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 variance parameters and the strength of selection at low and high population densities. Social effects of neighbours on the date of spring breeding were weak at low, but stronger at high population densities. Indirect phenotypic effects accounted for a larger amount of variation in the date of breeding than direct differences among-individuals, although the genetic component to these indirect

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37 effects was not statistically significant. Nevertheless, the estimated effect size was large

38 enough to suggest that indirect genetic effects could alter evolutionary change, resulting in

39 less change at high densities despite stronger selection. Despite the difficulty in estimating

40 them precisely, indirect genetic effects have clear potential to alter evolutionary trajectories

41 in any natural systems where organisms interact.

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

43 *Tamiasciurus*

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Introduction

46

47 An individual's phenotype is influenced by both its genotype and the environment it

48 experiences. When organisms live in a social world, mating, competing and cooperating with

49 conspecifics (Frank 2007), the environment they experience is partly made up of the

50 phenotypes of other individuals. This can allow an individual to influence others, and if this

51 trait has a genetic component, then a portion of any organism's phenotype will be influenced

52 by the genes of those with whom it interacts (Griffing 1967). These are known as indirect

53 genetic effects ("IGEs"), of which maternal genetic effects are a widely known example

54 (Moore et al. 1997; Wolf et al. 1998; McAdam et al. 2014). With maternal genetic effects, the

55 genes of a mother influence the traits of her offspring beyond those directly inherited (e.g. a

56 mammal's genes affecting milk production may influence the growth rate of her offspring;

57 Koch 1972; María et al. 1993). In the same way, the genes affecting hunting success of an

58 individual (so a direct genetic effect, "DGE", for condition) in a pack-hunting species may

59 influence the body condition of its pack mates (an IGE). Additionally, when competing for

60 limited resources, the genes for resource acquisition of one individual are expected to

61 negatively influence the resource acquisition, and so resource dependent traits, of

62 individuals with which it competes (Wilson 2014). Therefore, IGEs can be expected in almost

63 any system where conspecifics interact with each other (McAdam et al. 2014).

64 As IGEs are heritable by definition, they contribute additional heritable variation

65 within a population alongside DGEs (Moore et al. 1997; Bijma and Wade 2008). Similar to a

66 genetic correlation between any two traits (Lande 1979; Kirkpatrick 2009), an individual's

67 own phenotype for some focal trait and its indirect effect on that trait expressed by

68 neighbours can be genetically correlated (a DGE-IGE correlation). When IGEs are positively

69 correlated with DGEs, which we would expect for the trait of hunting success in the pack-

70 hunter example above, IGEs can enhance that trait's response to directional selection. This

71 happens because the standard response of the focal trait to selection results in a correlated

72 evolutionary change in the social environment. This in turn causes further change in focal

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73   trait mean - in the same direction - through a plastic response to the social environment

74   (Moore et al. 1997).

75   Conversely, if IGEs are negatively correlated with DGEs then the population

76   response to selection can be reduced, removed, or even reversed (Bijma and Wade 2008;

77   Wilson 2014). Negative correlations are expected for focal traits that are themselves

78   dependent on the outcome of competition for limited resources (Wilson 2014). For instance,

79   Wade (1976) observed a decrease in mean reproductive output across generations in flour

80   beetles (*Tribolium castaneum*) that were under individual selection for *increased*

81   reproduction. This was presumably due to a negative IGE-DGE correlation that caused each

82   subsequent generation to be composed of individuals that more strongly suppressed the

83   reproduction of others through competitive interactions. Similarly, Costa e Silva *et al.* (2013)

84   observed a strong negative DGE-IGE covariance for diameter at breast height in Eucalyptus

85   trees (*Eucalyptus globulus*). This meant that, despite tree growth rates being heritable in the

86   traditional sense (i.e. subject to DGEs), the total heritable variation in the population was

87   near zero, preventing a response to selection. Estimates of DGEs alone might, therefore,

88   provide a poor measure of the potential for a trait to respond to natural selection, yet most

89   estimates of response to selection or evolvability in the wild only consider DGEs (Houle

90   1992). More specifically, to the extent to which resources are limited in nature, we might

91   expect DGEs to consistently overestimate the adaptive potential of resource-dependent

92   traits because of negatively covarying IGEs (Wilson 2014). As such, IGEs arising from

93   competition represent one possible explanation for the "paradox of stasis", in which natural

94   selection on heritable traits often leads to stasis rather than evolutionary change (Merilä et

95   al. 2001), yet IGEs are very rarely quantified in the wild.

96   To date, empirical studies of IGEs in animals have focused on scenarios in which

97   within group interactions can be considered (approximately) uniform, and among-group

98   interactions are absent. This allows IGEs to be estimated from the covariance between

99   phenotypes of group mates, provided pedigree data spanning groups are available (Bijma

100   2010a). This approach is well suited to dyadic interactions, but also to larger discrete groups

101   (n > 2) of captive animals, where all individuals within a pen are assumed to interact equally,

102   but no interactions occur between individuals in different pens. It has now been applied in a

103   variety of taxa, such as mussels (*Mytilus galloprovincialis*; Brichette et al. 2001), flour beetles

104   (*T. castaneum*; Ellen et al. 2016), Nile tilapia (*Oreochromis niloticus*; Khaw et al. 2016),

105   domesticated chickens (*Gallus domesticus*; Muir 2005; Brinker et al. 2015) mink (*Neovison*

106   *vison*; Alemu et al. 2014), and domestic rabbits (*Oryctolagus cuniculus*; Piles et al. 2017).

107   This work has helped establish the importance of IGEs for trait evolution (see: Ellen *et al.*

108   2014, for a review in livestock), and has led to growing interest in studying IGEs in wild

109   populations.

110   Studies of IGEs in free-living animal populations, however, have thus far been
111   confined to dyadic interactions. For example, Wilson *et al.* (2011) demonstrated that the
112   tendency to win one-on-one fights in wild red deer (*Cervus elaphus*) is subject to both DGEs
113   and IGEs that are perfectly *negatively* correlated, resulting in a total heritable variation of
114   zero. This reconciles quantitative genetic predictions with a common sense approach that
115   sees that the tendency to win cannot evolve at the population level, as each contest must
116   always have one winner and one loser (see also: Wilson et al. 2009; Sartori and Mantovani
117   2013). Other estimates for IGEs have focused on maternal genetic effects (McAdam and
118   Boutin 2004; McFarlane et al. 2015) or influences of male partner on female bird laying
119   dates (Brommer and Rattiste 2008; Caro et al. 2009; Teplitsky et al. 2010; Liedvogel et al.
120   2012; Germain et al. 2016). Studies on social interactions in groups of wild animals larger
121   than two are, however, absent.

