Social selection is density dependent but makes little contribution to total selection in New Zealand giraffe weevils

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Abstract

13 Social selection occurs when traits of interaction partners influence an individual's fitness and can

14 fundamentally alter total selection strength. Unlike for direct selection, however, we have little idea

15 of what factors influence the strength of social selection. Further, social selection only contributes to

16 overall selection when there is phenotypic assortment, but simultaneous estimates of social

17 selection and phenotypic assortment are rare. Here we estimated social selection on body size in a

18 wild population of New Zealand giraffe weevils (*Lasiorhynchus barbicornis*). We did this in a range of

19 contexts and measured phenotypic assortment for both sexes. Social selection was mostly absent

20 and not affected by sex ratio or the body size of the focal individual. However, at high densities

21 selection was negative for both sexes, consistent with competitive interactions based on size for

22 access to mates. Phenotypic assortment was also density dependent, flipping from positive at low

23 densities to negative at high densities. However, it was always close to zero, indicating negative

24 social selection at high densities will not greatly impede the evolution of larger body sizes. Despite

25 its predicted importance, social selection may only influence evolutionary change in specific

26 contexts, leaving direct selection as the dominant driver of evolutionary change.

27 **Keywords:** brentine, density dependent, fitness, phenotypic assortment, social selection, weevil

Introduction

29   Selection is an important concept in evolutionary biology, describing the link between traits and

30   fitness. Typically, selection is characterised as a selection gradient or covariance between the trait of

31   a focal individual (e.g. its body size) and a measure of fitness (e.g. the number of adult offspring it

32   has over lifetime; [1]). This "direct" selection helps us understand the ultimate functional value of

33   traits and predict how they might evolve. Further, direct selection is known to vary across space [2],

34   time [3], and with ecological conditions [4,5], helping to generate the biodiversity of the natural

35   world. Other forms of selection are possible, however. For instance, when organisms interact with

36   others, such as by competing for access to resources or cooperating to raise young, they can

37   influence each other's fitness. The link between a partner's traits or the traits of group mates and a

38   focal individual's fitness is known as "social" selection [6]. Social selection may not align with direct

39   selection (see Table 3 of [7]), which can alter the direction of trait evolution [8]. For instance,

40   "selfish" traits may increase the fitness of an individual that bears them but be costly when

41   displayed by group mates. Conversely, "altruistic" traits may be costly for the individual that displays

42   them but be beneficial when possessed by group mates. Social selection can therefore be expected

43   to alter evolutionary change and trait optima away from that expected solely under direction

44   selection, making it a fundamentally important evolutionary parameter [6,9,10].

45   Social selection alone cannot alter evolution, however. For social selection to contribute to

46   total selection, and therefore evolutionary change, there must be non-zero phenotypic assortment

47   among interacting individuals [6]. Phenotypic assortment describes the covariation between the

48   traits of an individual and the traits of those it interacts with. Positive assortment indicates that

49   individuals with similar traits interact e.g., aggressive individuals interact with other aggressive

50   individuals. Negative assortment on the other hand indicates that individuals with dissimilar traits

51   interact e.g., resource producing individuals interact with resource consuming individuals.

52   Assortment has been often documented in groups of animals, and typically found to be positive (in

53   male great tits, *Parus major*, [11], Chacma baboons, *Papio ursinus*, [12]; guppies, *Poecilia reticulata*,

3

54   [13]). However, not all measures of assortment are equal, and only the interactant covariance (the

55   covariance between an individual's traits and the mean trait value of those it interacts with) is

56   correct for use in models of total selection [14]. Unfortunately, estimates of this parameter in

57   natural populations are rare, especially alongside estimates of social selection (but see: [15]).

58   Therefore, despite its predicted importance, we have very little knowledge of how social selection

59   contributes to total selection in natural populations.

