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

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8   Abstract

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

10   alter total selection strength. However, we have little idea of what factors influence social selection's

11   strength. Further, social selection only contributes to overall selection when there is phenotypic

12   assortment, but simultaneous estimates of social selection and phenotypic assortment are rare.

13   Here we estimated social selection on body size in a wild population of New Zealand giraffe weevils

14   (*Lasiorhynchus barbicornis*). We measured phenotypic assortment by body size and tested whether

15   social selection varied with sex-ratio, density, and interacted with the body size of the focal

16   individual. Social selection was limited and unaffected by sex ratio or the size of the focal individual.

17   However, at high densities social selection was negative for both sexes, consistent with size-based

18   competitive interactions for access to mates. Phenotypic assortment was always close to zero,

19   indicating negative social selection at high densities will not impede the evolution of larger body

20   sizes. Despite its predicted importance, social selection may only influence evolutionary change in

21   specific contexts, leaving direct selection to drive evolutionary change.

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

Introduction

Selection is an important concept in evolutionary biology, describing the link between traits and fitness. Typically, selection is characterised as a selection gradient or differential representing the relationship between the trait of a focal individual (e.g., body size) and a measure of fitness (e.g. its lifetime number of adult offspring; [1]). This "direct" selection helps us understand the functional value of traits and predict how they might evolve. Further, direct selection is known to vary across space [2], time [3], and with ecological conditions [4,5], helping to generate the biodiversity of the natural world. Other forms of selection are possible, however. For instance, when organisms interact with others, such as by competing for access to resources or cooperating to raise young, they can influence each other's fitness. The link between a partner's traits or the traits of group mates and a focal individual's fitness is known as "social" selection [6]. Estimating direct and social selection gradients is formally equivalent to estimating within- and among-group selection using contextual analysis, giving deep links between social selection theory and multilevel selection theory [6–8].

Social selection may not align with direct selection (see Table 3 of [9]), which can alter the direction and tempo of trait evolution [8], possibly leading to maladaptation [10]. For instance, "selfish" traits may increase the fitness of an individual that bears them but be costly when displayed by those they interact with. Conversely, "altruistic" traits may be costly for the individual that displays them but be beneficial when expressed by other individuals that interact with them. Social selection is one of the ways social interactions can alter evolutionary change, alongside individuals having heritable effects on each other's phenotypes (indirect genetic effects [11]), and individuals choosing who they interact with through social niche construction and therefore manipulating their environment and the selection pressures they are under [12, see 13 for a review]. Given how fundamentally social interactions can alter evolutionary change, it is therefore vital we estimate parameters such as social selection in natural populations in a range of contexts [6,14,15].

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

48   total selection, and therefore evolutionary change, there must be covariation between the traits of

49   an individual and the traits of those it interacts with (non-zero phenotypic assortment; [6]). The

50   overall selection differential is calculated as (following [16], see also [6]):

51     $$(\beta_D + \beta_S \beta_{z'z}) var(z)$$

52   Where β_D is the direct selection gradient, β_S is the social selection gradient, $\beta_{z'z}$ is the coefficient

53   from the regression of the mean partner phenotype on the focal individual's phenotype, also known

54   as the assortment coefficient, and $var(z)$ is the phenotypic variance across focal individuals.

55   Positive assortment indicates that individuals with similar traits interact e.g., aggressive individuals

56   interact with other aggressive individuals. Negative assortment on the other hand indicates that

57   individuals with dissimilar traits interact e.g., resource producing individuals interact with resource

58   consuming individuals. Assortment has been documented in groups of animals, and typically found

59   to be positive (in male great tits, *Parus major*, [17], Chacma baboons, *Papio ursinus*, [18]; guppies,

60   *Poecilia reticulata*, [19]). However, not all measures of assortment are equal, and only the

61   interactant covariance (the covariance between an individual's traits and the mean trait value of

62   those it interacts with) is correct for use in models of total selection [16]. Unfortunately, estimates of

63   this parameter in natural populations are rare, especially alongside estimates of social selection (but

64   see: [20,21]). Therefore, despite its predicted importance, we have very little knowledge of how

65   social selection contributes to total selection in natural populations.