122   While social processes in wild populations frequently involve interactions among
123   more than two individuals, it is often problematic to identify and define discrete groups where
124   n > 2. In many cases an individual will interact with multiple conspecifics, but not all at equal
125   intensity. Some interactions are frequent or strong while other interactions are brief or weak
126   (Lusseau et al. 2003; Croft et al. 2004, 2008). One possibility is that organisms interacting in
127   larger groups have generally weaker indirect effects on each of their group mates, as a
128   consequence of their phenotype being "diluted" among more group members (Muir 2005;
129   Hadfield and Wilson 2007; Bijma 2010b). However, within a continuous population (i.e. one
130   in which distinct groups cannot be identified) it seems likely the net effect of one individual
131   on the phenotype of any other may depend on distance or other factors (e.g. time
132   associating) that mediate interaction intensity or frequency (Muir 2005; Cappa and Cantet
133   2008). To model these situations, variation in interaction strengths can be incorporated as
134   "dilution" or "intensity of competition" factors in IGE models (Muir 2005; Cappa and Cantet
135   2008; Bijma 2010b). Here we refer to "intensity of association" factors, since social
136   interactions are not always competitive. This approach has proven useful in forestry genetics
137   to estimate DGEs, IGEs, and their covariance, on growth traits in Eucalyptus trees (Costa e
138   Silva et al. 2013, 2017). In this context, the inverse of the distance between each pair of
139   trees was used as the intensity of association factor. The important premise here is that
140   each focal individual has a potential indirect genetic effect on the phenotype of all its social
141   partners, but the degree to which each partner experiences that effect is contingent on its
142   distance from the focal individual. Incorporating intensity of association factors should be
143   equally useful for animal focused IGE models, as allows us to account for animals interacting
144   with multiple different individuals, in groups of varying sizes, and with different individuals at
145   different strengths; a realistic representation of social interactions in the natural world (Fisher
146   and McAdam 2017).

147   Here we used intensity of association factors to model IGEs amongst multiple

148   neighbours for the first time in a wild animal. We applied this framework to a population of

149   North American red squirrels (*Tamiasciurus hudsonicus*, hereafter "red squirrels") that have

150   been continuously studied since 1987. We looked at a resource-dependent, but also

151   heritable (h^2 = 0.14; Lane et al. 2018) life-history trait: parturition date (the date in the spring

152   on which a female squirrel gives birth to a litter; Réale et al. 2003; Boutin et al. 2006; Kerr et

153   al. 2007; Lane et al. 2018), which had the potential to show IGEs. Red squirrels of both

154   sexes in this population live on individual exclusive territories based around a central cache

155   of white spruce (*Picea glauca*) cones called a "midden". The seeds from stored spruce

156   cones represents their main food source during reproduction in the spring (Fletcher et al.

157   2013a). Individuals make territorial calls ("rattles") to delineate territory boundaries (Lair

158   1990) and deter intruders (Siracusa et al. 2017) from stealing cached resources (Gerhardt

159   2005; Donald and Boutin 2011). Previous analyses have shown that selection favours earlier

160   parturition dates (Réale et al. 2003), while a food supplementation experiment advanced the

161   timing of spring breeding (Kerr et al. 2007). Note, however, that females can upregulate

162   reproduction prior to a resource pulse (Boutin et al. 2006), and so typically are reproducing

163   below capacity (Boutin et al. 2013), so may not be absolutely food limited. Still, if neighbours

164   compete for food resources, we expect superior competitors to have access to more food

165   and breed earlier. Conversely, competitively inferior individuals are expected to acquire less

166   food and so breed later.

167   Population density is a key demographic parameter with which we expect IGEs to

168   vary. Selection on birth dates is particularly strong in years of high density (Williams et al.

169   2014; Fisher et al. 2017; although not found in Dantzer et al. 2013). Furthermore, red

170   squirrels respond behaviourally to both real and perceived increases in density (Dantzer et

171   al. 2012), while mothers adaptively increase the growth rates of their offspring under high

172   density conditions (Dantzer et al. 2013). Taken together, these findings are consistent with

173   the expectation that, all else being equal, high density means increased competition.

174

175   In light of the above, we had the following aims and predictions:

176   1) We expected individuals to have indirect effects on the parturition dates of their

177   neighbours, and that the covariance between direct and indirect effects would be

178   negative. That is, superior competitors will breed earlier and cause their neighbours to

179   breed later (following Costa e Silva et al. 2013; see also: Piles et al. 2017).

180   2) Parturition dates depend on resource acquisition and possess direct genetic variance,

181   so we expected the indirect effects to possess genetic variance (i.e. to be an IGE;

182   McAdam et al. 2014; Wilson 2014).

183   3) Increased competition in years of high density should result in stronger indirect effects
184   in high-density years, both in the magnitude of the indirect effects and the strength of
185   the covariance.

186   4) Finally, we applied the equations of Bijma and Wade (2008) and Costa e Silva et al.
187   (2013) to predict a response to selection in the presence of IGEs, across the whole
188   dataset and at low and high densities separately. This allowed us to assess how IGEs
189   would likely affect evolutionary responses to selection in this system.

190

Methods

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Data collection

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194 All data were collected as part of the Kluane Red Squirrel Project in the southwest Yukon,
195 Canada. Since 1987 we have monitored two adjacent and unmanipulated 40 ha. study areas
196 ("Kloo" and "Sulphur"), bisected by the Alaska highway. Red squirrels of both sexes defend
197 exclusive resource-based territories of around 0.3 ha (LaMontagne et al. 2013), centred
198 around a midden, an aggregation of discarded white spruce cone scales underneath which
199 red squirrels cache intact white spruce cones. Each study area is staked at 30m intervals in
200 a grid system and we recorded the x- and y-coordinates of the centre of each midden (to the
201 nearest tenth of a coordinate point, giving distances to the nearest 3m). In the spring of each
202 year we live trapped (Tomahawk Live Trap, Tomahawk, WI, USA) new individuals and gave
203 them unique ear tags in each ear. We also located females (based on vocalizations at
204 known and new territory locations), monitored them for signs of pregnancy and ear tagged
205 their pups once they were born. Based on the previously identified stages of female
206 pregnancy and the body mass of the pups once they were located, we then estimated the
207 female's parturition date. We analyse this date as the number of days since the 1st January
208 in the calendar year. We also conducted censuses twice yearly (once in spring, once in
209 autumn) using complete enumeration to ascertain the location of all individuals holding a
210 territory, and so estimate population density. See McAdam *et al.* (2007) for further details on
211 the study system.

212   Red squirrels collect food throughout the summer and autumn, cache it in their
213 middens and rely on it to survive over winter (Fletcher et al. 2013a). The number of cached
214 cones is positively associated with overwinter survival (juveniles: Larivée et al. 2010;
215 juveniles and adults: LaMontagne et al. 2013). Squirrels primarily forage close to their
216 midden, with occasional forays further afield, including small amounts of theft from other red
217 squirrels' hoards (Donald and Boutin 2011). We define the individuals a red squirrel
218 potentially *c*ompetes with as its *n* nearest neighbours (*n* was set at 6 for the majority of this

219　analysis, but see below for explorations with different numbers of neighbours). We defined

220　neighbourhoods and population densities based on our autumn census (August) rather than

221　our spring census (May), because autumn is when squirrels are potentially competing for

222　resources to hoard, and conception occurs well before May in most years. Gestation varies

223　little around 35 days (Lair 1985), hence parturition dates cannot be influenced by conditions

224　after conception. Squirrels occasionally defend a second adjacent midden, but as they rarely

225　store food in secondary middens we considered each squirrel's location to be the location of

226　its primary midden. We then analysed each female's parturition date the following spring as

227　influenced by her own genes (the DGE), and the identities and genotypes (the IGE) of those

228　competing individuals as identified in the autumn census. Some females gave birth in

229　multiple years, in which case they were included each year they did so, with an updated set

230　of nearest neighbours as necessary. Females may attempt multiple litters in years of high

231　resources, or if their first litter fails (Boutin et al. 2006; McAdam et al. 2007; Williams et al.

