Familiarity with neighbours, but not relatedness, is linked to enhanced fitness in a territorial mammal

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Abstract

Competition for limited resources is a defining feature of natural systems. Understanding the relative role of mutually beneficial behaviours versus kin selection in resolving conflict and facilitating cooperation remains a persistent enigma in evolutionary biology. Using 22 years of data from North American red squirrels, we assessed how kinship and familiarity with neighbours affected fitness in a solitary, territorial species. While living near kin did not enhance fitness, familiarity with neighbours was associated with both increased survival and annual reproductive success. These fitness benefits were strong enough to compensate for the effects of aging later in life, with potential consequences for the evolution of senescence. We suggest that such substantial fitness benefits provide the opportunity for the evolution of cooperation between otherwise adversarial neighbours, offering insight into the role that mutually beneficial behaviours might play in facilitating and stabilizing social systems.

Introduction

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 (Clutton-Brock 2002). The indirect fitness benefits gained from associating with kin are well established as an important pathway to conflict resolution (Hamilton 1964), however, other pathways to the evolution of cooperation may be more common than previously thought (Clutton-Brock 2002). 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 (Engh *et al.* 2006; Wittig *et al.* 2008), enhanced longevity (Silk *et al.* 2010; Brent *et*

al. 2017), and increased offspring production and survival (Silk 2003; Cameron *et al.* 2009; Vander Wal *et al.* 2015). Social connectedness is also positively associated with human health and longevity (Holt-Lunstad *et al.* 2010), and, in particular, may be important in later life for mitigating effects of aging (Steptoe *et al.* 2013).

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. Kin can help to mitigate territorial aggression and enhance fitness (Viblanc *et al.* 2010), but there is also potential for stable interactions between neighbours to play an important role in helping to resolve conflict over territorial space (Grabowska-Zhang *et al.* 2012; Bebbington *et al.* 2017). Although physical contact with conspecifics is typically limited, territorial individuals, like their group-living counterparts, engage in regular recurring interactions with neighbouring individuals, often through auditory signaling or olfactory signatures, which are central to the establishment of territorial boundaries (Nowicki *et al.* 1998; Siracusa *et al.* 2017b). It is well understood that familiarity among long-term neighbours allows for the formation of stable social relationships that can facilitate reduced aggression and territory defence, a phenomenon known as the 'dear enemy' effect (Temeles 1994). 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 (Liebgold & Cabe 2008), enhanced body condition (Seppä *et al.* 2001) and increased reproductive success (Beletsky & Orians 1989; Grabowska-Zhang *et al.* 2012).

68 Owing to the kin-structured nature of many animal societies, it has been difficult for
69 previous research to distinguish between the relative roles of kin selection and mutually
70 beneficial interactions in reducing conflict and facilitating cooperation. In many study systems
71 where the importance of social relationships have been investigated, interactions typically take
72 place between related individuals (Silk 2003; Brent *et al.* 2017) . Similarly, studies that look at
73 the benefits of relatedness within a social group (Silk 2007) may inherently be confounded by
74 affiliative relationships among stable social partners . As such, the benefits of kinship and stable
75 social relationships have rarely been parsed in the same system and so the relative importance of
76 each mechanism is difficult to assess (but see Bebbington *et al.* 2017).
77 Here we used a natural population of North American red squirrels (*Tamiasciurus*
78 *hudsonicus*) to assess the importance of familiarity with neighbours for resolving conflict over
79 territorial space and thereby enhancing reproductive success and survival, while simultaneously
80 accounting for effects of kinship. Red squirrels are arboreal rodents in which both sexes defend
81 exclusive territories (Smith 1968). Territories are important for overwinter survival (LaMontagne
82 *et al.* 2013) and are defended through vocalizations called 'rattles' (Siracusa *et al.* 2017b), which
83 are uniquely identifiable (Wilson *et al.* 2015). Juveniles typically disperse 100 m on average and
84 females are known to bequeath all or part of their territory to offspring (Berteaux & Boutin 2000).
85 As a result, neighbours are sometimes closely related and have been shown to exhibit affiliative
86 behaviour with kin. For example, red squirrels communally nest preferentially with kin
87 (Williams *et al.* 2013) and adopt orphaned pups from related neighbours (Gorrell *et al.* 2010).
88 Red squirrels also have potential to establish long-term familiarity with neighbours since
89 individuals rarely relocate to a vacant territory following natal dispersal (Larsen & Boutin 1995).
90 Squirrels regularly interact with these territory neighbours through auditory signals (Dantzer *et al.*

2012; 2013). Such reoccurring interactions mean that red squirrels establish social relationships with nearby conspecifics that have the potential to shape behaviour and fitness. Previous research has demonstrated, for instance, that neighbours can recognize one another's calls (Robertson *et al.* 2019) and that the risk of territory intrusion (Siracusa *et al.* 2017a) and the time spent on territory defence (Siracusa *et al.* 2019) is reduced among long-term (familiar) neighbours.