66   We also have little data on the contexts where social selection is strongest. A few studies to

67   date indicate that social selection and within- or among-group selection may vary with sex [20,22],

68   local density [21–23], or season [20], but we lack substantial evidence to make any strong

69   conclusions. Direct selection is known to vary based on demographic parameters such as population

70   density [24] and sex ratio [25], as well as depending on other individual characteristics (correlational

71   selection; [26]). A lack of knowledge of the conditions where social selection is strongest hampers

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72   our ability to predict how it may shape different populations, and therefore generate diversity. We

73   aimed to address this gap in a wild population of New Zealand giraffe weevils (*Lasiorhynchus*

74   *barbicornis;* Coleoptera: Brentidae). Both sexes are extremely variable in size [27–29], males bear an

75   elongated rostrum used as a weapon during contests for mates [30], and body length is under

76   positive linear selection in males and females (using number of mates as the fitness component;

77   [31]). As giraffe weevils form aggregations on trees and compete for access to mates, we predicted

78   that social selection for body size would be negative, where the presence of larger rivals reduces a

79   focal individual's fitness (following [21]). We included both sexes in all analyses as we wished to test

80   whether females experienced social selection, as there is often the implicit assumption that females

81   do not compete for access to mates, but whether females do in fact suffer a cost from competing

82   with large rivals is rarely tested (but see: [20]). We predicted that females would experience weaker

83   social selection than males as females do not actively guard their mates, unlike males, and so large

84   females should not be able to directly prevent others from mating.

85   We had a series of predictions for factors that could influence the strength of social

86   selection. As individuals mate more often but for shorter periods of time at higher densities (C.

87   Painting, unpublished data), we predicted that social selection would be more negative at high

88   densities and when the individual was of the more common sex (i.e., a male in a male-biased

89   population), as these are conditions when they might be competing most fiercely for mates. We also

90   predicted that smaller males would be less affected by the body size of rivals, as they can readily

91   switch between fighting with similar-sized rivals and "sneaker" tactics that allow them to gain

92   copulations without direct competition [32]. Finally, following previous work which found positive

93   assortment in various taxa (see above), we predicted that there would be positive assortment for

94   body size in the individuals present on trees in both sexes, causing social selection to reduce the

95   overall strength of selection on body size.

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Methods

Data collection

The giraffe weevil population we studied resides in Matuku Reserve (36° 51.92'S, 174° 28.32'E), a coastal broadleaf forest west of Auckland, New Zealand. We located aggregations of adult giraffe weevils on karaka trees (*Corynocarpus laevigatus*), which were subsequently used for behavioural observations. The observations and data collection used in the current study are described in full in a previous study [31] with the data available online [33], but we briefly outline them again here.

To determine variation in mating success among males and females of different sizes we conducted daily observations for one hour at three different trees (visited in a random order) that housed giraffe weevil aggregations. Aggregations typically covered only around 1m^2 of the tree trunk, making the complete observation of all individuals in the aggregation relatively straightforward. Observations took place over two periods between November 22 and December 22, 2013 (31 days, N = 120 females, 132 males), and January 22 to February 23, 2014 (33 days, N = 301 females, 366 males). For the analysis we excluded individuals only seen once, and those who were first seen in the last week of each observation period (following [31]). This left a dataset of 1234 records of 155 different females and 236 different males. At least two hours prior to observations each day, we removed all previously unrecorded giraffe weevils from the tree for measurement and marking. We measured total body length using digital callipers to nearest 0.01 mm; body length can vary between 15-90mm in males and 13-50 mm in females [34]. We also measured rostrum length (the weapon used by males during combat), but this and all morphological traits are highly correlated with body length [28]. We used body length in our selection analyses, as body length includes the length of the rostrum and is likely under fecundity selection in females. We then painted individuals on the pronotum and elytra with a unique colour combination using Queen bee marking paints (Lega, Italy) for identification before being released to the point of capture on

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the tree [35]. We observed all giraffe weevils present on each of the three trees for one hour on

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

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

each observation, we recorded the identity of all giraffe weevils present on the tree that day as well

as the occurrence of all matings using scan sampling with continuous recording. After observations,

we thoroughly searched the tree to check for any individuals that had been inactive or hiding in

cracks or under leaves, and we gave these individuals a mating frequency of zero. Within the hour it

is very unlikely that individuals were able to copulate in these hiding places and be missed by us.

