

## LETTER

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

April Robin Martinig,<sup>1\*</sup>   
 Andrew G. McAdam,<sup>2</sup>   
 Ben Dantzer,<sup>3,4</sup>   
 Jeffrey E. Lane,<sup>5</sup>   
 David W. Coltman<sup>1</sup>  and  
 Stan Boutin<sup>1</sup> 

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### 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 between-population 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.

### Keywords

Competition, cooperation, dispersal, fitness, inbreeding, kin selection, local resource enhancement, philopatry, sex-biased dispersal, *Tamiasciurus hudsonicus*.

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## 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, that is, movement between the site of birth 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 & Hatchwell 2018). The short-term costs of the act of dispersal (incurred during the 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 (Bowler & Benton 2005). The empirical data needed to test this are logistically challenging to collect as it requires following individuals across their lifetimes after they leave a study area or 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; Packer 1979; Clutton-Brock 1989; Perrin & Mazalov 2000), and kin selection, including local resource (Clarke 1978) and mate competition (Hamilton 1967; Moore & Ali 1984), and, most

recently, cooperation (i.e. local resource enhancement; Perrin & Lehmann 2001; Le Galliard *et al.* 2006; Lawson Handley & Perrin 2007; Green & Haldwell 2018) are the prevailing hypotheses for what drives the observed sex bias in dispersal (Greenwood 1980; Dobson 1982; Dobson & Jones 1985; Perrin & Mazalov 2000; Lawson Handley & Perrin 2007). 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 been 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 & Gaines 1990; Perrin & Mazalov 2000; Lawson Handley & Perrin 2007; 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 lifetime 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

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada

<sup>2</sup>Department of Integrative Biology, University of Guelph, Guelph, ON, Canada

<sup>3</sup>Department of Psychology, University of Michigan, Ann Arbor, MI, USA

<sup>4</sup>Department of Ecology & Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA

<sup>5</sup>Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada

\*Correspondence: E-mail: [aprilmartinig@hotmail.com](mailto:aprilmartinig@hotmail.com)

(average diameter of 60 m; Anderson & Boutin 2002) centred on a food cache referred to as a 'middens' (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 & Larsen 1993; Stuart-Smith & Boutin 1994), or show significant differences in territory size (Larsen 1993), territory acquisition (Hendrix, J.G., personal communication), or mortality during the transience phase (Martinig, A.R., & Boutin, S., personal communication). Red squirrels exhibit a scramble competition mating system, with females mating with an average of seven males during oestrus (Lane *et al.* 2008, 2009). 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-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 & Larsen 1993). Most red squirrels exhibit a degree of philopatry (Larsen & Boutin 1994; Haughland & Larsen 2004), recruiting an average of two territory widths from their natal site (Berteaux & 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 & 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 & 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 & Boutin 2000; Cooper *et al.* 2017), although females tend to recruit slightly closer to their natal site than do males (Berteaux & Boutin 2000) and are more likely to have a natal site bequeathed to them (Berteaux & 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 & 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 hypothesise dispersal costs and benefits to be intergenerational, we do not expect there to

be intergenerational effects. Earlier studies (Waser *et al.* 2013; Germain *et al.* 2017) reported results consistent with immigrants making the best of a bad lot, but found no sex differences.

## MATERIAL AND 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; c. 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 & Boutin 2007). Masting events are characterised by episodic, synchronised seed production by trees with an average inter-mast interval of approximately four years (Nienstaedt & 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 three 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 behavioural 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 radio 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) and living 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 (i.e. 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,  $464.78 \pm 241.44$  m 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 ( $96.00 \text{ m} \pm 94.00$  SD, Berteaux & Boutin 2000;  $102.00 \text{ m} \pm 107.00$  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 (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. breeding age/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  $\leq 220$  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 (Stuart-Smith & Boutin 1994; Larsen & Boutin 1995), breeding dispersal, which only involves adult females, is relatively infrequent (Price 1992; Price & Boutin 1993), and territory ownership significantly increases over winter survival of juveniles (Kemp & Keith 1970; Hendrix, J.G., Fisher, D.N., Martinig, A.R., Boutin, S., Dantzer, B., Lane, J.E., Krebs, C.J. & McAdam, A.G. personal communication).