60   Alongside limited knowledge of social selection's contribution to overall selection, we also

61   have little data on the contexts where social selection is strongest (but see: [16,17]). Direct selection

62   is known to vary based on demographic parameters such as population density [18] and sex ratio

63   [19], as well as depending on other individual characteristics (correlational selection; [20]). A lack of

64   knowledge of the conditions where social selection is strongest completely hampers our ability to

65   predict how it may shape different populations differently, and therefore generate diversity. We

66   aimed to fill gaps in our knowledge surrounding the contribution of social selection to total

67   selection, and the conditions it is strongest, in a wild population of New Zealand giraffe weevils

68   (*Lasiorhynchus barbicornis;* Coleoptera: Brentidae). Both sexes are extremely variable in size [21–

69   23], males bear an elongated rostrum used as a weapon during contests for mates [24], and body

70   length is under positive linear, but not quadratic, selection in males and females [25]. As giraffe

71   weevils form aggregations on trees and compete for access to mates, we predicted that social

72   selection for body size would be negative, where the presence of larger rivals reduces a focal

73   individual's fitness (following [26]). Further, we predicted that this social selection would be more

74   negative at high densities and when the individual was of the more common sex (i.e., a male in a

75   male-biased population), as these are conditions when they might be competing most fiercely for

76   access to mates. We also predicted that smaller males would be less affected by the body size of

77   rivals, as they can readily switch between fighting with similar-sized rivals and "sneaker" tactics that

78   allow them to gain copulations without direct competition [27]. Finally, following previous work

79   which found positive size-assortment among mating pairs [25], we predicted that there would be

80 positive assortment for body size in the individuals present on trees in both sexes, causing social

81 selection to reduce the overall strength of selection on body size.

82

83 ## Methods

84

85 ### Data collection

86 The giraffe weevil population we studied resides in Matuku Reserve (36° 51.92⬚S, 174° 28.32⬚E), an

87 area of native coastal broadleaf forest west of Auckland, New Zealand. We located aggregations of

88 adult giraffe weevils on karaka trees (*Corynocarpus laevigatus*), which were subsequently used for

89 behavioural observations. The observations and data collection used in the current study are

90 described in full in a previous study [25] with the data available online [28], but we briefly outline

91 them again here.

92 To determine variation in mating success among males and females of different sizes we

93 conducted daily observations for one hour at three different trees that housed giraffe weevil

94 aggregations. Observations took place over two periods between November 22 and December 22,

95 2013 (31 days, N = 120 females, 132 males), and January 22 to February 23, 2014 (33 days, N = 301

96 females, 366 males). For the analysis we excluded individuals only seen once, and those who were

97 first seen in the last week of each observation period (following [25]). This left a dataset of 1234

98 records of 155 different females and 236 different males. At least two hours prior to observations

99 each day, we removed all giraffe weevils from the tree for measurement and marking. We measured

100 total body length (tip of mandibles to distal end of elytra) using digital callipers to nearest 0.01 mm.

101 We also measured weapon size and other morphological traits, but these are all very highly

102 correlated with body length, while body length includes the rostrum (the weapon) and is likely under

103 fecundity selection in females, hence is an appropriate trait to use for our analysis [22]. We then

104   painted individuals on the pronotum and elytra with a unique colour combination using five Queen

105   bee marking paints (Lega, Italy) for identification before being released to the point of capture on

106   the tree [29]. We observed all giraffe weevils present on each of the three study trees for one hour

107   on each day of the observation period between 0800 h and 1800 h. We stood at least one metre

108   from the tree and used close range binoculars (Pentax, Papilio) to avoid disturbing the weevils.

109   During each observation, we recorded the identification of all giraffe weevils present on the tree

110   that day as well as all matings. After observations, we thoroughly searched the tree to check for any

111   individuals that had been inactive or hiding in cracks or under leaves, and we gave these individuals

112   a mating frequency of zero. We conducted no observations on days of heavy rainfall because giraffe

113   weevils are inactive during this time, resulting in two non-consecutive days being missed in the first

114   observation period, and three non-consecutive days during the second.

115

116   Data analysis

117   To assess the strength of social selection, we fitted a series of generalised linear mixed-effect models

118   using the R package "glmmTMB" [30]. For all models we mean-centred each continuous predictor

119   variable and divided by its standard deviation to improve model fit and interpretability (see [31]).

120   For quadratic terms we first mean centred and scaled the variable, then squared it and then divided

121   by two (see: [32]). Each model had the number of different individuals a focal weevil copulated with

122   in that day (our proxy for fitness) as the response variable, with date of observation, tree identity,

123   and weevil identity as random effects, and a Poisson error distribution with a log-link. This approach

124   gives fixed effect coefficients that are directly interpretable as selection gradients (see [32]).

