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Social effects of territorial neighbours on the timing of spring breeding in North American red squirrels

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Abstract

Organisms can affect one another’s phenotypes when they socially interact. Indirect genetic effects occur when an individual’s phenotype is affected by genes expressed in another individual. These heritable effects can enhance or reduce adaptive potential, thereby accelerating or reversing evolutionary change. Quantifying these social effects is therefore crucial for our understanding of evolution, yet estimates of indirect genetic effects in wild animals are limited to dyadic interactions. We estimated indirect phenotypic and genetic effects, and their covariance with direct effects, for the date of spring breeding in North American red squirrels (*Tamiasciurus hudsonicus*) living in an array of territories of varying spatial proximity. Additionally, we estimated indirect effects and the strength of selection at low and high population densities. Social effects of neighbours on the date of spring breeding were different from zero at high population densities but not at low population densities. Indirect phenotypic effects accounted for a larger amount of variation in the date of breeding than differences attributable to the among-individual variance, suggesting social interactions are important for determining breeding dates. The genetic component to these indirect effects was however not statistically significant. We therefore showcase a powerful and flexible method that will allow researchers working in organisms with a range of social systems to estimate indirect phenotypic and genetic effects, and demonstrate the degree to which social interactions can influence phenotypes, even in a solitary species.

Key words: evolution, indirect genetic effects, selection, social interactions, *Tamiasciurus*

Introduction

An individual’s phenotype is influenced by both its genotype and the environment it experiences. As organisms mate, compete and cooperate with conspecifics (Frank 2007), an important component of the environment they experience is social, and partly made up of the phenotypes of other

33 individuals. This can allow an individual to influence others, and if their influence is partly genetic-
34 based, then a portion of any organism's phenotype will be influenced by the genes of those with
35 whom it interacts (Griffing 1967). These are known as indirect genetic effects ("IGEs"), of which
36 maternal genetic effects are the best known example (Moore et al. 1997; Wolf et al. 1998; McAdam
37 et al. 2014). With maternal genetic effects, the genes of a mother influence the traits of her offspring
38 beyond those directly inherited (e.g. a mammal's genes affecting milk production may influence the
39 growth rate of her offspring; Koch 1972; María et al. 1993). In the same way, the genes affecting the
40 aggression level of an individual (so a direct genetic effect, "DGE") may influence the aggression of
41 any rival in a dominance contest (an IGE, e.g.: Wilson et al. 2009). Additionally, when competing for
42 limited resources, the genes for resource acquisition of one individual are expected to negatively
43 influence the resource acquisition, and so resource dependent traits, of individuals with which it
44 competes (Wilson 2014). Therefore, IGEs can be expected in almost any system where conspecifics
45 interact with each other (McAdam et al. 2014).

46 Indirect genetic effects contribute additional heritable variation within a population
47 alongside DGEs (Moore et al. 1997; Bijma and Wade 2008). Similar to a genetic correlation between
48 any two traits (Lande 1979; Kirkpatrick 2009), an individual's own phenotype for some focal trait and
49 its indirect effect on that trait expressed by neighbours can be genetically correlated (a DGE-IGE
50 correlation). When IGEs are positively correlated with DGEs, such as the example with aggression
51 above, IGEs can enhance that trait's response to directional selection. This happens because the
52 standard response of the focal trait to selection results in a correlated evolutionary change in the
53 social environment. This in turn causes further change in focal trait mean - in the same direction -
54 through a plastic response to the social environment (Moore et al. 1997).

55 Conversely, if IGEs are negatively correlated with DGEs then the population response to
56 selection can be reduced, removed, or even reversed (Bijma and Wade 2008; Wilson 2014). Negative
57 correlations are expected for focal traits that are themselves dependent on the outcome of
58 competition for limited resources (Wilson 2014). For instance, Wade (1976) observed a decrease in
59 mean reproductive output across generations in flour beetles (*Tribolium castaneum*) that were
60 under individual selection for *increased* reproduction. This was presumably due to a negative IGE-
61 DGE correlation that caused each subsequent generation to be composed of individuals that more
62 strongly suppressed the reproduction of others through competitive interactions. Similarly, Costa e
63 Silva *et al.* (2013) observed a strong negative DGE-IGE covariance for diameter at breast height in
64 eucalyptus trees (*Eucalyptus globulus*). This meant that, despite tree growth rates being heritable in
65 the traditional sense (i.e. subject to DGEs), the total heritable variation in the population was near
66 zero, preventing a response to selection. Estimates of DGEs alone might, therefore, provide a poor

67 measure of the potential for a trait to respond to natural selection, yet most estimates of response
68 to selection or evolvability in the wild only consider DGEs (Houle 1992). More specifically, to the
69 extent to which resources are limited in nature, we might expect DGEs to consistently overestimate
70 the adaptive potential of resource-dependent traits because of negatively covarying IGEs (Wilson
71 2014). As such, IGEs arising from competition represent one possible explanation for the “paradox of
72 stasis”, in which natural selection on heritable traits often leads to stasis rather than evolutionary
73 change (Merilä et al. 2001), yet IGEs are very rarely quantified in the wild.

74 To date, empirical studies of IGEs in animals have focused on scenarios in which within
75 group interactions can be considered (approximately) uniform, and among-group interactions are
76 absent. This allows IGEs to be estimated from the covariance between phenotypes of group mates,
77 provided pedigree data spanning groups are available (Bijma 2010a). This approach is well suited to
78 dyadic interactions, but also to larger discrete groups ($n > 2$) of captive animals, where all individuals
79 within a pen are assumed to interact equally, but no interactions occur between individuals in
80 different pens. It has now been applied in a variety of taxa, such as mussels (*Mytilus*
81 *galloprovincialis*; Brichette et al. 2001), flour beetles (*T. castaneum*; Ellen et al. 2016), Nile tilapia
82 (*Oreochromis niloticus*; Khaw et al. 2016), domesticated chickens (*Gallus domesticus*; Muir 2005;
83 Brinker et al. 2015) mink (*Neovison vison*; Alemu et al. 2014), and domestic rabbits (*Oryctolagus*
84 *cuniculus*; Piles et al. 2017). This work has helped establish the importance of IGEs for trait evolution
85 (see: Ellen et al. 2014, for a review in livestock), and has led to growing interest in studying IGEs in
86 wild populations.

87 Studies of IGEs in free-living animal populations, however, have thus far been confined to
88 dyadic interactions. For example, Wilson et al. (2011) demonstrated that the tendency to win one-
89 on-one fights in wild red deer (*Cervus elaphus*) is subject to both DGEs and IGEs that are perfectly
90 *negatively* correlated, resulting in a total heritable variation of zero. This reconciles quantitative
91 genetic predictions with a common sense approach that sees that the tendency to win cannot evolve
92 at the population level, as each contest must always have one winner and one loser (see also: Wilson
93 et al. 2009; Sartori and Mantovani 2013). Other estimates for IGEs have focused on maternal genetic
94 effects (McAdam and Boutin 2004; McFarlane et al. 2015) or influences of male partner on female
95 bird laying dates (Brommer and Rattiste 2008; Caro et al. 2009; Teplitsky et al. 2010; Liedvogel et al.
96 2012; Germain et al. 2016). Studies on social interactions in groups of wild animals larger than two
97 are, however, absent.

