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Population biology of a selfish sex ratio distorting element in a
booklouse (Psocodea: Liposcelis)

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August 2019

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Citation for this paper:

Hodson, C.N. & Perlman, S.J. (2019). Population biology of a selfish sex ratio distorting element in a booklouse (Psocodea: Liposcelis). *Journal of Evolutionary Biology*, 32(8), 825-832. <https://doi.org/10.1111/jeb.13484>

1 Accepted Manuscript:
2 Hodson CN, Perlman SJ. 2019. Population biology of a selfish sex ratio distorting element in
3 a booklouse (Psocodea: *Liposcelis*). *Journal of Evolutionary Biology*. 32, 825-832.
4

5 Population biology of a selfish sex ratio distorting element in a booklouse (Psocodea:
6 *Liposcelis*)

7

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15

16 **Abstract**

17 Arthropods harbour a variety of selfish genetic elements that manipulate reproduction
18 to be preferentially transmitted to future generations. A major ongoing question is to
19 understand how these elements persist in nature. In this study, we examine the population
20 dynamics of an unusual selfish sex ratio distorter in a recently discovered species of
21 booklouse, *Liposcelis* sp. (Psocodea: Liposcelididae) to gain a better understanding of some
22 of the factors that may affect the persistence of this element. Females that carry the selfish
23 genetic element only ever produce daughters, although they are obligately sexual. These
24 females also only transmit the maternal half of their genome. We performed a replicated
25 population cage experiment, varying the initial frequency of females that harbour the selfish
26 element, and following female frequencies for 20 months. The selfish genetic element
27 persisted in all cages, often reaching very high (and thus severely female-biased) frequencies.
28 Surprisingly, we also found that females that carry the selfish genetic element had much
29 lower fitness than their nondistorter counterparts, with lower lifetime fecundity, slower
30 development, and a shorter egg laying period. We suggest that differential fitness plays a role
31 in the maintenance of the selfish genetic element in this species. We believe that the genetic
32 system in this species, paternal genome elimination, which allows maternal control of
33 offspring sex ratio, may also be important in the persistence of the selfish genetic element,
34 highlighting the need to consider species with diverse ecologies and genetic systems when
35 investigating the effects of sex ratio manipulators on host populations.

36

37

38 **Keywords:** feminization, selfish genetic element, genetic conflict, *Wolbachia*, population
39 dynamics, paternal genome elimination

40

41 **Introduction**

42

43 There is growing evidence that selfish genetic elements (genes that subvert normal
44 inheritance rules to be transmitted to more offspring than expected) and genomic conflict in
45 general have an enormous impact on the evolution of species (Burt & Trivers, 2006; Rice,
46 2012). For instance, genomic conflict is implicated in the evolution of sex determination
47 (Bachtrog et al., 2014; Hurst & Werren, 2001) and meiosis (Fishman & Willis, 2005; Malik
48 & Bayes, 2006). Despite this, there are relatively few systems for which we have a clear
49 understanding of how selfish genetic elements persist in the wild. Partly, this is due to the
50 fact that genomic conflict is hard to observe in nature, since it does not always cause a visible
51 change in populations it occurs in. This is not the case, however, when it involves conflict
52 over the sex ratio. There are two main types of selfish genetic elements that manipulate the
53 sex ratio of their host in animals: cytoplasmically-inherited bacteria and selfish genetic
54 elements on sex chromosomes. Because male hosts are dead ends for maternally transmitted
55 microbes, inherited endosymbionts have evolved a number of ways to increase the fitness of
56 female hosts at the expense of males, including male killing, parthenogenesis induction, and
57 feminization of genetic males (Engelstädter & Hurst, 2009). In the case of selfish genetic
58 elements on sex chromosomes, they generally cause the destruction of gametes that contain
59 the alternate sex chromosome in the heterogametic sex, thereby manipulating the sex ratio of
60 their host (Jaenike, 2001).

61

62 *Liposcelis sp.* (Psocodea: Liposcelididae) is a recently discovered booklouse species
63 that harbours an intriguing selfish genetic element (Perlman et al., 2015; Hamilton et al.,
64 2018). This species was recently discovered in the Chiricahua Mountains, Arizona, on *Yucca*
65 plants. Laboratory populations set up from the original collections are extremely female

66 biased. This is because some females in the population, which we refer to as distorters, carry
67 a maternally transmitted selfish genetic element which causes them to produce exclusively
68 female progeny who also carry the element (while other females in the population, referred to
69 as nondistorters, produce offspring of both sexes). Distorter females are still obligately
70 sexual, however (i.e. virgin females do not produce offspring) (Perlman et al., 2015), mating
71 with the sons of nondistorters. There is no evidence of microbial infection causing the
72 distortion (Perlman et al., 2015).