232　2014), but we limited our analyses to each female's first litter of each year (e.g. Dantzer et

233　al. 2013).

234　　　　We tagged pups while they were still on their mother's territory, so maternity is known

235　for all non-immigrants. Male red squirrels provide no parental care. From 2003 onwards,

236　paternities were, therefore, assigned by collecting tissues samples from the ears of adults

237　and neonatal pups. We used these tissue samples to genotype all adults and pups since

238　2003 at 16 microsatellites (Gunn et al. 2005) analysed with 99% confidence using CERVUS

239　3.0 (Kalinowski *et al.* 2007; see Lane *et al.* 2007, 2008 for further details). This method gives

240　an estimated error rate of paternities, based on mismatches between known mother–

241　offspring pairs, of around 2% (Lane et al. 2008), which we consider acceptable.

242　Approximately 90% of yearly pups are assigned paternities with known males while the

243　remaining 10% are analysed further in Colony 2.0 (Jones and Wang 2010) to determine

244　whether they might still be full or half siblings from unknown sires using 95% confidence in

245　maximum likelihoods.

246

247　Data analysis

248　Data on the locations of squirrel territories were available from the autumns in 1991-2015,

249　and so we looked at parturition dates in the following springs (i.e. 1992-2016). All squirrels

250　identified as holding a territory in an autumn census were included in this analysis, including

251　females that did not attempt a litter in the following spring, and males. These individuals had

252　missing values entered for their parturition dates. Their inclusion was nonetheless necessary

253　as they acted as potential competitors during the autumn for those squirrels that did have a

254　litter.

255   We initially fitted two mixed-effects linear models to our data, the first to estimate

256 indirect effects (the "phenotypic model"), and second to split these indirect effects into

257 genetic and non-genetic components (the "genetic model"). All models we fitted in the

258 software "ASReml" ver 4.1; (Gilmour et al. 2015). We divided raw parturition dates by the

259 standard deviation of all observations, giving a sample with a variance of 1, making the

260 variance components easier to interpret (Schielzeth 2010). In each model we included the

261 fixed effects of study area (a two-level factor), year (as a continuous linear covariate),

262 whether or not the spruce trees "masted" ((produced a super-abundance of cones;

263 Silvertown 1980; Kelly 1994; Lamontagne and Boutin 2007) in the year of the autumn

264 census (a two-level factor), age and age^2 of the squirrel, and the random effects of year and

265 squirrel identity, to account for repeated measures on squirrels across years. If the age of

266 the squirrel was not known, the mean age of all other squirrels in that breeding season was

267 entered. Estimating the squirrel identity random effect allowed the calculation of the

268 (conditional) repeatability of individual squirrel parturition dates (Nakagawa and Schielzeth

269 2010). Additionally, while we predicted a negative covariance between neighbours due to

270 competition for resources (especially during high-density conditions), this could be masked

271 by positive spatial autocorrelation in resource availability within a study-area. This would

272 generate a net signal of positive phenotypic covariance among-neighbours (Stopher et al.

273 2012; Regan et al. 2016; Thomson et al. 2018). To control for this we fitted a term

274 accounting for (non-socially determined) environmental heterogeneity in resource

275 abundance. In our multiyear data set we were unable to obtain convergence from our data

276 with a model in which a separate spatial autocorrelation term for each year was fitted (since

277 the spatial distribution of territory quality is not consistent year-to-year; LaMontagne et al.

278 2013). As a simpler alternative, we assigned each red squirrel within each year to one 150 m

279 x 150 m square within a grid of non-overlapping squares that encompassed the study area

280 (hereafter referred to as "squares"). Each square was given a unique label comprising its

281 location and the year, and so by fitting this as a random effect we could account for any

282 similarity among red squirrels within each 150 m x 150 m area in each year. This is similar to

283 the approach of Germain et al (2016), who found that an equivalent "grid" term fitted their

284 data better than a matrix of local overlap (c.f. Stopher et al. 2012), or a modelling spatial

285 autocorrelation in the residuals (c.f. Costa e Silva et al. 2013). We repeated this analysis

286 with squares of 75 m x 75 m or 300m x 300 m. These results were qualitatively similar to the

287 analysis with the intermediate size squares, and so are presented in the supplementary

288 materials (Table S1).

289   To estimate indirect effects, we added the identities of the six nearest squirrels as six

290 random effects (see below for our explorations of other possible neighbourhood sizes),

291 assuming that all random competitor effects came from the same distribution, with a mean of

292 zero and a single variance to be estimated. This allowed us to estimate a single indirect

293 phenotypic effect, and the covariance between this term and the direct effect of squirrel

294 identity. We based "nearest" on location of the primary midden during the autumn census.

295 We associated each neighbour (*j*) of each focal individual (*i*) with variable intensity of

296 association factors (f_{ij}). This allowed the indirect effect of each neighbour *j* actually

297 experienced by *i* to be mediated by their spatial proximity, with f_{ij} = 1/ (1 + distance), where

298 distance was the Euclidean distance between the center of individuals' territories, measured

299 in units of 30m. This value is bounded between 0 and 1, with low values representing

300 individuals that were far apart and high values representing individual that were close. We

301 used the inverse of distance here, but any biologically relevant measure representing

302 intensity of social interaction could be used (Fisher and McAdam 2017). To weight the

303 strength of the indirect effects, we replaced all 1s in the indirect effect design matrix with

304 these terms (Muir 2005; Cappa and Cantet 2008). All individuals farther than the 6 nearest

305 neighbours were not modelled as having an indirect effect (but see below). The phenotypic

306 model therefore used the following form, with a population mean accounting for the fixed

307 effects for *i* (*μ_Fi*), a direct phenotypic effect (P_{Di}) and a total indirect influence arising from the

308 sum of competitor specific indirect effects (P_{Sj}) for the 6 nearest neighbours. Note, a single

309 variance for the indirect effect is estimated, from a distribution made up of all competitor

310 effects (see above). Additionally, there are multiple measures per squirrel across years,

311 hence we include the random effect for the year *t* (K_t). Our model predicts a parturition date

312 for the *i*th individual in a given year (y_{it}) and so the residual term is specific to an individual

313 in a year (e_{it}).

314

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

316

317 This phenotypic model estimated the variance among squirrels in their parturition dates, the

318 variance in parturition dates caused by repeatable effects of neighbour identities, and the

319 within-individual covariance between direct and indirect phenotypic effects (i.e. *Cov(P_{Di},*

320 *P_{Si})*). For our genetic model, we split these phenotypic effects into additive genetic and

321 permanent environment effects by the incorporation of a pedigree (Kruuk 2004; Wilson et al.

322 2010). We estimated the DGEs and IGEs on parturition dates, their covariance, and the

323 equivalent terms for the permanent environmental effects:

324

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

326

327 Where individual i's parturition date in year t, is comprised of the fixed effect mean, a direct

328 additive genetic effect (A_{Di}), a direct permanent environmental effect (PE_{Di}), both the

329 additive genetic (A_{Sj}) and non-additive genetic (E_{Sj}) indirect effects of all the n neighbours (j)

330 that i interacts with, a year term (K_t), and an individual by year specific residual term (e_{it}).