125   To estimate direct and social selection, in our first model we fitted individual body size and

126   the mean body size of all other individuals of the same sex on the same tree in that day as

127   predictors. The latter term specifically excludes the focal individual from the calculation of the mean

128   [7,14,33]. We also included quadratic versions of these terms to determine whether social selection

129   was non-linear. We included sex as a fixed effect, and the interactions between sex and both focal

130   and rival body size for both linear and quadratic terms to test whether males and females

131   experienced different selection. Females were set as the default sex and so the interaction was

132   modelled as the difference between males and females. We evaluated the "clarity" (see [34]) of the

133   effect of all fixed effects using Wald χ^2 tests with type II sum of squares using the *Anova* function

134   within the R package "cars" [35]. The degrees of freedom were 1 for all tests unless a subscript is

135   given stating otherwise.

136   To determine under which conditions social selection is strongest we then fitted a series of

137   models. We used the same starting model as above except we did not include quadratic terms as

138   they had no clear effect (see Results). For the first model, we included an interaction between focal

139   body size and the mean size of its rivals to determine if smaller individuals experienced weaker social

140   selection than larger individuals. We also included the three-way interaction between sex, focal

141   body size, and rival body size, to see if males and females differed in this relationship. As males of

142   only smaller sizes (typically under 40mm, see [27]) may engage in "sneaky" copulations, we also

143   fitted a model where sex was a three-level categorical variable, either "female", "male over 40mm",

144   or "male 40mm or under", and retained the interactions between this new variable and both focal

145   and rival body size. We then fitted two models to test which demographic parameters influenced

146   social selection. The first included weevil density (number of weevils observed on the tree on that

147   day) as a fixed effect and its interactions with both focal and rival body size, including the three-way

148   interactions between density, sex, and either focal or rival mean body size. The second model was

149   equivalent to the density model but included sex-ratio (proportion of weevils on the tree on that day

150   that were male) instead of density. In these two models the key terms are the interactions between

151   density/sex-ratio and the mean body size of rivals, as these terms indicate whether the impact of

152   rival body size on focal individual fitness (and so the strength of social selection) increases or

153   decreases with density/sex-ratio (while the interaction between this term and sex indicates whether

154   this effect differs between the sexes or not).

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155   To estimate the overall phenotypic assortment within each sex we calculated the Pearson

156   correlation between the body size of a focal individual and the mean body size of its rivals, where

157   the variables had been mean centred and divided by their standard deviation [14]. Following our

158   detection of density dependent social selection (see Results), we then decided to test whether

159   phenotypic assortment was density dependent. We stress this was a decision made after viewing

160   our initial results and so should be interpreted appropriately. To do this we fitted a linear model with

161   the mean body size of same-sex rivals as the response variable, the body size of a focal individual,

162   the density of weevils on the tree, the focal individual's sex, and all two- and three-way interactions

163   between these variables as fixed effects. We also included date, weevil identity, and tree identity as

164   random effects. The response variable and all continuous predictor variables were mean centred

165   and divided by their own standard deviation. The key term here is the interaction between density

166   and the body size of the focal individual, as this indicates whether the relationship between the focal

167   individual and the mean body size of its rivals changes with density (while the interaction between

168   this term and sex indicates whether this effect differs between the sexes or not).

169

Results

171   There was no linear or quadratic social selection in either sex when not taking into account variation

172   in body size, density, or sex ratio (linear social selection = 0.479, se = 0.563, χ^2 = 0.029, p = 0.864; sex

173   interaction = -0.494, se = 0.591, χ^2 = 0.700, p = 0.403; quadratic social selection = 0.485, se = 0.498,

174   χ^2 = 0.268, p = 0.604; interaction = -0.674, se = 0.527, χ^2 = 1.633, p = 0.201). As previously found [25]

175   both sexes were under approximately equal positive linear direct selection for body size (linear

176   direct selection = 0.232, se = 0.382, χ^2 = 11.477, p < 0.001; sex interaction = 0.038, se = 0.391, χ^2 =

177   0.009, p = 0.923; quadratic direct selection = -0.470 se = 0.669, χ^2 = 1.551, p = 0.213, sex interaction

178   = 0.395, se = 0.671, χ^2 = 0.347, p = 0.556). The strength of social selection did not depend on the size