These individuals were included in the calculation of the social environment (see below) as they

could have interacted with the other weevils in the aggregation but chose not to. We conducted no

observations on days of heavy rainfall because giraffe weevils are inactive during this time, resulting

in two non-consecutive days being missed in the first observation period, and three non-consecutive

days during the second.

Data analysis

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

using the R package "glmmTMB" [36]. For all models we mean-centred each continuous predictor

variable and divided by its standard deviation to improve model fit and interpretability (see [37]).

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

by two (see: [38]). Each model had the number of different individuals a focal weevil copulated with

in that day (the component of absolute fitness) as the response variable, time of day as both linear

and quadratic terms as fixed effects, tree identity, weevil identity, and an Ornstein–Uhlenbeck

temporal autocorrelation term (as dates were not evenly spaced), modelling both variation among

dates and the similarity of measurements made closer in time on the same individual, as random

effects, and a Poisson error distribution with a log-link. This approach gives fixed effect coefficients

147   that can be readily transformed into selection gradients (see [38,39]) and means we do not scale

148   fitness by the mean of the group, instead effectively looking at the strength of selection at the

149   population level [40], matching the scale at which we calculate assortment (see below). We use

150   number of different mating partners as a component of fitness in females (i.e., the rate of

151   polyandry) as this was used by LeGrice *et al*. when estimating selection in both males and females in

152   this species ([31], note that number of mating partners and both survival and recapture probability

153   increase with body size). While laboratory studies suggest female fitness plateaus at higher mating

154   rates [41], in studies on wild insects the lifetime rate of polyandry can predict the number of

155   offspring produced that survive to adulthood (e.g., the field cricket *Gryllus campestris*; [42]). As such

156   we think this is an appropriate measure of a component of fitness.

157   To estimate social selection, we must define which other weevils an individual is interacting

158   with and calculate their mean body size, specifically excluding the focal individual from the

159   calculation of the mean [7,9,16]. Estimating social selection is related to "contextual analysis", where

160   the within-group and among-group selection gradients are estimated [7,43], and one can transform

161   the estimates of direct and social selection into estimates of within- and among-group selection

162   (see: [8], although note that phenotypic assortment is not required for among-group selection to

163   contribute to overall selection). We used social selection rather than contextual analysis as we felt

164   the parameters of direct and social selection were more intuitive when applied to the biology of our

165   study species. We defined an individual's interaction partners as all same sex-individuals found in

166   the same aggregation as a focal weevil on the same day, including those that achieved no mating

167   success and were hiding in cracks (hereafter "rival mean body size"). The rival mean body size

168   accurately represents the social environment as the aggregations we observed covered only a small

169   area, meaning that all weevils, even those in cracks, could easily interact with others in the

170   aggregation if they chose to. Further, daily survival probabilities based on mark-recapture data are

171   high (around 0.9 to 0.95; [31]) and we observed only 27 out of 391 individuals at more than one

172   tree, suggesting high site fidelity (although there is still variation within a tree in density and mean

173   size of rivals across days, see Figs. S1 & S2).

174   To estimate direct and social selection, we fit individual body size and the rival mean body

175   size as predictors (model 1). We also included quadratic versions of both direct and social selection

176   to determine whether either form of selection was non-linear (terms were mean centred and scaled

177   to unit variance, then squared, then halved). We included sex as a fixed effect, and the interactions

178   between sex and both focal and rival body size for both linear and quadratic terms to test whether

179   males and females experienced different selection, although we removed these interactions to

180   calculate linear and quadratic selection gradients. Males were set as the default sex and so the

181   interaction was modelled as the difference between females and males. We evaluated the "clarity"

182   (replacing the word "significant" with "clarity" avoids implying that finding a lack of a difference

183   from zero is not important and emphasises that effects not different from zero can still be positive or

184   negative, but not "clearly" so; see [44]) of the effect of all fixed effects using Wald χ^2 tests with type

185   III sum of squares using the *Anova* function within the R package "cars" [45]. The degrees of freedom

186   were 1 for all tests unless stated otherwise.