331 This model has not been applied to wild animals before, and we fully acknowledge

332 that our choice to consider only the 6 nearest neighbours here is somewhat arbitrary, as

333 indeed is the scaling of f_{ij}. Therefore, we also explored different numbers of neighbours,

334 and different methods for defining our f_{ij} terms. We then monitored how this influenced the

335 estimates of the variance parameters, to determine whether the model was particularly

336 sensitive to altering these factors (see also: Costa e Silva *et al.* 2017). We present results

337 using f_{ij} = 1/(1 + distance^2) in the supplementary materials (Table S1). In the supplementary

338 materials we also present results where we defined the competitors as all those within 60,

339 130 or 200 metres, without weighting by distance, up to 24 competitors (Table S1), and

340 investigations with varying numbers of neighbours 1-5, 9, 12, 15, 18 & 24; Table S2). Neither

341 changing the number of neighbours nor rescaling intensity of association terms changed the

342 number of model parameters estimated. Therefore, information criteria-based approaches

343 for comparing model fits were not appropriate. Additionally, we were primarily interested in

344 our ability to estimate, and the magnitude and significance of, certain parameters (our

345 indirect effects), hence finding the most parsimonious model of parturition date was not a

346 goal of ours. Instead we simply assessed the change in variance components, noting the

347 size of the parameter estimates and size of the standard errors. We focus on the results with

348 the 6 closest neighbours, as this seemed the median result among the variations we tried.

349 Using the inverse of distance^2 squared led to a large increase in the standard errors of the

350 DGE estimate, which only occurred in this model, hence we considered simply the inverse of

351 distance as more appropriate.

352 We tested the significance of the direct-indirect phenotypic covariance in the

353 phenotypic model using a likelihood ratio-test (LRT) between a model with the covariance

354 freely estimated and one with it fixed to zero, and tested the significance of the indirect

355 phenotypic effect using a LRT between the model with the indirect effect (and a zero

356 covariance) and a model without it. With the genetic model, we tested the significance of the

357 DGE-IGE covariance, and the IGE variance, in the same way, in models that still estimated

358 the full direct-indirect phenotypic covariance matrix. We assumed the LRT statistic was

359 distributed as a 50:50 mixture of χ^2_1 and χ^2_0 when testing single variance components

360 (following Self and Liang 1987) but as χ^2_1 when testing covariances. Note that, even where

361 terms were non-significant, they were retained as our best estimate of the corresponding

362 parameter for our estimates of predicted responses to selection (as described below). We

10

363   report correlations, although if the variance of either the direct or indirect effect was very

364   small (<0.0001), then we assumed it was essentially zero, and so then we report the

365   correlation as "undefined". Although they were not directly relevant to the biological

366   hypotheses being tested, the statistical significance of the fixed effects in the genetic model

367   was tested using conditional Wald tests (see: Gilmour et al. 2015). This approach to testing

368   the significance of fixed effects in mixed linear models performs well in situations with limited

369   sample sizes (Kenward and Roger 1997). We then calculated partial R^2 for each fixed effect,

370   following Edwards et al. (2008), using the residual degrees of freedom as calculated by

371   ASReml (1174 for the genetic model).

372

373   Influence of population density on indirect effects

374   We consider population density during the resource caching period to be key to resource

375   acquisition. Consequently, for any given year of parturition the relevant measure of density

376   was obtained from the census in the autumn of the year *prior* to parturition, i.e. at the same

377   time as when the territory ownership was defined. As the study area has grown marginally

378   since the start of the project, we restricted counts to individuals holding a territory within a

379   defined 38ha area that has been constant throughout the entire study period. Across both

380   study areas in all years the median population density in the autumn was 1.69 squirrels ha^{-1}

381   (Fig. 1). We, therefore, labelled each study area within each year with a density higher than

382   this as "high density" (1994, 1998-2000, 2006 and 2015 for both study areas, 1991-1993,

383   1995-1997, 2001 and 2002 for Sulphur only and 2011-2014 for Kloo only), and so the

384   remainder as "low density" There were, therefore, 26 instances of low density conditions,

385   and 24 instances of high density conditions. There are several instances of study areas

386   having exactly the median density, hence why there are more low- than high-density

387   conditions.

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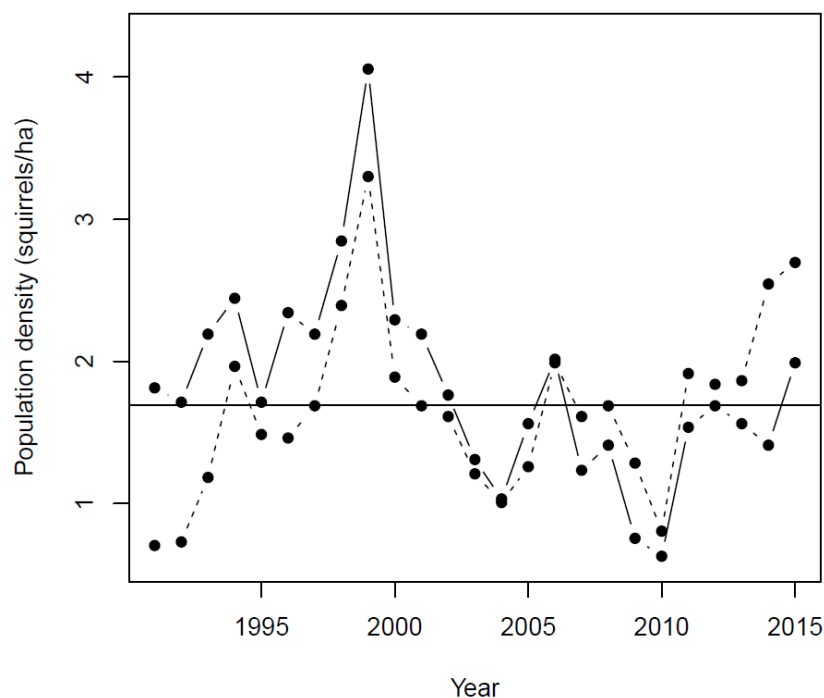
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391
392   Figure 1. Estimated population densities across both study areas in our study ("Kloo" is
393   solid line, "Sulphur" is dashed line). Points above the line (the median density: 1.69
394   squirrels ha.$^{-1}$) were counted as "high density", points below the line as "low density".

395
396   For both the phenotypic and the genetic models, we fitted an interaction between population
397   density (low or high) and each random effect. This gave us separate density-specific
398   estimates of each of the variances (DGEs, IGES, and non-genetic versions) and
399   covariances, the among-year variances and the among-square variances for low- and high-
400   density study areas. To obtain stable model convergence in the genetic model, we were
401   required to fix the direct permanent environment effect in low-density years to 0.1×10^{-4}, but
402   since this term was estimated to be very small in the model across all years, this is likely not
403   problematic. There was a single residual variance in each model. We also included density
404   as two-level factor in the fixed effects, and an interaction between this term and each of the
405   other fixed effects, to allow them to vary between low- high-density conditions. We tested for
406   significance of indirect effects in both low- and high-density conditions in the same way as
407   for the full models. When testing the significance of terms for low-density, we maintained the
408   full structure (e.g. IGEs and their covariance with DGEs in the genetic model) for high-
409   density conditions, and vice versa.

