

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

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11

12 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

28 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*,

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).

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

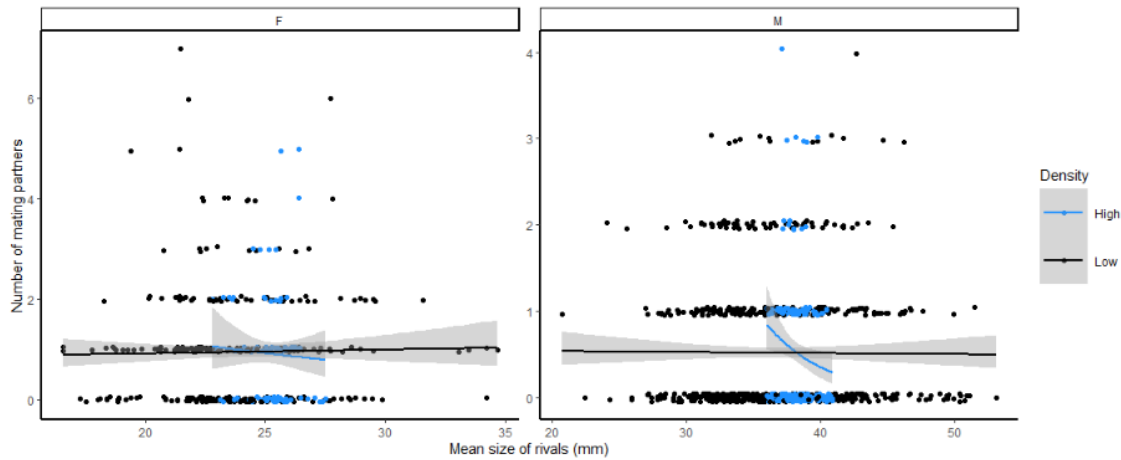
170 Results

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, $\chi^2 = 0.029$, p = 0.864; sex
173 interaction = -0.494, se = 0.591, $\chi^2 = 0.700$, p = 0.403; quadratic social selection = 0.485, se = 0.498,
174 $\chi^2 = 0.268$, p = 0.604; interaction = -0.674, se = 0.527, $\chi^2 = 1.633$, 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, $\chi^2 = 11.477$, p < 0.001; sex interaction = 0.038, se = 0.391, $\chi^2 =$
177 0.009, p = 0.923; quadratic direct selection = -0.470 se = 0.669, $\chi^2 = 1.551$, p = 0.213, sex interaction
178 = 0.395, se = 0.671, $\chi^2 = 0.347$, 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, $\chi^2 =$

180 1.781, $p = 0.182$; sex interaction = 0.093, $se = 0.380$, $\chi^2 = 0.060$, $p = 0.806$), 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, $se = 0.204$, $\chi^2_2 = 1.262$, $p = 0.532$). 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, $se = 0.207$, $\chi^2_2 = 4.087$, $p = 0.532$).
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, $se = 0.301$, $\chi^2 = 4.340$, $p = 0.037$, sex interaction =
187 0.358, $se = 0.370$, $\chi^2 = 0.934$, $p = 0.334$), 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, $se = 0.146$, $\chi^2 = 2.170$, $p = 0.141$; sex interaction = 0.125,
190 $se = 0.154$, $\chi^2 = 0.652$, $p = 0.419$). Sex-ratio did not influence social selection (rival body size and sex-
191 ratio interaction = -0.158, $se = 0.156$, $\chi^2 = 0.060$, $p = 0.806$; sex interaction = 0.175, $se = 0.174$, $\chi^2 =$
192 1.006, $p = 0.316$) or direct selection in either sex (focal body size and sex-ratio interaction = -0.006,
193 $se = 0.167$, $\chi^2 = 1.209$, $p = 0.272$; sex interaction = 0.070, $se = 0.176$, $\chi^2 = 0.159$, $p = 0.690$); 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 $\chi^2 = 18.800$, $p < 0.001$; focal body size and density interaction = -0.021, $se = 0.057$, $\chi^2 = 4.564$, $p =$
200 0.033; sex interaction = 0.056, $se = 0.059$, $\chi^2 = 0.915$, $p = 0.339$; 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).

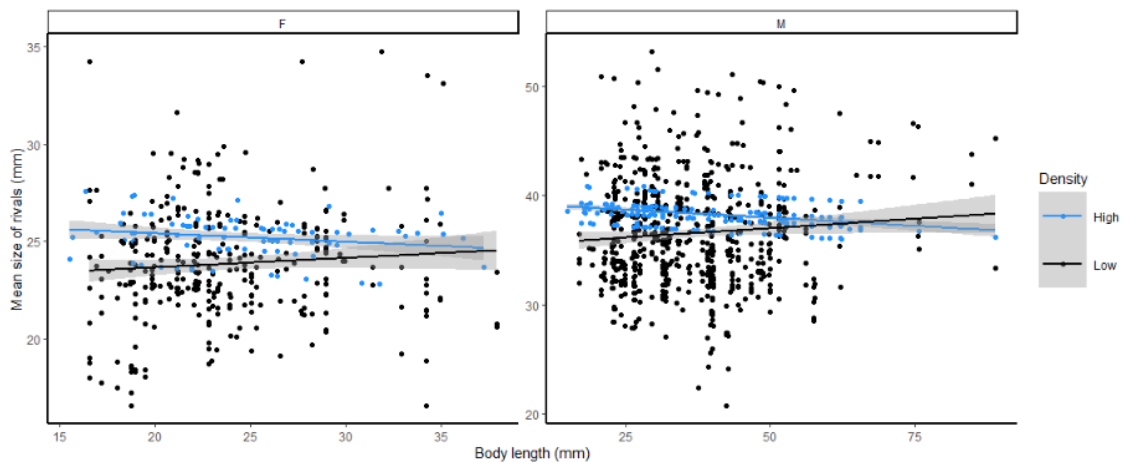
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204

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.

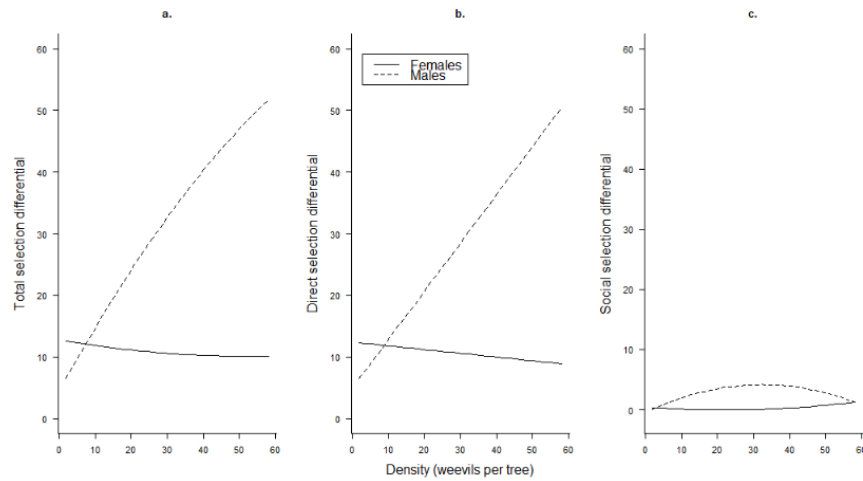
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211

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
214 densities (40 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

229 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

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

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.

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

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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342

343 Authors' contributions

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

348

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