Familiar neighbors, but not relatives, enhance fitness in a territorial mammal

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Abstract: Resolving conflict amongst solitary adversaries provides the first steps toward the evolution of sociality. Kin selection and mutually beneficial interactions among unrelated individuals are two important pathways to conflict resolution, but the relative importance of these mechanisms has been difficult to assess in the wild. Using 22 years of data from North American red squirrels, we assessed how kinship and familiarity with neighbors affected fitness in this solitary, territorial species. While living near kin did not enhance fitness, social familiarity increased survival by up to 17% and annual reproductive success by at least 40%. These fitness benefits were strong enough to compensate for the effects of aging later in life, with potential consequences for the evolution of senescence. Mutually beneficial interactions stemming from social familiarity can, therefore, provide the opportunity for the evolution of cooperation between adversarial neighbors, even in the absence of kin benefits.

One Sentence Summary: Stable social relationships increase reproductive success and survival in solitary red squirrels and can offset the negative effects of aging.

Main Text:

One of the outstanding questions in evolutionary biology is the extent to which mutualistic benefits and kin-selection can facilitate the evolution of cooperation through mitigation of conflict between interacting organisms (*1*). The indirect fitness benefits gained from associating with kin are well established as an important pathway to conflict resolution (*2*), however, other pathways to the evolution of cooperation may be more common than previously thought (*1*). It has been widely demonstrated that mutually beneficial interactions in the form of stable social bonds among conspecifics can play an important role in mitigating intragroup conflict and enhancing fitness in group-living organisms. For example, stable social relationships are known to be associated with reduced stress levels (*3*, *4*), enhanced longevity (*5*, *6*), and increased offspring production and survival (*7-9*). Social connectedness is also positively associated with human health and longevity (*10*), and, in particular, may be important in later life for mitigating effects of aging (*11*).

While the majority of research has focused on group-living species, where much conflict resolution has already taken place, the question of how cooperation can first be favored in solitary species where interactions are primarily agonistic, remains a key question in our understanding of how sociality can evolve. Kin can help to mitigate territorial aggression and enhance fitness (*12*), but there is also substantial potential for social stability to play an important role in helping to resolve conflict over territorial space. For example, stable social relationships, in the form of familiarity with neighbours, can lead to a cooperative 'agreement' of reduced aggression and territory defence, a phenomenon known as the 'dear enemy' effect (*13*). Given

that these stable social relationships help to minimize negotiation of territory boundaries and alleviate costs of territoriality for both individuals, social familiarity is illustrative of a mutualism-based pathway to conflict resolution. Familiarity with neighbours is known to have benefits for a variety of individual traits including faster growth rates (*14*), enhanced body condition (*15*) and, in a few cases, increased reproductive success (*16*, *17*).

However, previous research has struggled to distinguish between the relative roles of kin selection and mutually beneficial interactions in reducing conflict and facilitating cooperation. In many study systems where the importance of stable social relationships have been investigated, social interactions typically take place between related individuals (*6*, *18*). Similarly, studies that look at the benefits of relatedness in a social group (reviewed in *19*) may inherently be confounded by familiarity. However, the effects of kinship and familiarity are rarely studied concurrently in the same system and so the relative importance of each mechanism is difficult to assess (cf. *20*).

Here we used a natural population of North American red squirrels (*Tamiasciurus hudsonicus*) to assess the importance of familiarity with neighbours for resolving conflict over territorial space and thereby enhancing reproductive success and survival, while simultaneously accounting for effects of kinship. Red squirrels are arboreal rodents in which both sexes defend exclusive territories (*21*). Territories are important for overwinter survival (*22*) and are defended through vocalizations called 'rattles' (*23*), which are uniquely identifiable (*24*). Following natal dispersal, individuals rarely relocate to a vacant territory (*25*), allowing for the establishment of long-term familiarity among neighbouring individuals. Despite the fact that relationships with territory neighbours are primarily antagonistic, living near familiar neighbours provides

important benefits for red squirrels, including reducing the risk of territory intrusion (*26*) and time spent on territory defence (*27*).

In this study we tested whether red squirrels that were more familiar with neighbouring conspecifics had increased annual reproductive success (ARS) and a higher probability of surviving to the following year, than squirrels that were less familiar with their social neighbourhood (i.e. squirrels within a 130 m radius; Fig. 1). We measured ARS as the number of pups sired for males and as the number of pups surviving to the following year (i.e. recruited) for females. Given that in humans, strong social connections in old age have been demonstrated to reduce mortality risk and enhance longevity (*11*), we also tested whether stable social relationships might help to buffer organisms against the effects of senescence. To do this, we looked for effects of familiarity on survival and reproductive success in red squirrels specifically during the 'senescent' period (squirrels ≥ 4 years old; *28*, *29*). We tested these hypotheses using 22 years of data from a natural population of red squirrels in the Yukon, Canada. Through genetic analysis and monitoring of red squirrel pups in the natal nest we were able to establish a long-term pedigree, allowing us to assess effects of social familiarity while simultaneously accounting for relatedness between neighbours.

We found no effect of average relatedness of the social neighbourhood on male or female survival, number of pups sired, or number of pups recruited in either the full models or senescent models (all $|z| < 1.48$, all $P > 0.13$; Table 1). In contrast, familiarity with neighbouring individuals increased male and female survival by 6% ($\beta = 0.18 \pm 0.06$, $z = 2.78$, $P = 0.005$), and the number of pups sired by 40% ($\beta = 0.18 \pm 0.09$, $z = 2.04$, $P = 0.04$; Table 1). There was no overall effect of social familiarity on the number of pups recruited by females ($\beta = 0.06 \pm 0.05$, $z = 1.38$, $P = 0.17$; Table 1). When analyzing effects of familiarity in the senescent period alone,

the benefits of social familiarity for all fitness measures were even greater. For squirrels aged 4 and older, living near familiar neighbours increased the probability of annual survival by 17% for both sexes ($\beta = 0.45 \pm 0.11$, $z = 3.40$, $P < 0.001$), increased the number of pups sired by 89% ($\beta = 0.39 \pm 0.15$, $z = 2.67$, $P = 0.008$), and the number of pups recruited by 40% ($\beta = 0.23 \pm 0.09$, $z = 2.52$, $P = 0.01$; Fig. 1, 2; Table 1).