179   of the focal individual for either sex (focal and rival body size interaction = -0.200, se = 0.368, χ^2 =

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180   1.781, p = 0.182; sex interaction = 0.093, se = 0.380, χ^2 = 0.060, p = 0.806), nor was it different

181   among different classes of male (contrast between female and large male = -0.197, se = 0.218,

182   contrast between female and small male = -0.014, se = 0.204, χ^2_2 = 1.262, p = 0.532). Direct selection

183   also did not differ among different classes of male (contrast between female and large male= -0.311,

184   se = 0.180, contrast between female and small male= -0.390, se = 0.207, χ^2_2 = 4.087, p = 0.532).

185   Social selection was density dependent; at higher densities it was clear and negative for both sexes

186   (rival body size and density interaction = -0.563, se = 0.301, χ^2 = 4.340, p = 0.037, sex interaction =

187   0.358, se= 0.370, χ^2 = 0.934, p = 0.334), indicating that larger rivals reduce an individual's fitness, but

188   only at high densities (Figure 1). Direct selection was not dependent on density for either sex (focal

189   body size and density interaction = -0.043, se = 0.146, χ^2 = 2.170, p = 0.141; sex interaction = 0.125,

190   se = 0.154, χ^2 = 0.652, p = 0.419). Sex-ratio did not influence social selection (rival body size and sex-

191   ratio interaction = -0.158, se = 0.156, χ^2 = 0.060, p = 0.806; sex interaction = 0.175, se = 0.174, χ^2 =

192   1.006, p = 0.316) or direct selection in either sex (focal body size and sex-ratio interaction = -0.006,

193   se = 0.167, χ^2 = 1.209, p = 0.272; sex interaction = 0.070, se = 0.176, χ^2 = 0.159, p = 0.690;). Full

194   results from each model are reported in the supplementary materials (Tables S1-5).

195   Phenotypic assortment overall was near zero for both females ($r_{females}$ = 0.066, t = 1.336, df =

196   406, p = 0.182) and males (r_{males} = 0.053, t = 1.521, df = 824, p = 0.129). Our subsequent test of

197   whether phenotypic assortment was density dependent revealed that, for both sexes, assortment

198   switched from being positive to negative as densities increased (focal body size = 0.012, se = 0.064,

199   χ^2 = 18.800, p < 0.001; focal body size and density interaction = -0.021, se = 0.057, χ^2 = 4.564, p =

200   0.033; sex interaction = 0.056, se = 0.059, χ^2 = 0.915, p = 0.339; Figure 2). However, at no density

201   was it especially far from zero, and therefore social selection does not ever greatly alter the total

202   selection differential (Figure 3).

203
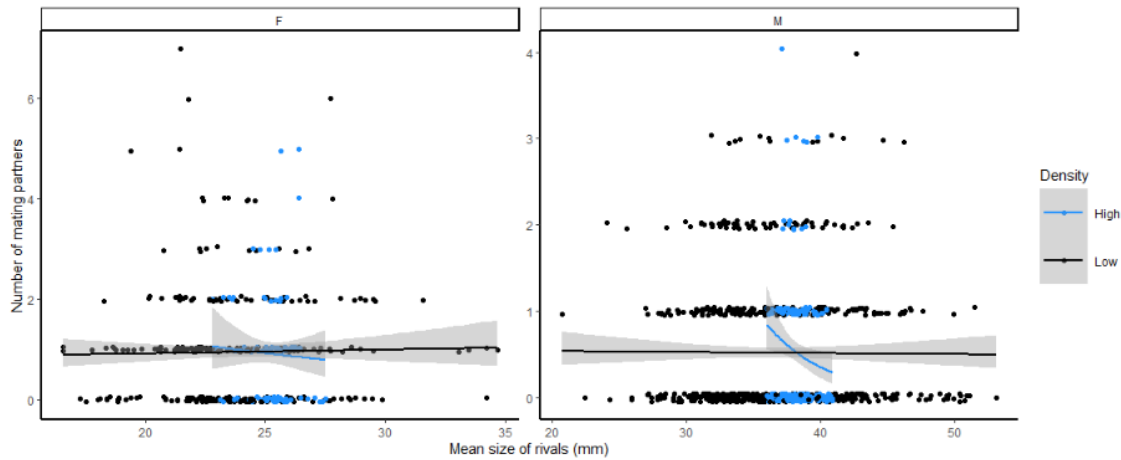
204

205 **Figure 1.** The strength of social selection was density dependent, becoming more