98 For social processes in wild populations it is often problematic to identify and define discrete
99 groups when individuals interact with multiple individuals but not all at equal intensity. Some
100 interactions are frequent or strong while other interactions are brief or weak, and interactions may

101 be indirect e.g. competition for resources (Lusseau et al. 2003; Croft et al. 2004, 2008). Organisms
102 interacting in larger groups may have generally weaker indirect effects on each of their group mates,
103 as a consequence of their phenotype being “diluted” among more group members (Muir 2005;
104 Hadfield and Wilson 2007; Bijma 2010b). However, within a continuous population (i.e. one in which
105 distinct groups cannot be identified) the net effect of one individual on the phenotype of any other
106 may depend on distance or other factors (e.g. time associating) that mediate interaction intensity or
107 frequency (Muir 2005; Cappa and Cantet 2008). To model these situations, variation in interaction
108 strengths can be incorporated as “dilution” or “intensity of competition” factors in IGE models (Muir
109 2005; Cappa and Cantet 2008; Bijma 2010b). Here we refer to “intensity of association” factors,
110 since social interactions are not always competitive. In eucalyptus trees the inverse of the distance
111 between pairs of trees was used as the intensity of association factors to estimate DGEs, IGEs, and
112 their covariance, on growth traits in (Costa e Silva et al. 2013, 2017). The important premise here is
113 that each focal individual has a potential indirect genetic effect on the phenotype of all its social
114 partners, but the degree to which each partner experiences that effect depends on its distance from
115 the focal individual. Incorporating intensity of association factors should be equally useful for animal
116 focused IGE models, as this allows us to account for animals interacting with multiple different
117 individuals, in groups of varying sizes, and with different individuals at different strengths; a realistic
118 representation of social interactions in the natural world (Fisher and McAdam 2017).

119 Here we used intensity of association factors to model IGEs amongst multiple neighbours for
120 the first time in a wild animal (but see Formica et al. 2011 and; Farine and Sheldon 2015 who
121 weighted interacting phenotypes by distance to estimate social selection). We applied this
122 framework to a population of North American red squirrels (*Tamiasciurus hudsonicus*, hereafter “red
123 squirrels”) that have been continuously studied since 1987. We looked at a resource-dependent, but
124 also heritable ($h^2 = 0.14$; Lane et al. 2018) life-history trait: parturition date (the date in the spring on
125 which a female squirrel gives birth to a litter; Réale et al. 2003; Boutin et al. 2006; Kerr et al. 2007;
126 Lane et al. 2018), which could depend on competition for limited resources and, therefore,
127 incorporate IGEs. Red squirrels of both sexes in this population live on individual exclusive territories
128 based around a central cache of white spruce (*Picea glauca*) cones called a “midden”. The seeds
129 from stored spruce cones represents their main food source during reproduction in the spring
130 (Fletcher et al. 2013a). Individuals make territorial calls (“rattles”) to delineate territory boundaries
131 (Lair 1990) and deter intruders (Siracusa et al. 2017) from stealing cached resources (Gerhardt 2005;
132 Donald and Boutin 2011). Previous analyses have shown that selection favours earlier parturition
133 dates (Réale et al. 2003), while a food supplementation experiment advanced the timing of spring
134 breeding (Kerr et al. 2007). Note, however, that females can upregulate reproduction prior to a

135 resource pulse (Boutin et al. 2006), and so typically are reproducing below capacity (Boutin et al.
136 2013). Therefore, although reproduction is food dependent, they can still increase reproductive
137 output if necessary (see also: Dantzer et al. 2013). Still, if neighbours compete for food resources, we
138 expect superior competitors to have access to more food and breed earlier. Conversely,
139 competitively inferior individuals are expected to acquire less food and so breed later.

140 Population density is a key demographic parameter that we expect will influence the
141 magnitude of IGEs. Selection on birth dates is particularly strong in years of high density (Williams et
142 al. 2014; Fisher et al. 2017; although not found in Dantzer et al. 2013). Furthermore, red squirrels
143 respond behaviourally to both real and perceived increases in density (Dantzer et al. 2012), while
144 mothers adaptively increase the growth rates of their offspring under high density conditions
145 (Dantzer et al. 2013). Taken together, these findings are consistent with the expectation that, all else
146 being equal, high density means increased competition.

147

148 In light of the above, we had the following predictions:

- 149 1) We expected individuals to have indirect effects on the parturition dates of their neighbours,
150 and that the covariance between direct and indirect effects would be negative. That is,
151 superior competitors will both breed earlier and cause their neighbours to breed later
152 (following Costa e Silva et al. 2013; see also: Piles et al. 2017).
- 153 2) Parturition dates depend on resource acquisition and possess direct genetic variance, so we
154 expected the indirect effects to possess genetic variance (i.e. to be an IGE; McAdam et al.
155 2014; Wilson 2014).
- 156 3) Increased competition in years of high density should result in stronger indirect effects in
157 high-density years, both in the magnitude of the indirect effects and the strength of the
158 negative covariance (Fisher and McAdam 2019).

159

160

161 [Methods](#)

162

163 [Data collection](#)

164 All data were collected as part of the Kluane Red Squirrel Project (KRSP) in the southwest Yukon,
165 Canada. Since 1987 we have monitored two adjacent and unmanipulated 40 ha. study areas (“Kloo”
166 and “Sulphur”), bisected by the Alaska highway. Red squirrels of both sexes defend exclusive
167 resource-based territories of around 0.3 ha (LaMontagne et al. 2013), centred around a midden, an
168 aggregation of discarded white spruce cone scales underneath which red squirrels cache intact white

169 spruce cones. Each study area is staked at 30m intervals in a grid system and we recorded the x- and
170 y-coordinates of the centre of each midden (to the nearest tenth of a coordinate point, giving
171 distances to the nearest 3m). In the spring of each year we live trapped (Tomahawk Live Trap,
172 Tomahawk, WI, USA) new individuals and gave them unique ear tags in each ear. We also located
173 females (based on vocalizations at known and new territory locations), monitored them for signs of
174 pregnancy and ear tagged their pups once they were born. Based on the previously identified stages
175 of female pregnancy and the body mass of the pups once they were located, we then estimated the
176 female's parturition date. We analyse this date as the number of days since the 1st January in the
177 calendar year. We also conducted censuses twice yearly (once in spring, once in autumn) using
178 complete enumeration to ascertain the location of all individuals holding a territory, and so estimate
179 population density. See McAdam *et al.* (2007) for further details on the study system.

180 Red squirrels collect food throughout the summer and autumn, cache it in their middens and
181 rely on it to survive over winter (Fletcher *et al.* 2013a). The number of cached cones is positively
182 associated with overwinter survival (juveniles: Larivée *et al.* 2010; juveniles and adults: LaMontagne
183 *et al.* 2013). Squirrels primarily forage close to their midden, with occasional forays further afield,
184 including small amounts of theft from other red squirrels' hoards (Donald and Boutin 2011). We
185 define the individuals a red squirrel potentially competes with as its n nearest neighbours (n was set
186 at 6 for the majority of this analysis, but see below for explorations with different numbers of
187 neighbours). We defined neighbourhoods and population densities based on our autumn census
188 (August) rather than our spring census (May), because autumn is when squirrels are potentially
189 competing for resources to hoard, and conception occurs well before May in most years. Gestation
190 varies little around 35 days (Lair 2014), hence parturition dates cannot be influenced by conditions
191 after conception. Squirrels occasionally defend a second adjacent midden, but as they rarely store
192 food in secondary middens we considered each squirrel's location to be the location of its primary
193 midden. We then analysed each female's parturition date the following spring as influenced by her
194 own genes (the DGE), and the identities and genotypes (the IGE) of those competing individuals as
195 identified in the autumn census. Some females gave birth in multiple years, in which case they were
196 included each year they did so, with an updated set of nearest neighbours as necessary. Females
197 may attempt multiple litters in years of high resources, or if their first litter fails (Boutin *et al.* 2006;
198 McAdam *et al.* 2007; Williams *et al.* 2014), but we limited our analyses to each female's first litter of
199 each year (e.g. Dantzer *et al.* 2013).

200 We tagged pups while they were still on their mother's territory, so maternity was known
201 for all non-immigrants. Male red squirrels provide no parental care. From 2003 onwards, paternities
202 were, therefore, assigned by collecting tissues samples from the ears of adults and neonatal pups.