73

74 A recent study by Hamilton et al. (2018) has shed light on the mechanism of sex ratio
75 distortion in this system. Distorter females exhibit drive of the entire maternal genome. This
76 means that distorter females exclusively transmit genes passed on to them from their mother
77 and that the maternal half of the distorter female genome is effectively genetically isolated
78 from the nondistorter genome. Distorter females also possess several genes that are absent
79 from nondistorters. Interestingly, some of these genes have been horizontally transferred
80 from *Wolbachia* to the distorter female genome. Since *Wolbachia* is a maternally-inherited
81 bacterium that often manipulates reproduction in its host (Werren et al., 2008), it is possible
82 that the horizontally transmitted DNA is responsible for the fascinating reproductive
83 dynamics found in distorter females (especially since this segment is absent from
84 nondistorters) (Hamilton et al., 2018).

85

86 Sex in *Liposcelis* and its relatives is determined by a genetic system known as
87 paternal genome elimination (Hodson et al., 2017; de la Filia et al., 2018), a mode of sex
88 determination that has evolved independently in several groups of terrestrial microarthropods
89 (Gardner & Ross, 2014). In *Liposcelis* sp. (and several other species with paternal genome
90 elimination), sex is associated with modification of the paternally inherited chromosomes in

91 males (Hodson et al., 2017). These chromosomes are heterochromatized (epigenetically
92 silenced) and are therefore not expressed in males. Males also only transmit maternally
93 inherited chromosomes to offspring, similar to haplodiploid sex determination. This means
94 that both distorter females and males have asymmetric chromosome transmission dynamics,
95 with both only transmitting maternally inherited chromosomes to offspring, and only
96 nondistorter females exhibiting Mendelian transmission dynamics. The chromosome
97 transmission dynamics in this system are remarkable, but ecologically, this system is similar
98 to those in which inherited microbes cause feminization of their host. The persistence of these
99 systems is somewhat of a mystery, since feminized females theoretically have a reproductive
100 advantage over normal females (since like parthenogenetic females they avoid the cost of
101 producing males) and so should outcompete their normal counterparts in time (Hatcher &
102 Dunn, 1995). This would lead to a population collapse due to the absence of males.

103

104 In natural systems, however, there are several examples in which feminizers exist and
105 seem to be able to persist over time (Hatcher, 2000). A number of factors may enable
106 individuals that harbour feminizers to coexist with their normal counterparts, including
107 fitness costs to carrying the feminizer (which would equalize to some degree the advantage
108 individuals carrying feminizers have due to not producing males) (Kelly et al., 2001),
109 metapopulation dynamics (i.e. local populations are unstable with frequent population
110 collapse followed by migration of individuals carrying the feminizer to new populations)
111 (Hatcher et al., 1999; Rigaud et al., 1992), and mating dynamics that favour females that do
112 not carry the feminizer (e.g. mate choice against individuals carrying the feminizer) (Moreau
113 et al., 2001).

114

115 Very little is known about the ecology of *Liposcelis* sp. in nature, or about the
116 frequency of distorters, since this species has only been collected once from the wild
117 (Perlman et al., 2015). However, it has been estimated by comparing the distorter female
118 restricted part of the genome to the nondistorter part that the distorter phenotype originated in
119 populations between 450,000-820,000 years ago (Hamilton et al., 2018). Distorter females
120 have a shorter longevity than nondistorter females in the lab, suggesting that there is a cost to
121 carrying the distorting element (Perlman et al., 2015), but other fitness costs to carrying the
122 distorting element are unknown. Another factor that may be important in this system is the
123 sex ratio produced by nondistorter females since the reproductive advantage that feminizers
124 have is based on the assumption that other females in the population produce an equal sex
125 ratio. In cases where this is untrue (such as in a species with paternal genome elimination
126 where there is often maternal control of sex ratio) (Hodson et al., 2017; Nagelkerke &
127 Sabelis, 1998; Ross et al., 2010; Varndell & Godfray, 1996), females may be able to alleviate
128 the cost of producing males by altering the sex ratio of their offspring. Additionally, we
129 know very little about the frequency of the sex ratio manipulator, either in laboratory or wild
130 populations.

131

132 In order to better understand how distorter and nondistorter females may coexist in
133 nature, we examined the cost of carrying the sex ratio distorting element by assessing
134 differences in lifetime fecundity and development time between nondistorter and distorter
135 females. We also looked at the frequency of distorter females in experimental laboratory
136 population cages, and in wild populations. We found that the distorter phenotype likely
137 persists in part due to fitness costs of carrying the element, as distorter females have a lower
138 lifetime fecundity, longer development time, and shorter reproductive period than
139 nondistorter females. Additionally, over their life, nondistorter females produce a female

140 biased sex ratio. Interestingly, in spite of this, we found that distorter females can reach high
141 frequencies in laboratory populations, and high distorter female frequency does not seem to
142 cause population collapse. Along with the fitness costs to carrying the distorting element
143 identified in this study, it is probable that the genetic system in this species and male mating
144 dynamics may also have an effect on the persistence of the distorting element in these
145 populations.

