

Artificial selection for increased dispersal results in lower fitness

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1 *Abstract*

2 Dispersal often covaries with other traits and this covariation was shown to have a genetic basis.
3 Here, we wanted to explore to what extent genetic constraints and correlational selection can
4 explain patterns of covariation between dispersal and key life-history traits – lifespan and
5 reproduction. A prediction from the fitness-associated dispersal hypothesis was that lower
6 genetic quality is associated with higher dispersal propensity as driven by the benefits of genetic
7 mixing. We wanted to contrast it with a prediction from a different model that individuals
8 putting more emphasis on current rather than future reproduction disperse more, as they are
9 expected to be more risk-prone and exploratory. However, if dispersal has inherent costs this
10 will also result in a negative genetic correlation between higher rates of dispersal and some
11 aspects of performance. To explore this issue we used the dioecious nematode *Caenorhabditis*
12 *remanei* and selected for increased and decreased dispersal propensity for 10 generations,
13 followed by 5 generations of relaxed selection. Dispersal propensity responded to selection and
14 females from high-dispersal lines dispersed more than females from low-dispersal lines.
15 Females selected for increased dispersal propensity produced fewer offspring and were more
16 likely to die from matricide, which is associated with a low physiological condition in
17 *Caenorhabditis* nematodes. There was no evidence for differences in age-specific reproductive
18 effort between high- and low-dispersal females. Rather, reproductive output of high-dispersal
19 females was consistently reduced. We argue that our data provides support for the fitness-
20 associated dispersal hypothesis.

21 **Keywords:** fitness-associated dispersal, dispersal syndromes, artificial selection, life-history
22 theory, *Caenorhabditis*

23 *Introduction*

24 Dispersal is defined as any movement that results in gene flow across space, regardless
25 of the mechanisms underlying it (Clobert, Baguette, Benton, & Bullock, 2012, Ronce, 2007), and
26 as such is of a great evolutionary and ecological importance. The interest in the associations
27 between dispersal and morphological, behavioural or life-history traits – also named dispersal
28 syndromes, was spurred by studies which demonstrated that dispersing and philopatric
29 individuals differ in suits of traits (Clobert, Baguette, Benton, & Bullock, 2012). The study of
30 phenotypic associations between dispersal and other traits (Bensch, Hasselquist, Nielsen, &
31 Hansson, 1998; Forero, Donázar, & Hiraldo, 2002; García-Navas, Ferrer, & Sanz, 2014; Germain,
32 Pärt, & Gustafsson, 2017; Gienapp & Merilä, 2011; Hansson, Bensch, & Hasselquist, 2004;
33 Maccoll & Hatchwell, 2004; Nevoux, Arlt, Nicoll, Jones, & Norris, 2013; Pasinelli, Schiegg, &
34 Walters, 2004; Pärn, Jensen, & Ringsby, 2009; Robbins & Robbins, 2005; Serrano & Tella, 2012;
35 Verhulst & Eck, 1996; Wauters, Matthysen, & Dhondt, 1994) revealed a high context-
36 dependency and plasticity of dispersal decisions. At the same time research on the genetic
37 architecture of dispersal and dispersal syndromes revealed significant heritability of dispersal
38 and genetic integration between dispersal and other traits (Bal, Michel & Grewal, 2014;
39 Duckworth & Kruuk, 2009; Edelsparre, Vesterberg, Lim & Anwari, 2014; Gu & Danthanarayana,
40 1992; Korsten, van Overveld, Adriaensen, & Matthysen, 2013; Nachappa, Margolies & Nechols,
41 2010; Roff & Gelinas, 2003; Roff, Tucker & Stirling, 1999; Tung et al., 2017; van Overveld,
42 Adriaensen & Matthysen, 2015). The challenge is therefore to understand the forces behind the
43 evolution of genetically integrated dispersal strategies.