Given these benefits of established social relationships with familiar neighbours, 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. 3). Given that in humans, strong social connections in old age have been demonstrated to reduce mortality risk and enhance longevity (Steptoe *et al.* 2013), we also tested whether familiar 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; McAdam *et al.* 2007; Descamps *et al.* 2008). 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. Our findings demonstrate that, even in the absence of kin benefits, stable social relationships with territory neighbours are associated with substantial fitness benefits that may offset the negative effects of aging.

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 ('Kloo' and 'Sulphur'). 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 (Berteaux & Boutin 2000; McAdam *et al.* 2007). 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 (Lane *et al.* 2008), with an average of three pups per litter (Humphries & Boutin 2000). 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.

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 whose middens (i.e. the center of the territory) were within a 130 m radius of the focal squirrel's midden (Fig. 3). One hundred and thirty meters is the farthest distance that red squirrel territorial vocalizations ('rattles') are known to be detectable to the human ear (Smith 1978), and is similar to the distance at which red squirrels have been demonstrated to be most responsive to changes in local density (150 m; Dantzer *et al.* 2012). This therefore suggests that 130 m is a reasonable measure of the distance at which squirrels can

receive and respond to information about their social environment. 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 neighbours. The timing of our semi-annual censuses meant that we could only update each squirrel's familiarity with its neighbours twice per year. Therefore, an individual's average familiarity could increase by 90 days if all neighbours were maintained from the May census to the August census, and by 270 days if all neighbours were maintained from August to May of the following year.

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 (Gunn *et al.* 2005) and assigned paternity with 99% confidence using CERVUS 3.0 (Kalinowski *et al.* 2007). 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

158 For individuals alive between 1994 and 2015, we measured annual survival as the probability of
159 surviving to the following year (*N* = 2346 records over 1009 individuals). Given that long-term
160 monitoring of individuals in this population first began in 1987, we excluded data prior to 1994
161 to ensure accurate measurement of familiarity between neighbours. Our ability to successfully
162 redetect adults in the population each year is estimated to be 1.0 (Descamps *et al.* 2009).
163 We measured female ARS as the number of pups recruited each year (i.e. surviving
164 overwinter). We included data from 450 breeding females between 1994 and 2015 (*N* = 981
165 records). All females with a known parturition date were considered to have bred; all other non-
166 breeding females were excluded from analysis. Since red squirrel males do not contribute to the
167 raising of pups and the male's social environment is, therefore, unlikely to affect pup recruitment,
168 we defined male ARS as the number of pups sired each year. We used data from 207 males
169 between 2003 and 2014 (*N* = 412 records). We excluded male reproductive success outside of
170 this timeframe because paternity data was not available prior to 2003 and after 2014. For all
171 analyses we only used data for adults (≥ 1 year old) whose age could be assigned with certainty
172 (i.e. individuals tagged in nest as juveniles).
173 It is possible that our ability to accurately assess recruitment is somewhat confounded by
174 dispersal beyond the borders of our study grids (Martinig *et al.* 2020). On average, juveniles
175 typically disperse less than 100 m (Berteaux & Boutin 2000; Cooper *et al.* 2017), and estimates
176 of juvenile survival do not differ between the center and edge of our study grids, which might be
177 expected if dispersing juveniles were mistakenly considered to have died (McAdam *et al.* 2007).
178 However, 37% of our population is comprised of immigrants from outside our study grids
179 (Martinig *et al.* 2020), which suggests that some juvenile recruitment outside the study area is
180 likely to have been missed by our methods.

Ethical note

This study required trapping individuals using Tomahawk live traps to determine territory ownership and assess reproductive status. Traps were checked every 60-90 min and squirrels were never left in a trap for longer than 120 min. We also entered the natal nest when pups were 1-2 days old and 25 days old to collect DNA, measure pup growth, and tag individuals. We returned the pups to the natal nest immediately after processing to minimize time spent away from the dam. These procedures had no detectable negative effects on the survival or welfare of the study animals. This research was approved by the University of Guelph Animal Care Committee (AUP number 1807).

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 study grid as a categorical fixed effect (Table 1). 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 (Table S1). To account for inherent spatial structure in our data, we grouped squirrels into 150 m squares (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

203 senescent period included the same covariates as the full models described above, but only
204 included a linear effect of age.