146

147 **Methods**

148 *Colony Information*

149 *Liposcelis* sp. used in experiments were collected from the Chiricahua Mountains,
150 Arizona in 2010. Cultures are maintained at 27°C and 75% RH. Distorter female and
151 nondistorter female cultures are maintained separately in 125ml glass jars containing a 1:10
152 (by weight) mixture of Rice Krispies (Kellogg's) and organic cracked wheat (Bob's Red
153 Mill). Distorter and nondistorter female types were initially identified by their reproductive
154 biology (i.e. distorter females only produce female offspring) (and later via molecular means)
155 (Perlman et al., 2015; Hamilton et al., 2018). Since distorter females need to mate with males
156 in order to reproduce we added males from the nondistorter female colonies into the distorter
157 female colonies weekly.

158

159 *Costs to carrying the sex ratio manipulator*

160 To better understand the fitness costs associated with the sex ratio manipulator, we
161 conducted an experiment comparing fecundity of distorter and nondistorter females. We
162 produced separate jars containing approximately equal numbers of age matched individuals
163 for each female type. Immediately after these individuals completed development (i.e. before
164 the female's cuticle reached full pigmentation), we isolated single females in a 35mm² petri

165 dish containing 0.5g of food. We placed two males into each of these containers and made 20
166 containers for each female type in total. Each week, we would transfer the female (and males)
167 into a new container with the same amount of food and count the number of eggs she had laid
168 in the past week. We continued to do this until the female died. After counting the eggs, we
169 left the offspring to develop and recorded the number and sex of offspring (housing offspring
170 laid by each female every three weeks together). This allowed us to measure the number of
171 eggs each female laid each week, the total lifetime fecundity of each female, and the sex ratio
172 and number of offspring that reached adulthood for each female. We analysed all data in
173 Rstudio v3.1.0. (R Core Team, 2014). We compared the total amount of offspring produced
174 by nondistorter and distorter females (via egg counts) using a generalized linear model with a
175 quasipoisson distribution, and analysed the amount of eggs laid over time with a generalized
176 linear mixed model (Bates et al., 2015), including individual ID as a random effect and the
177 week eggs were laid as a quadratic term. We also compared adult longevity of distorter and
178 nondistorter females (measured from the start of the experiment to when each female died)
179 and female egg laying period (measured from the first to last time each female produced
180 eggs) using Cox proportional hazards survival analyses (Therneau & Granbsch, 2000).

181

182 In conjunction with the analysis of longevity in nondistorter and distorter females
183 published in Perlman et al. (2015), we also measured development time in the same
184 experiment to determine if distorter and nondistorter females differ in this trait. For a detailed
185 description of methods see Perlman et al. (2015). Briefly, we placed 10 eggs laid by either
186 nondistorter or distorter females in a petri dish with abundant food. We made 10 of these
187 containers for each female type. We checked them three times a week and recorded when
188 individuals developed into adults (i.e. when females completed their final nymphal molt). We
189 analysed whether there was a difference in development time between nondistorter and

190 distorter females using a Cox proportional hazards survival analyses (Therneau & Granbsch,
191 2000), clustering observations by the container the females were raised in.

192

193 *Distorter female frequency in laboratory and wild populations*

194 We wanted to determine if populations with distorter females reach an equilibrium of
195 the selfish genetic element over time. To do this, we conducted a laboratory experiment
196 where we transferred 300 individuals into glass jars (125ml) containing 20g of food (1:7.5
197 mixture of Rice Krispies to cracked wheat). We started all jars with 100 males and 200
198 females but had two different treatments with different ratios of nondistorter to distorter
199 females (100 nondistorter females and 100 distorter females (1:1) or 175 nondistorter females
200 and 25 distorter females (7:1)).

201

202 We prepared 8 replicates for each treatment. We sampled population jars every 4
203 months for 20 months. We also froze four jars of each treatment over the first two collection
204 times to get an idea of the overall number of individuals in jars and the sex ratio (but only
205 counted the individuals collected at four months and when we terminated the experiment due
206 to time constraints) (Supplementary Table 3). We therefore followed four replicates for each
207 treatment over the entire 20 month period. Sampling consisted of extracting total DNA from
208 40 females using 20ul of PrepMan Ultra (life technologies) to obtain 10ul of DNA. In order
209 to determine whether an individual was a nondistorter or distorter female, we made use of
210 mitochondrial primers that would amplify either nondistorter or distorter female DNA (since,
211 like mitochondria, the selfish genetic element is maternally transmitted so mitochondrial
212 primers can be used to determine the identity of females) (Perlman et al., 2015)
213 (Supplementary Table 1 for primer sequence and thermocycling conditions). We performed
214 PCRs for each individual with both of these primer sets. If we were unable to amplify DNA

215 using either of these primer sets we would run both PCRs again. We compared the frequency
216 of distorter females in the two treatments at the end of the experiment to determine if the
217 frequency of distorter females from different treatments reached the same stable frequency
218 over time.

219

220 We also collected *Liposcelis* sp. from the Chiricahua Mountains, Arizona (where the
221 lines were originally collected) in August, 2014, to determine whether distorters were still
222 present and at what frequency. We collected specimens from nine sites over four days by
223 shaking the branches of Yucca plants onto a sheet and collecting all *Liposcelis* individuals.
224 We grouped specimens by site, sexed individuals, and identified them morphologically to
225 species. We also identified individuals to species (all individuals that appeared to be
226 *Liposcelis* sp. and a few individuals from all other morphotypes) with a 400 bp region of the
227 mitochondrial CO1 gene (using primers L6625 and H7005 [Hafner et al., 1994]) and an
228 approximately 900bp region of the rRNA region 18S (using primers 18Sai and 18Sbi
229 [Desalle et al., 1992]) (Supplementary Table 2).