206 negative at high densities (more than 40 weevils per tree, light blue) compared to low

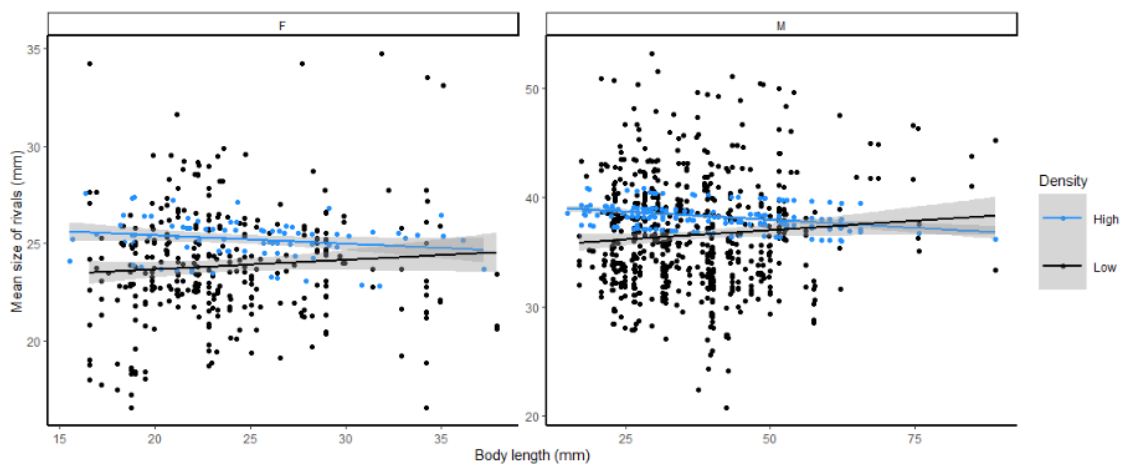207 densities (40 or fewer weevils per tree, black). This was true for both females (left

208 panel) and males (right panel). Note that we analysed density as a continuous variable,

209 but we have used a categorical representation when plotting for ease of viewing.

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211

212 **Figure 2.** Phenotypic assortment was density dependent, becoming more negative at
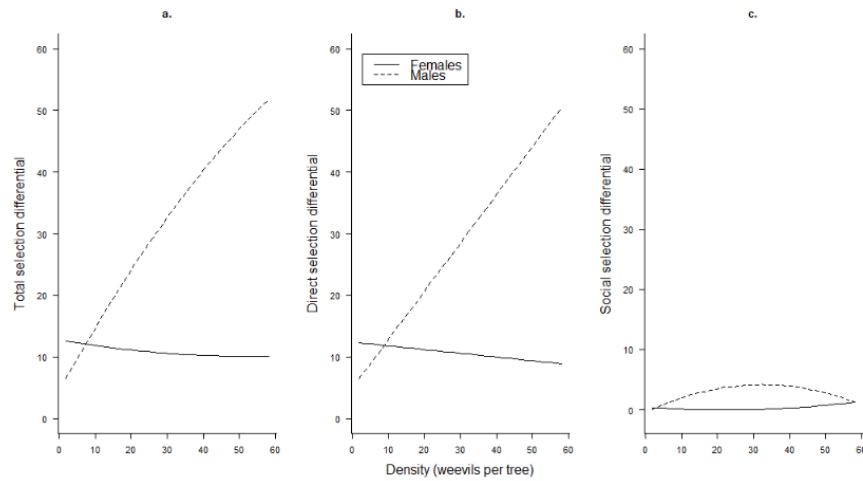
213 high densities (more than 40 weevils per tree, light blue) compared to low densities (40

214 or fewer weevils per tree, black). This was true for both females (left panel) and males

215   (right panel). Note that we analysed density as a continuous variable, but we have used

216   a categorical representation when plotting for ease of viewing.