410
411   Calculating variance parameters and the predicted response to selection

412   To assess the contribution of indirect effects to phenotypic and genetic variances, we

413   estimated the variance in individuals' phenotypic effects on the population mean parturition

414   date ($\hat{\sigma}^2_{PE}$, incorporating both consistent direct and indirect phenotypic effects; for the

415   phenotypic model), and variance in individuals' heritable influence on the population mean

416   parturition date ($\hat{\sigma}^2_H$; for the genetic model, commonly referred to as the "total heritable

417   variance"). Following Bijma (2011) and Costa e Silva *et al.* (2013) these are:

418

419    $$\hat{\sigma}^2_{PE} = V_{PD} + 2n\overline{f_{ij}}Cov(P_D, P_I) + (n\overline{f_{ij}})^2 V_{PI} \qquad 3$$

420

421    $$\hat{\sigma}^2_H = V_{AD} + 2n\overline{f_{ij}}\,Cov(A_D, A_I) + (n\overline{f_{ij}})^2 V_{AI} \qquad 4$$

422

423   Where *n* is the number of neighbours (excluding the focal individual, so 6), $\overline{f_{ij}}$ is the mean

424   intensity of association factor, V_{PD} and V_{AD} are the direct phenotypic and additive genetic

425   variances respectively, $Cov(P_D, P_I)$ and $Cov(A_D, A_I)$ are the phenotypic and genetic direct-

426   indirect covariances respectively, and V_{PI} and V_{AI} are the indirect phenotypic and additive

427   genetic variances respectively. The $\overline{f_{ij}}$ was calculated as 0.330 across the whole dataset,

428   0.298 at low densities and 0.352 at high densities, which means a squirrel's 6 nearest

429   neighbours were on average, 60.9m, 70.7m and 55.2m from it across the whole dataset, at

430   low densities, or at high densities respectively. Note that $\hat{\sigma}^2_H$, unlike traditional heritability, can

431   exceed 1; see Bijma (2011) for the mathematical demonstration of this, and Ellen *et al.*

432   (2014) for empirical examples in livestock.

433   In order to calculate the predicted response to selection in the presence of IGEs

434   among related individuals, we combined equation 15 of Bijma and Wade (2008), and

435   equation S5_2 of Costa e Silva et al. (2013), setting total phenotypic variance as 1. In a

436   previous study (Fisher et al. 2017) we determined that selection on parturition date acts

437   primarily among neighbours within 130m, and, so the relative strength of multilevel selection

438   (*g*) is approximately zero, giving:

439

440    $$\Delta\bar{P} = \beta_{W_D P}\{r\hat{\sigma}^2_H + (1 - r)[V_{A_D} + n\overline{f_{ij}}Cov(A_D, A_I)]\} \qquad 5$$

441

442   Note that as we have already defined *n* as the number of neighbours excluding the focal

443   individual, we have altered *n-1* in eq. 15 of Bijma and Wade (2008) to *n*.

444   In eq. 5 the change in the mean phenotype ($\Delta\bar{P}$) is predicted by the selection gradient

445   of the phenotype on relative direct fitness ($\beta_{W_D P}$), multiplied by a term encompassing the

446   genetic variance parameters. We estimated $\beta_{W_D P}$ across all females in the whole dataset by

13

447   regressing relative fitness (number of pups born to each individual in a given year that

448   recruited to the population as adults, divided by the population average for that year) on

449   standardised parturition dates (mean centred and divided by the standard deviation across

450   the whole dataset). This measure of fitness maps individuals that recruited into our

451   population (and hence held territories, necessary to be included in our analysis) to the

452   number of recruits they have. Arguably, early survival is a trait of the juvenile, not the parent,

453   and hence this fitness component should not be assigned to the parent (Thomson and

454   Hadfield 2017). However, as parturition dates are only expressed by females, and do not

455   influence adult survival (Lane et al. unpublished), our estimates of selection should not be

456   biased. We re-estimated selection gradients at low and high densities by fitting an interaction

457   with low/high density to parturition date, to give different estimates for $\beta_{W_D P}$ in each

458   condition. Densities (and competitive neighbourhoods) in the autumn of a given year were

459   associated with parturition dates and fitness in the following spring (year +1). Relatedness (r)

460   is the mean coefficient of relatedness among the 7 squirrels in each neighbourhood (the

461   focal squirrel and its 6 nearest neighbours). We used the pedigree to calculate r as 0.094

462   across the entire data set, 0.087 at low densities and 0.098 at high densities. We multiplied

463    $\Delta \bar{P}$ by the standard deviation of parturition date, to give the result as "days per generation".

464   We compare this to a case where IGEs were equal to zero, and so the response to selection

465   was equal to $\beta_{W_D P}$ V_{AD}.

466

Results

468

469   In total, 1862 unique red squirrels were recorded a total of 4362 times in autumn censuses

470   as holding territories, and so were included in the analysis. There were 555 unique females

471   that had at least one litter, with a mean of 2.1 (range = 1-8, standard deviation = 1.3)

472   recorded parturition dates each. The median date of first litters was 23rd April, with

473   interquartile ranges of 6th April to 11th May. There were 364 females that had no recorded

474   parturition dates, and 943 males. 1196 squirrels had a known mother, and 498 had a known

475   father, with 481 of those having both parents known.

476   Parturition dates differed greatly among years and less so among squares, with

477   variance among-years accounting for 32.0% of the variance in the genetic model, while

478   variance among-squares accounted for 4.0% of the total variance (all variance component

479   estimates are shown in Table 1, with fixed effect estimates shown in Table 2). While there

480   was no linear trend across years, parturition dates were significantly earlier following mast

481   years by approximately 40 days.

482   Alongside these environmental variations, individuals showed some degree of

483   consistency in their parturition dates, with the direct variance among-individuals in parturition

484   date in the phenotypic model accounting for 3.8% of the phenotypic variance. Indirect

485   phenotypic effects of neighbours were significant (LRT, $\chi^2_{0.5}$ = 13.755, p < 0.001), but the

486   covariance between the direct and indirect phenotypic effects was not (cor = -0.094, LRT, χ^2_1

487   = 0.111, p = 0.739), indicating that individuals that give birth earlier do not influence their

488   neighbours in any particular direction relative to their own parturition date. Individuals'

489   consistent differences in their own phenotypes and consistent effects on neighbours ($\hat{\sigma}^2_{PE}$)

490   was calculated as 31.4% of the phenotypic variation, indicating that social effects account for

491   a large amount of the variation in parturition date. Alongside this consistency, individuals

492   showed a degree of plasticity, with older squirrels having earlier parturition dates, while the

493   positive quadratic effect indicates a nonlinear effect of age in which squirrels began to breed

494   later at older ages.

495   Parturition date showed direct heritability, with V_{AD} in the genetic model accounting

496   for 4.8% of the phenotypic variance (note this differs from previous estimates of h^2 for this

497   trait in this system as here we include the among-year variation in V_P). The estimate for the

498   IGEs was not different from zero (LRT, $\chi^2_{0.5}$ = 0.003, p = 0.480), as was the DGE-IGE

499   covariance (cor = undefined, LRT, $\chi^2_{0.5}$ = 0.119, p = 0.729). We calculated the total heritable

500   variance of parturition date, $\hat{\sigma}^2_H$, as 6.8%, a modest increase over V_{AD}. The very small DGE-

501   IGE covariance indicates that genotypes for early parturition dates did not affect their

502   neighbours in any consistent direction relative to their own parturition date.