230

231 **Results**

232 *1. Distorter females have reduced fitness*

233 Distorter females laid fewer eggs than nondistorter females over their lifetime
234 (generalized linear model: $t_{38}=4.959$, $p<0.0001$) (Fig. 1A) with distorter females laying on
235 average 49 eggs and nondistorter females laying 78 eggs. Additionally, nondistorter females
236 and distorter females have different egg laying patterns over time, with a significant
237 interaction between the female type and the number of eggs females lay in a week
238 (generalized linear mixed model: $z_{677}=9.107$, $p<0.0001$) (Fig. 1B). One distorter female never

239 produced eggs and was therefore not included in the analysis of fecundity (but was included
240 in the adult longevity analysis).

241

242 The differences in the number of eggs females laid translated into a difference in the
243 number of adults produced by each female type, with distorter females producing fewer adult
244 offspring than nondistorter females (generalized linear model: $z_{38}=14.95$, $p<0.0001$) (Fig.
245 1C). Nondistorter females produced offspring with a skewed sex ratio, with 78.5% ($\pm 11.7\%$)
246 of the offspring being female. As expected, distorter females never produced sons.
247 Nondistorter females produced a more female biased sex ratio over time (Supplementary Fig.
248 1). For example, at the beginning of their reproductive period (i.e. weeks 1-3) they produced
249 on average 64.1% females, while later in their reproductive period (weeks 15-23) they
250 produced an average of 85.7% females.

251

252 Similar to Perlman et al. (2015), we also found that distorter females did not live as
253 long as nondistorter females ($z_{39}=2.076$, $p=0.038$) (Fig. 3A) (although we measured adult
254 longevity rather than their total lifespan), and additionally had a shorter reproductive period
255 compared to nondistorter females ($z_{39}=3.438$, $p=0.0006$) (Fig 3B) (measured as the time from
256 when they produced their first egg to their last egg). Distorter female lived an average of 111
257 days (as adults) with an average reproductive period of 97 days while nondistorter females
258 lived an average of 130 days with an average reproductive period of 122 days. Distorter
259 females also take longer to develop than nondistorter females (Fig. 3) (Cox proportional
260 hazard, $z_{86}= 3.186$, $p=0.0014$), with distorter females taking on average 50.2 ± 2.3 days to
261 develop while nondistorter females take 41.1 ± 1.5 days to develop.

262

263 *2. Distorter females reach high frequencies in population cages*

264 The frequency of distorter females (compared to the total number of females)
265 increased in all eight population cages at the end of the 20 months of the experiment, and in
266 two of the populations distorters reached frequencies greater than 80% (Fig. 4). None of the
267 cages went extinct, nor were distorter females lost in any of them. Although the proportion of
268 distorter females relative to nondistorter females increased for all populations, the
269 populations that were started with fewer distorter females still had significantly fewer
270 distorter females than those started with an equal amount of distorter and nondistorter females
271 at the end of 20 months ($t = 2.5781$, $p = 0.04232$). The frequency of distorter females in
272 populations that were started with fewer distorter females was not different than the initial
273 frequency of distorter females in the populations with an equal amount of distorter and
274 nondistorter females ($t = 1.1596$, $p = 0.3301$). This indicates that we did not find a stable
275 frequency of the selfish genetic element in our laboratory population cages. The four cages in
276 which we counted all booklice at the end of the experiment were all female-biased, but with a
277 wide range of sex ratios, ranging from 7% to 40% male, and a total of 2692-5345 individual
278 booklice in each cage (Table S3).

279

280 *3. Distorter females are microsympatric with nondistorter females in the wild*

281 We collected a total of 15 *Liposcelis* sp. from the same area of the Chiricahua
282 Mountains where we collected the initial population (Table 1); there were 10, 5, and 0
283 nondistorter females, distorter females, and males in this sample, respectively. These
284 collections were made over the course of 4 days. In the site where the majority of *Liposcelis*
285 sp. specimens were collected (site 8), we found both nondistorter and distorter females.

286

287 **Discussion**

288 In this study, we use fitness and population cage experiments, and field collections, to
289 examine the population biology of an unusual selfish sex-ratio distorter in a booklouse,
290 *Liposcelis* sp., that produces an effect similar to a feminizing agent. Although they are
291 obligately sexual, distorter females produce exclusively daughters and only pass on the
292 maternally inherited half of their genome (Hamilton et al., 2018). Distorters produce similar
293 population effects to those in which feminizers have invaded (specifically that distorter
294 females have a reproductive advantage over other females due to their exclusive production
295 of female offspring). However, the known arthropod systems with feminizers exhibit either
296 an XO sex determination system (i.e. in the leafhopper *Zyginidia pullula*) (Negri et al., 2006),
297 or a ZW sex determination system (i.e. in the isopod *Armadillium vulgare* and *Eurema*
298 butterflies) (Hiroki et al., 2002; Rigaud et al., 1992). *Liposcelis* sp. exhibits paternal genome
299 elimination, with different chromosome transmission dynamics from these other systems
300 (Hodson et al., 2017; Hamilton et al., 2018), which may alter the rules governing how its sex
301 ratio distorter persists.