217

218   **Figure 3**. Plots showing how the total selection differential (a.), and its components the

219   direct selection differential (b.) and the social selection differential multiplied by

220   phenotypic assortment (c.) change with density for females (solid lines) and males

221   (dashed lines). Note that direct selection was not clearly density dependent for either

222   sex, but the high phenotypic variance in male body size means small changes in the

223   selection gradient have large consequences for the selection differential. While social

224   selection became more negative with increased density, phenotypic assortment

225   changed from positive at low densities to negative at high densities and was always

226   near zero, meaning the contribution of social selection to the total selection differential

227   was always small.

228

Discussion

230   We estimated the strength of social selection across a range of contexts for both male and female

231   giraffe weevils. In contrast to our predictions, we found that social selection was typically absent,

232   although it was clearly negative at high densities, a result in line with our predictions. An increase in

233   the strength of negative social selection as densities increase is consistent with the idea that weevils

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234   are engaging in higher competition for access to mates. Interestingly, this is true for males and

235   females, and so females experience reduced mating success at high densities when there are large

236   females on the same tree. The mechanism for this social selection in females remains to be

237   explored, although there is some evidence larger males prefer to mate with larger females [25],

238   which might lead to fewer matings for smaller females. Another possibility is that at high densities

239   males are spending more of their time fighting other males, leaving less time to copulate with

240   females, resulting in choosier males to the detriment of small females sharing trees with large

241   females. However, as phenotypic assortment was always close to zero the social selection we

242   observed will only make very small contributions to overall selection. At low densities, social

243   selection is weakly positive or absent and so will only very slightly increase total selection (which is

244   positive) due to the positive assortment, while at high densities social selection will also slightly

245   increase overall selection as both it and assortment are negative. Despite this effect, ultimately it

246   seems that direct selection, in interaction with costs and benefits stemming from natural selection

247   [25], will govern the evolution of body and weapon size in giraffe weevils

248   Our results are consistent with several previous studies on direct and social selection for

249   body size and related traits (see also [7] for a list of direct and social selection in other types of

250   traits). Formica *et al.* [26] found positive direct selection and negative social selection for body size

251   (when using mating success as a proxy for fitness, but this is not true when using survival) in fungus

252   beetles (*Bolitotherus cornutus*), matching our result for high densities. Similarly, Tsuji [36] and

253   Santostefano *et al.* [15] found positive direct selection and negative social selection for body size in

254   an ant (*Pristomyrmex pungens*) and in male chipmunks (*Tamias striatus* ; but only in summer, and

255   never for females), respectively. These results have also been repeated in plants, in both *Arabidopsis*

256   *thaliana* [37] and sea rocket (*Cakile edentula*) [38] positive direct selection and negative social

257   selection for size has been detected, although in sea rocket this is only true at low densities, while

258   both selection gradients are reversed at medium and high densities. Other studies however either

259   find positive direct selection and either positive or mixed social selection for size or growth rate

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260   (black-throated blue warblers, *Setophaga caerulescens*, [39]; North American red squirrels,

261   *Tamiasciurus hudsonicus*, [16]; great tits, *P. major*, [40]; *Silene tatarica* [41]), while Stevens *et al.* [42]

262   found both direct and social selection for size to be negative in Jewelweed (*Impatiens capensis*).

263   Therefore, while opposing direct and social selection for body size may be more common than any

264   other situation, consistent with size-based competition for limited resources which are key for

265   fitness (such as food or members of the time-limited sex), it is by no means the rule. More estimates

266   of direct and social selection need to be accumulated before we can start to identify general rules.

267   Sex-ratio had no effect on social or direct selection. No effect on social selection surprised us

268   given we assumed social selection represents competition for mates, which should be stronger in

269   males when an aggregation is more male-biased, and potentially vice versa for females. Sex ratio

270   varied from 0-1.0 (median = 0.66, 25% quantile = 0.61, 75% quantile = 0.71) so we do not think it is a

271   lack of variation in our dataset preventing us from finding a pattern. Possibly, many males on a tree

272   on any given day are not participating in the competition for mates, therefore rendering the

273   measure of sex-ratio uninformative. We also found a focal individual's body size (either measured

274   continuously or where males were split into "small" and "large" male either side of 40mm) did not

275   influence the impact of rivals on fitness. We had expected smaller males to be less severely affected

276   by large rivals, as they are able to obtain matings by switching from a female-defence strategy to