203 We used these tissue samples to genotype all adults and pups since 2003 at 16 microsatellites (Gunn
204 et al. 2005) analysed with 99% confidence using CERVUS 3.0 (Kalinowski *et al.* 2007; see Lane *et al.*
205 2007, 2008 for further details). This method gives an estimated error rate of paternities, based on
206 mismatches between known mother–offspring pairs, of around 2% (Lane et al. 2008), which we
207 consider acceptable. Approximately 90% of yearly pups are assigned paternities with known males
208 while the remaining 10% are analysed further in Colony 2.0 (Jones and Wang 2010) to determine
209 whether they might still be full or half siblings from unknown sires using 95% confidence in
210 maximum likelihoods.

211

212 Data analysis

213 Data on the locations of squirrel territories were available from the autumns in 1991-2015, and so
214 we looked at parturition dates in the following springs (i.e. 1992-2016). All squirrels identified as
215 holding a territory in an autumn census were included in this analysis, including females that did not
216 attempt a litter in the following spring, and males. These individuals had missing values entered for
217 their parturition dates. As all males have missing values, we did not include an effect of sex. Their
218 inclusion was nonetheless necessary as they acted as potential competitors during the autumn for
219 those squirrels that did have a litter.

220 We initially fitted two mixed-effects linear models to our data, the first to estimate indirect
221 effects (the “phenotypic model”), and second to split these indirect effects into genetic and non-
222 genetic components (the “genetic model”). All models we fitted in the software “ASReml” ver 4.1;
223 (Gilmour et al. 2015). We divided raw parturition dates by the standard deviation of all observations,
224 giving a sample with a variance of 1, making the variance components easier to interpret (Schielzeth
225 2010). In each model we included the fixed effects of study area (a two-level factor), year (to test for
226 a continuous linear trend), whether or not the spruce trees “masted” (produced a super-abundance
227 of cones; Silvertown 1980; Kelly 1994; LaMontagne and Boutin 2007) in the year of the autumn
228 census (a two-level factor), age and age² of the squirrel, and the separate random effects of year and
229 squirrel identity, to account for repeated measures within each year and within each squirrel
230 respectively. If the age of the squirrel was not known, the mean age of all other squirrels in that
231 breeding season was entered. Estimating the squirrel identity random effect allowed the calculation
232 of the (conditional) repeatability of individual squirrel parturition dates (Nakagawa and Schielzeth
233 2010). Additionally, while we predicted a negative covariance between neighbours due to
234 competition for resources (especially during high-density conditions), this could be masked by
235 positive spatial autocorrelation in resource availability within a study-area. This would generate a
236 net signal of positive phenotypic covariance among-neighbours (Stopher et al. 2012; Regan et al.

237 2016; Thomson et al. 2018). To avoid this, we fitted a term (hereafter referred to as the “square
 238 term” or differences among “squares”) to control for spatial auto-correlation (see Supplementary
 239 materials for details, and Table S1 for results of varying the scale at which we modelled this).

240 To estimate indirect effects, we added the identities of the six nearest squirrels as six
 241 random effects (see below for our explorations of other possible neighbourhood sizes). However,
 242 unlike most mixed effect models, these six random effects were assumed to come from the same
 243 distribution, with a mean of zero and a single variance which we estimated. This allowed us to
 244 estimate a single indirect phenotypic effect, and the covariance between this term and the direct
 245 effect of squirrel identity. We based “nearest” on location of the primary midden during the autumn
 246 census. We associated each neighbour (j) of each focal individual (i) with variable intensity of
 247 association factors (f_{ij}). This allowed the indirect effect of each neighbour j actually experienced by
 248 i to be mediated by their spatial proximity, with $f_{ij} = 1 / (1 + \text{distance})$, where distance was the
 249 Euclidean distance between the center of individuals’ territories, measured in units of 30m. This
 250 value is bounded between 0 and 1, with low values representing individuals that were far apart and
 251 high values representing individual that were close. We used the inverse of distance here, but any
 252 biologically relevant measure representing intensity of social interaction could be used (Fisher and
 253 McAdam 2017). To weight the strength of the indirect effects, we replaced all 1s in the indirect
 254 effect design matrix with these terms (Muir 2005; Cappa and Cantet 2008). These terms link and
 255 scale indirect effects of individuals with the phenotypes of the focal individuals. All individuals
 256 farther than the 6 nearest neighbours were not modelled as having an indirect effect (but see
 257 below). The phenotypic model therefore used the following form, with a population mean
 258 accounting for the fixed effects for i (μ_{Fi}), a direct phenotypic effect (P_{Di}) and a total indirect
 259 influence arising from the sum of competitor specific indirect effects (P_{Sj}) for the 6 nearest
 260 neighbours. Note, a single variance for the indirect effect is estimated, from a distribution made up
 261 of all competitor effects (see above). Additionally, there are multiple measures per squirrel across
 262 years, hence we include the random effect for the year t (K_t). Our model predicts a parturition date
 263 for the i th individual in a given year (y_{it}) and so the residual term is specific to an individual in a year
 264 (e_{it}).

265

$$266 \quad y_{it} = \mu_{Fi} + P_{Di} + \sum_{i \neq j}^n f_{ij}(P_{Sj}) + K_t + e_{it} \quad 1$$

267

268 This phenotypic model estimated the variance among squirrels in their parturition dates, the
 269 consistent variance in parturition dates associated with the identity of the neighbour, and the
 270 covariance within-individuals between their own parturition date and how they influence their

271 neighbours ($Cov(P_{Di}, P_{Sj})$). For our genetic model, we split these phenotypic effects into additive
272 genetic and permanent environment effects (consistent differences among-individuals not due to
273 additive genetic differences) by the incorporation of a pedigree (Kruuk 2004; Wilson et al. 2010). We
274 estimated the DGEs and IGEs on parturition dates, their covariance, and the equivalent terms for the
275 permanent environmental effects:

$$276$$
$$277 \quad y_{it} = \mu_{Fi} + A_{Di} + PE_{Di} + \sum_{i \neq j}^n f_{ij} (A_{Sj} + E_{Sj}) + K_t + e_{it} \quad 2$$
$$278$$

279 Where individual i 's parturition date in year t , is comprised of the fixed effect mean, a direct additive
280 genetic effect (A_{Di}), a direct permanent environmental effect (PE_{Di}), both the additive genetic (A_{Sj})
281 and non-additive genetic (E_{Sj}) indirect effects of all the n neighbours (j) that i interacts with, a year
282 term (K_t), and an individual by year specific residual term (e_{it}).

283 This model has not been applied to wild animals before, and we fully acknowledge that our
284 choice to consider only the 6 nearest neighbours here is somewhat arbitrary, as indeed is the scaling
285 of f_{ij} . Therefore, we also explored different numbers of neighbours, and different methods for
286 defining our f_{ij} terms. We then monitored how this influenced the estimates of the variance
287 parameters, to determine whether the model was particularly sensitive to altering these factors (see
288 also: Costa e Silva *et al.* 2017). We present results using $f_{ij} = 1/(1 + \text{distance}^2)$ in the supplementary
289 materials (Table S1). In the supplementary materials we also present results where we defined the
290 competitors as all those within 60, 130 or 200 metres, without weighting by distance, up to 24
291 competitors (Table S1), and investigations with varying numbers of neighbours 1-5, 9, 12, 15, 18 &
292 24; Table S2). Neither changing the number of neighbours nor rescaling intensity of association
293 terms changed the number of model parameters estimated (either a single indirect phenotypic
294 effect, or both genetic and permanent environmental indirect effects, and their respective
295 covariances). Therefore, information criteria-based approaches for comparing model fits were not
296 appropriate as biological complexity (e.g. number of neighbours) changed but the degree of
297 penalisation did not (i.e. still one neighbour variance estimated). Additionally, we were primarily
298 interested in our ability to estimate, and the magnitude and significance of, certain parameters (our
299 indirect effects), hence finding the most parsimonious model of parturition date was not a goal of
300 ours. Instead we simply assessed the change in variance components, noting the size of the
301 parameter estimates and size of the standard errors. We focus on the results with the 6 closest
302 neighbours, as this seemed the median result among the variations we tried. Using the inverse of
303 distance² squared led to a large increase in the standard errors of the DGE estimate, which only
304 occurred in this model, hence we considered simply the inverse of distance as more appropriate.