### 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.* (2008).

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 maximise 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 2018), 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  $\pm$  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%;  $G = 33.77$ , d.f. = 1,  $P < 0.001$ ), while immigrants were male biased (64%;  $G = 57.97$ , d.f. = 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 ( $2.81 \pm 0.04$  vs.  $2.43 \pm 0.06$  years, respectively), more breeding attempts ( $2.63 \pm 0.03$  vs.  $2.32 \pm 0.07$  litters, respectively), and larger litter sizes ( $3.17 \pm 0.01$  vs.  $3.02 \pm 0.01$  pups per litter, respectively), but none of these

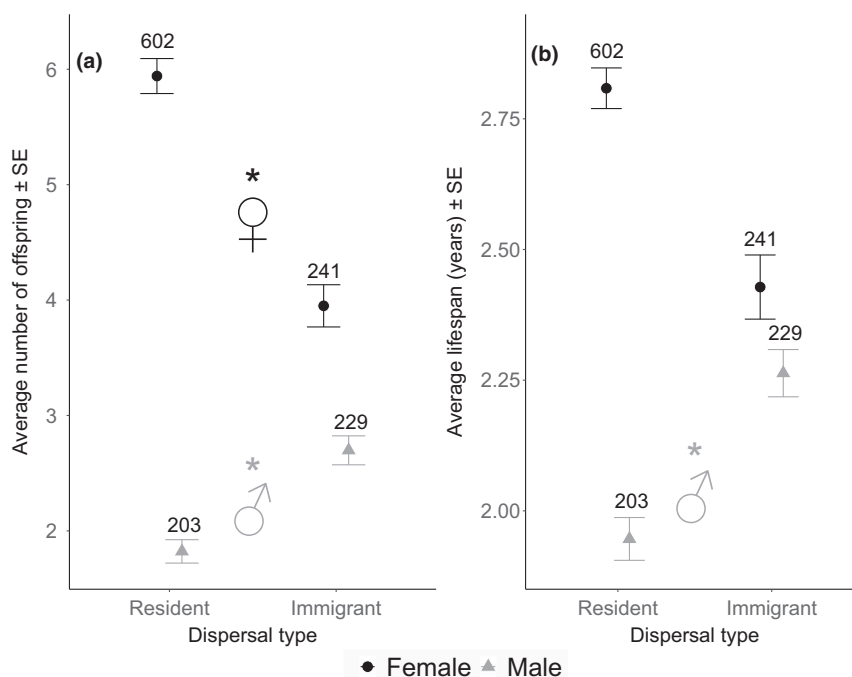
differences were statistically significant (Table 2; Table S4; Table S5; Fig. 1b). These combined differences led to resident females having 23% more offspring over their lifetime relative to immigrant females ( $5.94 \pm 0.15$  vs.  $3.95 \pm 0.18$  offspring, respectively;  $\beta: -0.26$ , 95% CI:  $-0.34$  to  $-0.19$ ; Table 1; Fig. 1a).

In contrast, resident males sired 29% less offspring over their lifetime relative to immigrant males ( $1.82 \pm 0.10$  vs.  $2.70 \pm 0.13$  offspring, respectively;  $\beta: 0.25$ , 95% CI:  $0.12$  to  $0.39$ ; Table 1; Fig. 1a). Resident males' lifespan was also 16% shorter than immigrant males ( $1.94 \pm 0.04$  vs.  $2.26 \pm 0.05$  years, respectively;  $\beta: 0.15$ , 95% CI:  $0.04$  to  $0.26$ ; Table 2; Fig. 1b). While no direct interest to this study, there were significant differences between populations and if individuals encountered a mast year or not (Table 1; Table 2).

### Intergenerational effects of immigration

Daughters born to resident females had no differences in longevity relative to daughters of immigrant females ( $2.85 \pm 0.05$  vs.  $2.85 \pm 0.08$  years, respectively), but they did have more breeding attempts ( $2.69 \pm 0.04$  vs.  $2.57 \pm 0.07$  litters, respectively), and larger litter sizes ( $3.19 \pm 0.01$  vs.  $2.99 \pm 0.01$  pups per litter, respectively), but none of these differences were statistically significant (Tables S4–S6; Fig. 2b). These combined differences led to daughters born to resident females having 15% more offspring over their lifetime relative to daughters of immigrant females ( $6.13 \pm 0.19$  vs.  $5.56 \pm 0.27$  offspring, respectively;  $\beta: -0.16$ , 95% CI:  $-0.25$  to  $-0.08$ ; Table 1; Fig. 2a).