We hypothesized that this large observed increase in siring success associated with social familiarity could result either from increased energetic resources (*26*, *27*) that allow male squirrels in familiar social neighbourhoods to travel farther to obtain mating opportunities (*30*, *31*), or that social familiarity might directly benefit males through increased mating success within their more familiar social neighbourhoods. Analysis of the spatial locations of male paternity success revealed that males traveled farther to mate as familiarity with neighbours increased ($\beta = 19.93 \pm 8.83$, $t = 2.26$, $P = 0.03$; Fig. 3). This does not appear to be due to inbreeding avoidance (see Table S2). Additionally, while the number of pups sired outside the social neighbourhood (130 m radius) was positively associated with social familiarity ($\beta = 0.39 \pm 0.10$, $z = 3.79$, $P < 0.001$), there was no association between familiarity and siring success within a male's social neighbourhood ($\beta = 0.12 \pm 0.10$, $t = 1.25$, $P = 0.21$; Fig. 3; Table S2). These results suggest that stable social relationships with neighbours increased the energy stores available to males, either through reduced territory defence (*27*) or reduced cache pilfering by neighbours (*26*), which allowed them to travel farther and increase their siring success (*31*).

This study is the first to simultaneously assess effects of kinship and familiarity on fitness outcomes, and demonstrates that mutualistic benefits provided through social familiarity can facilitate reduced conflict and enhance fitness, even in the absence of inclusive fitness benefits. Importantly, we've demonstrated that the benefits of stable social relationships are not exclusive

to group-living organisms, but can extend to solitary species whose primary social interactions are defined by competition for limited resources, suggesting a common evolutionary basis for social benefits across the animal kingdom. By exploring the fitness benefits of social relationships in a solitary, territorial species we've shown the potential for familiarity to stabilize social groups even in the simplest and least cooperative of situations. Future studies, even in complex social systems, should therefore not only assess the benefits of interacting with relatives, but should consider simultaneously assessing how familiar social relationships might enhance the cooperative potential of a group.

Our findings also demonstrate a previously unappreciated benefit of maintaining social relationships into later life. The magnitudes of the benefits of social familiarity in the senescent period were sufficient to offset age-related declines in survival and reproductive success (*32*). Specifically, for an average 4-year old squirrel, aging by one year decreases the probability of survival from 68% to 59%. But if that individual were to maintain all of its neighbours, such that average familiarity increased by one year, the maintenance of those stable social relationships would more than compensate for the change in age, resulting in an increase in survival probability from 68% to 74%. However, despite the large individual benefits of increased social familiarity late in life, few squirrels currently enjoy this fitness advantage. For example, only 4% of 4-year olds surviving to age 5 maintain all of their neighbours, and mean familiarity does not continue to increase with age through the senescent period (Fig. S1). As a result, our observed fitness increases in later life associated with social stability are not currently widespread enough to affect the decline in the force of natural selection with age and the arrival of the mutational 'wall of death' (see Supplementary Materials; Fig. S2; *33*).

Nevertheless, such individual fitness benefits of familiarity provide strong incentive for squirrels to reduce turnover in their social neighbourhood. While squirrels compete with territorial neighbours for resources (*34*), space (*21*), and reproductive success (*35*), here we have shown that individuals also benefit from the enhanced survival of neighbours. The idea that territorial neighbours might engage in cooperative behaviours to prevent neighbourhood turnover has been theorized (*36*). Here our documented benefits of social familiarity provide the opportunity for the evolution of cooperative behaviour toward otherwise adversarial neighbours. Specifically, while the loss of an unfamiliar neighbour would have no effect on survival probability, the loss of a neighbour with 6 years of familiarity would decrease the owner's probability of survival by 7%. A squirrel should, therefore, be willing to engage in behaviours that ensure their neighbours survival as long as this does not reduce the actor's survival by more than 7%. This scope for altruism is comparable to kin selection interactions between first cousins once removed ($r = 0.06$; *2*). It is possible then that reduced aggression when interacting with familiar neighbours (i.e. the dear-enemy phenomenon; *13*) is a mechanism that not only serves to reduce an individual's own time and energy spent on defence, but also enhances the survival of familiar neighbours, which, in turn, provides indirect fitness returns through increased social familiarity. Ultimately, if cooperative behaviours enhancing the survival of familiar neighbours were to become widespread enough that mean social familiarity increased with age across the population, then this socially driven increase in fitness late in life could influence the force of selection and consequently the evolution of senescence.

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Data and materials availability: All data and code associated with the analyses will be made available on the Figshare Repository following acceptance of the manuscript.