503

504   Low vs high density comparison

505   In low density conditions, both the variance in indirect phenotypic effects (LRT, $\chi^2_{0.5}$ = 0.808,

506   p = 0.184) and the direct-indirect phenotypic covariance (cor = 0.737, LRT, $\chi^2_{0.5}$ = 0.1.206, p

507   = 0.272) were not significantly different from zero. At high densities there were significant

508   phenotypic indirect effects (Table 1; LRT, $\chi^2_{0.5}$= 9.523, p = 0.001), although the covariance

509   was not different from zero (cor = -0.023, LRT, $\chi^2_{0.5}$ = 0.004, p = 0.952).

510   Given that we detected no phenotypic indirect effects in low-density conditions, it is

511   unsurprising that the IGEs (LRT, $\chi^2_{0.5}$ = 0.000, p = 0.500) and the DGE-IGE covariance in

512   these conditions were also not different from zero (cor = undefined, LRT, χ^2_1 = 0.566, p =

513   0.452). For high densities, IGEs were considerably stronger than across the whole dataset,

514   and more than one standard error from zero, although still not significantly different from

515   zero (LRT, $\chi^2_{0.5}$ = 0.607, p = 0.218). The covariance between DGEs and IGEs was negative

516   but not different from zero (cor = -0.401, LRT, $\chi^2_{0.5}$ = 0.688, p = 0.407). Although we reiterate

517   that neither covariance was statistically significant, based on our parameter estimates in low-

518   density conditions $\hat{\sigma}^2_H$ was 14.3%, which was higher than V_{AD}, as this calculation includes the

519   positive DGE-IGE covariance estimate (despite the lack of variance in IGEs rendering the

520   correlation undefined). In high-density conditions $\hat{\sigma}^2_H$ was 14.2%, much higher than with

521   direct genetic effects alone due to the additional genetic variance from IGEs. We stress that,

522   as the estimates for the IGEs and their covariances with the DGEs were not significantly

523   different from zero, the estimates of $\hat{\sigma}^2_H$ should be interpreted with caution.

524   The square term revealed that there was some variation attributable to spatial

525   location in both conditions, accounting for 4.2% in low-density, and 3.1% in high-density

526   conditions, of the variance in the genetic model split between low and high densities. Finally,

527   there was also substantial among-year variance in both conditions, accounting for 32.2%

528   and 38.4% for the observed variance in low and high-density conditions respectively. We

529   present estimates for fixed effects at low and high densities from the genetic model in the

530   supplemental materials (Table S3); for the calculation of partial R^2s, we calculated the

531   residual degrees of freedom to be 1169.

532

533   Predicted response to selection

534   Across all years, selection favoured squirrels with earlier parturition dates (linear selection

535   gradient β = -0.249). The standard deviation of parturition date was 23.32. From eq. 5, this

536   gives a predicted response when accounting for IGEs across the entire data set of -0.342

537   days generation^{-1}, or -0.279 days generation^{-1} if IGEs were not considered. While the

538   magnitude of selection differed, breeding earlier was still favoured whether squirrels were

539   breeding under low (β = -0.239) or high densities (β = -0.286). At high densities, despite

540   stronger selection, we calculated a slower predicted evolutionary response, due to the

541   negative DGE-IGE covariance. At low densities, updating all parameters except *n*, the

542   predicted response was -0.553 days generation^{-1}, while at high densities it was -0.183 days

543   generation^{-1}. Predictions solely based on additive genetic variance multiplied by the

544   selection gradient were -0.262, and -0.353 days generation^{-1}, for low densities and high

545   densities respectively, therefore giving a faster response when selection is strongest, as is

546   typical.

547

548   ## Discussion

549

550   Indirect effects are present and change with population density

551   Red squirrels live in territories surrounded by conspecifics, with whom they engage in social

552   interactions through vocalizations, competition for resources, and mating interactions. Our

553   analyses show that these interactions can lead to substantial indirect effects on female

554   squirrel reproductive traits. These are detected here as a repeatable influence of competitor

555   identity on the parturition date of focal individuals – which accounted for a much greater

556   amount of variation in parturition date than direct effects of individual identity alone. Our

557   results also suggest that these indirect effects are more important determinants of focal

558   phenotypes at high densities than at low densities. Specifically, at high densities, there is

559   significant variation in the extent to which squirrels influence each other's parturition dates,

560   but this is not the case at low densities.

561
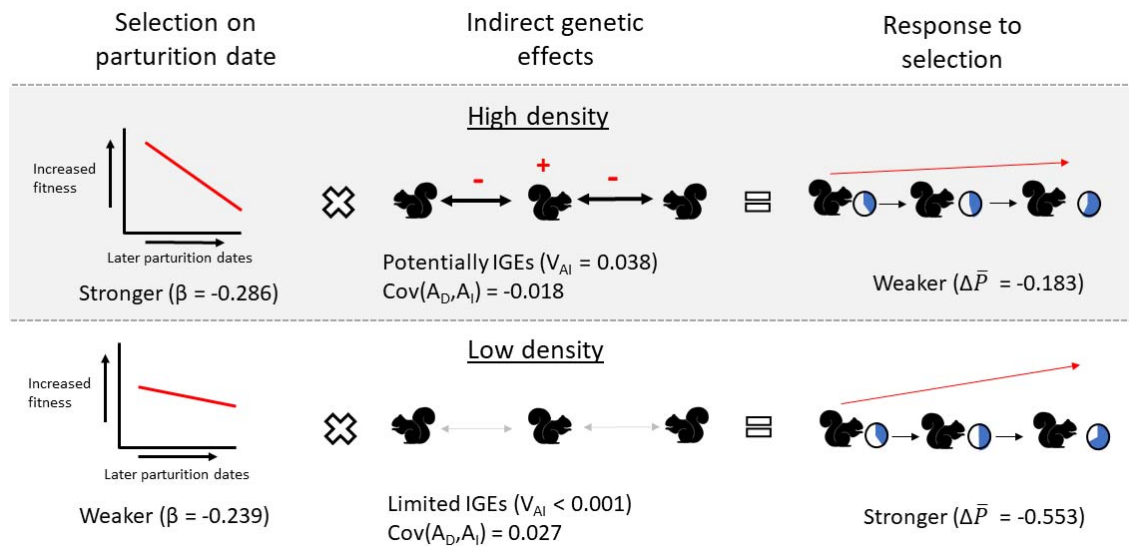
562

563   Figure 2. A summary of our results for the analysis of indirect genetic effects at low and high

564   densities. At high density selection was stronger (β = -0.286), and there were direct genetic

565   effects (variance = 0.053). There were significant phenotypic indirect effects, and non-zero

566   but statistically non-significant indirect genetic effects (variance = 0.038). The DGE-IGE

567   covariance ($Cov(A_D,A_I)$) was estimated to be negative (estimate = -0.018). These

568   parameters gave a weaker response to selection ($\Delta\bar{P}$ = -0.183 days.generation^{-1}). At low

569   density selection was weaker (β = -0.239), while there were direct genetic effects of a similar

570   magnitude to at high densities (variance = 0.047), but indirect genetic effects were absent

571   (variance = < 0.001). The DGE-IGE covariance was estimated still (estimate = 0.027). These

572   parameters gave a moderate response to selection ($\Delta\bar{P}$ = -0.553 days.generation^{-1}). Note in

573   all cases negative $\Delta\bar{P}$ values indicate the evolution of earlier parturition dates. For the

574   response to selection, more full circles represent later parturition dates. Red symbols

575   represent the DGE-IGE covariance, showing that individuals with genes to be early (red

576   plus) cause their neighbours to give birth later (red minus).