277   "sneaking" copulations with females guarded by large males [27]. However, given we only detected

278   any negative effect of larger rivals at high densities, we might have to focus on high densities to look

279   for our predicted pattern, and the current dataset does not contain enough samples of trees with a

280   high density of giraffe weevils to do this. While correlational direct selection has received some

281   attention [43], we possess very limited information about which traits of individuals influence the

282   strength of social selection (but see [16] for an interaction between sex and multilevel selection on

283   birth date in North American red squirrels, *T. hudsonicus*). Beyond body size, certain behavioural

284   traits, such as sensitivity or susceptibility, might modulate how strongly an individual is influenced by

285   rivals, but this remains to be tested.

13

286   We found phenotypic assortment was typically near zero, although was more positive at low

287   densities and more negative at high densities, for both sexes. Due to this near-zero assortment,

288   social selection will only ever contribute a small amount to total selection. Limited phenotypic

289   assortment is consistent with individuals mostly randomly aggregating on trees without respect to

290   the body size of other individuals on the tree. In giraffe weevils, assortment by body size has been

291   observed in mating pairs [25], but this pattern could emerge following arrival at trees rather than

292   before. We did see negative phenotypic assortment at high densities, which is consistent with large

293   individuals avoiding large rivals at high densities, when the fitness consequences of interacting with

294   them is strongest. However, this effect is relatively weak, probably due to individuals of all sizes

295   benefiting from avoiding large rivals, in which case no strong assortment can arise.

296   Although estimates of phenotypic assortment have been accumulated in the literature and

297   are often positive, they tend not to be specifically measures of the interactant covariance (the

298   covariance between an individual's traits and the mean trait value of those it interacts with), the key

299   parameter for models of social selection [14]. For example, Farine and Sheldon [44] estimated

300   positive assortment on lay date in great tits (*P. major*) but used a social network measure of

301   assortment which underestimates the true interactant covariance substantially [14]. If positive

302   phenotypic assortment is indeed common, then social selection will often contribute to total

303   selection, and if social selection is typically in the opposite direction to direct selection [7], will

304   therefore tend to reduce overall selection. Formica *et al.* [26] estimated the interactant covariance

305   for body size in aggregations of forked fungus beetles (*B. cornutus*) and found a negative covariance.

306   This would then end up causing negative social selection for body size to increase the magnitude of

307   the overall positive selection for body size. In contrast, while Santostefano *et al.* [15] found a

308   negative covariance among female chipmunks (*T. striatus*) for body mass, they found no covariance

309   among males for body mass. Since social selection was only present in males, social selection would

310   not contribute to overall selection in either sex. In summary then, while we may expect social

311   selection to weaken overall selection, evidence from systems where both social selection and

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312   phenotypic assortment have been estimated suggests that it often does not contribute at all.

313   Further, a lack of estimates of how phenotypic assortment changes with key demographic

314   parameters such as density prevents us from understanding whether there are some contexts social

315   selection does contribute to total selection. Given both direct and social selection can also vary with

316   conditions, context-dependent phenotypic assortment raises the possibility that evolution can have

317   very different outcomes in different environments, but we lack the data to assess this suggestion.

318   Overall, we have contributed to our knowledge of how selection operates in wild animals. As

319   predicted, social selection was in the opposite direction to direct selection and was stronger at high

320   densities. However, social selection was not clearly different from zero in average conditions and did

321   not vary with sex-ratio or the size of the focal individual. Further, although phenotypic assortment

322   changed with density it was rarely far from zero, indicating that social selection will have a limited

323   contribution to overall selection even at high densities. Therefore, despite its predicted importance,

324   social selection will only have a minor impact on the evolutionary change of body size in New

325   Zealand giraffe weevils.

326

327   ## Data accessibility

328   The data used here have previously been made publicly available, see: [28]. We have chosen to

329   provide copies of the exact spreadsheets and the R code used to create the dataset, analyse the

330   data, and produce all figures, as supplementary materials for ease of access for reviewers. Upon

331   acceptance we will make these files available in Dryad or another suitable public repository.

332

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Authors' contributions

DNF developed the main ideas for the manuscript, analysed the data, and lead the writing of the manuscript. RLG collected and curated the data. CJP helped collect the data and design the study, provided assistance during the statistical analysis, and contributed to the writing. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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