Daughters sired by resident males had shorter lifespans compared to daughters sired by immigrant males ( $2.45 \pm 0.13$  vs.



**Figure 1** Resident and immigrant North American red squirrels (*Tamiasciurus hudsonicus*) had differential fitness after recruitment to our southwestern Yukon, Canada populations 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 1 and 2). Error bars indicate  $\pm$  SE. Sample sizes above bars.

**Table 1** Parameter estimates (d.f. = 4) from the generalised 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<sup>†</sup> North American red squirrels (*Tamiasciurus hudsonicus*) in southwestern Yukon, Canada from 1989 (females) and 2002 (males) to 2017

Fixed and random effects <sup>‡</sup>	Estimate	SE	Z	2.5% CI	97.5% CI
Model: adult female, $n = 843$					
Immigrants	-0.26	0.04	-6.42	<b>-0.32</b>	<b>-0.17</b>
Population (SU)	-0.01	0.03	-0.36	-0.07	0.05
Encountered most year	2.00	0.06	31.04	<b>1.88</b>	<b>2.14</b>
Birth year <sup>§</sup>	0.66	0.81	NA	NA	NA
Model: adult male, $n = 432$					
Immigrants	0.25	0.07	3.69	<b>0.12</b>	<b>0.39</b>
Population (SU)	-0.16	0.07	-2.38	<b>-0.29</b>	<b>-0.03</b>
Encountered most year	1.90	0.14	13.21	<b>1.61</b>	<b>2.18</b>
Birth year <sup>§</sup>	1.29	1.14	NA	NA	NA
Model: daughter – known maternity, $n = 582$					
Immigrant mother	-0.16	0.04	-3.67	<b>-0.25</b>	<b>-0.08</b>
Population (SU)	-0.06	0.04	-1.62	-0.13	0.01
Encountered most year	1.91	0.08	24.12	<b>1.75</b>	<b>2.06</b>
Birth year <sup>§</sup>	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 most year	2.12	0.26	8.30	<b>1.62</b>	<b>2.62</b>
Birth year <sup>§</sup>	1.11	1.06	NA	NA	NA
Model: daughter – known paternity, $n = 174$					
Immigrant father	-0.17	0.07	-2.46	<b>-0.30</b>	<b>-0.03</b>
Population (SU)	-0.04	0.07	-0.55	-0.18	0.10
Encountered most year	1.60	0.13	12.28	<b>1.34</b>	<b>1.85</b>
Birth year <sup>§</sup>	1.95	1.40	NA	NA	NA
Model: son – known paternity, $n = 139$					
Immigrant father	-0.55	0.13	-4.29	<b>-0.81</b>	<b>-0.30</b>
Population (SU)	-0.45	0.14	-3.18	<b>-0.72</b>	<b>-0.17</b>
Encountered most year	2.27	0.32	7.05	<b>1.64</b>	<b>2.91</b>
Birth year <sup>§</sup>	1.19	1.09	NA	NA	NA

Bold terms denote significance at  $\alpha = 0.05$ .

<sup>†</sup>Offspring with known maternity ( $n = 771$ ) or known paternity ( $n = 313$ ).

<sup>‡</sup>Reference categories for fixed effects were set to 'residents' (for 'immigrants'), 'KL' (for 'population (SU)'), 'did not encounter most year' (for 'encountered most year'), 'resident mothers' (for 'immigrant mothers'), and 'resident fathers' (for 'immigrant fathers').

<sup>§</sup>Random effect; estimate column is variance ( $\sigma^2$ ) and SE column is standard deviation.

2.64  $\pm$  0.09 years, respectively), but more breeding attempts (3.03  $\pm$  0.11 vs. 2.54  $\pm$  0.06 litters, respectively), and smaller litter sizes (3.07  $\pm$  0.02 vs. 3.39  $\pm$  0.01 pups per litter, respectively), but none of these differences were statistically significant (Table 1; Table S4; Table S5; Table S6; Fig. 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  $\pm$  0.57 vs. 5.59  $\pm$  0.36 offspring, respectively;  $\beta$ : -0.17, 95% CI: -0.30 to -0.03; Table 1; Fig. 2a).