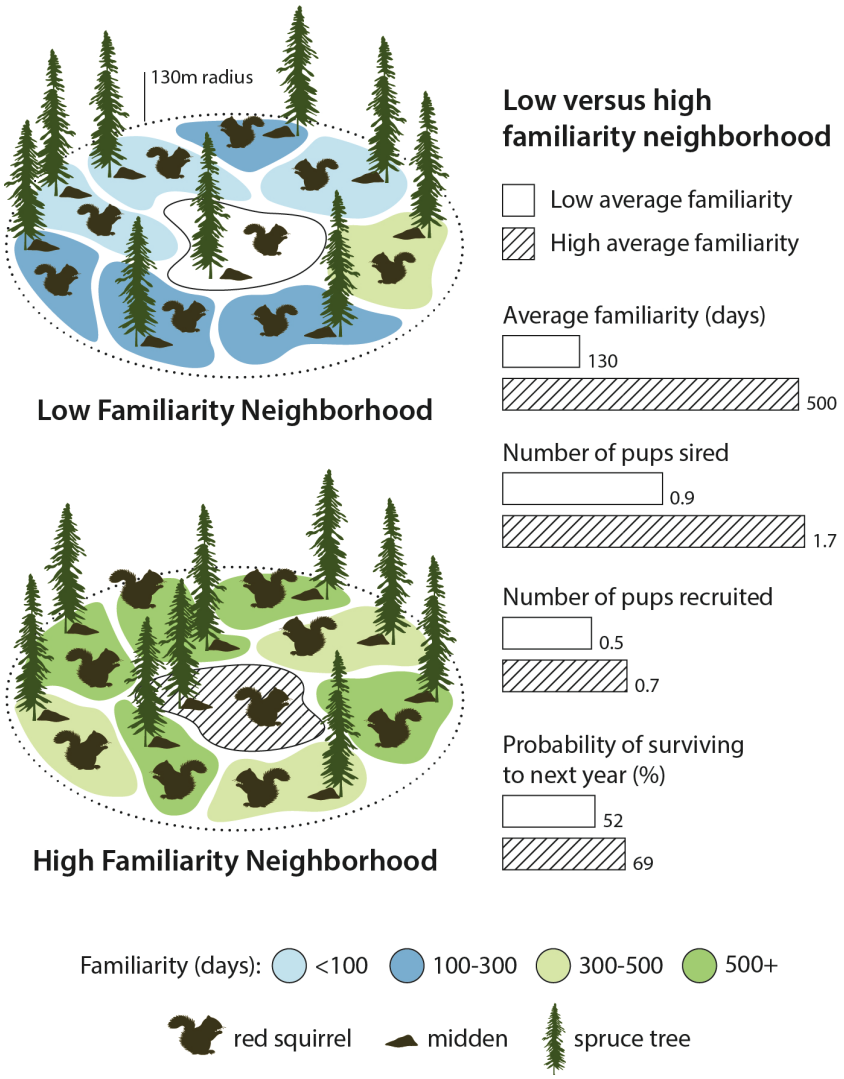

Fig. 1. Schematic depiction of a low and high familiarity red squirrel neighborhood with associated fitness metrics. Low and high familiarity are based on first and third quartile familiarity values. Neighborhoods include all squirrels within a 130 m radius of the focal squirrel's midden, this reflects the acoustic social environment as 130 m is the farthest distance that red squirrel rattles (unique territorial vocalizations) carry. Although simplified here for sake of space, on average squirrels have 13 neighbors. Effect sizes are based on models from the senescent period.

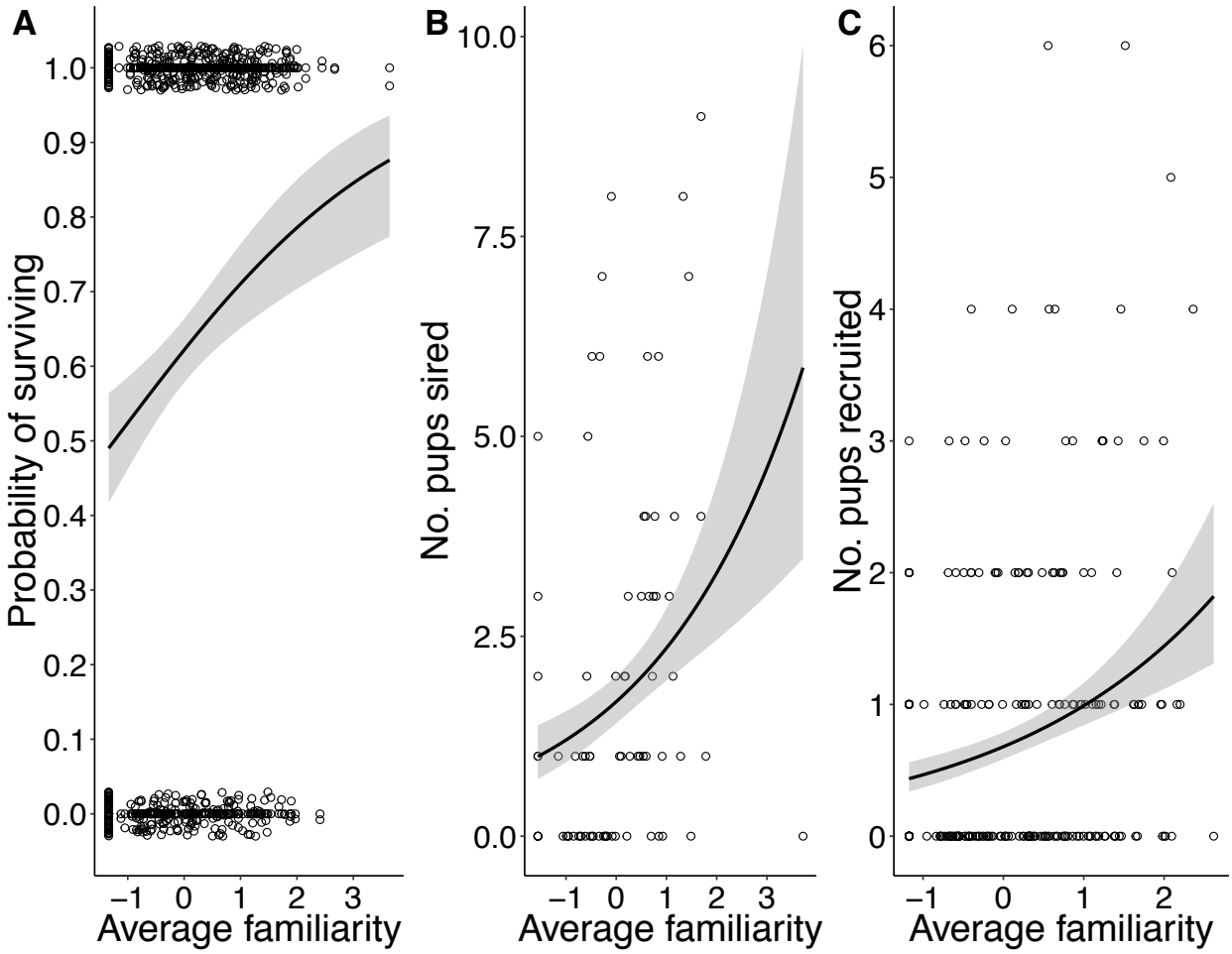

Fig. 2. Effects of average neighborhood familiarity on a) annual survival (N = 512), b) male annual reproductive success (ARS; N = 78), and c) female ARS (N = 268) during the senescent period (≥ 4 years old). Shaded grey bars indicate 95% confidence intervals. Values on x-axis are standardized measures of average familiarity. Points indicate raw data with a small amount of jitter introduced to show overlapping points.