305 Nevertheless, we direct readers to the supplementary material to view the range of possible results
306 depending on the model specification.

307 We tested the significance of the direct-indirect phenotypic covariance in the phenotypic
308 model using a likelihood ratio-test (LRT) between a model with the covariance freely estimated and
309 one with it fixed to zero, and tested the significance of the indirect phenotypic effect using a LRT
310 between the model with the indirect effect (and a zero covariance) and a model without it. With the
311 genetic model, we tested the significance of the DGE-IGE covariance, and the IGE variance, in the
312 same way, in models that still estimated the full direct-indirect phenotypic covariance matrix. We
313 assumed the LRT statistic was distributed as a 50:50 mixture of χ^2_1 and χ^2_0 when testing single
314 variance components (following Self and Liang 1987) but as χ^2_1 when testing covariances. We report
315 correlations, although if the variance of either the direct or indirect effect was very small (<0.0001),
316 then we assumed it was essentially zero, and so then we report the correlation as “undefined”.
317 Although they were not directly relevant to the biological hypotheses being tested, the statistical
318 significance of the fixed effects in the genetic model was tested using conditional Wald tests (see:
319 Gilmour et al. 2015). This approach to testing the significance of fixed effects in mixed linear models
320 performs well in situations with limited sample sizes (Kenward and Roger 1997). We then calculated
321 partial R^2 for each fixed effect, following Edwards et al. (2008), using the residual degrees of freedom
322 as calculated by ASReml (1174 for the genetic model).

323

324 Influence of population density on indirect effects

325 We consider population density during the resource caching period to be key to resource
326 acquisition. Consequently, for any given year of parturition the relevant measure of density was
327 obtained from the census in the autumn of the year *prior* to parturition, i.e. at the same time as
328 when the territory ownership was defined. As the study area has grown marginally since the start of
329 the project, we restricted counts to individuals holding a territory within a defined 38ha area that
330 has been constant throughout the entire study period. Across both study areas in all years the
331 median population density in the autumn was 1.69 squirrels ha^{-1} (Fig. 1). We, therefore, labelled
332 each study area within each year with a density higher than this as “high density” (1994, 1998-2000,
333 2006 and 2015 for both study areas, 1991-1993, 1995-1997, 2001 and 2002 for Sulphur only and
334 2011-2014 for Kloof only), and so the remainder as “low density” There were, therefore, 26 instances
335 of low density conditions, and 24 instances of high density conditions. There are several instances of
336 study areas having exactly the median density, hence why there are more low- than high-density
337 conditions.

338 For both the phenotypic and the genetic models, we fitted an interaction between
 339 population density (low or high) and each random effect. This gave us separate density-specific
 340 estimates of each of the variances (DGEs, IGES, and non-genetic versions) and covariances, the
 341 among-year variances and the among-square variances for low- and high-density study areas. To
 342 obtain stable model convergence in the genetic model, we were required to fix the direct permanent
 343 environment effect in low-density years to 0.1×10^{-4} , but since this term was estimated to be very
 344 small in the model across all years, this is likely not problematic. There was a single residual variance
 345 in each model. We also included density as two-level factor in the fixed effects, and an interaction
 346 between this term and each of the other fixed effects, to allow them to vary between low- and high-
 347 density conditions. We tested for significance of indirect effects in both low- and high-density
 348 conditions in the same way as for the full models. When testing the significance of terms for low-
 349 density, we maintained the full model structure (e.g. IGES and their covariance with DGEs, and the
 350 equivalent permanent environmental effects in the genetic model) for high-density conditions, and
 351 vice versa for when testing the significance of terms for low-density.

352

353 Calculating total variance parameters

354 When traits are influence by social effects, their total variance (both phenotypic among-individual
 355 variance and genetic variance) is not only defined by direct effects. How individuals' influence those
 356 they interact with, and how this social effect covaries with their own trait values, must be
 357 incorporated. These composite values represent how much individuals vary in their effect (both
 358 direct and indirect) on trait values, and how much genetic variance (including direct and indirect
 359 effects) there is for selection to act on (Bijma 2011). To this end, we estimated the total variance in
 360 individuals' phenotypic effects on the population mean parturition date ($\hat{\sigma}_{PE}^2$, incorporating both
 361 consistent direct and indirect phenotypic effects; for the phenotypic model), and the total variance
 362 in individuals' heritable influence on the population mean parturition date ($\hat{\sigma}_H^2$; for the genetic
 363 model, commonly referred to as the "total heritable variance"). Following Bijma (2011) and Costa e
 364 Silva *et al.* (2013) these are:

365

$$366 \quad \hat{\sigma}_{PE}^2 = V_{PD} + 2n\bar{f}_{ij}Cov(P_D, P_I) + (n\bar{f}_{ij})^2V_{PI} \quad 3$$

367

$$368 \quad \hat{\sigma}_H^2 = V_{AD} + 2n\bar{f}_{ij}Cov(A_D, A_I) + (n\bar{f}_{ij})^2V_{AI} \quad 4$$

369

370 Where n is the number of neighbours (excluding the focal individual, so 6), \bar{f}_{ij} is the mean intensity
 371 of association factor, V_{PD} and V_{AD} are the direct phenotypic and additive genetic variances

372 respectively, $Cov(P_D, P_I)$ and $Cov(A_D, A_I)$ are the phenotypic and genetic direct-indirect
373 covariances respectively, and V_{PI} and V_{AI} are the indirect phenotypic and additive genetic variances
374 respectively. The $\overline{f_{ij}}$ was calculated as 0.330 across the whole dataset, 0.298 at low densities and
375 0.352 at high densities, which means a squirrel's 6 nearest neighbours were on average, 60.9m,
376 70.7m and 55.2m from it across the whole dataset, at low densities, or at high densities respectively.
377 Note that $\hat{\sigma}_H^2$, unlike traditional heritability, can exceed 1; see Bijma (2011) for the mathematical
378 demonstration of this, and Ellen *et al.* (2014) for empirical examples in livestock.

379

380 Results

381

382 In total, 1862 unique red squirrels were recorded a total of 4362 times in autumn censuses as
383 holding territories, and so were included in the analysis. There were 555 unique females that had at
384 least one litter, with a mean of 2.1 (range = 1-8, standard deviation = 1.3) recorded parturition dates
385 each. The median date of first litters was 23rd April, with interquartile ranges of 6th April to 11th
386 May. There were 364 females that had no recorded parturition dates, and 943 males. 1196 squirrels
387 had a known mother, and 498 had a known father, with 481 of those having both parents known.

388 Parturition dates differed greatly among years and less so among squares, with variance
389 among years accounting for 32.0% of the variance in the genetic model, while variance among
390 squares accounted for 4.0% of the total variance (all variance component estimates are shown in
391 Table 1, with fixed effect estimates shown in Table 2). While there was no linear trend across years,
392 parturition dates were significantly earlier following mast years by approximately 40 days.