205 *Mechanisms underlying male reproductive success*

206 We conducted a post-hoc analysis to reveal potential mechanisms by which familiarity with
207 neighbours might lead to increased male reproductive success. We had two hypotheses: 1) that
208 familiarity with neighbours leads to increased energetic resources, allowing males to travel
209 farther to mate or 2) that familiarity with females provides males with more mating opportunities
210 within the males' social neighbourhood. To test hypothesis one, we assessed whether familiarity
211 with neighbours affected the farthest distance that a male traveled to mate using a linear mixed
212 effect model (LMM) with average familiarity, average relatedness, age, and grid density as
213 continuous fixed effects and squirrel ID and year as random effects (Table S2, S3). To test
214 hypothesis two, we measured whether average familiarity affected the number of pups that a
215 male sired inside or outside his neighbourhood. We fitted both these models using a Poisson
216 GLMM with the same fixed and random effects structure as above.

217 *Data analysis*

218 We conducted statistical analyses using R version 3.4.1 (R Core Team 2017) and fitted models
219 using the lme4 package (version 1.1-13; Bates *et al.* 2015). We obtained *P* values for the LMMs
220 using the package lmerTest (version 3.0-1; Kuznetsova *et al.* 2017). For all models, we checked
221 for significant non-linearities between the predictor and response variables by fitting generalized
222 additive models. For GLMMs we checked for overdispersion by assessing whether the sum of
223 squared Pearson residuals approximated a Chi-squared distribution with *N-P* degrees of freedom
224 (Bolker *et al.* 2009). Of the 1009 squirrels used in this analysis 12 individuals were not in the

225 pedigree, meaning there were 25 neighbourhoods for which we could not calculate relatedness
226 with neighbours. We assigned these neighbourhoods the mean average neighbourhood
227 relatedness (r = 0.05). To facilitate direct comparison of effect sizes (Schielzeth 2010) we
228 standardized all continuous predictors to a mean of zero and unit variance. We estimated all
229 effect sizes by using first and third quartile familiarity values while holding all other variables
230 constant at their mean and using 'Kloo' as the study grid. We present all means ± SE, unless
231 otherwise stated, and consider all differences statistically significant at $\alpha < 0.05$.

232 **Results**

233 **Survival**

234 We analyzed 2346 records of annual survival from 1009 squirrels. Over the 22-year period in
235 which we analyzed survival (1994-2015), average familiarity ranged between 0 and 1186 days
236 (mean = 191 ± 4 days) and average relatedness ranged between 0 and 0.5 (mean = 0.05 ± 0.001).
237 We found no effect of average relatedness of the social neighbourhood on male or female
238 survival in either the full models or senescent models (all $|z| < 1.21$, all $P > 0.22$; Table 1). Based
239 on the full models, increased familiarity with neighbouring individuals was associated with a 6%
240 increase in male and female survival ($\beta = 0.18 \pm 0.06$, $z = 2.78$, $P = 0.005$; Table 1). In the
241 senescent period (≥ 4 years old; $N = 512$ records over 288 individuals), living near familiar
242 neighbours was associated with a 17% increase in the probability of annual survival for both
243 sexes ($\beta = 0.45 \pm 0.11$, $z = 3.40$, $P < 0.001$; Fig. 1; Table 1). For example, squirrels with high
244 familiarity with their neighbours (500 days; third quartile) had a 69% chance of surviving to the
245 next year, while squirrels with low familiarity with their neighbours (130 days; first quartile) had
246 a 52% chance of surviving to the next year.

247 **Male ARS**

248 We analyzed 412 records of 207 males between 2003 and 2014. Over this timespan, average
249 familiarity ranged between 0 and 1186 days (mean = 167 ± 9 days) and average relatedness
250 ranged between 0 and 0.33 (mean = 0.04 ± 0.003). There was no effect of average relatedness of
251 the social neighbourhood on number of pups sired in either the full models or senescent models
252 (all |z| < 1.48, all P > 0.13; Table 1). In contrast, in full models including all data increased
253 familiarity with neighbouring individuals was associated with a 40% increase in the number of
254 pups sired (β = 0.18 ± 0.09, z = 2.04, P =0.04; Table 1). In the senescent period alone, the
255 fitness benefits associated with increased social familiarity were even more substantial. For
256 squirrels aged 4 and older (N = 78 records over 60 individuals), living near familiar neighbours
257 was associated with an 89% increase in the number of pups sired (β = 0.39 ± 0.15, z = 2.67, P =
258 0.008; Fig. 1; Table 1). Males with high familiarity with their neighbours (500 days, third
259 quartile) sired 1.7 pups annually while males with low familiarity with their neighbours (130
260 days, first quartile) sired 0.9 pups annually.

261 **Female ARS**

262 We analyzed 981 records of 450 breeding females between 1994 and 2015. Over this period,
263 average familiarity ranged between 0 and 892 days (mean = 213 ± 6 days) and average
264 relatedness ranged between 0 and 0.5 (mean = 0.07 ± 0.002). We found no effect of average
265 relatedness of the social neighbourhood on number of pups recruited in either the full models or
266 senescent models (all |z| < 0.80, all P > 0.42; Table 1). In the full model, there was also no effect
267 of familiarity on number of pups recruited (β = 0.06 ± 0.05, z = 1.38, P =0.17; Fig. 4.1).
268 However, in the senescent period (≥ 4 years old; N = 268 over 170 individuals), familiarity with
269 neighbours was associated with a 40% increase in the number of pups recruited (β = 0.23 ± 0.09,
270 z = 2.52, P =0.01; Fig. 1; Table 1). Females with high familiarity with their neighbours (500

days; third quartile) recruited 0.7 pups annually compared to females with low average familiarity with their neighbours (130 days; first quartile) that recruited 0.5 pups annually.