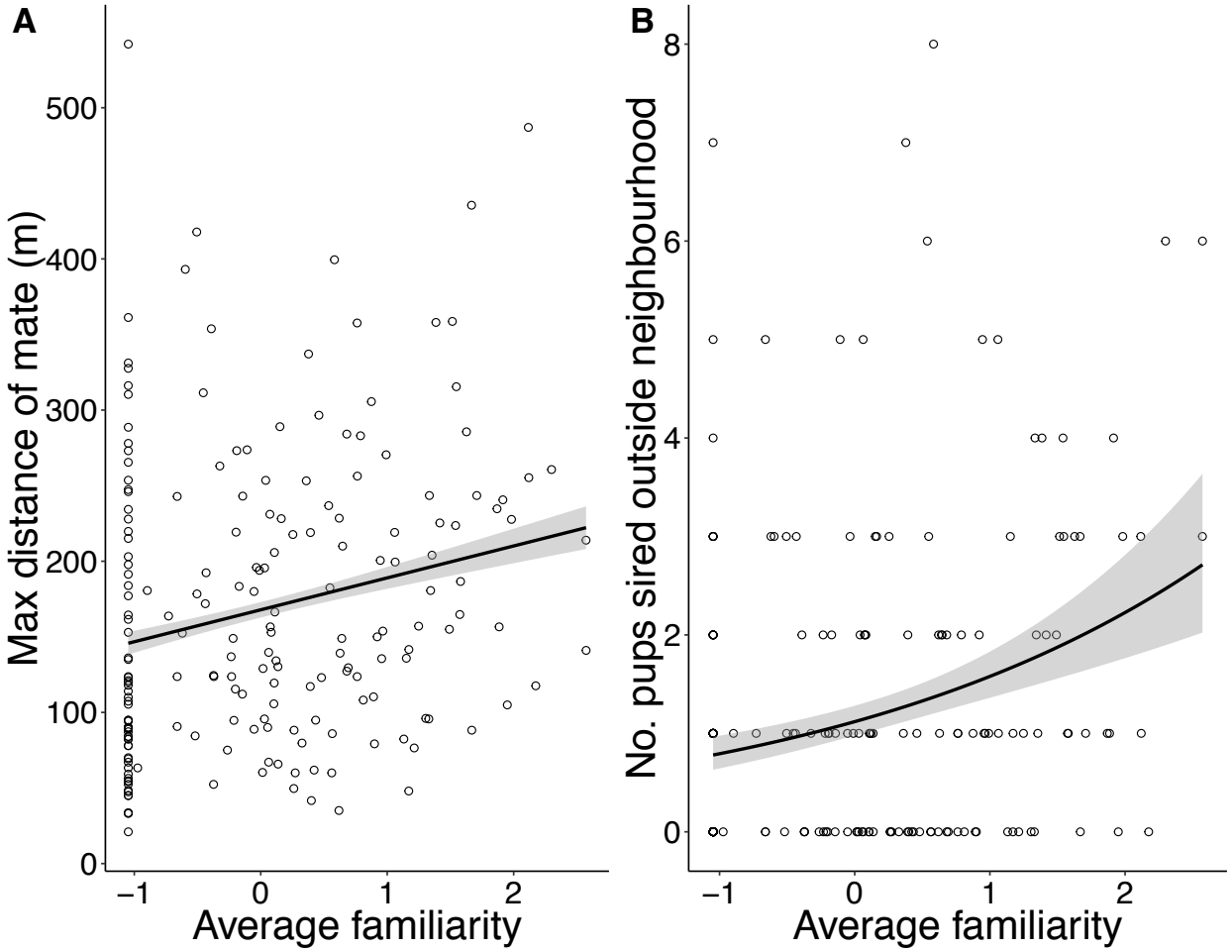

Fig. 3. Effects of average neighborhood familiarity on a) the distance that males traveled to mate and b) number of pups sired outside the social neighborhood (i.e. 130 m radius; N = 199). Shaded grey bars indicate 95% confidence intervals. Values on x-axis are standardized measures of average familiarity. Points indicate raw data.

Table 1. Fixed effects from annual survival, male annual reproductive success (ARS), and female ARS generalized linear mixed-effects models. Models are based on the full and senescent (≥ 4 years old) datasets are shown with significant effects indicated in bold. Regression coefficients are standardized.

Data set	N	Response	Fixed effect	Parameter ± SE	*z*	*P*
Full data						
	2346	Probability of survival	**Familiarity**	**0.18 ± 0.06**	**2.78**	**0.005**
			Age	**-0.27 ± 0.09**	**-2.94**	**0.003**
			Age^2	**-0.11 ± 0.04**	**-2.57**	**0.01**
			Relatedness	0.008 ± 0.05	0.15	0.88
			Density	0.10 ± 0.11	0.92	0.36
			Grid-SU	0.17 ± 0.10	1.67	0.10
	412	No. pups sired *(Male ARS)*	**Familiarity**	**0.18 ± 0.09**	**2.04**	**0.04**
			Age	**0.68 ± 0.14**	**4.75**	**<0.001**
			Age2	**-0.41 ± 0.08**	**-5.32**	**<0.001**
			Relatedness	-0.11 ± 0.08	-1.47	0.14
			Density	0.04 ± 0.12	0.37	0.71
			Grid-SU	-0.07 ± 0.19	-0.38	0.70
	981	No. pups recruited *(Female ARS)*	Familiarity	0.06 ± 0.05	1.38	0.17
			Age	0.08 ± 0.05	1.42	0.16
			Age^2	**-0.10 ± 0.04**	**-2.72**	**0.007**
			Relatedness	0.02 ± 0.04	0.63	0.53
			Density	**-0.37 ± 0.13**	**-2.78**	**0.005**
			Grid-SU	-0.06 ± 0.08	-0.78	0.43
Senescent data						
	512	Probability of survival	**Familiarity**	**0.45 ± 0.11**	**3.40**	**<0.001**
			Age	**-0.36 ± 0.10**	**-3.42**	**<0.001**
			Relatedness	0.13 ± 0.11	1.20	0.23
			Density	0.15 ± 0.11	1.33	0.18
			Grid-SU	0.14 ± 0.21	0.68	0.49
	78	No. pups sired *(Male ARS)*	**Familiarity**	**0.39 ± 0.15**	**2.67**	**0.008**
			Age	**-0.39 ± 0.19**	**-2.01**	**0.04**
			Relatedness	0.05 ± 0.14	0.37	0.72
			Density	0.11 ± 0.19	0.60	0.55
			Grid-SU	0.26 ± 0.32	0.82	0.41
	268	No. pups recruited *(Female ARS)*	**Familiarity**	**0.23 ± 0.09**	**2.52**	**0.01**
			Age	**-0.29 ± 0.10**	**-2.79**	**0.005**
			Relatedness	0.06 ± 0.08	0.79	0.43