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

188   models. We used the same starting model as above, excluding quadratic terms as they had no clear

189   effect (see Results). For model 2, we included an interaction between focal body size and rival mean

190   body size to determine if smaller individuals experienced weaker social selection than larger

191   individuals. Such interactive effects can be important in determining how social interactions

192   contribute to evolution [46]. We also included the three-way interaction between sex, focal body

193   size, and rival mean body size, to see if males and females differed in the focal-rival relationship. As

194   males of only smaller sizes (typically under 40mm, see [32]) may engage in "sneaky" copulations, we

195   also fitted a model (model 3) where sex was a three-level categorical variable, either "female",

196   "male over 40mm", or "male 40mm or under", including the interactions between this new variable

197   and both focal and rival mean body size. We then fitted two models to test whether demographic

198   parameters influenced social selection. Model 4 included weevil density (number of weevils

199   observed on the tree on that day; median = 16, 25% quantile = 10, 75% quantile = 25) as a fixed

200   effect and its interactions with both focal and rival mean body size, including the three-way

201   interactions between density, sex, and either focal or rival mean body size. Model 5 was equivalent

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

203   male; median = 0.64, 25% quantile = 0.60, 75% quantile = 0.71) instead of density. In models 4 and 5

204   the key terms are the interactions between density/sex-ratio and the rival mean body size, as these

205   terms indicate whether the impact of rival body size on focal individual fitness (i.e., the strength of

206   social selection) increases or decreases with density/sex-ratio (while the interaction between this

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

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

209   correlation between the body size of a focal individual and the rival mean body size, where the

210   variables had been mean centred and divided by their standard deviation [16]. Note that small group

211   sizes can lead to negative phenotypic assortment by chance [16], but our mean group size was 21

212   which is above the threshold where we expect negative assortment to occur by chance. Following

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

214   phenotypic assortment was density dependent (as has been found before, see [21], although note

215   caveats above about negative assortment "appearing" at low group sizes). We stress that we did this

216   analysis after viewing our initial results and so should be interpreted appropriately. To do this we

217   fitted a linear model with the rival mean body size as the response variable, the body size of a focal

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

219   interactions between these variables as fixed effects. Random effect structure was the same as for

220   the selection models, including the temporal autocorrelation term. The response variable and all

221   continuous predictor variables were mean centred and divided by their own standard deviation. The

222   key term here is the interaction between density and the body size of the focal individual, as this

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223   indicates whether the relationship between the focal individual and the rival mean body size

224   changes with density (while the interaction between this term and sex indicates whether this effect

225   differs between the sexes or not).

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Results

228   Key model results are summarised in Table 1, while full results from each model are reported in the

229   supplementary materials (Tables S1-5). There was no linear or quadratic social selection in either sex

230   when not taking into account interactions with body size, density, or sex ratio. We re-fitted a model

231   without interactions between selection gradients and sex to estimate the direct (note not

232   "directional") linear and quadratic selection gradients as: $\beta_D = 0.277 \pm 0.181$, $\gamma_D = -0.005 \pm 0.254$ and

233   the social linear and quadratic selection gradients as: $\beta_S = -0.085$, $\gamma_S = -0.128$ (standard errors for

234   social selection gradients could not be calculated).

235   The strength of social selection did not depend on the size of the focal individual for either

236   sex, and it was not different among size classes of male. Direct selection also did not differ between

237   large males and small males. When controlling for density, social selection was clearly negative for

238   both sexes, and became stronger at higher densities (Figure 1). Direct selection was clearly positive

239   for both sexes and stronger for females in model 4, but not dependent on density for either sex. Sex-

240   ratio did not influence social selection or direct selection in either sex, while females had higher

241   mating success at more male-biased sex ratios. Mating success tended to decline linearly throughout

242   the day, with no quadratic effect. In all models there was essentially no variance among weevils

243   beyond the temporal autocorrelation term which indicated there were positive correlations

244   between measurements on the same individual on close dates (Fig. S3). There was some variance

245   among trees and among dates.