Mechanisms underlying male reproductive success

Analysis of the spatial locations of male paternity success revealed that males traveled farther to mate as familiarity with neighbours increased (β = 19.93 ± 8.83, t = 2.26, P =0.03; Fig. 2). 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 (β = 0.39 ± 0.10, z = 3.79, P <0.001; Fig. 2; Table S2), there was no association between familiarity and siring success within a male's social neighbourhood (β = 0.12 ± 0.10, t = 1.25, P =0.21; Table S2).

Discussion

Stable social relationships among group-living species are known to play an important role in mediating intragroup conflict and enhancing fitness (Silk 2003; Cameron *et al.* 2009; Vander Wal *et al.* 2015). For territorial species, maintaining territorial boundaries can be a costly endeavor and long-term associations among neighbours may serve an equally important role in helping to alleviate the negative effects of competition (Fisher 1954; Temeles 1994). Here we used 22 years of data from a population of territorial red squirrels to test the direct fitness effects of long-term familiarity with neighbouring conspecifics (Fig. 3). We tested for these effects while controlling for kinship to help elucidate the importance of mutualistic interactions relative to inclusive fitness benefits, the relative importance of which has previously been difficult to disentangle (c.f. Cameron *et al.* 2009; Bebbington *et al.* 2017). Our findings demonstrate that stable social relationships with neighbouring competitors are associated with increased survival

294 and reproductive success in solitary red squirrels, particularly in the senescent period, while
295 relatedness with neighbours is not (Fig. 3).
296 While we did not find evidence that kin provide fitness benefits for red squirrels, we
297 acknowledge that low average relatedness among neighbours (average neighbourhood
298 relatedness = 0.05 ± 0.001) could have constrained the potential for kin selection to act in this
299 system. We recognize that our findings do not mean that neighbour relatedness has no
300 biologically meaningful effects on red squirrel fitness, but simply that the scale at which we
301 attempted to measure these effects did not detect any influence of kinship. If, for instance, the
302 primary benefits of kinship come from sharing food (Siracusa *et al.* 2017a), relatedness of
303 nearest neighbours may be a more relevant measure to assess whether red squirrels obtain
304 benefits from kin. Future work should attempt to use other measures of the social environment to
305 offer additional insight as to the relative importance of kin-selection in this system. Regardless,
306 our results demonstrate that stable social relationships are associated with increased fitness in red
307 squirrels, independent of kinship, suggesting that inclusive fitness benefits are not a necessary
308 prerequisite to facilitate cooperation between social partners.
309 Although we do not have direct evidence for the mechanism by which familiarity with
310 neighbours might lead to increased reproductive success, previous work in this this study system
311 has shown that social familiarity results in reduced risk of pilfering (Siracusa *et al.* 2017a) and
312 reduced time spent on territory defence (Siracusa *et al.* 2019). Conceivably then, these direct
313 fitness benefits may result from cooperative agreements of non-intrusion among long-term
314 neighbours, which might increase food stores or reduce time and energy allocated to territory
315 defence. We sought to provide some mechanistic understanding of how familiarity contributes to
316 fitness by exploring two hypotheses in male red squirrels. We first hypothesized that if

317 familiarity is providing an increase in energetic resources (Siracusa *et al.* 2017a; 2019) this
318 might allow male squirrels in familiar social neighbourhoods to travel farther to obtain mating
319 opportunities (Lane *et al.* 2009; 2010), which might explain the large observed increase in siring
320 success associated with social familiarity. Alternatively, we hypothesized that social familiarity
321 might directly benefit males through increased mating success within their more familiar social
322 neighbourhoods. Our analyses revealed that males traveled farther to mate and sired more pups
323 outside their social neighbourhood (>130 m away) when more familiar with their neighbours
324 (those within 130 m; Fig. 2). However, we found no association between familiarity and a male's
325 siring success within his social neighbourhood. Together, these results suggest that stable social
326 relationships with neighbours enhance male fitness by allowing them to travel farther and
327 increase their siring success (Lane *et al.* 2009). This might result from familiarity with
328 neighbours increasing the energetic resources available to males through reduced territory
329 defence (Siracusa *et al.* 2019) or reduced cache pilfering by neighbours (Siracusa *et al.* 2017a).
330 Our findings also demonstrate a previously unappreciated benefit of maintaining social
331 relationships into later life. The magnitudes of the benefits of social familiarity in the senescent
332 period were sufficient to offset age-related declines in survival and reproductive success (Nussey
333 *et al.* 2013). Specifically, for an average 4-year old squirrel, aging by one year decreases the
334 probability of survival from 68% to 59%. But if that individual were to maintain all of its
335 neighbours, such that average familiarity increased by one year (from the mean familiarity of
336 318 days to 679 days), the maintenance of those stable social relationships would more than
337 compensate for the change in age, resulting in an increase in survival probability from 68% to
338 74%. However, despite the large individual benefits of increased social familiarity late in life,
339 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' (Hamilton 1966; see Supplementary Materials for methods and a more in-depth discussion of these results; Fig. S2).