Sons born to resident females sired more offspring over their lifetime than sons born to immigrant females (1.75  $\pm$  0.13 vs. 1.32  $\pm$  0.17 offspring) and lived longer (1.94  $\pm$  0.05 vs. 1.77  $\pm$  0.09 years, respectively), but these differences were not statistically significant (Table 1; Table S6; Fig. 2). In contrast, sons born to resident males sired 43% more offspring over their lifetime relative to sons of immigrant males (2.45  $\pm$  0.32 vs.

**Table 2** Parameter estimates (d.f. = 4) from the generalised linear mixed effects model output with longevity (days alive) as a response variable for resident and immigrant North American red squirrels (*Tamiasciurus hudsonicus*;  $n = 1275$ ) in southwestern Yukon, Canada from 1989 (females) and 2002 (males) to 2017

Fixed and random effects <sup>†</sup>	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 most year	1.04	0.06	17.49	<b>0.92</b>	<b>1.16</b>
Birth year <sup>‡</sup>	0.10	0.32	NA	NA	NA
Model: adult male, $n = 432$					
Immigrants	0.15	0.06	2.62	<b>0.04</b>	<b>0.26</b>
Population (SU)	0.03	0.05	0.61	-0.07	0.14
Encountered most year	0.83	0.09	9.55	<b>0.66</b>	<b>1.00</b>
Birth year <sup>‡</sup>	0.06	0.24	NA	NA	NA

Bold terms denote significance at  $\alpha = 0.05$ .

<sup>†</sup>Reference categories for fixed effects were set to 'residents' (for 'immigrants'), 'KL' (for 'population (SU)'), 'did not encounter most year' (for 'encountered most year'), 'resident mothers' (for 'immigrant mothers'), and 'resident fathers' (for 'immigrant fathers').

<sup>‡</sup>Random effect; estimate column is variance ( $\sigma^2$ ) and SE column is standard deviation.

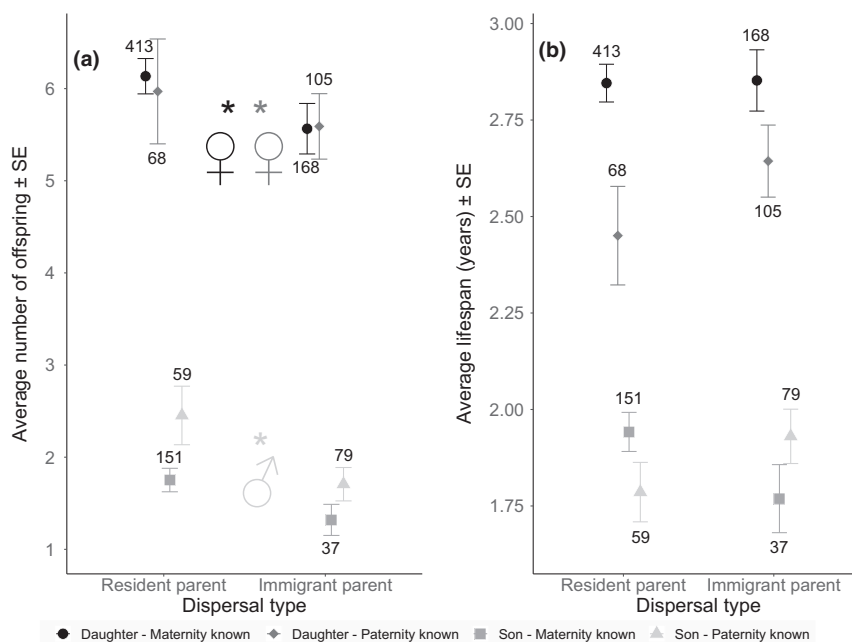
1.71  $\pm$  0.18 offspring, respectively;  $\beta$ : -0.55, 95% CI: -0.81 to -0.30) but had no significant difference in lifespan (1.79  $\pm$  0.07 vs. 1.93  $\pm$  0.07 years, respectively; Table 1; Table S6; Fig. 2). While of no direct interest to this study, there were significant differences between populations and if individuals encountered a mast year or not (Table 1; Table S6).