Density	**-0.38 ± 0.17**	**-2.20**	**0.03**
Grid-SU	-0.32 ± 0.17	-1.85	0.07

Supplementary Materials for

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Supplementary Text

Effects of familiarity on patterns of senescence

If the fitness benefits of stable social relationships were sufficiently widespread in the red squirrel system then an increase in the mean number of reproductive opportunities later in life associated with social familiarity would lead to a less rapid decline in the force of natural selection with age. This would delay the arrival of the 'wall of death', a spike in mortality caused by the accumulation of deleterious alleles, leading to the evolution of slower rates of aging (*33*). We explored this possibility in red squirrels by creating a 'simulated' population where social interactions were excluded from the calculation of age-specific survival and fecundity, but found that the observed effects of social familiarity on patterns of aging were negligible (Fig. S2). Under natural conditions, where red squirrels experienced the social benefits of familiar neighbours, the force of selection was marginally stronger than in a 'simulated' population where social interactions were excluded from the calculation of age-specific survival and fecundity (Fig S2a, S2b). However, this ultimately had no influence on when the wall of death occurred (Fig. S2c, S2d). This is likely due to the fact that currently, in red squirrels, familiarity does not increase linearly with age (Fig. S1), meaning that while some individuals experience stable social environments and their associated fitness benefits, others have substantial turnover in neighbours and as a result have reduced survival and reproductive success. Given that not all squirrels experience the benefits of familiarity in old age, this limits the extent to which social relationships might currently affect patterns of senescence at the population level.

Potential for spatial confounds to drive fitness effects

Although we discuss red squirrel neighbourhoods as if they were discrete units, individuals were actually distributed fairly continuously across our study areas, meaning that

individually defined neighbourhoods were spatially overlapping. It is possible then that our observed fitness effects could be confounded by spatial variation in resource availability or predation risk. In particular, areas with low survival would have high turnover and hence low average familiarity locally. If this kind of spatial autocorrelation in survival were present, low neighbourhood familiarity might be linked to low survival in the absence of a causal relationship. While this is a relevant concern that warrants consideration, there are several reasons why we do not think this is likely to be the case. First, there is no evidence of consistent spatial variation in spruce cone production (the primary food source for red squirrels *37*, *38*) across years in this study system (*22*). Therefore, there should not be locations that are consistently rich or poor in food resources. Second, we added a spatial random effect ('spatial ID') to our models by grouping squirrels into 150 m squares (within each grid and within each year) based on their known spatial locations. This spatial random effect was only significant in the male ARS models (Table S2) and all effects of familiarity we observed were robust to its inclusion (Table 1). Given that we would expect spatial variation in resource availability or predation risk to affect males and females similarly, this result suggests that some additional spatial factor, unique to males, might be at play. It is possible that if there are spatial clusters of females, males that are located near those clusters are particularly successful at breeding with multiple females and thus siring many pups.

Materials and Methods

Study population

We studied a wild population of North American red squirrels located in the southwest Yukon, Canada (61° N, 138° W). This population has been followed since 1987 on two 40-ha study grids separated by the Alaska Highway. We monitored squirrels annually from March to August and

used a combination of live-trapping and behavioural observations to assess territory ownership, track reproduction and survival, and determine offspring recruitment. We trapped squirrels using Tomahawk live-traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) baited with peanut butter. During their single-day oestrous, female red squirrels mate with multiple males and produce multiply-sired litters (*39*), with an average of three pups per litter (*40*). We monitored the reproductive statuses and parturition dates of females through palpation, mass changes, and evidence of lactation. After parturition, we used radio telemetry and/or behavioural observations to follow females to their nests. We fitted pups with unique alphanumeric metal ear tags (Monel #1; National Band and Tag, Newport, KY, USA) at 25 days old, allowing us to follow individuals throughout their lifetimes. A detailed description of project protocols can be found in (*29*, *41*).

Measuring familiarity

We completed a full census of the population twice annually in May and August and determined territory ownership using the aforementioned methods. We defined each squirrel's social neighbourhood to be all conspecifics within a 130 m radius of the focal squirrel's midden (i.e. the centre of the territory). Red squirrel territorial vocalizations ('rattles') typically carry up to 130 m (*42*), so this radius defines the acoustic social environment that an individual experiences. Furthermore, 130 meters is similar to the distance at which red squirrels have been demonstrated to respond to changes in local density (150 m; *43*). We measured the pairwise familiarity between the territory owner and each neighbour as the number of days that both individuals had occupied their current territories within 130 m of each other. We then averaged all pairwise

measures of familiarity to obtain a measure of each individual's average familiarity with its surrounding neighbours.