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 (Donald & Boutin 2011), space (Smith 1968), and reproductive success (Fisher *et al.* 2017), 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 (Getty 1987). 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 neighbour's survival as long as this does not reduce the actor's survival by more than 7%. This scope for cooperation is comparable to kin selection interactions between first cousins once removed ($r = 0.06$; Hamilton 1964). It is possible then that reduced aggression when interacting with familiar neighbours (i.e. the dear-enemy phenomenon; Temeles 1994) 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 provides indirect fitness returns through increased social familiarity. In red

363 squirrels, reduced territory defence toward familiar individuals (Siracusa *et al.* 2019) may
364 convey survival benefits to neighbours through reduced aggression or lowered defense of food
365 resources. Red squirrels have also been known to nest communally during cold temperatures
366 (Williams *et al.* 2013), which might enhance neighbour survival. Other mechanisms by which
367 red squirrels might reduce neighbourhood turnover such as predator alarm calling, or forming
368 defensive coalitions (e.g. Getty 1987) to prevent a territory takeover, have yet to be tested.
369 Ultimately, if cooperative behaviours enhancing the survival of familiar neighbours were to
370 become widespread enough that mean social familiarity increased with age across the population,
371 then this socially driven increase in fitness late in life could influence the force of selection and
372 consequently the evolution of senescence (Fig. S2).

373 Finally, it is important that we address the potential issues associated with spatial
374 confounds in this study. Individual squirrels are distributed fairly continuously across our study
375 areas, so individually defined neighbourhoods are spatially overlapping. It is possible that our
376 observed fitness effects could be confounded by spatial variation in resource availability or
377 predation risk. In particular, areas with consistently low survival would have high turnover and
378 hence low average familiarity locally. If this kind of spatial autocorrelation in survival were
379 present, low neighbourhood familiarity might be linked to low survival in the absence of a causal
380 relationship. While this is a relevant concern that warrants consideration, there are several
381 reasons why we do not think this is likely.

382 First, there is no evidence of consistent spatial variation in spruce cone production (the
383 primary food for red squirrels; Boutin *et al.* 2006; Fletcher *et al.* 2010) across years in this study
384 system (LaMontagne *et al.* 2013). Therefore, there should not be locations that are consistently
385 rich or poor in food resources. Second, given this lack of consistency in the spatial distribution of

resource availability, it would have been inappropriate to fit a constant spatial autocorrelation term in our models (Fisher *et al.* 2019). Fitting separate spatial autocorrelation terms for each year would have been ideal, however, it was not possible to obtain convergence from our data using this method. Therefore, as a simpler alternative, we added a spatial random effect ('spatial ID') to our models by grouping squirrels into 150 m squares (within each year) based on their known spatial locations (Fisher *et al.* 2019). Fitting this as a random effect allowed us to account for any similarity among squirrels within each 150 m x 150 m area in each year (Table S1). All effects of familiarity we observed were robust to its inclusion (Table 1), and our results remained unchanged even when this spatial grouping term was defined to be a 75 m or 300 m square (see Table S4).

Third, we calculated Moran's I (ape package, version 5.1; Paradis & Schliep 2019) for each study grid and year to test whether similarity in ARS or probability of survival was related to the spatial proximity of any two individuals. We found only 9 out of 112 year/grid combinations in which the observed Moran's I value was significantly greater than the expected value, indicating that the trait in question demonstrated positive spatial autocorrelation (Table S5). We then proceeded to remove those year/grid combinations with positive autocorrelation from our analyses and found that our conclusions remained the same when our analyses were rerun with this limited dataset (Table S6).

Ultimately all of these concerns stem from the possibility that our findings might result from among individual differences in familiarity that result from covariation with individuals or locations of high quality. By refitting our ARS models using a within-individual mean centering approach (van de Pol & Wright 2009) we were able to demonstrate why this is unlikely to be the case. We split our familiarity term into an among-individual effect (the mean familiarity score

409 for an individual across all observations) and a within-individual effect (the deviation in each
410 familiarity observation for each individual from their mean score), and found that associations
411 between familiarity and fitness are primarily driven by within individual changes in familiarity
412 rather than among individual differences in familiarity (Table S7). In other words, it appears that
413 some individuals do not consistently experience high familiarity environments and others low
414 familiarity environments due to some intrinsic (individual quality) or extrinsic (habitat quality)
415 factor. It is instead the within individual changes in familiarity that occur within an individual's
416 lifetime that are associated with variation in fitness, resulting in the patterns observed in our data.