44 In this study we were specifically interested in the evolution of genetic integration
45 between dispersal and life-history traits – lifespan and reproduction. Correlational selection –
46 selection for optimal trait combination, can be one force behind the evolution of such
47 integration. For instance, the trade-off between current and future reproduction is predicted to
48 lead to the evolution of polymorphic populations where some individuals put more emphasis on
49 current reproduction while others on future reproduction. Individuals that put more emphasis
50 on current reproduction have lower expected future reproduction and are selected to be more
51 risk-prone than individuals that put more emphasis on future reproduction (Clark, 1994; Roff,
52 2002; Wolf, Doorn, Leimar, & Weissing, 2007). Dispersal poses considerable risks (Bonte et al.,
53 2012), and, following the outlined logic individuals with lower expected future reproduction
54 should be selected to disperse more readily than individuals with higher expected future
55 reproduction. Fitness-associated dispersal hypothesis, an extension of fitness-associated
56 recombination framework (Hadany & Beker, 2003), offers another explanation of how a
57 correlation between life-history traits and dispersal could have arisen. According to this
58 hypothesis the evolution of higher dispersal rates for bad quality genotypes, associated with
59 lower fitness, is driven by the benefits of genetic mixing and underlain by a regulatory gene that
60 allows for conditional dispersal (Gueijman, Ayali, Ram, & Hadany, 2013; Hadany, Eshel, &
61 Motro, 2004). Theoretical models show that fitness-associated dispersal can evolve even in the
62 absence of kin competition and in homogenous environments (Gueijman, Ayali, Ram, & Hadany,
63 2013). While long-term correlational selection can lead to genetic integration of dispersal and
64 life-history traits, such integration can be a direct result of an inherent cost of dispersal
65 underlain by, for instance, resource/energy allocation trade-offs. This cost can be constitutive -

66 paid by all individuals with higher dispersal propensity, regardless of actual dispersal decisions
67 or induced - paid only by individuals that disperse.

68 In this paper we took advantage of the experimental tractability of the dioecious
69 nematode *Caenorhabditis remanei* and selected bidirectionally for increased (HD – high-
70 dispersal) and decreased (LD – low-dispersal) dispersal propensity. *Caenorhabditis* nematodes
71 inhabit ephemeral substrates and disperse in both adult and larval stages. Closely related *C.*
72 *elegans* has been previously employed to study aspects of dispersal (Bono & Bargmann, 1998;
73 Friedenber, 2003a; 2003b; Harvey, 2009). In our study, we used *C. remanei* because this
74 dioecious species harbours much higher levels of standing genetic variation than
75 hermaphroditic *C. elegans* (Graustein, Gaspar, Walters, & Palopoli, 2002; Jovelin, Ajie, & Phillips,
76 2003), allowing for fast responses to artificial selection. The selection lasted for 10 generations,
77 followed by five generations of relaxed selection. After selection we measured age-specific
78 reproductive performance and lifespan of females from our experimental lines.

79 Using our experimental lines we tested predictions derived from life-history theory and
80 two theoretical models discussed above. The predictions were as follows: 1) if the relationship
81 between dispersal propensity and age-specific reproductive effort reflects the current versus
82 future reproduction trade-off (Clark, 1994; Roff, 2002; Wolf, Doorn, Leimar, & Weissing, 2007),
83 then the HD selection regime should consist of individuals selected at their reproductive peak.
84 Reproductive peak of individuals from the LD regime should be observed at a different age, but
85 their overall reproductive output should not be depressed; 2) if lower genetic quality is reflected
86 in higher dispersal rates (Gueijman, Ayali, Ram, & Hadany, 2013; Hadany, Eshel, & Motro, 2004)
87 then the HD selection regime should consist of individuals of lower overall quality, and their

88 lower performance should be observed across different contexts. Finally, 3) if inherent, intrinsic
89 costs of dispersal shape its relationship with life-history traits then the HD regime would be
90 expected pay such costs in terms of reproduction and/or lifespan. Nonetheless, rather than
91 being the best of a bad situation as in scenario 2), one would expect that under circumstances in
92 which fitness benefits of dispersal can be acquired HD individuals would perform as good or
93 better than LD individuals.

94 *Materials and Methods*

95 (a) *General maintenance*

96 The strain *C. remanei* SP8, a genetically diverse strain created by crossing three wild-type
97 isolates (Fritzsche, Timmermeyer, Wolter, & Michiels, 2014), was used for all experiments. The
98 strain was provided by N. Timmermeyer from the Department of Biology, Tuebingen University,
99 Germany and was maintained in our laboratory for 15 generations before being frozen to create
100 stock populations. In the beginning of our experiments these *C. remanei* SP8 stock populations
101 were recovered from freezing and propagated for two to three generations. Standard
102 cultivation conditions were employed; worms were kept on 92 mm Petri plates poured with
103 Nematode Growth Medium (NGM) agar and seeded with 1-1.5 ml of food source *Escherichia*
104 *coli* (Stiernagle, 2006). Because antibiotics – streptomycin, kanamycin and nystatin were added
105 to agar (and to LB bacterial medium) (Lionaki & Tavernarakis, 2013) antibiotic resistant *E. coli*
106 OP50-1 (pUC4K) (provided by J. Ewbank from Centre d'Immunologie de Marseille-Luminy) was
107 used as nematode food. Worms were kept in climate chambers at 20°C, 60% humidity and in

108 darkness. Hypochlorite treatment (bleaching), which leaves eggs, killing all other stages, was
109 used to obtain age-synchronized populations (Stiernagle, 2006).