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

247   406, p = 0.182) and males ($r_{males} = 0.053$, t = 1.521, df = 824, p = 0.129). Our subsequent test of

248   whether phenotypic assortment was density dependent indicated that it was not for either sex (focal

249   body size = -0.015, se = 0.036, χ^2 = 0.173, p = 0.677; focal body size and density interaction = -0.007,

250   se = 0.032, χ^2 = 0.042, p = 0.838; sex interaction = -0.009, se = 0.032, χ^2 = 0.087, p = 0.768; Figure 2).

251   As phenotypic assortment was never clearly different from zero social selection does not ever alter

252   the total selection differential, which is the phenotypic variance in body length (149.222) multiplied

253   by the direct selection gradient (above), giving 41.358.

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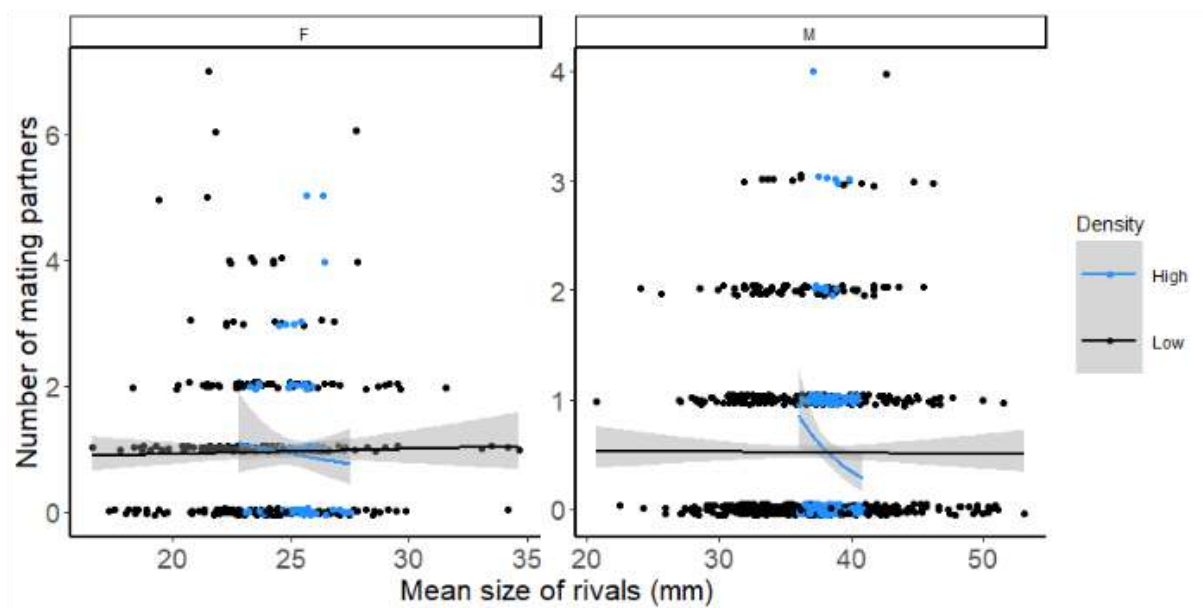
255

256   **Figure 1.** There was negative social selection when controlling for density, and the

257   strength of social selection tended to become more negative at high densities (more than

258   40 weevils per tree, light blue) compared to low densities (40 or fewer weevils per tree,

259   black). This was true for both females (left panel) and males (right panel). Note that we

260   analysed density as a continuous variable, but we have used a categorical representation

261   when plotting for ease of viewing. The grey areas around the trend lines indicate the 95%

262   confidence intervals.