Measuring relatedness

We temporarily removed juveniles from their natal nest immediately following parturition to weigh, sex, and take ear tissue samples. Observing pups in the natal nest also allowed us to assign maternity with certainty. Starting in 2003, we determined paternity by genotyping all individuals at 16 microsatellite loci (*44*) and assigned paternity with 99% confidence using CERVUS 3.0 (*45*). Genotyping error based on known mother-offspring pairs was 2%. Additional details on the genetic methods can be found in Lane et al. (2008). Using the established multigenerational pedigree, we calculated the coefficient of relatedness between the territory owner and each neighbour. We averaged all pairwise measures of relatedness to provide a measure of the average relatedness between each squirrel and all of its neighbours.

Fitness measures

For individuals alive between 1994 and 2015, we measured annual survival as the probability of surviving to January 1st of the following year (N = 2346 records over 1009 individuals). Given that long-term monitoring of individuals in this population first began in 1987, we excluded data prior to 1994 to ensure accurate measurement of familiarity between neighbours. Our ability to successfully redetect adults in the population on a yearly basis is estimated to be 1.0 (*46*).

We measured female ARS as the number of pups recruited each year (i.e. surviving overwinter). We included data from 450 breeding females between 1994 and 2015 (N = 981 records). All females with a known parturition date were considered to have bred; all other non-

breeding females were excluded from analysis. Since red squirrel males do not contribute to the raising of pups and the male's social environment is, therefore, unlikely to affect pup recruitment, we defined male ARS as the number of pups sired each year. We used data from 207 males between 2003 and 2014 ($N = 412$ records). We excluded data prior to 2003 and after 2014 because pedigree data was incomplete. For all analyses we only used data for adults (≥ 1 year old) whose age could be assigned with certainty (i.e. individuals tagged in nest as juveniles).

Although our ability to accurately assess survival and recruitment has the potential to be confounded by dispersal beyond the borders of our study grids, this does not appear to be a problem. Juveniles typically disperse less than 100 m (*41*, *47*), and estimates of juvenile survival do not differ between the centre and edge of grid, which might be expected if dispersing juveniles were mistakenly considered to have died (*29*).

Statistical analyses

Annual survival and ARS

To assess the effects of familiarity on ARS and survival, we used generalized linear mixed effects models (GLMMs) with a BOBYQA optimizer. We used a binomial distribution (logit-link) to assess probability of annual survival and a Poisson distribution (log-link) for male and female ARS. For all models we fitted average familiarity, a linear and quadratic term for age, grid density, and average relatedness as continuous predictors and included grid as a categorical fixed effect. For the survival models we checked for an effect of sex, but sex was not significant and so was not considered further. We included a random effect of squirrel ID and year to account for repeated measures of individuals and temporal variation in resource availability, respectively. To account for inherent spatial structure in our data that could be related to

familiarity we grouped squirrels into 150 m squares (within each grid and within each year) based on their known spatial locations and included this 'spatial ID' as a random effect in all of our models. Models for the senescent period included the same covariates as the full models described above, except that these models only included a linear effect of age.

Force of selection

To assess whether familiarity with neighbours might increase the force of selection in later life, we fitted the same models as above, except that we included both breeding and non-breeding females and the response variable for females was now number of pups born rather than number recruited. For the first set of models we included age, a quadratic term for age, density and grid as fixed effects, as well as squirrel ID and year as random effects. We extracted the parameter estimates for age in each of these models and used those parameters to estimate age-specific fecundity and survival for females and males separately. This represented our 'natural' population, and provided us with the estimates of age-specific fecundity and survival as observed and as potentially confounded by social familiarity among squirrels. We then measured what the effects of age would have been had there not be been variation in familiarity by including familiarity as a continuous predictor in the same models described above, and thus statistically controlling for its effects. Our parameter estimates for age now represented the effects of age in the absence of social effects. We again used these parameters to estimate age-specific fecundity and survival for both sexes. We calculated force of selection separately for males and female in our 'natural' population and simulated 'non-social' population using the following formula (*48*):

$$S(x) = \sum_{y=x+1} e^{-ry}\, l(y)m(y)$$

Here $S(x)$ represents the force of selection against a deleterious allele in the population, where r is the intrinsic rate of increase, $l(y)$ and $m(y)$ are the survivorship and fecundity functions and y is used to sum up the net expected reproduction over all ages after age x.

Mechanisms underlying male reproductive success

To test hypothesis #1 (that familiarity with neighbours leads to increased energetic resources, allowing males to travel farther to mate) we assessed whether familiarity with neighbours affected the farthest distance that a male traveled to mate using a linear mixed effect model (LMM) with average familiarity, average relatedness, age, and grid density as continuous fixed effects and squirrel ID and year as random effects. To test hypothesis #2 (that familiarity with neighbours provides males with more mating opportunities within his social neighbourhood) we measured whether average familiarity affected the number of pups that a male sired inside or outside his neighbourhood. We fitted both these models using a Poisson GLMM with the same fixed and random effects structure as above.

Data analysis

We conducted statistical analyses using R version 3.4.1 (R Core Team, 2017) and fitted models using the lme4 package (version 1.1-13: *49*). We obtained *P* values for the LMMs using the package lmerTest (version 3.0-1: *50*). For all models, we checked for significant non-linearities between the predictor and response variables by fitting generalized additive models. For GLMMs we checked for overdispersion by assessing whether the sum of squared Pearson residuals approximated a Chi-squared distribution with *N-P* degrees of freedom (*51*). Of the 1013 squirrels used in this analysis 12 individuals were not in the pedigree, meaning that there

were 25 neighbourhoods for which we could not calculate relatedness with neighbours. We assigned these neighbourhoods the mean average neighbourhood relatedness (r = 0.05). To facilitate direct comparison of effect sizes (*52*) we standardized all continuous predictors to a mean of zero and unit variance. We present all means ± SE, unless otherwise stated, and consider all differences statistically significant at $\alpha < 0.05$.