110 *(b) Selection*

111 The experiment employed a bidirectional selection for increased and decreased dispersal
112 propensity for 10 generations. The population density was kept roughly at 300-700 of worms
113 per generation making inbreeding during the selection experiment unlikely. Four replicate lines
114 for high (HD) and low (LD) dispersal were established. However, due to problems with
115 cryopreservation of experimental lines, one line from each of the selection regimes was
116 eventually lost, such that three replicate lines from each selection regime were used for
117 experimental assays. For the first five rounds of selection, two replicate assay plates for each
118 replicate line were established and after that only one assay plate for each replicate line was
119 established. The assays were conducted on 150 mm Petri plates poured with NGM agar. Each
120 assay plate had two patches of food (200 μ l of *E. coli*) – one on each side of a plate. The distance
121 between the centres of the two patches was 10 cm. Dispersal was operationally defined as a
122 movement from one half of the plate to another half. While the scope of such movement was
123 not big, in natural settings this should be enough to move between different
124 microenvironmental patches allowing for gene flow. Before the beginning of the assays, worms
125 (day 2 adults) were collected from 92 mm population plates by pipetting them in M9 buffer to
126 10 ml plastic tubes. After they settled at the bottom of a plastic tube, supernatant was
127 removed, and worms were placed around one of the two food patches, which marked the
128 beginning of the assay. During the assay, worms were free to move on the plates, which were
129 monitored regularly to check if any worms reached the second food patch. Worms that reached

130 the second bacterial patch were transferred onto a new 92 mm plate with food, until 50 males
131 and 50 females were collected for each replicate line in HD regime. After that, 50 males and 50
132 females remaining around the first patch were picked haphazardly to establish LD replicate
133 lines. The duration of the assays ranged from 7 to 10 hours. After selection worms that were
134 collected mated overnight, and plates with eggs were bleached the following day. Once 10
135 generations of selection were completed worms were propagated for two more generations
136 before being cryopreserved at -80 °C.

137 *(c) Dispersal assays*

138 Selected populations were recovered from freezing and propagated for three generations to
139 obtain sufficient numbers of worms for assays. The duration of post-selection dispersal assays
140 was about 7 hours. After this time assays were terminated by cooling plates in the fridge. The
141 worms were later killed by inverting plates over chloroform, and then hand-counted. The
142 number of worms (males and females) on each half of a plate, as well as on each patch was
143 hand-counted. The number of worms per plate ranged from 239 to 954 (mean = 494.30, median
144 = 485, standard deviation = 134.07). 40 dispersal assays for LD lines and 41 dispersal assays for
145 HD lines were run, with the number of replicate assays per replicate line ranging from 8 to 17
146 (due to problems with cryopreservation for some lines only a limited number of worms was
147 available for assays).

148 *(d) Fecundity and lifespan*

149 To measure fecundity and lifespan of mated females (as males did not show response to
150 selection, see Results) 34 females were isolated from each replicate line (giving 102 females per

151 selection regime) on 35 mm Petri plates seeded with 100 μ l of bacteria. The isolation was done
152 at last (L4) larval stage and each female was subsequently paired with two standard males from
153 the base SP8 population. Females and two accompanying males were transferred to new plates
154 every day. Males that died were replaced. The number of progeny (larvae) was counted over
155 the first seven days of adulthood. Previous findings indicate that in lab conditions *C. remanei*
156 females lay about 93% of eggs during the first week of adulthood (Lind, Zwoinska, Meurling,
157 Carlsson, & Maklakov, 2015; Zwoinska, Kolm, & Maklakov, 2013). Given this and that age-
158 specific reproduction followed similar trajectories in both selection regimes (see Results and
159 Supp. Fig. 1) we assumed that our measure accurately represents lifetime reproductive success
160 for both selection regimes. After the first week of adulthood, females were transferred to the
161 new plates every second day (because they largely stopped laying eggs) but deaths were scored
162 daily. This continued until the last female died. In *Caenorhabditis* nematodes,
163 females/hermaphrodites (genus consists of dioecious and androdioecious species) have two
164 distinct causes of death. Mothers in poor condition often die by matricide when eggs hatch
165 internally as triggered by stress, low nutrient availability or age-related degeneration of the egg-
166 laying system (Pickett & Kornfeld, 2013). Mothers that do not commit matricide survive for
167 longer and die in late ages from other age-related causes. We scored these two types of deaths
168 separately.