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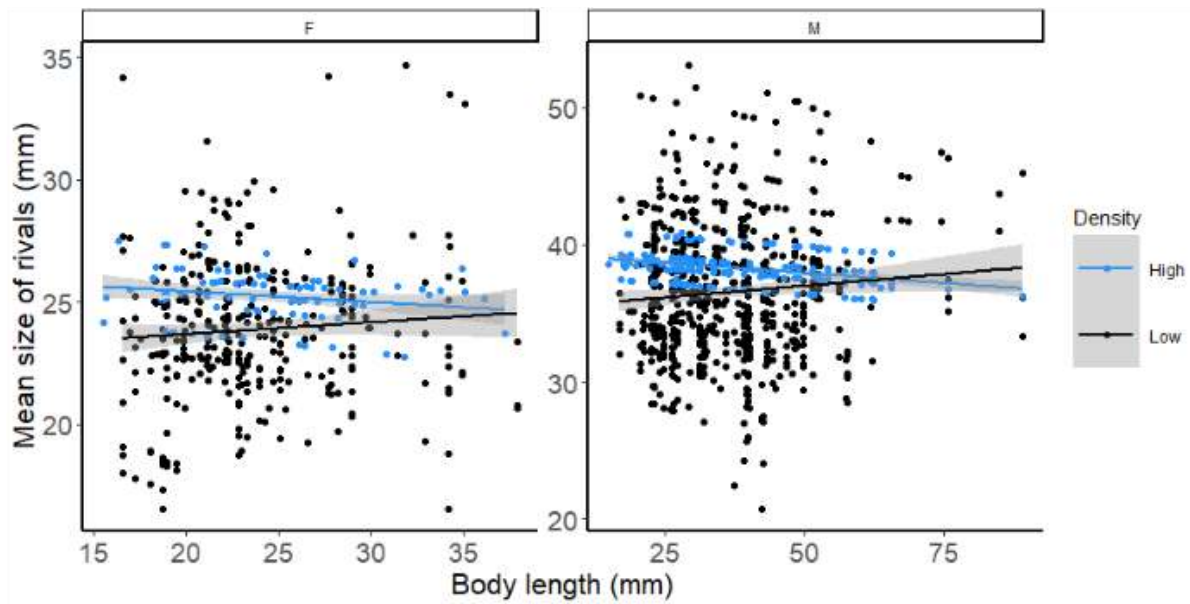
Figure 2. Phenotypic assortment was not different from zero at any density. The graph shows the predicted phenotypic assortments at high densities (more than 40 weevils per tree, light blue) compared to low densities (40 or fewer weevils per tree, black), but note that we analysed density as a continuous variable; we have used a categorical representation when plotting for ease of viewing. The grey areas around the trend lines indicate the 95% confidence intervals.

Discussion

We estimated the strength of social selection across a range of contexts for both male and female giraffe weevils. In contrast to our predictions, we found that social selection was typically absent, although negative social selection was apparent when controlling for density, and social selection increased in strength at high densities, a result in line with our predictions. An increase in the strength of negative social selection as densities increase is consistent with the idea that weevils are engaging in higher competition for access to mates at high densities. However, as phenotypic assortment was always close to zero, the social selection we observed will make limited

280   contributions to overall selection. Therefore, it seems that direct selection will govern the evolution

281   of body and weapon size in giraffe weevils.

282   Our results are consistent with several previous studies exploring how traits like body size

283   can benefit focal individuals while being costly when expressed in interacting individuals. Formica *et*

284   *al.* [21] found positive direct selection and negative social selection for body size (when using mating

285   success as a proxy for fitness, but this is not true when using survival) in fungus beetles (*Bolitotherus*

286   *cornutus*), matching our result when we accounted for variation in density. Similarly, Santostefano *et*

287   *al.* [20] found positive direct selection and negative social selection for body size in male chipmunks

288   (*Tamias striatus*) in the summer (but never for females). In an equivalent result using contextual

289   analysis, jewelweed (*Impatiens capensis*) show positive within-group selection and negative among-

290   group selection for size [47]. Meanwhile, several studies have used a "mixed" method, which should

291   not differ substantially from a social selection approach if groups are large enough (see [9]). These

292   studies have found positive direct and negative social selection for size in the ant *Pristomyrmex*

293   *pungens* [48] and sea rocket (*Cakile edentula*) at low densities [23]. Other studies however find

294   positive direct selection and either positive or variable social selection for size (black-throated blue

295   warblers, *Setophaga caerulescens*, [49]; *Silene tatarica* [50], note latter study used the "mixed"

296   method), or, using contextual analysis, find within- and among- group selection to be aligned (for

297   growth rate in juvenile North American red squirrels, *Tamiasciurus hudsonicus*, [22]; for body mass

298   in fledgling great tits, *P. major*, [51]). Therefore, while opposing direct and social selection for body

299   size may be more common than any other situation, consistent with competition for limited

300   resources (such as food or members of the limiting sex, [52]) where larger individuals gain the most

301   and therefore cause their rivals to suffer relative losses, it is by no means the rule. Given we have

302   clear theoretical reasons to expect social selection (and social interactions more broadly) to alter the

303   speed and direction of evolutionary change, we need to gather more estimates of direct and social

304   selection so that we can identify general rules for when social interactions do fundamentally alter

305   evolution.