302

303 Fitness costs are one way in which feminizers may be able to persist in nature. For
304 instance, in the amphipod *Gammarus duebeni*, females that carry the feminizing
305 microsporidian *Nosema granulosis* have a slightly lower fecundity than uninfected females
306 (Kelly et al., 2001). The selfish genetic element in *Liposcelis* sp. is already known to reduce
307 the longevity of individuals that carry it (Perlman et al., 2015). In this study, we show that
308 there are multiple fitness costs to being a distorter females. These females have a lower
309 lifetime fecundity, longer development time, shorter reproductive period, and shorter adult
310 lifespan compared to nondistorter females. It is possible that the lower fecundity we observed
311 for distorter females is in part a consequence of the differences in lifespan between the adult
312 types (since nondistorter females lived an average of ~2.5 weeks longer than distorter

313 females and had a reproductive period ~3.5 weeks longer) . Old distorter females have an
314 unusual mitochondrial structure in some tissues, reminiscent of damaged mitochondria (in
315 contrast to similar-aged nondistorter females). Mitochondria, are maternally transmitted (like
316 the element that causes sex ratio distortion in this system) and also affect longevity (Melvin
317 & Ballard, 2006). Nondistorter and distorter females also have radically different
318 mitochondrial organization and sequence (Perlman et al., 2015). Therefore, differences in
319 longevity (and also potentially fecundity) between distorter and nondistorter females may
320 stem from differences in mitochondrial function, although this idea has not yet been tested.

321

322 Although fitness differences between the two female types in *Liposcelis* sp.
323 populations likely plays a role in their coexistence in the wild, it is probable that there are
324 other factors which are also important in this system. In our population cage experiment, we
325 found the frequency of males in populations was often very low (i.e. sometimes as low as 8%
326 males in the population). This observation suggests male mating dynamics may be important
327 in this system. In *Armadillium vulgare* isopods (another species that carries a feminizer), for
328 instance, males preferentially mate with, and transfer more sperm to, females that are not
329 infected with a feminizing *Wolbachia* (Moreau et al., 2001; Moreau & Rigaud, 2003; Rigaud
330 & Moreau, 2004). Male mate choice has also been suggested to be important in the
331 maintenance of gynogenetic species, asexual lineages that require mating with males of
332 closely related sexual species in order to trigger embryonic development (Mee & Otto, 2010;
333 Schlupp, 2010). *Armadillium vulgare* males can also mate with more females than related
334 species that do not carry the feminizer (Moreau & Rigaud, 2003) (suggesting the feminizer is
335 associated with males with a higher mating capacity). Studies looking at how many females
336 *Liposcelis* sp. males can mate with as well as whether they are able to distinguish between
337 nondistorter and distorter females would be useful to gain a more complete understanding of

338 the factors that contribute to the persistence of the distorter phenotype. In this system, we
339 would expect males to have a strong selection pressure to be able to perceive and avoid
340 mating with distorter females, since these females will not transmit genes from their partner
341 to the next generation (Hamilton et al., 2018).

342

343 Another avenue of research suggested from the results of this study is understanding
344 how the sex ratio produced by nondistorter females affects population dynamics. We found
345 that over their entire reproductive period, *Liposcelis* sp. females produce a female biased
346 offspring sex ratio which seems to become more female biased over time. Similar to
347 haplodiploids, females of species that exhibit paternal genome elimination are often able to
348 control the sex of their offspring (Varndell & Godfray, 1996; Nagelkerke & Sabelis, 1998;
349 Ross et al., 2010) and there is some evidence that female *Liposcelis* sp. may be able adjust
350 the sex ratio of their offspring (Hodson et al., 2017). It may be particularly important in this
351 system if nondistorter females can control their offspring sex ratio, as it may allow the
352 population to persist at varying levels of the selfish genetic element. For instance, we might
353 expect nondistorter females to produce more male offspring when female frequencies are
354 high, since in these conditions males would be expected to have a higher reproductive value
355 than females (i.e. be able to produce more offspring than their sisters). We speculate that sex
356 ratio adjustment by nondistorter females may explain why population cages in which more
357 than 90% of females were distorter females did not result in extinction. In general, classic sex
358 ratio theory does not account very well for the type of polymorphic system found in
359 *Liposcelis* sp., with a sex ratio distorter, nonmendelian inheritance in some members of the
360 population, and parental control over the offspring sex ratio (Fisher, 1930; Bull & Charnov,
361 1988).