169 (e) *Statistical analysis*

170 All analyses were conducted in R software v. 3.2.2. To analyse dispersal beta-binomial models
171 with a logit link function available in the package *glmmadmb* (Skaug, Fournier, Bolker,
172 Magnusson, & Nielsen, 2015) were used, because our data were over-dispersed. Our response

173 variable was a number of “successes” – worms that dispersed and “failures” – worms that did
174 not disperse and remained on the same half of a plate they were placed on. Selection regime,
175 total number of worms on plate, sex and their interactions were fitted as fixed predictors. The
176 total number of worms on a plate refers to worms of both sexes. For our analysis, we decided to
177 remove 2 assays with the highest number of worms (836 and 954 worms) because they both
178 belonged to the HD treatment, and this number was well above the maximum number of
179 worms observed in the LD treatment assays (maximum 707 worms). The conclusion about the
180 significantly higher dispersal rates of HD females holds regardless of the treatment of these
181 outliers. Replicate line (nested within selection regime) and day of assay were fitted as random
182 factors. Males and females were also analysed in separate models.

183 Negative binomial models with the log link function from the package *glmmadmb* were
184 used to analyse the fecundity data as our count data were over-dispersed. Selection regime was
185 fitted as a fixed factor and replicate line nested within selection regime as a random factor. The
186 response variable was the total number of offspring (measured as larvae). We also analysed
187 age-specific reproduction to test for the interaction between selection regime and age, i.e. the
188 evidence for differences in age-specific reproductive effort between the selection regimes.

189 Cox proportional hazards model with Gaussian random effects available in the package
190 *coxme* (Therneau, 2015) was employed to analyse our survival data. Selection regime was fitted
191 as a fixed factor and replicate line nested within selection regime as a random factor. We run
192 models in which matricidal and non-matricidal deaths were analysed separately.

193 *Results*

194 *(a) Dispersal*

195 We found a significant interaction between selection regime and sex (selection regime x sex: $z =$
196 2.76 , $P = 0.0057$, Table 1) - only females responded to selection on dispersal (Fig. 1). The total
197 number of worms on a plate was also significant ($z = 4.04$, $P < 0.001$), as dispersal increased with
198 increasing density (Fig. 1(a) and (b)). A model in which only females were included confirmed a
199 significant effect of selection regime on dispersal (selection regime: $z = -1.74$, $P = 0.031$). Indeed,
200 HD females dispersed more than LD females (Fig. 1(a)). In males the only significant effect was
201 the total number of worms on a plate reflecting increasing dispersal with increasing density ($z =$
202 2.59 , $P = 0.010$) (Fig. 1(b)).

203 *(b) Reproduction*

204 We analysed lifetime reproductive success of females and found a significant effect of selection
205 regime ($z = 2.43$, $P = 0.015$), where LD lines had higher lifetime reproductive success than HD
206 lines (Fig. 2). We also tested if reproduction followed similar trajectories in both treatments in a
207 model of with age (including 2nd and 3rd degree polynomials of age) and an interaction between
208 selection regime and all age terms. None of the interactions was significant (Table 1). In general,
209 we only found evidence for differences in total reproduction between the treatments.

210 *(c) Survival*

211 Approximately 39% of females died from matricide (71 out of 182). Females from LD regime
212 had a lower risk of death from matricide than females from HD regime ($z = -2.26$, $P = 0.024$)

213 (Fig. 3(a)). We did not observe survival differences between females that died of causes other
214 than matricide ($z = -0.54$, $P = 0.59$) (Fig. 3(b)).