417 **Conclusion**

418 Although interactions among territorial individuals are fundamentally defined by
419 competition for food, mates, or other resources, here we have shown that stable social
420 relationships can limit these competitive interactions and provide important fitness benefits that
421 might feed back to maintain strong affiliative relationships among territorial neighbours. Similar
422 fitness benefits of social familiarity have also been demonstrated in territorial birds such as red-
423 winged blackbirds (Beletsky & Orians 1989) and great tits (Grabowska-Zhang *et al.* 2012). Our
424 findings, in conjunction with these previous studies, demonstrate that the benefits of stable social
425 relationships are not exclusive to group-living organisms but can extend to solitary species,
426 suggesting a shared evolutionary importance of stable relationships across a range of social
427 complexities. The strength of the effects of familiarity, particularly in the senescent period, was
428 surprising. We suggest that by increasing the force of selection later in life, stable social
429 relationships have the potential to lead to the evolution of slower rates of aging, although these
430 late-life social benefits are not currently widespread enough to affect senescence in red squirrels.
431 Importantly, our results indicate that intraspecific conflict can be mitigated through mutualistic

432 pathways, with resulting fitness benefits, independent of kinship effects (see also Cameron *et al.*
433 2009; Bebbington *et al.* 2017). Consequently, stable social relationships with neighbours may be
434 an important and overlooked contributor to fitness in territorial species, and may offer insight
435 into the relative importance of mutualistic behaviours for facilitating conflict resolution.

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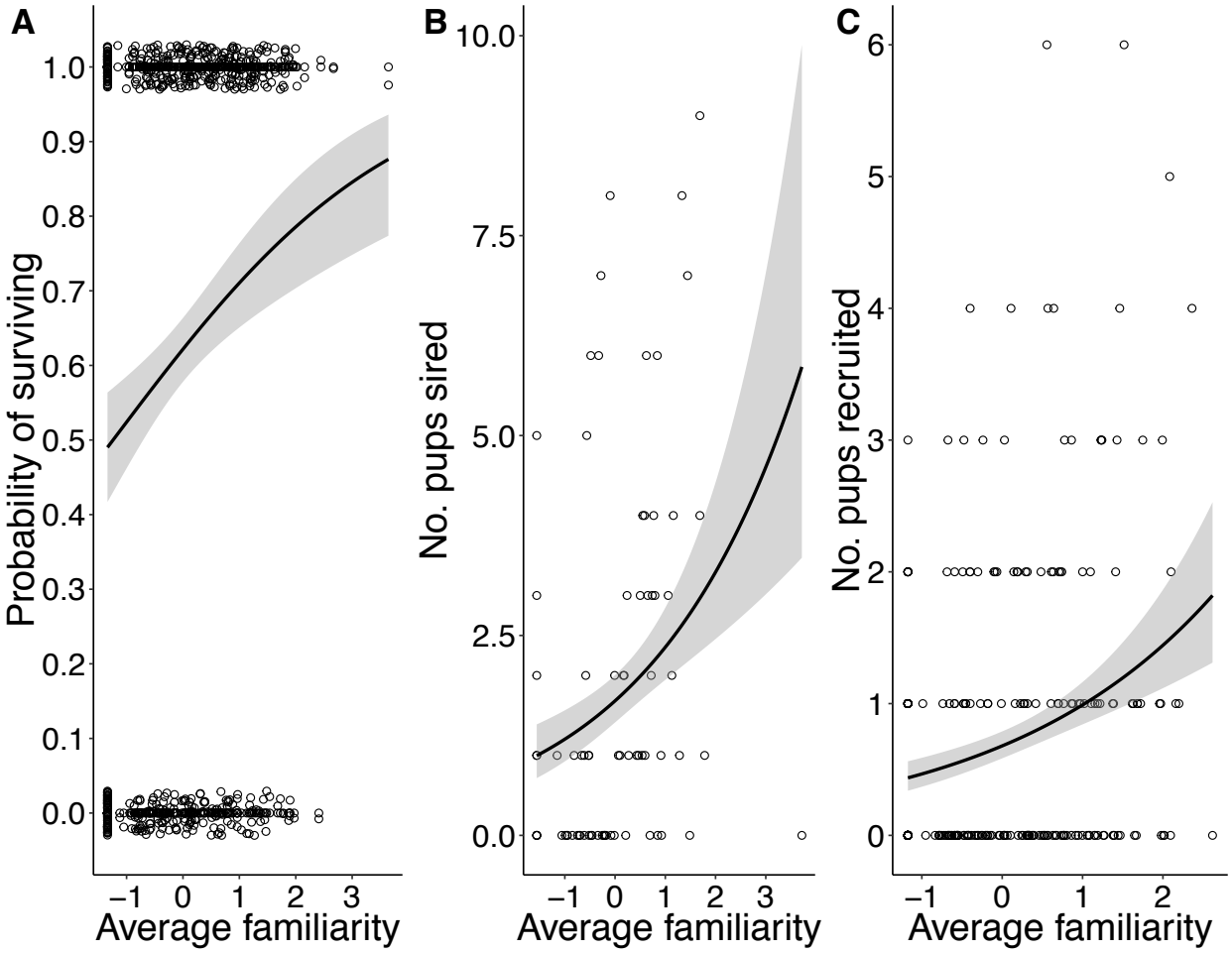