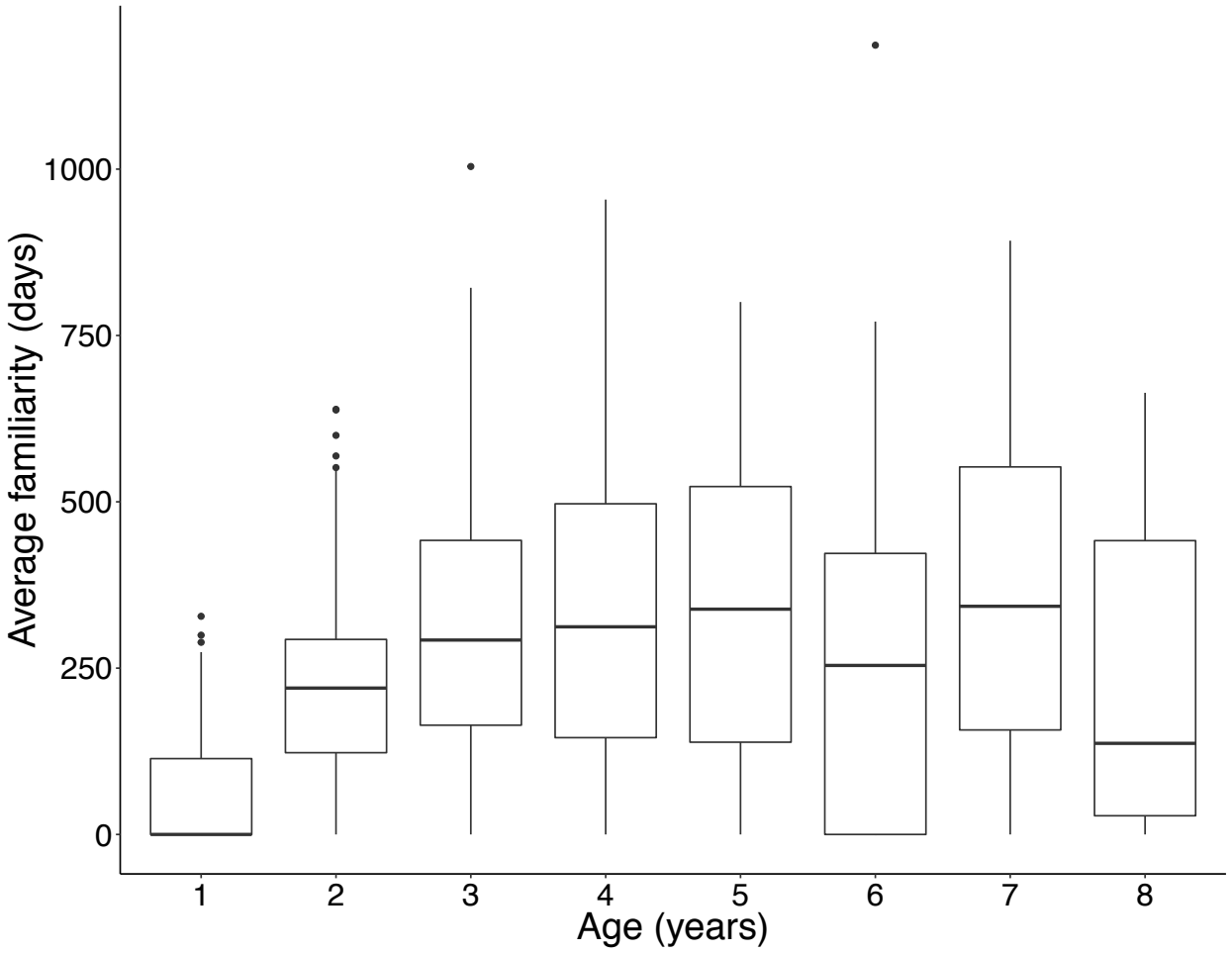

Fig. S1. Relationship between red squirrel age and the average familiarity of the social neighborhood (conspecifics within 130 m). Before age four, age and familiarity are strongly correlated (Pearson r = 0.60). However, in the senescent period (≥ 4 years old) familiarity in squirrels is driven by other demographic factors in the population such that age and familiarity become decoupled (Pearson r = -0.04).