215 *Discussion*

216 In this study we investigated the patterns of reproduction and survival in *C. remanei*
217 lines selected for high (HD) and low (LD) dispersal propensity. We found heritable variation in
218 dispersal as females from HD lines evolved higher dispersal compared to females from LD lines.
219 Differences in dispersal propensity evolved within short evolutionary time, after only 10
220 generations of artificial selection. Dispersal was genetically integrated with life-history traits as
221 HD females selected for higher dispersal propensity had lower lifetime reproductive success
222 compared with LD females. While some previous studies demonstrated a negative correlation
223 between dispersal-related traits and aspects of reproductive performance (e.g. Bal, Michel &
224 Grewal 2014; Gu & Danthararyana 1992a; Roff, Tucker & Stirling 1999; Roff & Gelinas 2003),
225 here we were able to link dispersal propensity to reproductive performance across the lifespan
226 and contrast observed patterns with predictions derived from theory. In our experiments HD
227 females also had a higher risk of dying from matricide, which is one of the major contributors to
228 death in female nematodes. Females in low nutritional condition are more likely to undergo
229 matricide, which also increases with female reproductive ageing (Pickett & Kornfeld, 2013).
230 Overall, these results suggest that HD females were of poorer condition than their LD
231 counterparts. This is inconsistent with our prediction 1), where dispersal decisions reflect life-
232 history strategies rooted in the trade-off between current and future reproduction (Wolf,
233 Doorn, Leimar, & Weissing, 2007). In this scenario we would expect differences in age-specific
234 reproductive effort (linked to differences in dispersal propensity) but not consistently lower

235 reproductive output. According to life-history theory we could also expect individuals with
236 higher reproductive output (our LD lines) to die younger as a result of the survival-reproduction
237 trade-off, while the opposite was true.

238 Both of our two remaining predictions outlined in the introduction assume that aspects
239 of performance are reduced, at least in some contexts, in highly dispersive individuals. In the
240 fitness-associated dispersal framework, dispersal is a way to make the best of a bad situation for
241 lower quality individuals due to benefits of genetic mixing (Gueijman, Ayali, Ram, & Hadany,
242 2013; Hadany, Eshel, & Motro, 2004). The fitness-associated dispersal framework appears
243 therefore to provide a good fit to our data, where HD females are the “bad quality” ones.
244 However, we cannot rule out the possibility that the HD females would have an advantage
245 under different environmental settings, if allowed to acquire fitness through dispersal and this
246 issue requires further study. Interestingly, a study on mountain goats, which used genetic and
247 population-monitoring data also found evidence for fitness-associated dispersal. In this study
248 dispersing goats had lower levels of heterozygosity than non-dispersers. The study also found
249 that as density increased, more higher rank individuals dispersed (Shaffer et al. 2011). We also
250 found that a higher proportion of individuals dispersed with increasing densities and this was
251 true for both sexes. However, the difference between dispersal rates between LD and HD lines
252 remained constant across different population densities. In the future it would be worth testing
253 whether under more stressful conditions than the ones used in our assays the proportion of
254 higher quality individuals among dispersers increases. This issue is worth further study because
255 higher quality individuals are more likely to survive dispersal and settle successfully in a new

256 environment. This can lead to a situation in which the majority of emigrants are of a higher
257 quality despite lower baseline dispersal propensity.

258 Interestingly, we found no differences in dispersal propensity between males from HD
259 and LD lines. The way we applied selection on dispersal propensity could have weakened
260 selection on males; specifically, although equal numbers of males and females were collected at
261 the end of an assay for each treatment, females were mating freely through the duration of
262 assays. Consequently, in the HD treatment in each generation we would exclusively select for
263 dispersive mothers but their progeny would be sired to a large degree by less dispersive males,
264 rather than by co-selected dispersive males. Still, male dispersal propensity could also have
265 evolved by intersexual genetic correlation. For example, in another study where we specifically
266 selected for female learning performance, male learning performance evolved as a correlated
267 response to selection (Zwoinska, Lind, Cortazar-Chinarro, Ramsden, & Maklakov, 2016). The
268 results of this study therefore suggest that dispersal propensity in *C. remanei* harbours
269 substantial sex-specific genetic variation. Differences between the sexes can also exist in the
270 amount of genetic variation available. There is currently an increased interest in the sex-biased
271 dispersal (eg Li & Kokko 2018; Trochet et al. 2016). It would be insightful to use *Caenorhabditis*
272 nematodes to select separately on male and female dispersal propensity and investigate
273 whether the strength and direction of genetic correlations between dispersal and other traits
274 are the same in males and females.