Figure 1. Effects of average neighbourhood familiarity on a) annual survival (N = 512), b) male annual reproductive success (ARS; N = 78), and c) female ARS (N = 268) during the senescent period (≥ 4 years old). Shaded grey bars indicate 95% confidence intervals. Values on x-axis are standardized measures of average familiarity. Points indicate raw data with a small amount of jitter introduced to show overlapping points.

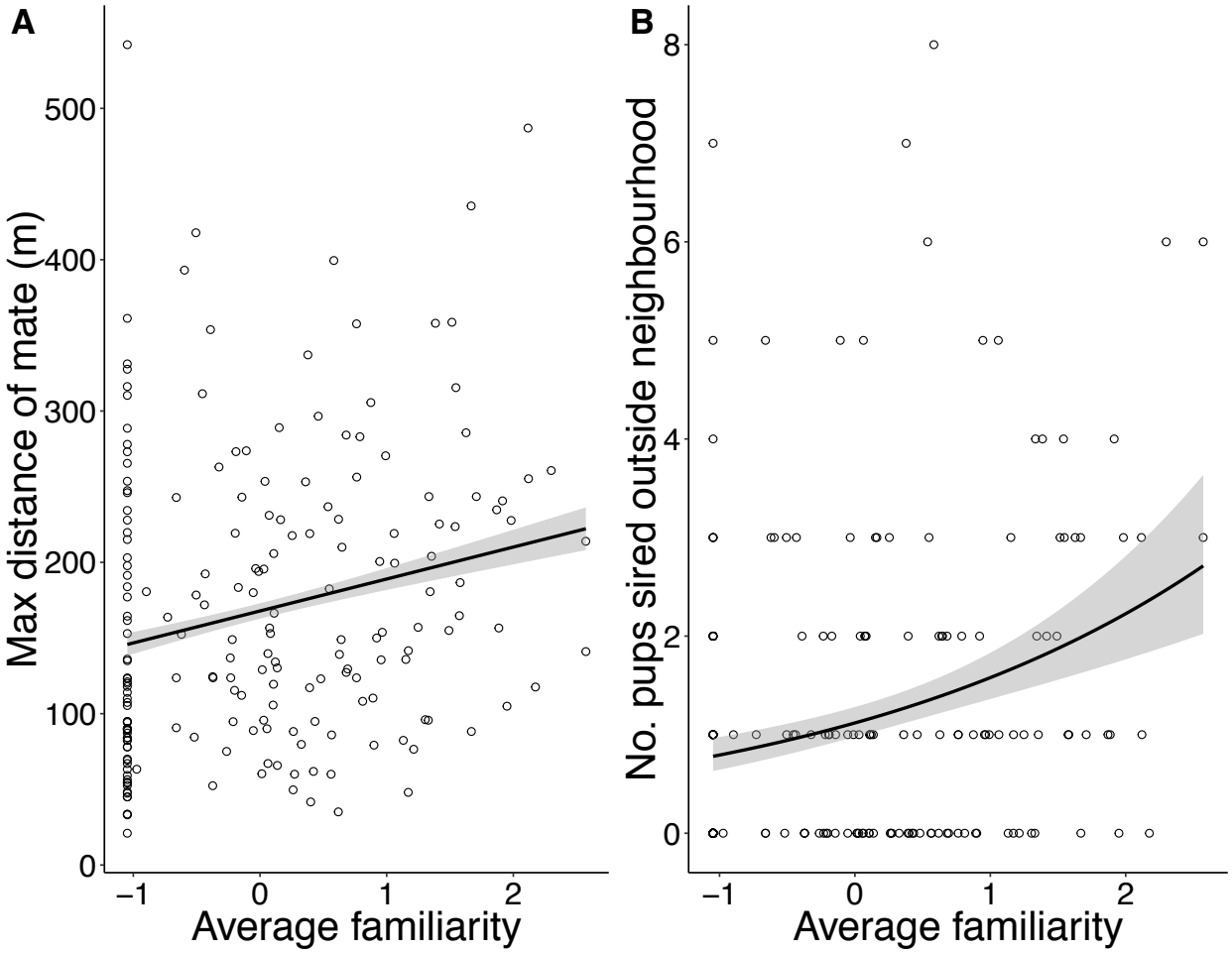

Figure 2. Effects of average neighbourhood familiarity on a) the distance that males traveled to mate and b) number of pups sired outside the social neighbourhood (i.e. 130 m radius; N = 199). Shaded grey bars indicate 95% confidence intervals. Values on x-axis are standardized measures of average familiarity. Points indicate raw data.