577 **Table 1**. Variance component estimates (with their approximate standard errors in brackets) for each element of the variance-covariance

578 structure from our models. Terms that were bound to values very close to zero will not have a standard error estimated, and so have "-"

579 instead. Models without a given term have "NA" entered in that cell. Terms highlighted in bold were >2 times greater than their standard errors,

580 while terms underlined were between 1 and 2 times greater than their standard errors. Variance in direct genetic effects are indicated by V_{AD}, in

581 indirect genetic effects by V_{AI}, and their covariance by $Cov(A_D,A_I)$. Equivalent notation with "P" instead of "A" refers to variance in purely

582 phenotypic effects for the phenotypic model, and permanent environment effects in the genetic model. V_S is the among-square variance (with

583 squares of size 150mx150m), V_Y is the among-year variance, and V_R is the 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)	

18

584 **Table 2**. Estimates and relevant statistics for fixed effects from final model with all years.

585 Study area was a two-level factor, with "Kloo" as the reference level, hence the shown

586 estimate is for the deviation of the "Sulphur" study area. Following a mast was a two-level

587 factor, with not following a mast as the default, hence the estimate is for the deviation in

588 parturition dates following a mast year. The denominator degrees of freedom are indicated

589 by df_d, while the numerator degrees of freedom were 1 in all cases.

Term	Estimate	Standard error	df_d	F-statistic	P-value	R^2
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
Age^2	< 0.001	< 0.001	1164.0	95.59	< 0.001	0.075

590

591 The social effects on parturition date we documented indicate that much more of an

592 individual's phenotype is under the control of those it socially interacts with than is

593 determined by its own identity, even in a solitary and territorial species. Work on Eucalyptus

594 trees (Costa e Silva et al. 2013) implicated competition for limited resources as the source of

595 indirect effects, and our results are consistent with this idea, hence highly competitive red

596 squirrels may acquire larger amounts of resources from the environment, leaving less for

597 other individuals. Earlier studies have shown that red squirrel females may be food limited to

598 some degree, aside from in years following a mast event. For example, earlier parturition

599 dates and lower levels of oxidative protein damage and higher levels of antioxidants were

600 found when food was supplemented (Kerr et al. 2007; Fletcher et al. 2013b; Williams et al.

601 2014), and individuals are more likely to survive over winter with a larger food cache (Larivée

602 et al. 2010; LaMontagne et al. 2013), suggesting that not all individuals have enough stored

603 food. However, female squirrels appear to reproduce below capacity in non-mast years, and

604 upregulate their reproduction *before* pulsed resources are available (Boutin et al. 2006,

605 2013), and so they are likely not completely food-limited. The additional insight from the

606 current study is that, for focal individuals, competitive effects on phenotype depend not

607 simply on high density, but also on the identities – and so phenotypes - of their nearest

608 neighbours.

609 Our analysis did not explore the specific mechanism (or trait(s)) that mediate indirect

610 phenotypic effects from competition, hence we have not confirmed that red squirrels are

611 competing for limited food resources, although this explanation seems likely. We can

612 however, suggest a second explanation based on prior knowledge of the system: red

19

613 squirrels might influence each other's parturition dates through acoustic territorial

614 interactions. Red squirrels give territorial calls ("rattles"), to which neighbours behaviourally

615 respond (Shonfield 2010) and which function to maintain their territory from conspecifics

616 (Smith 1978; Lair 1990; Siracusa et al. 2017). Additionally, red squirrels rattle more when

617 they have a higher local population density (Dantzer et al., 2012; Shonfield et al. 2012),

618 while red squirrel mothers increase the growth rate of their pups when playback of territorial

619 vocalizations leads to the perception of higher local population density (Dantzer et al. 2013).

620 This is through upregulation of maternal glucocorticoids, part of the stress axis (Dantzer et

621 al. 2013). Other life history traits, such as parturition date, may be influenced by rattles at

622 high densities, allowing individuals to influence each other's parturition dates. Therefore,

623 acoustic interactions among-neighbours, which enable neighbours to influence each other's

624 reproduction, may be a source of indirect effects, particularly in high-density conditions.

625

626 Indirect effects with a limited heritable basis

627 While our analyses provide statistical support for considerable indirect effects of competitors

628 on a focal individual's parturition date, we were unable to conclusively demonstrate that

629 these indirect effects were underpinned by genetic variation. Estimated effect sizes were

630 larger at high densities, in line with our predictions and the phenotypic effects. If we

631 incorporated the estimates of variance attributable to IGEs, and the DGE-IGE covariances,

632 into our predicted response to selection, we expected a faster response to selection in low-

633 density conditions (-0.553 days generation^{-1}) when selection was weakest, while a slower

634 response to selection in high-density conditions (-0.183 days generation^{-1}) when selection

635 was strongest, compared to across the whole data set (-0.342 days generation^{-1}). Therefore,

636 a negative DGE-IGE covariance counteracted stronger selection at high densities to give a

637 slower evolutionary response. However, while the point estimates of predicted change

638 indicate IGEs are potentially strong enough to make a meaningful difference to evolutionary

639 dynamics, we acknowledge they are estimated with high uncertainty.

640 　　　　Previous work on livestock has shown that IGEs negatively correlated with DGEs can

641 reduce or even reverse the expected response to selection (Costa e Silva et al. 2013; Muir

642 et al. 2013; Ellen et al. 2014), as we have found. The evolutionary stasis of heritable traits

643 under directional selection is a well-known observation in need of an explanation in the study

644 of trait evolution in wild populations (Merilä et al. 2001; Kokko et al. 2017). IGEs that

645 consistently counteract selection responses (compared to a DGE-only scenario) would

646 reduce evolutionary change, as we have shown under high-densities, and so could

647 contribute to a lack of evolutionary change. Whether this is a general explanation for

648 evolutionary stasis remains to be explored (Wilson 2014). In our study population, despite

649   phenotypic selection on parturition dates (which as noted above are heritable), we have

650   observed no evolution in this trait over 20 years (Lane et al. 2018). However, Lane et al

651   (2018) found that the association between parturition date and fitness was entirely a residual

652   correlation, rather than a genetic one, so no alternative explanation for evolutionary stasis

653   (such as IGEs) is required.

654   The contribution of the variance of the IGEs, and the DGE-IGE covariance to the

655   expected response to selection is not certain, as these estimates were not statistically

656   significant. If IGEs are not different from zero, then the expected response to selection may

657   not differ from that predicted by the breeder's equation (Bijma and Wade 2008). We note

658   that the non-significance of our IGE variance estimates may have been driven by a high

659   degree of uncertainty (large standard errors), rather than the magnitude of the effect, as in

660   high density years the V_{AI} was quite close in absolute size to V_{AD}, and their contribution to

661   total heritable variance and the predicted response to selection was large enough to change

662   the expected response in different conditions. As such, the value of incorporating these

663   estimates into predictive models is possibly large, but uncertain.