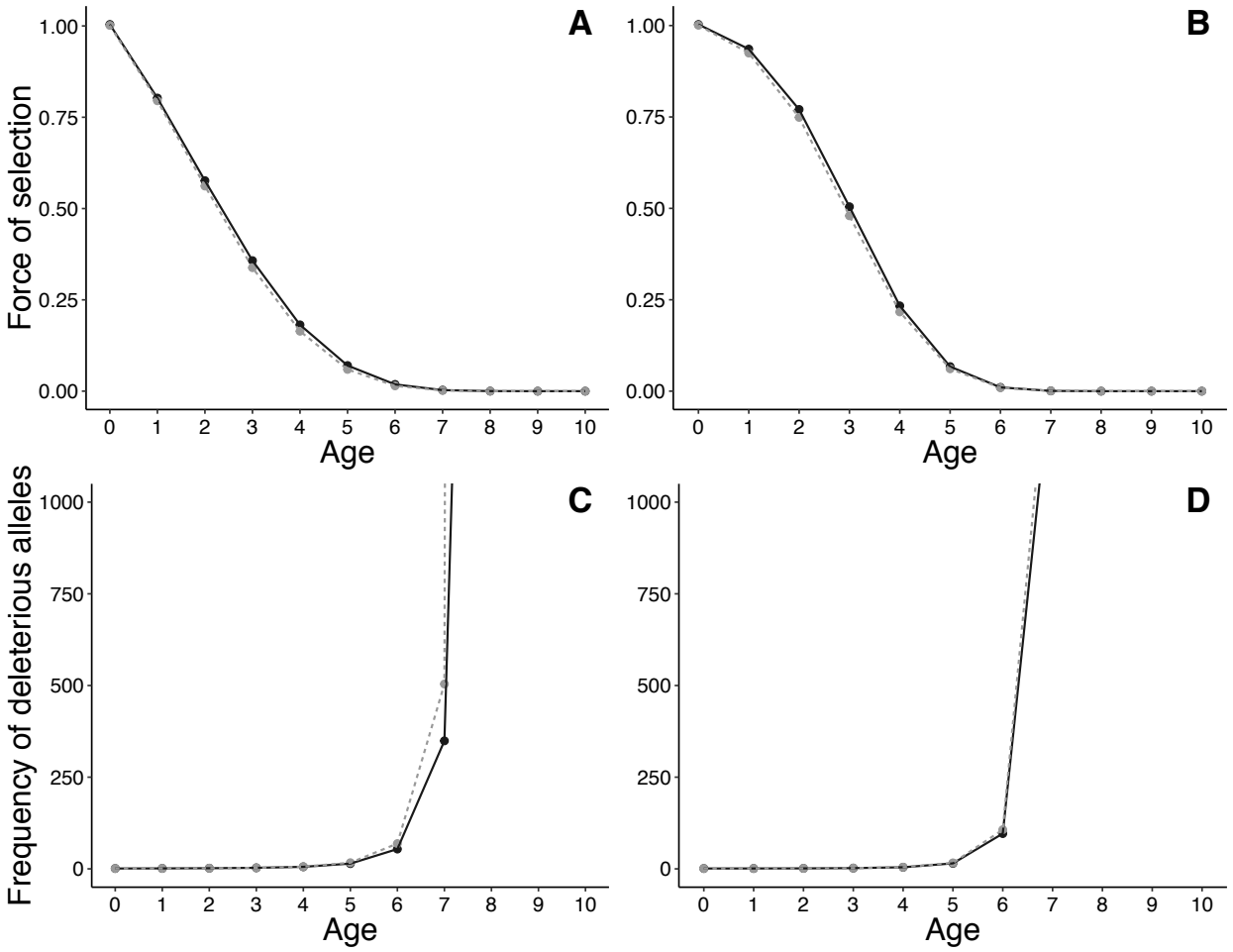

Fig. S2. The top two panels of this figure show Hamilton's force of selection ($S(x)$) by age for a) females and b) males. The force of selection falls to zero as the remaining survival-weighted reproduction for each sex declines. The bottom two panels of this figures show the inverse of the force of selection as an indicator of age-specific mortality for c) females and d) males. The rate of accumulation of deleterious alleles in the population is expected to be proportional to $1/S(x)$. The rapid increase in deleterious alleles observed when the force of selection drops to zero is referred to as the 'wall of death'. The solid black lines show the squirrel population under natural conditions where squirrels experience the social benefits of familiar neighbors. The dashed grey lines show the 'simulated' squirrel population without the benefits of social relationships.

Table S1. Random effects from annual survival, male annual reproductive success (ARS), and female ARS generalized linear mixed-effects models. Significance assessed using a log-likelihood ratio test (LRT) with one degree of freedom to compare models with and without the listed random effect. Significant effects are indicated in bold.

Data set	Response	Random effect	Variance	χ^2	*P*
Full data					
	Probability of survival	Squirrel ID	0.007	0.002	0.96
		Year	**0.18**	**29.00**	**<0.001**
		Spatial ID	0.07	0.55	0.46
	No. pups sired *(Male ARS)*	**Squirrel ID**	**0.47**	**35.60**	**<0.001**
		Year	**0.08**	**6.19**	**0.01**
		Spatial ID	**0.44**	**39.28**	**<0.001**
	No. pups recruited *(Female ARS)*	Squirrel ID	0.03	0.69	0.40
		Year	**0.34**	**128.12**	**<0.001**
		Spatial ID	0.01	0.08	0.78
Senescent data					
	Probability of survival	Squirrel ID	<0.01	<0.01	>0.999
		Year	0.06	0.60	0.44
		Spatial ID	0.27	1.24	0.26
	No. pups sired *(Male ARS)*	**Squirrel ID**	**0.45**	**5.96**	**0.01**
		Year	<0.01	<0.01	>0.999
		Spatial ID	**0.37**	**4.50**	**0.03**
	No. pups recruited *(Female ARS)*	Squirrel ID	<0.01	<0.01	>0.999
		Year	**0.30**	**18.84**	**<0.001**
		Spatial ID	0.11	1.31	0.25

Table S2. Fixed effects from models assessing effects of familiarity on (i) the furthest distance that males traveled to mate, (ii) the number of pups sired inside the neighborhood, and (iii) the number of pups sired outside the neighborhood (N = 199 observations over 129 males). Regression coefficients are standardized and significant effects are indicated in bold.

Response	Fixed Effect	Parameter ± SE	Test-statistic	*P*
Distance of furthest mate	**Familiarity**	**19.93 ± 8.83**	**2.26**	**0.03**
	Relatedness	6.91 ± 6.82	1.01	0.31
	Age	-4.67 ± 9.56	-0.49	0.63
	Density	**-24.86 ± 7.49**	**-3.32**	**0.001**
No. pups sired inside	Familiarity	0.12 ± 0.10	1.24	0.21
	Relatedness	0.01 ± 0.07	0.18	0.85
	Age	0.03 ± 0.11	0.24	0.810
	Density	**0.27 ± 0.12**	**2.32**	**0.02**
No. pups sired outside	**Familiarity**	**0.39 ± 0.10**	**3.78**	**<0.001**
	Relatedness	-0.003 ± 0.09	-0.04	0.97
	Age	-0.09 ± 0.12	-0.77	0.44
	Density	**-0.25 ± 0.09**	**-2.66**	**0.008**

Table S3. Random effects from models assessing effects of familiarity on (i) the furthest distance that males travels to mate, (ii) the number of pups sired inside the neighborhood, and (iii) the number of pups sired outside the neighborhood (N = 199 observations over 129 males). Significance assessed using a log-likelihood ratio test (LRT) with one degree of freedom to compare models with and without the listed random effect. Significant effects are indicated in bold.

Response	Random Effect	Variance	χ^2	*P*
Distance of furthest mate	Squirrel ID	2415	2.92	0.09
	Year	<0.01	<0.01	>0.999
No. pups sired inside	**Squirrel ID**	**0.20**	**11.60**	**<0.001**
	Year	**0.08**	**6.21**	**0.01**
No. pups sired outside	**Squirrel ID**	**0.41**	**28.52**	**<0.001**
	Year	<0.01	<0.01	>0.999

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