306   Interestingly, we found clear density dependent social selection for both males and females,

307   and so females experience reduced mating success at high densities when there are large females on

308   the same tree. This finding challenges the implicit assumption that females do not compete for

309   mating partners. The mechanism for this social selection in females remains to be explored,

310   although there is evidence larger males prefer to mate with larger females [31], which might lead to

311   fewer matings for smaller females. Another possibility is that at high densities males are spending

312   more of their time fighting other males, leaving less time to copulate with females, resulting in

313   choosier males to the detriment of small females sharing trees with large females.

314   Several contextual factors we had predicted would influence social selection did not. Sex-

315   ratio had no effect on social selection, which surprised us given we assumed social selection

316   represents competition for mates, which should be stronger for the sex which is more common. Sex

317   ratio varied from 0-1.0 so we do not think a lack of variation in our dataset prevented us from

318   finding a pattern. Possibly, many males or females on a tree on any given day are not competing for

319   mates, making our measure of sex-ratio uninformative. We also found a focal individual's body size

320   did not influence the impact of rivals on fitness. We had expected smaller males to be less severely

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

322   strategy to "sneaking" copulations with females guarded by large males [32]. However, given we

323   only detected any negative effect of larger rivals at high densities, we might require a dataset with

324   more samples of trees with a high density of giraffe weevils to test this prediction. While

325   correlational direct selection has received some attention [53], we possess very limited information

326   about which traits of individuals influence the strength of social selection (but see [22]). Beyond

327   body size, certain behavioural traits, such as how responsive an individual's behaviour is to the traits

328   of others, or how susceptible its phenotype is to being modified by the actions of others, might

329   modulate how strongly an individual is influenced by rivals and could alter evolutionary trajectories

330   [46], but this remains to be tested.

331   We found phenotypic assortment was never clearly different from zero for both sexes. Due

332   to this near-zero assortment, social selection on giraffe weevil body size will not contribute to total

333   selection. Note that, although taking a contextual analysis approach is equivalent to the social

334   selection approach we used, in contextual analysis there is no requirement for phenotypic

335   assortment to allow among-group selection to contribute to the response to selection (see: [8]).

336   Limited phenotypic assortment is consistent with individuals mostly randomly aggregating on trees

337   without respect to the body size of other individuals on the tree. In giraffe weevils, assortment by

338   body size has been observed in mating pairs [31], suggesting there is some capacity for partner

339   choice once a weevil has arrived at an aggregation, but our current results show limited assortment

340   occurs in the process of forming aggregations on trees. There may be environmental factors, such as

341   the distance between suitable trees, that prevent strong assortment from occurring. If a giraffe

342   weevil can only access a single or small number of suitable trees, and body sizes are initially evenly

343   spread across the landscape, then no strong assortment could occur regardless of whether

344   individuals have preferences for certain sized rivals or not.

345   Estimates of phenotypic assortment are accumulating in the literature and are often

346   positive. Positive assortment can arise through environment by phenotype associations, through

347   active selection for like individuals, or from individual's confirming to match their social partners

348   [18]. If positive phenotypic assortment is indeed common, then social selection will often contribute

349   to total selection, and if social selection is typically in the opposite direction to direct selection [9],

350   will therefore tend to reduce overall selection. However, there are only a few estimates of the

351   interactant covariance, the specific parameter used in social selection models [16]. Formica *et al.*

352   [21] estimated the interactant covariance for body size in aggregations of forked fungus beetles (*B.*

353   *cornutus*) and found a negative covariance. This would cause negative social selection for body size

354   to increase the magnitude of the overall positive selection for body size. In contrast, while