393 Alongside these environmental effects, individuals showed some degree of consistency in
394 their parturition dates, with the direct variance among-individuals in parturition date in the
395 phenotypic model accounting for 3.8% of the phenotypic variance. Indirect phenotypic effects of
396 neighbours were significant ($V_{PI} = 0.076$, LRT, $\chi^2_{0,1} = 13.755$, $p < 0.001$), but the covariance between
397 the direct and indirect phenotypic effects was not ($cor = -0.094$, LRT, $\chi^2_1 = 0.111$, $p = 0.739$),
398 indicating that individuals that give birth earlier do not influence their neighbours in any particular
399 direction relative to their own parturition date. Individuals' consistent differences in their own
400 phenotypes and consistent effects on neighbours ($\hat{\sigma}_{PE}^2$ from eq. 3) was calculated as 31.4% of the
401 phenotypic variation, much larger because each individual affects multiple neighbours and indicating
402 that social effects account for a large amount of the variation in parturition date. Alongside this
403 consistency, individuals showed a degree of plasticity, with older squirrels having earlier parturition
404 dates, while the positive quadratic effect indicates a nonlinear effect of age in which squirrels began
405 to breed later at older ages.

406 Parturition date showed direct heritability, with V_{AD} in the genetic model accounting for
407 4.8% of the phenotypic variance (note this differs from previous estimates of h^2 for this trait in this
408 system as here we include the among-year variation and the variance attributable to fixed effects in
409 V_P , see also Wilson (2008)). The estimate for the IGEs was not different from zero ($V_{AI} < 0.001$, LRT,
410 $\chi^2_{0,1} = 0.003$, $p = 0.480$), as was the DGE-IGE covariance ($cor = \text{undefined}$, LRT, $\chi^2_1 = 0.119$, $p = 0.729$).
411 We calculated the total heritable variance of parturition date, $\hat{\sigma}_H^2$ from eq. 4, as 6.8%, a modest
412 increase over V_{AD} . The very small DGE-IGE covariance indicated that genotypes for early parturition
413 dates did not affect their neighbours in any consistent direction relative to their own parturition
414 date.

415

416 Low vs high density comparison

417 In low density conditions, both the variance in indirect phenotypic effects ($V_{PI} = 0.031$, LRT, $\chi^2_{0,1} =$
418 0.808 , $p = 0.184$) and the direct-indirect phenotypic covariance ($cor = 0.737$, LRT, $\chi^2_1 = 0.1206$, $p =$
419 0.272) were not significantly different from zero. At high densities there were significant phenotypic
420 indirect effects ($V_{PI} = 0.078$, LRT, $\chi^2_{0,1} = 9.523$, $p = 0.001$), although the covariance was not different
421 from zero ($cor = -0.023$, LRT, $\chi^2_1 = 0.004$, $p = 0.952$). We note here that size of the standard errors
422 suggests that the indirect phenotypic effects at low and high densities are not different from each
423 other, but we did not test this formally.

424 Given that we detected no phenotypic indirect effects in low-density conditions, it is
425 unsurprising that the IGEs ($V_{AI} < 0.001$, LRT, $\chi^2_{0,1} = 0.000$, $p = 0.500$) and the DGE-IGE covariance in
426 these conditions were also not different from zero ($cor = \text{undefined}$, LRT, $\chi^2_1 = 0.566$, $p = 0.452$). For
427 high densities, IGEs were considerably stronger than across the whole dataset, and more than one
428 standard error from zero, although still not significantly different from zero ($V_{AI} = 0.038$, LRT, $\chi^2_{0,1} =$
429 0.607 , $p = 0.218$). The covariance between DGEs and IGEs was negative but not different from zero
430 ($cor = -0.401$, LRT, $\chi^2_1 = 0.688$, $p = 0.407$). Although we reiterate that neither covariance was
431 statistically significant, based on our parameter estimates in low-density conditions $\hat{\sigma}_H^2$ was 14.3%,
432 which was higher than V_{AD} , as this calculation includes the positive DGE-IGE covariance estimate
433 (despite the lack of variance in IGEs rendering the correlation undefined). In high-density conditions
434 $\hat{\sigma}_H^2$ was 14.2%, much higher than with direct genetic effects alone due to the additional genetic
435 variance from IGEs. We stress that, as the estimates for the IGEs and their covariances with the DGEs
436 were not significantly different from zero, the estimates of $\hat{\sigma}_H^2$ should be interpreted with caution.

437 Variation attributable to spatial location accounted for 4.2% of the variation in parturition
438 dates in low-density, and 3.1% in high-density conditions (from the genetic model split between low
439 and high densities). Finally, there was also substantial among-year variance in both conditions,

440 accounting for 32.2% and 38.4% for the observed variance in low and high-density conditions
441 respectively. We present estimates for fixed effects at low and high densities from the genetic model
442 in the supplemental materials (Table S3); for the calculation of partial R^2 s, we calculated the residual
443 degrees of freedom to be 1169.

444

445

446 Discussion

447

448 Indirect effects are present and change with population density

449 Red squirrels live in territories surrounded by conspecifics, with whom they engage in social
450 interactions through vocalizations, competition for resources, and mating interactions. Our analyses
451 show that these interactions can lead to substantial indirect effects on female squirrel reproductive
452 traits. These are detected here as a repeatable influence of competitor identity on the parturition
453 date of focal individuals – which accounted for a much greater amount of variation in parturition
454 date than direct effects of individual identity alone. Our results also suggest that these indirect
455 effects are significant determinants of focal phenotypes at high densities, but they are not at low
456 densities. Specifically, at high densities, there is significant variation in the extent to which squirrels
457 influence each other's parturition dates, but this is not the case at low densities.

458 The social effects on parturition date we documented indicate that much more of an
459 individual's phenotype is under the control of those it socially interacts with than is determined by
460 its own identity ($\hat{\sigma}_{PE}^2$ was large compared to within-individual repeatability), even in a solitary and
461 territorial species. Work on eucalyptus trees (Costa e Silva et al. 2013) implicated competition for
462 limited resources as the source of indirect effects, and our results are broadly consistent with this
463 idea. Highly competitive red squirrels may acquire larger amounts of resources from the
464 environment, leaving less for other individuals. Earlier studies have shown that red squirrel females
465 may be food limited to some degree, aside from in years following a mast event. For example, earlier
466 parturition dates and lower levels of oxidative protein damage and higher levels of antioxidants
467 were found when food was supplemented (Kerr et al. 2007; Fletcher et al. 2013b; Williams et al.
468 2014), and individuals are more likely to survive over winter with a larger food cache (Larivée et al.
469 2010; LaMontagne et al. 2013), suggesting that not all individuals have enough stored food.
470 However, female squirrels appear to reproduce below capacity in non-mast years, and upregulate
471 their reproduction *before* pulsed resources are available (Boutin et al. 2006, 2013), and so they are
472 likely not completely food-limited. The additional insight from the current study is that, for focal

473 individuals, competitive effects on phenotype depend not simply on high density, but also on the
474 identities – and so phenotypes - of their nearest neighbours.

475 Our analysis did not explore the specific mechanism (or trait(s)) that mediate indirect
476 phenotypic effects from competition, hence we have not confirmed that red squirrels are competing
477 for limited food resources, although this explanation seems likely. While direct physical interactions
478 are rare (Dantzer et al. 2012) and thus an unlikely mechanism, red squirrels might instead influence
479 each other's parturition dates through acoustic territorial interactions. Red squirrels give territorial
480 calls ("rattles"), to which neighbours behaviourally respond (Shonfield et al. 2012; Wilson et al.
481 2015) and which function to maintain their territory from conspecifics (Smith 1978; Lair 1990;
482 Siracusa et al. 2017). Additionally, red squirrels rattle more when they have a higher local population
483 density (Dantzer et al., 2012; Shonfield et al. 2012), while red squirrel mothers increase the growth
484 rate of their pups when playback of territorial vocalizations leads to the perception of higher local
485 population density (Dantzer et al. 2013). This is through upregulation of maternal glucocorticoids
486 (Dantzer et al. 2013), part of the stress axis. Other life history traits, such as parturition date, may be
487 influenced by rattles at high densities, allowing individuals to influence each other's parturition
488 dates. Therefore, acoustic interactions among-neighbours, which enable neighbours to influence
489 each other's reproduction, may be a source of indirect effects, particularly in high-density
490 conditions.