275 At this stage it is important to note that not all studies found a genetic correlation
276 between dispersal and life-history traits. For example, a selection experiment on increased
277 dispersal in *Drosophila melanogaster* (Tung et al., 2017) found increased aggression, exploratory

278 tendency and locomotory activity in lines selected for dispersal but no relationship with life-
279 history traits. While both in our experiment and in the *Drosophila* study life-history traits were
280 measured in ad libitum conditions, the *Drosophila* study used a dispersal assay in which no food
281 was provided in order to encourage dispersal. It would be interesting to investigate whether
282 food conditions during the selection for dispersal can lead to different associations between life-
283 history traits. Dispersal is a plastic trait and some individuals may disperse under one set of
284 conditions but not under another set of conditions (e.g. density-dependent effects found in
285 Shaffer et al. 2011). The absence of food can mobilize a higher proportion of individuals, with
286 more diverse genetic backgrounds, to disperse.

287 To summarize, we showed that dispersal propensity, reproduction and survival have
288 shared genetic basis and high dispersal is associated with reduced reproduction and higher
289 mortality from matricide in *C. remanei* females. We argue that our findings are largely
290 consistent with the fitness-associated dispersal model, in which lower quality individuals are
291 predicted to disperse more as driven by the benefits of genetic mixing.

292

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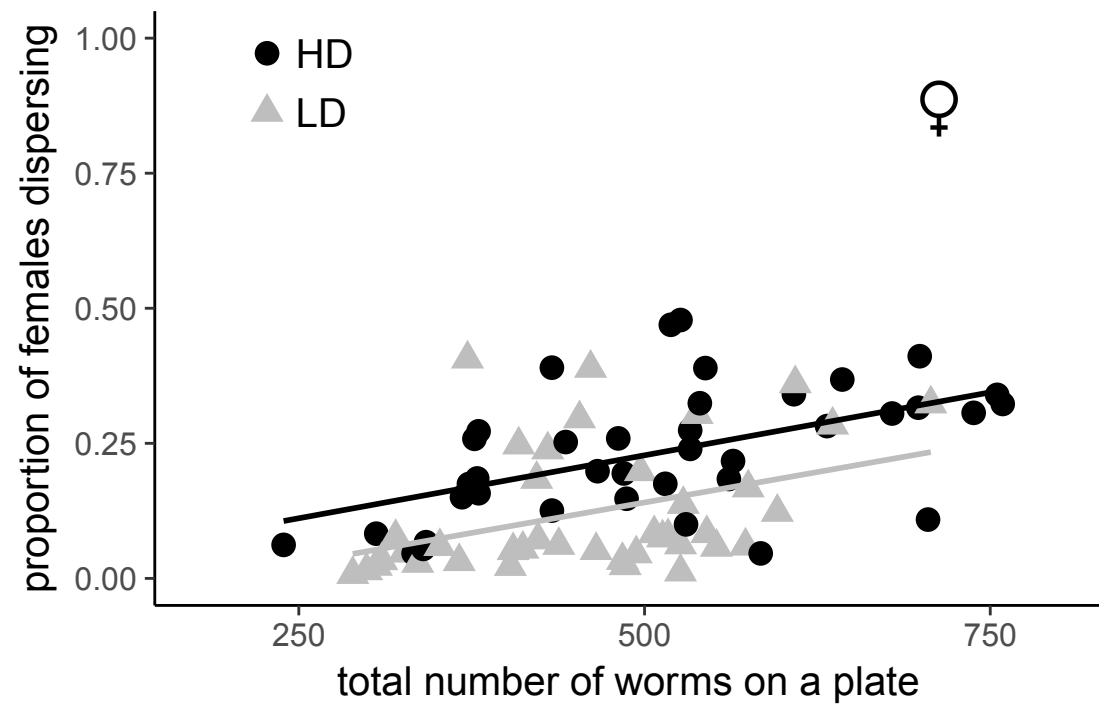
435 **Figure 1.** Dispersal propensity of worms selected for increased (HD) or decreased (LD) dispersal
436 expressed as the number of males/females on a new “dispersal” half of a plate divided by the
437 total number of males/females on a plate. (a) females and (b) males.

438 **Figure 2.** Lifetime reproductive success of females coming from HD and LD regimes expressed as
439 a mean of each replicate line \pm SEM.

440 **Figure 3.** Survival of females from HD and LD regimes that died of matricide (a) and when
441 matricidal worms were excluded (b).