355   Santostefano *et al.* [20] found a negative interactant covariance among female chipmunks (*T.*

356   *striatus*) for body mass, they found no covariance among males for body mass. Since social selection

357   was only present in males, social selection would not contribute to overall selection in either sex. In

358   summary, while we may expect social selection to weaken overall selection, evidence from systems

359   where both social selection and the interactant covariance have been estimated suggests that it

360   often does not contribute at all. Further, a lack of estimates of how phenotypic assortment changes

361   with key demographic parameters such as density prevents us from understanding whether there

362   are some contexts social selection does contribute to total selection. Each of direct selection, social

363   selection, the phenotypic variance, and phenotypic assortment can vary with conditions. Therefore,

364   evolution may vary substantially in both direction and speed in different environments, and further

365   could change differently across environments for traits that show a higher degree of social selection,

366   or a greater tendency towards positive assortment, and so on. While we currently lack the data to

367   assess this possibility, it represents an exciting future line of work.

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

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

370   densities. However, social selection was not clearly different from zero when not controlling for

371   variation in density and did not vary with sex-ratio or the size of the focal individual. Further,

372   phenotypic assortment was never different from zero, indicating that social selection will have a

373   limited contribution to overall selection even at high densities. Therefore, despite its predicted

374   importance, social selection will only have a minor impact on the evolutionary change of body size in

375   New Zealand giraffe weevils.

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Data accessibility

378   The data used here have previously been made publicly available, see: [33]. We have chosen to

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

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

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

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 and edited the manuscript. 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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Tables

537

538 **Table 1**. Key model results from models 1-5. Given are the effect estimate, associated standard

539 error, the Chi-squared value (with a note if the degrees of freedom were other than 1) and the p-

540 value. For the difference between large males and both females and small males a single Chi-

541 squared statistic and p-value are given for the clarity of the three-level categorical variable ("sex

542 type factor") we used to test this effect. We also note which model the term stems from, see Data

543 analysis, and the variance attributed to each random effect in model 1. Full results from each model

544 are given in the supplementary materials (Tables S1-5).

545

	Estimate	Standard Error	Chi-squared	P value	Model
Intercept	-0.287	0.211	1.857	0.173	1
Sex (Female contrast)	0.470	0.167	7.888	0.005	1
Direct selection - linear	0.239	0.205	1.352	0.245	1
Social selection - linear	0.105	0.277	0.144	0.704	1
Direct selection - quadratic	-0.301	0.353	0.724	0.395	1
Social selection - quadratic	-0.126	0.260	0.233	0.630	1
Time of day - linear	-0.105	0.044	5.719	0.017	1
Time of day - quadratic	-0.005	0.086	0.003	0.953	1
Sex:Direct selection - linear	-0.026	0.207	0.016	0.900	1
Sex:Social selection - linear	0.029	0.281	0.011	0.917	1
Sex:Direct selection - quadratic	-0.219	0.353	0.387	0.534	1
Sex:Social selection - quadratic	0.266	0.255	1.083	0.298	1
Focal body length:Social selection	-0.089	0.181	0.242	0.623	2
Sex:Focal body length:Social selection	0.010	0.183	0.003	0.956	2
Female:Direct selection	0.253	0.122	*sex type factor*	(df = 2)	3
Small male:Direct selection	-0.083	0.101	4.337	0.114	3
Female:Social selection	0.116	0.125	*sex type factor*	(df = 2)	3
Small male:Social selection	-0.143	0.112	1.663	0.435	3
Density:Direct selection	0.017	0.078	0.050	0.822	4
Density:Social selection	-0.441	0.161	7.526	0.006	4
Sex:Density:Direct selection	-0.063	0.078	0.659	0.417	4

Sex:Density:Social selection	-0.150	0.171	0.773	0.379	4
Sex ratio:Direct selection	0.033	0.089	0.139	0.709	5
Sex ratio:Social selection	-0.059	0.081	0.540	0.462	5
Sex:Sex ratio:Direct selection	-0.042	0.089	0.221	0.639	5
Sex:Sex ratio:Social selection	-0.062	0.081	0.587	0.443	5

	Random effect	Variance	
Weevil	0.000	1
Tree	0.101	1
Date	0.181	1

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