491

492 Indirect effects with a limited heritable basis

493 While our analyses provide statistical support for considerable indirect effects of competitors on a
494 focal individual's parturition date, we did not conclusively demonstrate that these indirect effects
495 were underpinned by genetic variation. Estimated effect sizes were larger at high densities, in line
496 with our predictions and the phenotypic effects, but standard errors remained quite wide.
497 Therefore, while the point estimates of predicted change indicate IGEs are potentially strong enough
498 to make a meaningful difference to evolutionary dynamics, they were estimated with high
499 uncertainty so should be interpreted with caution.

500 Previous work on livestock has shown that IGEs negatively correlated with DGEs can reduce
501 or even reverse the expected response to selection (Costa e Silva et al. 2013; Muir et al. 2013; Ellen
502 et al. 2014). The evolutionary stasis of heritable traits under directional selection is a well-known
503 observation in need of an explanation in the study of trait evolution in wild populations (Merilä et al.
504 2001; Kokko et al. 2017; Pujol et al. 2018). The negative DGE-IGE covariance found here at high
505 densities would counteract selection responses (compared to a DGE-only scenario) and so reduce
506 evolutionary change. Whether this is a general explanation for evolutionary stasis remains to be

507 explored (Wilson 2014). In our study population, despite phenotypic selection on parturition dates
508 (which as noted above are heritable), we have observed no evolution in this trait over 20 years (Lane
509 et al. 2018). However, Lane et al (2018) found that the association between parturition date and
510 fitness was entirely a residual correlation, rather than a genetic one, so no alternative explanation
511 for evolutionary stasis (such as IGEs) is required.

512 If IGEs are not different from zero and so all social effects are solely phenotypic, then the
513 expected response to selection will not differ from that predicted by the breeder's equation (Bijma
514 and Wade 2008). We note that the non-significance of our IGE variance estimates may have been
515 driven by a high degree of uncertainty (large standard errors), rather than the magnitude of the
516 effect, as in high density years the V_{AI} was quite close in absolute size to V_{AD} , and their contribution
517 to total heritable variance was large. By demonstrating this possibly important but uncertain effect,
518 we hope to stimulate others to estimate more precisely these parameters, and so help the field
519 achieve a general understanding of their importance.

520

521 Altering competition indices and neighbourhood size

522 Varying the intensity of association factors (i.e. how strongly we weighted neighbours at different
523 distances) and the size of the neighbourhood did alter the balance between the estimated direct and
524 indirect effects, as well as estimated relative contribution of genetic and environmental influences
525 (see Tables S1-2 in the supplementary materials). Weighting the closest individuals more strongly, by
526 only including the 1-3 nearest neighbours, or using the inverse of distance or distance², or by only
527 including individuals within 60 m, gave similar results. In all these versions, the variance arising from
528 DGEs increased marginally compared to the model where all neighbours were weighted equally. This
529 effect was more pronounced when using the inverse of distance² to define the intensity of
530 association factors. We note that the standard errors of estimates for direct additive genetic
531 variance (V_{AD}) in the model using the inverse of distance² were greatly increased, causing the
532 estimate to be within two standard errors of zero (i.e. nominally non-significant). This was the only
533 model explored where this occurred. Weighting farther individuals as strongly as close individuals,
534 either by not including any intensity of association factors for the 6 closest individuals, or by
535 including all individuals within 200 m and weighting them equally, gave very low estimates for the
536 IGEs. This could suggest that individuals at greater distances do not influence their neighbours as
537 much as close individuals.

538 Increasing the number of neighbours considered in the analysis beyond six led to larger
539 estimates for the variance arising from the non-genetic indirect effects (V_{PI}). A larger estimate for
540 the V_{PI} was also present in the model before the square term was added (not shown). This suggests

541 the apparent non-genetic influence of neighbours at large spatial scales, as indicated by V_{PI} , may be
542 driven by shared environmental factors at the larger scale causing sets of neighbours to be
543 consistently different from other sets, rather than by social interactions of the focal individual
544 causing their neighbours to be consistently different. Decreasing the number of neighbours tended
545 to increase the variance attributed to the DGE, while IGEs showed a non-linear trend, peaking in
546 magnitude with 4 neighbours and then falling back down towards zero. At these neighbourhood
547 sizes, V_{PI} was typically estimated near zero, but grew in size once 5 or more neighbours were
548 considered. Overall, these results do not indicate that inferences from our model with the six closest
549 neighbours, weighted by the inverse of distance, are inappropriate for the system.

550 The approach we used, based on the work of Muir (2005) and Cappa and Cantet (2008) can
551 be applied to organisms in a range of social structures. Due to the relatively recent increase in usage
552 of techniques such as social network analysis (Krause et al. 2007, 2014; Croft et al. 2008), estimates
553 of pairwise associations within populations of animals have been made in many systems. These
554 values can be used as the intensity of association factors, as we used the inverse of distance, to scale
555 indirect effects (Fisher and McAdam 2017). To estimate IGEs, this must be twinned with information
556 on the phenotypes and relatedness of the individuals in the population. We had a large dataset with
557 good information on phenotypes and relatedness of individuals, yet high uncertainty around
558 moderately large estimates of IGEs did not distinguish them from zero. The requirement to
559 phenotype, genotype and assess the social relationships of many individuals within a population may
560 well limit the range of study systems this approach can be used in (Kruuk and Wilson 2018).
561 Simulations to provide guidelines for sample sizes may well be useful. However, with decreases in the
562 cost of tracking technologies and in the cost of assessing the genetic relatedness of animals (Bérénos
563 et al. 2014), more study systems will begin to be able to apply this and similar models, increasing the
564 number of estimates for these difficult-to-estimate quantitative genetic parameters, which could
565 then be aggregated in a meta-analysis to detect general patterns (Reid 2012), such as that by Wilson
566 and Réale (2005) for the direct-maternal genetic correlation.

567

568 Conclusions

569 Previous to this study, IGEs had only ever been estimated for wild animals in the context of pairwise
570 (dyadic) social interactions. We extended this to estimate IGEs on a life-history trait with links to
571 fitness in a population of wild animals that do not interact in discretely defined groups. We also
572 incorporated varying strengths of closeness of association between individuals to more accurately
573 represent the heterogeneous and complex nature of social interactions in the natural world. We
574 found that indirect effects of neighbours were a significant contributor to parturition dates at high

575 densities, and this effect may have a heritable component. However, the point estimates for genetic
576 parameters are characterised by high uncertainty and, as noted, we cannot exclude the possibility
577 that the indirect effects have a non-genetic basis. Nonetheless, significant indirect phenotypic
578 effects were detected and appear to increase in importance at high density. This is consistent with
579 competition for limited food resources being the source of neighbour influences on focal life-history
580 traits. Exactly how this competition is mediated remains to be determined. The estimation of
581 indirect effects, and IGEs specifically, should be extended to more systems where densities and
582 resource availabilities vary (either naturally or artificially) to determine whether the patterns we
583 have observed are general. While we did not conclusively demonstrate IGEs are present, we think
584 wider estimation of effect sizes is useful even if power is limiting to make strong inferences in any
585 single case. The method we have used is flexible enough to be applied to alternative systems, hence
586 we look forward to the accumulation of more estimates of IGEs in the wild to detect general
587 patterns.

588

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827 Figure legends

828

829 Figure 1. Estimated population densities across both study areas in our study (“Kloo” is the solid line,
830 “Sulphur” the dashed line). Points above the line (the median density: 1.69 squirrels ha.⁻¹) were
831 counted as “high density”, points at or below the line as “low density”.