362

363 Given that distorter females over their lifetime produced less than half the total
364 surviving offspring that nondistorter females produced (and approximately half the number of
365 females compared to nondistorter females), we were surprised that they were able to invade
366 the population cages (and appear to have persisted for at least 400,000 years [Hamilton et al.,
367 2018]). It is possible that the fitness of distorter females compared to nondistorter females
368 may depend on ecological conditions. For instance, there was a larger difference in fecundity
369 between females late in their life compared to their early reproductive period. However, we
370 do not know how long females live in natural conditions, so differences between the total
371 lifetime fecundity between the two female types may not be as striking in natural conditions
372 where both may have a shorter lifespan. Understanding more about the ecological conditions
373 in wild *Liposcelis* sp. populations, and investigating whether fitness differences between
374 nondistorter and distorter females depend on these factors will go a long way to answering
375 this question.

376

377 *Liposcelis* sp. is an intriguing species. Although it shares some similarities to other
378 systems in which feminizers have been found, the genetic differences between *Liposcelis* sp.
379 and systems with feminizers (i.e. that *Liposcelis* sp. exhibits paternal genome elimination and
380 that distorter females also exhibit maternal chromosome drive) means that further
381 investigation into this system will provide valuable information about how reproductive
382 manipulators affect species' evolution. This will help us to determine how important the
383 genetic system as opposed to other factors (such as ecological factors) are in determining
384 whether and how reproductive manipulators persist.

385

386 **Acknowledgements**

387 We would like to thank members of the Perlman lab for useful discussion on this
388 work, and Ed Mockford for help with collecting *Liposcelis*. This research was supported by a
389 Natural Sciences and Engineering Council of Canada Discovery Grant. We acknowledge
390 support from the Integrated Microbial Biodiversity Program of the Canadian Institute for
391 Advanced Research.

392

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486

487 **Tables**

488 Table 1. Summary of sex and type of *Liposcelis* sp. collected from Chiricahua Mountain field
489 collections in 2014. No male *Liposcelis* sp. were found. These collections were made from 9
490 sites over a period of 4 days.

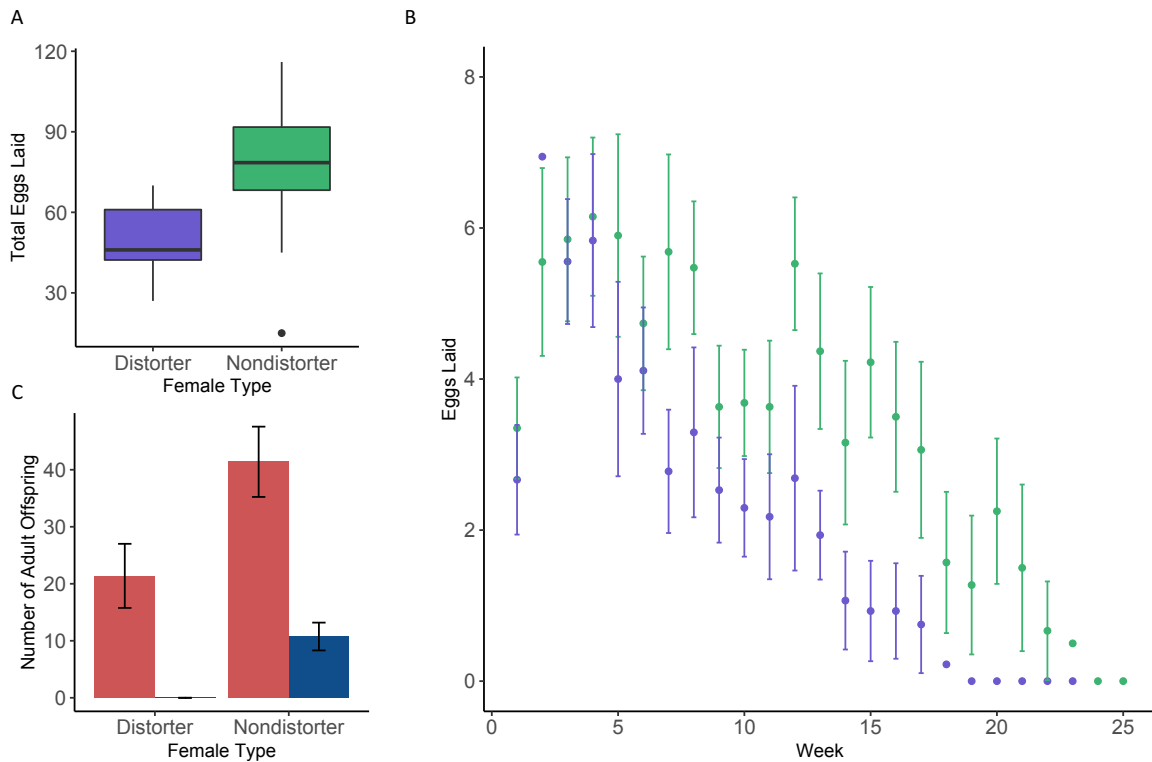
Site	Nondistorter	Distorter
1	0	1
3	1	0
5	1	1
6	1	0
8	7	3
Total	10	5