664   Predictions about the speed of evolution based on V_{AD} or σ_H^2 can be misleading,

665   because, as we have demonstrated, a negative DGE-IGE covariance detracts from the

666   response to selection (see eq. 5), even if there is a large amount of genetic variance. This is

667   similar to how negative genetic correlations between traits under equivalent selection can

668   limit their evolution (Lande 1979; Kirkpatrick and Lande 1989). Additionally, there are several

669   reasons why not all of σ_H^2 may be utilized in the response to selection. As can be seen from

670   eq. 5, the response to selection in the presence of IGEs is not simply σ_H^2 multiplied by

671   selection. Neighbourhoods or groups made up of unrelated individuals, small group sizes,

672   and a near-zero or negative covariance between DGEs and IGEs will also cause the σ_H^2 to

673   be somewhat discounted when calculating the response. However, given their prevalence

674   among livestock (Ellen et al. 2014), IGEs may well influence the response to selection more

675   broadly, hence they need to be considered more often when attempting to predict the

676   microevolution of populations, and to explain phenomena such as evolutionary stasis (Merilä

677   et al. 2001; Ellen et al. 2014; McAdam et al. 2014). This is true even in populations of wild

678   animals that do not live in clearly defined groups, but in an irregular network of territories

679   (see also Nunney (1985) for related work on the evolution of altruism in "continuous arrays"

680   of animals).

681

682   Altering competition indices and neighbourhood size

683   Varying the intensity of association factors (i.e. how strongly we weighted neighbours at

684   different distances) and the size of the neighbourhood did alter the balance between the

685   estimated direct and indirect effects, as well as estimated relative contribution of genetic and

686   environmental influences (see Tables S1-2 in the supplementary materials). Weighting the

687   closest individuals more strongly, by only including the 1-3 nearest neighbours, or using the

688   inverse of distance or distance^2, or by only including individuals within 60 m, gave similar

689   results. In all these versions, the variance arising from DGEs increased marginally compared

690   to the model where all neighbours were weighted equally. This effect was more pronounced

691   when using the inverse of distance^2 to define the intensity of association factors. We note

692   that the standard errors of estimates for direct additive genetic variance (V_{AD}) in the model

693   using the inverse of distance^2 were greatly increased, causing the estimate to be within two

694   standard errors of zero (i.e. nominally non-significant). This was the only model explored

695   where this occurred. Weighting farther individuals as strongly as close individuals, either by

696   not including any intensity of association factors for the 6 closest individuals, or by including

697   all individuals within 200 m and weighting them equally, gave very low estimates for the

698   IGEs. This could suggest that individuals at greater distances do not influence their

699   neighbours as much as close individuals.

700   Increasing the number of neighbours considered in the analysis beyond six led to

701   larger estimates for the variance arising from the non-genetic indirect effects (V_{PI}). A larger

702   estimate for the V_{PI} was also present in the model before the square term was added (not

703   shown). This suggests the apparent non-genetic influence of neighbours at large spatial

704   scales, as indicated by V_{PI}, may be driven by shared environmental factors at the larger

705   scale causing sets of neighbours to be consistently different from other sets, rather than by

706   social interactions of the focal individual causing their neighbours to be consistently different.

707   Decreasing the number of neighbours tended to increase the variance attributed to the DGE,

708   while IGEs showed a non-linear trend, peaking in magnitude with 4 neighbours and then

709   falling back down towards zero. At these neighbourhood sizes, V_{PI} was typically estimated

710   near zero, but grew in size once 5 or more neighbours were considered. Overall, these

711   results do not indicate that inferences from our model with the six closest neighbours,

712   weighted by the inverse of distance, are inappropriate for the system.

713   The approach we used, based on the work of Muir (2005) and Cappa and Cantet

714   (2008) can be applied to organisms in a range of social structures. Due to the relatively

715   recent increase in usage of techniques such as social network analysis (Krause et al. 2007,

716   2014; Croft et al. 2008), estimates of pairwise associations within populations of animals

717   have been made in many systems. These values can be used as the intensity of association

718   factors, as we used the inverse of distance, to scale indirect effects (Fisher and McAdam

719   2017). To estimate IGEs, this must be twinned with information on the phenotypes and

720   relatedness of the individuals in the population. We had a large dataset with good

22

721   information on phenotypes and relatedness of individuals, yet high uncertainty around

722   moderately large estimates of IGEs did not distinguish them from zero. The requirement to

723   phenotype, genotype and assess the social relationships of many individuals within a

724   population may well limit the range of study systems this approach can be used in (Kruuk

725   and Wilson 2018). However, with decreases in the cost of tracking technologies and in the

726   cost of assessing the genetic relatedness of animals (Bérénos et al. 2014), more study

727   systems will begin to be able to apply this and similar models, increasing the number of

728   estimates for these difficult-to-estimate quantitative genetic parameters, which could then be

729   aggregated in a meta-analysis to detect general patterns (Reid 2012), such as that by

730   Wilson and Réale (2005) for the direct-maternal genetic correlation.

731

732   Conclusions

733   Previous to this study, IGEs had only ever been estimated for wild animals in the context of

734   pairwise (dyadic) social interactions. We extended this to estimate IGEs on a life-history trait

735   with links to fitness in a population of wild animals that do not interact in discretely defined

736   groups. We also incorporated varying strengths of closeness of association between

737   individuals to more accurately represent the heterogeneous and complex nature of social

738   interactions in the natural world. We found that indirect effects of neighbours were a very

739   important contributor to parturition dates, especially at high densities, and may have a

740   heritable component. Predicting selection responses from a model that incorporated IGEs

741   indicates that they can both slow down (at high population density) and speed up (at low

742   density) the expected response to selection for earlier parturition dates. This is despite

743   selection actually being stronger at high densities. However, these patterns are based on

744   point estimates for genetic parameters that are characterised by high uncertainty and, as

745   noted, we cannot exclude the possibility that the indirect effects have a non-genetic basis.

746   Nonetheless, significant indirect phenotypic effects were detected and appear to increase in

747   importance at high density. This is consistent with competition for limited food resources

748   being the source of neighbour influences on focal life-history traits. Exactly how this

749   competition is mediated remains to be determined. The estimation of indirect effects, and

750   IGEs specifically, should be extended to more systems where densities and resource

751   availabilities vary (either naturally or artificially) to determine whether the patterns we have

752   observed are general. While we did not conclusively demonstrate IGEs are present, we think

753   wider estimation of effect sizes is useful even if power is limiting to make strong inferences in

754   any single case. The method we have used is flexible enough to be applied to alternative

755   systems, hence we look forward to the accumulation of more estimates of IGEs in the wild to

756   detect general patterns.

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Author contributions

766 AGM, AJW, and DNF conceived of the research question. SB initiated the long-term study

767 and all authors contributed to field logistics, data collection and the writing of the manuscript.

768 DNF drafted the manuscript and conducted the data analysis, with guidance from AJW and

769 AGM. All authors approved of the final manuscript for submission.

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