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835 **Table 1.** Variance component estimates (with their approximate standard errors in brackets) for each element of the variance-covariance structure from
836 our models. Terms that were bound to values very close to zero will not have a standard error estimated, and so have “-” instead. Models without a given
837 term have “NA” entered in that cell. Terms highlighted in bold were >2 times greater than their standard errors, while terms underlined were between 1
838 and 2 times greater than their standard errors. Variance in direct genetic effects are indicated by V_{AD} , in indirect genetic effects by V_{AI} , and their covariance
839 by $Cov(A_D, A_I)$. Equivalent notation with “P” instead of “A” refers to variance in purely phenotypic effects for the phenotypic model, and permanent
840 environment effects in the genetic model. V_S is the among-square variance (with squares of size 150m x 150m), V_Y is the among-year variance, and V_R is the
841 residual variance.

Model		V_{AD}	V_{AI}	$Cov(A_D, A_I)$	V_{PD}	V_{PI}	$Cov(P_D, P_I)$	V_Y	V_S	V_R
Whole dataset										
Phenotypic model		NA	NA	NA	0.038 (0.012)	0.076 (0.023)	-0.005 (0.014)	0.317 (0.098)	0.038 (0.014)	0.197 (0.017)
Genetic model		0.048 (0.012)	<0.001 (-)	0.005 (0.015)	<0.001 (-)	0.063 (0.023)	-0.018 (0.020)	0.320 (0.099)	0.040 (0.014)	0.192 (0.016)
Low vs. high density comparison										
Phenotypic model split by density	Low density	NA	NA	NA	<u>0.043</u> (0.022)	0.031 (0.046)	<u>0.027</u> (0.024)	0.316 (0.123)	<u>0.040</u> <u>(0.024)</u>	0.205 (0.019)
	High density	NA	NA	NA	0.040 (0.019)	0.078 (0.030)	-0.001 (0.022)	0.380 (0.150)	<u>0.028</u> (0.178)	
Genetic model split by density	Low density	0.047 (0.020)	<0.001 (-)	0.027 (0.030)	<0.001 (-)	0.021 (0.045)	-0.003 (0.036)	0.322 (0.126)	<u>0.042</u> (0.024)	0.189 (0.017)
	High density	0.053 (0.018)	<u>0.038</u> (0.037)	-0.018 (0.023)	<0.001 (-)	0.033 (0.046)	-0.001 (0.026)	0.384 (0.151)	<u>0.031</u> (0.018)	

842

843 **Table 2.** Estimates and relevant statistics for fixed effects from final model with all years. Study area
 844 was a two-level factor, with “Kloo” as the reference level, hence the shown estimate is for the
 845 deviation of the “Sulphur” study area. Following a mast was a two-level factor, with not following a
 846 mast as the default, hence the estimate is for the deviation in parturition dates following a mast
 847 year. The denominator degrees of freedom are indicated by df_d, while the numerator degrees of
 848 freedom were 1 in all cases.

Term	Estimate	Standard error	df_d	F-statistic	P-value	R²
Intercept	-6.684	32.355	23.3	0.06	0.810	NA
Study area (SU)	0.176	0.054	5.72	10.68	0.002	0.009
Year	0.006	0.016	23.1	0.16	0.693	< 0.001
Following a mast (yes)	-1.71	0.288	22	35.57	< 0.001	0.029
Age	-0.002	< 0.001	1091.5	145.85	< 0.001	0.111
Age²	< 0.001	< 0.001	1164.0	95.59	< 0.001	0.075

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Social effects of territorial neighbours on the timing of spring breeding in North American red squirrels: Supplementary materials

Spatial autocorrelation

We predicted a negative covariance (either genetic or solely phenotypic) between neighbours for parturition date due to competition for resources (especially during high-density conditions). However, this could be masked by positive spatial autocorrelation in resource availability within a study-area. This would generate a net signal of positive phenotypic covariance among-neighbours (Stopher et al. 2012; Regan et al. 2016; Thomson et al. 2018). To control for this, we fitted a term accounting for (non-socially determined) environmental heterogeneity in resource abundance. In our multiyear data set we were unable to obtain convergence from our data with a model in which a separate spatial autocorrelation term for each year was fitted (since the spatial distribution of territory quality is not consistent year-to-year; LaMontagne et al. 2013). As a simpler alternative, we assigned each red squirrel within each year to one 150 m x 150 m square within a grid of non-overlapping squares that encompassed the study area (hereafter referred to as “squares”). Each square was given a unique label comprising its location and the year, and so by fitting this as a random effect we could account for any similarity among red squirrels within each 150 m x 150 m area in each year. This is similar to the approach of Germain et al (2016), who found that an equivalent “grid” term fitted their data better than a matrix of local overlap (c.f. Stopher et al. 2012), or a modelling spatial autocorrelation in the residuals (c.f. Costa e Silva et al. 2013). We repeated this analysis with squares of 75 m x 75 m or 300m x 300 m. These results were qualitatively similar to the analysis with the intermediate size squares, and so are presented below (Table S1).

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Model variations

Key

VAD	additive direct genetic variance (DGEs)
VAI	additive indirect genetic variance (IGEs)
C-AD, AI	additive direct-indirect genetic covariance (DGE-IGE covariance)
VPED	Permanent environmental direct effect
VPEI	Permanent environmental indirect effect
C-PED, PEI	direct-indirect permanent environment covariance
Year	among year variance
Square	among square variance

Point estimates are provided in the tables, with the standard error of the estimate in parentheses

Table S1. Variance components from models with modifications from the “genetic model” presented in the text, as well as in line 1 of this table. The “75m square” and “300m square” models use smaller or larger areas respectively to define the term controlling for spatial autocorrelation. The “6 closest, no f_{ij} ” model includes the 6 nearest neighbours, but does not scale their effects by any factor. The “6 closest, inverse of $dist^2$ ” model includes the 6 nearest neighbours and scales their effects by the inverse of the square of the distance between the two squirrels. The “within XXm” models include all squirrels with 60, 130 or 200 metres of the focal individual respectively, without scaling their effect by any factor, up to a maximum of 24 individuals.

Model	VAD	VAI	C-AD, AI	VPED	VPEI	C-PED, PEI	Year	Square	Residual	Notes
150m square	0.0480 (0.0124)	< 0.0001 (0)	0.0051 (0.0145)	< 0.0001 (0)	0.0626 (0.0227)	-0.0177 (0.0198)	0.3199 (0.0991)	0.0402 (0.0139)	0.1922 (0.0164)	Genetic model
75m square	0.0442 (0.0123)	0.0078 (0.0259)	<0.001 (0.0020)	0 (0)	0.0765 (0.0364)	-0.00576 (0.02057)	0.3167 (0.0981)	0.0491 (0.0237)	0.1744 (0.0242)	
300m square	0.0479 (0.0121)	0.0026 (0.0258)	0.0022 (0.0154)	0 (0)	0.0723 (0.0349)	-0.0135 (0.0195)	0.3144 (0.0979)	0.0423 (0.0111)	0.1890 (0.0145)	
6 closest, no f_{ij}	0.0399 (0.0117)	< 0.0001 (0)	0.0018 (0.0053)	< 0.001 (0)	0.0121 (0.0030)	-0.0079 (0.0072)	0.3187 (0.9900)	0.0335 (0.0131)	0.1805 (0.0156)	
6 closest, inverse of $dist^2$	<u>0.0676</u> <u>(0.0598)</u>	0.0064 (0.0320)	0.00311 (0.0388)	0.0184 (0.0593)	0.00427 (0.0475)	-0.0248 (0.0487)	0.3222 (0.0998)	0.0539 (0.0139)	0.2133 (0.0170)	
within 60m	0.0535 (0.0123)	< 0.0001 (0)	0.0092 (0.0069)	< 0.0001 (0)	< 0.0001 (0)	-0.0054 (0.0877)	0.3244 (0.1004)	0.0535 (0.0135)	0.2140 (0.0156)	
within 130m	0.0439 (0.0121)	0.0006 (0.0015)	0.0021 (0.0038)	< 0.0001 (0)	0.0026 (0.0056)	-0.0022 (0.0056)	0.3205 (0.0995)	0.0255 (0.0139)	0.2021 (0.0160)	
within 200m	0.0445 (0.0120)	< 0.0001 (0)	0.0020 (0.0030)	< 0.0001 (0)	0.00397 (0.0010)	-0.00162 (0.00463)	0.3157 (0.0993)	<u>0.0187</u> <u>(0.0129)</u>	0.2012 (0.0154)	

Table S2. Variance components from models with varying numbers of neighbours, with the “genetic model” used in the main text in row 6.