491

492

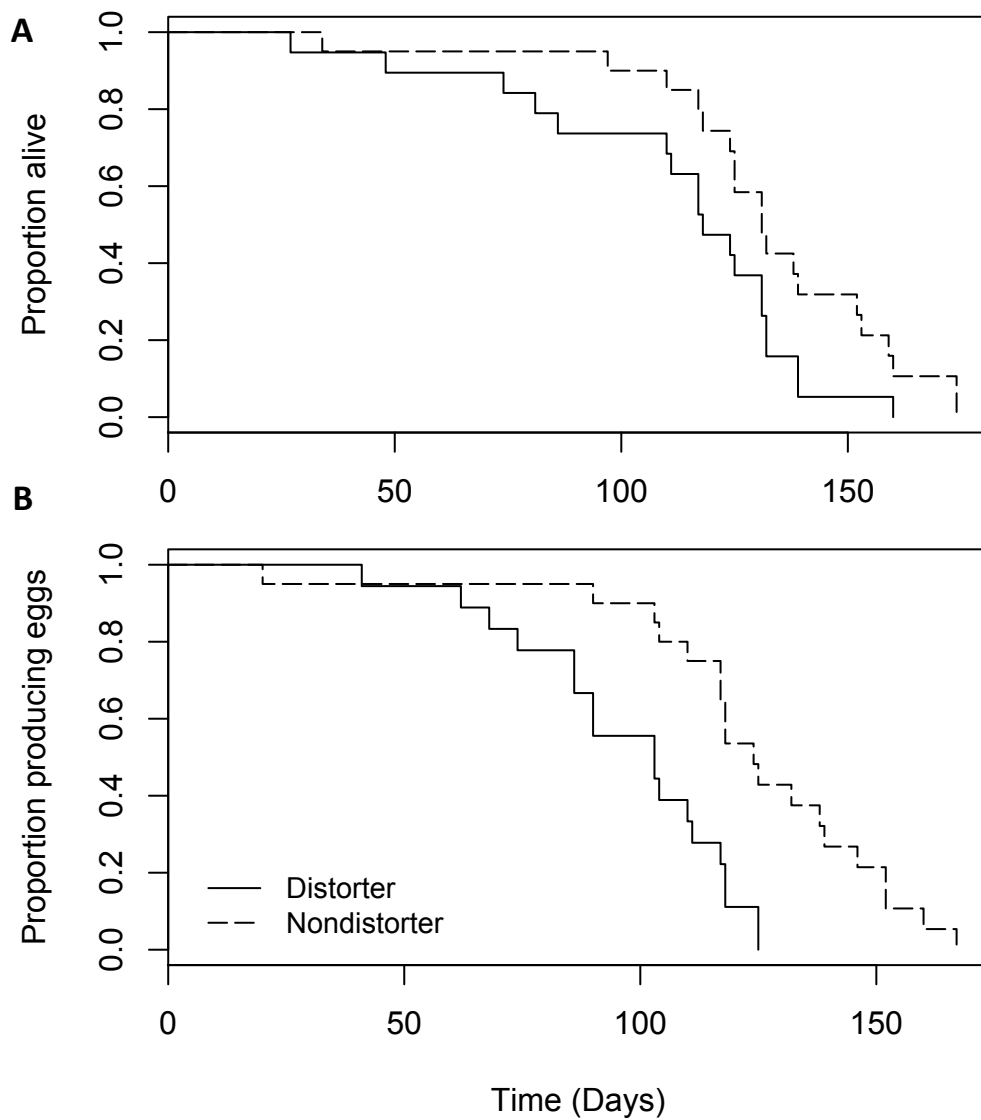
493

494 **Figures**



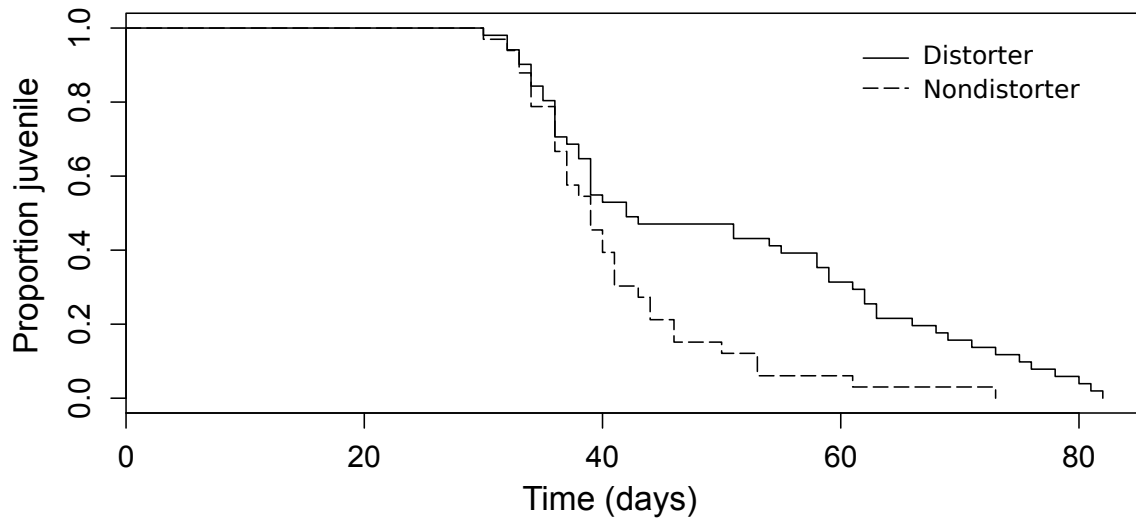
495

496 Fig. 1. Differences in fecundity between distorter females (purple) and nondistorter females
497 (green). A. Distorter females lay fewer eggs than nondistorter females over their life. B.
498 Differences in fecundity between the two female types are greater later in life compared to
499 early in their reproductive period. C. Nondistorter females produce fewer male offspring
500 (blue) than female offspring (red), and distorter female produce fewer adult offspring than
501 nondistorter females. Error bars indicate the 95% confidence interval for each measurement.



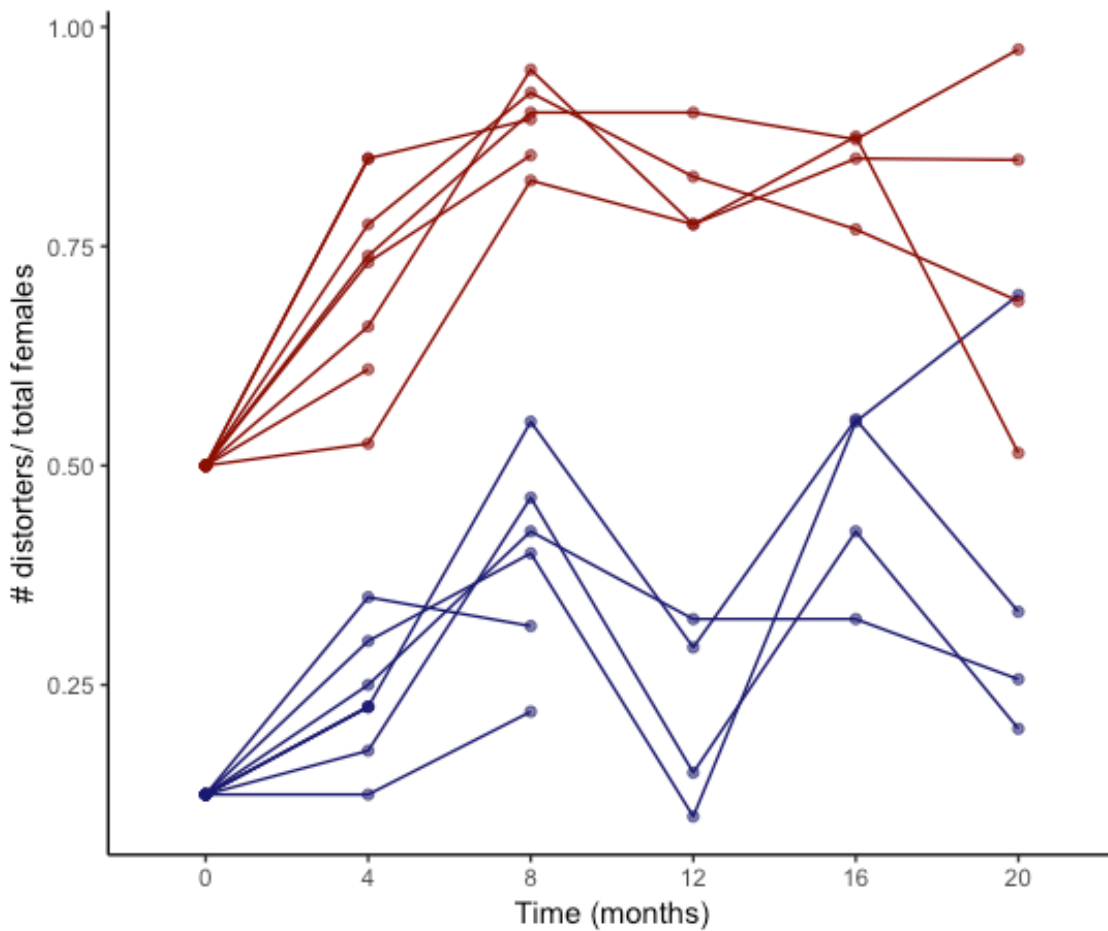
502

503 Fig. 2. Adult longevity (A) and adult reproduction period (B) (measured as the time egg
 504 production began to the time the last egg was laid) for distorter (solid line) and nondistorter
 505 (dashed line) females over the course of the fecundity experiment. Distorter females did not
 506 live as long as nondistorter females and had a shorter egg laying period.



507

508 Fig. 3. Development time (shown as the proportion of individuals who are still juvenile) of
 509 nondistorter (dashed line) and distorter (solid line) females. Nondistorter females take less
 510 time to develop than distorter females.



511

512

513 Fig. 4. Frequency of distorter females (compared to the total number of females) in *Liposcelis*
514 *sp.* populations started at an initial frequency of either 50% distorter females (red) or 12.5%
515 distorter females (blue). Lines indicate the trajectory of each replicate over time.
516