Daughters born to resident females were more likely to recruit in the population than their sons ( $G = 3.89$ , d.f. = 1,  $P = 0.049$ ), while there was no sex difference in recruitment for offspring produced by immigrant females ( $G = 0.927$ , d.f. = 1,  $P = 0.34$ ) or for offspring sired by resident males ( $G = 2.34$ ,  $P = 0.13$ ) or immigrant males ( $G = 2.53$ , d.f. = 1,  $P = 0.11$ ) (Table S7). Resident females ( $G = 8.40$ , d.f. = 1,  $P = 0.004$ ) and immigrant females ( $G = 8.55$ , d.f. = 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 than resident males, 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 (Greenwood 1980; Dobson 1982), in red squirrels, both sexes disperse similar distances (Berteaux & Boutin 2000; Cooper *et al.* 2017). Despite these previous studies



**Figure 2** Offspring born to resident and immigrant North American red squirrels (*Tamiasciurus hudsonicus*) had differential fitness after recruitment to our southwestern Yukon, Canada populations 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 (Tables 1 and 2). Error bars indicate  $\pm$  SE. Sample sizes by bars.

documenting a lack of sex-difference in dispersal 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 (Gienapp & Merilä 2011; Waser *et al.* 2013; Germain *et al.* 2017) 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 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.

In males, though, 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 & May 1977; Waser 1985) and inbreeding depression (Bengtsson 1978) (Lehmann & Perrin 2003).

Female choice may play a part too. Females in other species show selection for mating with unfamiliar males (e.g. olive baboons (*Papio anubis*; Packer 1979; Smuts 1983), house mice (*Mus musculus*; Winn & Vestal 1986), and naked mole-rats (*Heterocephalus glaber*; Clarke & 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 (Richard 1974; Kurland 1977), such as the ability to survive dispersal. It is unlikely that female red squirrels favour mating with unfamiliar males (Winn & Vestal 1986; Hughes *et al.* 1999) as an inbreeding avoidance mechanism (Bengtsson 1978; Lehmann & 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 & Stebbins 1965; Duckworth 2008; Bonte *et al.* 2012 and references therein)), 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 (Stuart-Smith & Boutin 1995; Rémy *et al.* 2011); the so-called silver-spoon effect (Stamps 2006; Descamps *et al.* 2008; Bonte *et al.* 2012). 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 (Greenwood 1980; Dobson 1982).

Immigrant females may be making the best of a bad lot (see also Waser *et al.* 2013). This is in line with various theoretical models that assume an advantage to remaining close to the natal site (Hamilton & May 1977; Shields 1982, 1983; Waser 1987, 1988; Green & Haldwell 2018). While the mechanism of selection is unknown, resident females may benefit from local resource enhancement (Perrin & Lehmann 2001; Le Galliard *et al.* 2006; Lawson Handley & Perrin 2007) through kin-selected cooperation (Green & Hatchwell 2018) in the form of bequeathals (Bertheaux & Boutin 2000; Williams *et al.* 2013). Immigrant females are not expected to benefit from increased familiarity with the environment or their neighbours (Beletsky & 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 maximise their own chance for reproduction (Murray 1967; Hamilton & May 1977; Johnson & Gaines 1990).

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 realise the same advantages that residents may transfer to their offspring (e.g. maternal investment through bequeathals (Bertheaux & Boutin 2000; Williams *et al.* 2013)). Phenotype matching of offspring to the local environment through directed gene flow (Davis & Stamps 2004; Edelaar *et al.* 2008) would also explain these results, as this would impact competitive ability and fitness in the next generation (Doligez & Pärt 2008; Burton *et al.* 2010; 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 have been able to detect 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 lifetime 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 resource 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 after settlement costs experienced by immigrants are not compensated for in the next generation.

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## AUTHORSHIP

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

## DATA AVAILABILITY STATEMENT

All data are archived on figshare and will be available from <https://doi.org/10.6084/m9.figshare.10261016> after January 1, 2022 (Martinig *et al.* 2019).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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