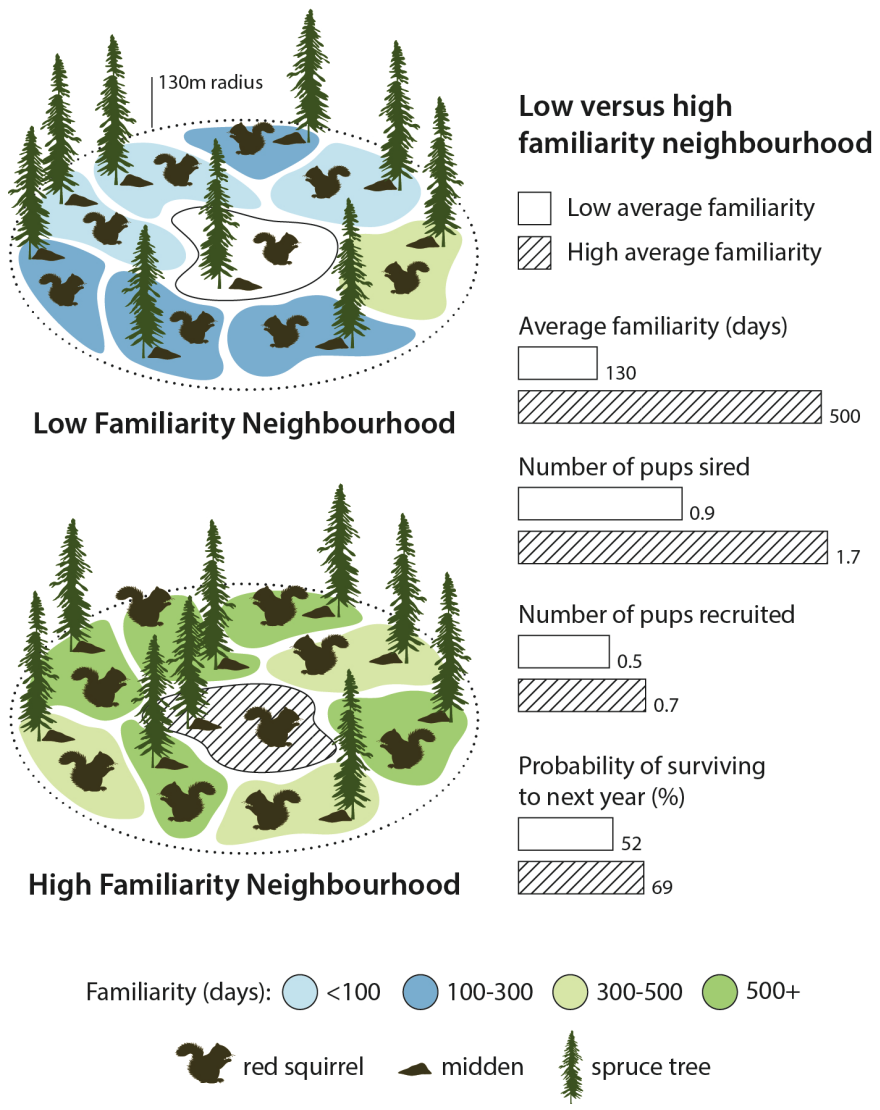

Figure 3. Schematic depiction of a low and high familiarity red squirrel neighbourhood with associated fitness metrics. Low and high familiarity are based on first and third quartile familiarity values. Neighbourhoods include all squirrels within a 130 m radius of the focal squirrel's midden, this reflects the acoustic social environment as 130 m is the farthest distance that red squirrel rattles (unique territorial vocalizations) carry. The biology of the system is simplified here for sake of space and clarity. On average squirrels have 13 neighbours and multiple spruce trees per territory. Familiarity with neighbours can only be updated twice per

year, see methods for details. Effect sizes reported here are based on models from the senescent period. Confidence intervals around the predicted effects of familiarity on these three measures of fitness can be found in Figure 1.

687 **Table 1.** Fixed effects from annual survival, male annual reproductive success (ARS), and

688 female ARS generalized linear mixed-effects models. Models are based on the full and senescent

689 (≥ 4 years old) datasets are shown with significant effects indicated in bold. Regression

690 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