Number of neighbours	VAD	VAI	C-AD,AI	VPED	VPEI	C-PED,PEI	Year	Square	Residual	Notes
1	0.0562 (0.0123)	<0.0001 (0)	0.0183 (0.0265)	<0.0001 (0)	<0.0001 (0)	-0.0093 (0.0275)	0.3285 (0.1003)	0.0539 (0.0135)	0.2132 (0.0155)	
2	0.0560 (0.0126)	<0.0001 (0)	0.0091 (0.0199)	<0.0001 (0)	0.0140 (0.0341)	-0.0099 (0.0231)	0.3233 (0.1001)	0.0539 (0.0127)	0.2085 (0.0173)	
3	0.05545 (0.0126)	0.0009 (0.0186)	0.0139 (0.0174)	<0.0001 (0)	<0.0001 (0)	-0.0241 (0.0221)	0.3234 (0.1001)	0.0569 (0.0140)	0.2091 (0.0162)	
4	0.0513 (0.0125)	0.0107 (0.0290)	0.0142 (0.0169)	<0.0001 (0)	<0.0001 (0)	-0.0206 (0.0108)	0.3217 (0.0996)	0.0499 (0.0140)	0.2038 (0.0168)	
5	0.0518 (0.0126)	0.0018 (0.0255)	0.0038 (0.0159)	<0.0001 (0)	<u>0.0416</u> <u>(0.0358)</u>	-0.0131 (0.0202)	0.3205 (0.0992)	0.0463 (0.0141)	0.1984 (0.0166)	
6	0.0480 (0.0124)	<0.0001 (0)	0.0051 (0.0145)	<0.0001 (0)	0.0626 (0.0227)	-0.0177 (0.0198)	0.3199 (0.0991)	0.0402 (0.0139)	0.1922 (0.0164)	Genetic model
9	0.0421 (0.0119)	<0.0001 (0)	0.0070 (0.0136)	<0.0001 (0)	0.0756 (0.01980)	-0.0294 (0.0196)	0.3168 (0.0984)	0.0311 (0.0136)	0.1877 (0.0156)	
12	0.0435 (0.0120)	0.0041 (0.0177)	0.0081 (0.0132)	<0.0001 (0)	0.0551 (0.0266)	-0.0201 (0.0192)	0.3203 (0.0998)	0.0284 (0.0138)	0.1970 (0.0160)	
15	0.0447 (0.0121)	<0.0001 (0)	0.0064 (0.0119)	<0.0001 (0)	0.0476 (0.0156)	-0.0101 (0.0183)	0.3202 (0.0998)	0.0291 (0.0139)	0.2041 (0.0161)	
18	0.04580 (0.0121)	<0.0001 (0)	0.0006 (0.0112)	<0.0001 (0)	0.0573 (0.0160)	0.0031 (0.0182)	0.3171 (0.0991)	0.0194 (0.0136)	0.2067 (0.0161)	
24	0.0450 (0.0120)	< 0.0001 (0)	0.0067 (0.0115)	<0.0001 (0)	0.0536 (0.0146)	-0.0120 (0.0184)	0.3189 (0.0100)	0.0206 (0.0135)	0.2047 (0.0159)	

Table S3. Estimates of the fixed effects, including interactions with density. The intercept and main effects are for low densities, with the main effect of density, and the interaction between density and other fixed effects (interactions indicated with colons), indicating the difference at high densities.

Name	Effect estimate	Numerator degrees of freedom	Denominator degrees of freedom	F (conditional)	p value	R ²
Intercept	-40.71	1	29.3	0	0.97	NA
density (high)	19.58	1	28.9	0.57	0.457	0.0005
mast (true)	-1.713	1	25.3	38.67	< 0.001	0.0320
study area (Sulphur)	0.1341	1	119.3	18.05	< 0.001	0.0152
gr:density (Sulphur at high density)	0.1867	1	126.7	2.56	0.112	0.0022
year	0.0235	1	28.4	1.67	0.207	0.0014
year:density (high)	-0.1000	1	28.6	0.12	0.731	0.0001
age	-0.0181	1	1007	140.2	< 0.001	0.1071
age:density (high)	0.0037	1	1151	1.88	0.17	0.0016
age ²	< 0.001	1	1030.2	89.8	< 0.001	0.0713
age ² :density (high)	> -0.001	1	1151	1.77	0.184	0.0015

ASREML Code

Code for indirect effects on red squirrel parturition date analysis

#This incorporates multiple neighbours through the use of "and(neigh2..." and scales by distance by interacting neighbour ID with the *inverse* of distance "neigh1.dist1"

```
animal !P #unique ID of each individual to link to the pedigree
gr !A #grid or study area
year !A !L 1991 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2013 2012 2014
2015 #loading year to be fitted as a random effect
yearp1 #continuous effect of year
part_date !/23.32 #dividing by the standard deviation
age
mast !A !L FALSE TRUE
neigh1 !P #unique ID of closest neighbouring individual to link to the pedigree
dist1 #inverse of the distance between neighbour 1's territory and focal squirrel's territory
neigh2 !P #and so on for neighbours 2-6
dist2
neigh3 !P
dist3
neigh4 !P
dist4
neigh5 !P
dist5
neigh6 !P
dist6
square !A
spr_density
```

```
high_density !A !L FALSE TRUE
```

```
age2 !=age !*age
```

```
SQped.ped !ALPHA !SKIP 1 #loading the pedigree
```

```
SQpart.data.neigh.txt !SKIP 1 !maxit 100 !FCON !DDF 2 #loading the data file
```

```
part_date ~ mu gr yearp1 mast age age2 +
```

```
!r year square + #set up parturition date, influenced by fixed effects, and random effects of year and square
```

```
animal + #animal term estimates additive genetic variance
```

```
neigh1.dist1 and(neigh2.dist2) and(neigh3.dist3) + #neighbours 1-6 estimate indirect effects
```

```
and(neigh4.dist4) and(neigh5.dist5) and(neigh6.dist6) +
```

```
ide(animal) + #ide(animal) term estimates permanent environmental effect
```

```
ide(neigh1).dist1 and(ide(neigh2).dist2) + #non-genetic indirect effects
```

```
and(ide(neigh3).dist3) and(ide(neigh4).dist4) +
```

```
and(ide(neigh5).dist5) and(ide(neigh6).dist6) !f mv
```

```
1 1 4
```

```
0 0 IDV 0.8 !S2==1
```

```
year 1
```

```
year 0 IDV 0.1
```

```
square 1
```

square 0 IDV 0.1

#covariance matrix for direct-indirect genetic effects and covariance

anim 2
2 0 US #!GUUU
0.4E-01
0.1E-02 0.1E-02
anim 0 AINV

#covariance matrix for direct-indirect non-genetic effects and covariance

ide(animal) 2
2 0 US !GPUU
0.1E-5
0.01 0.01
ide(animal) 0