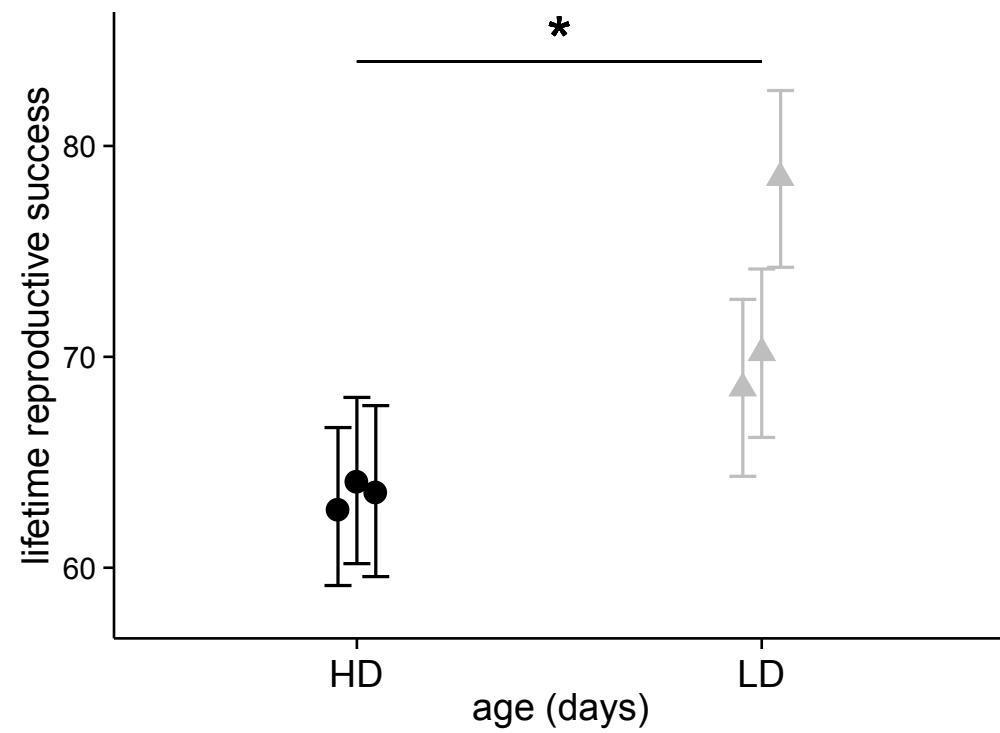
442 **Supplementary Figure 1.** Age-specific reproductive effort in high-dispersal (HD) and low-
443 dispersal (LD) lines.

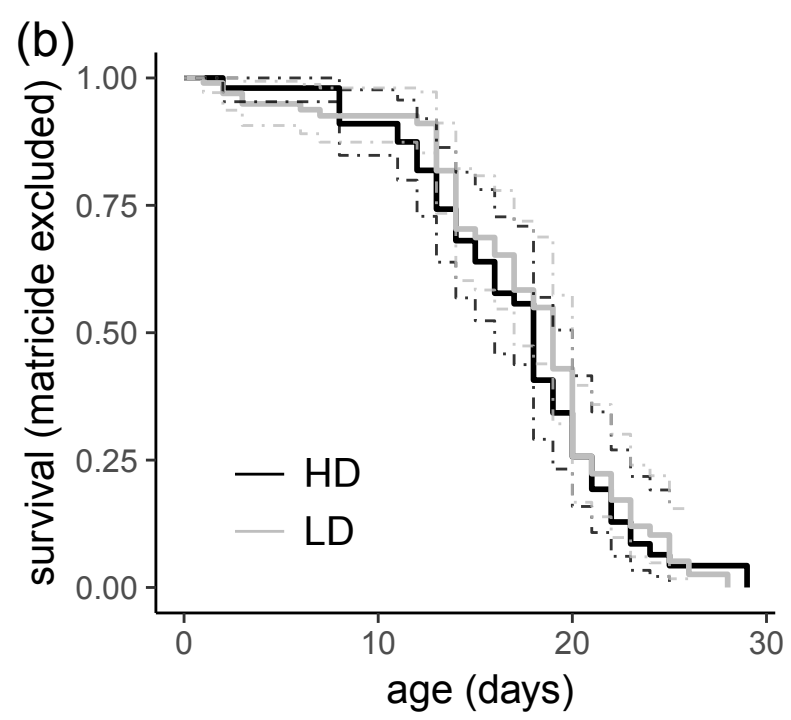
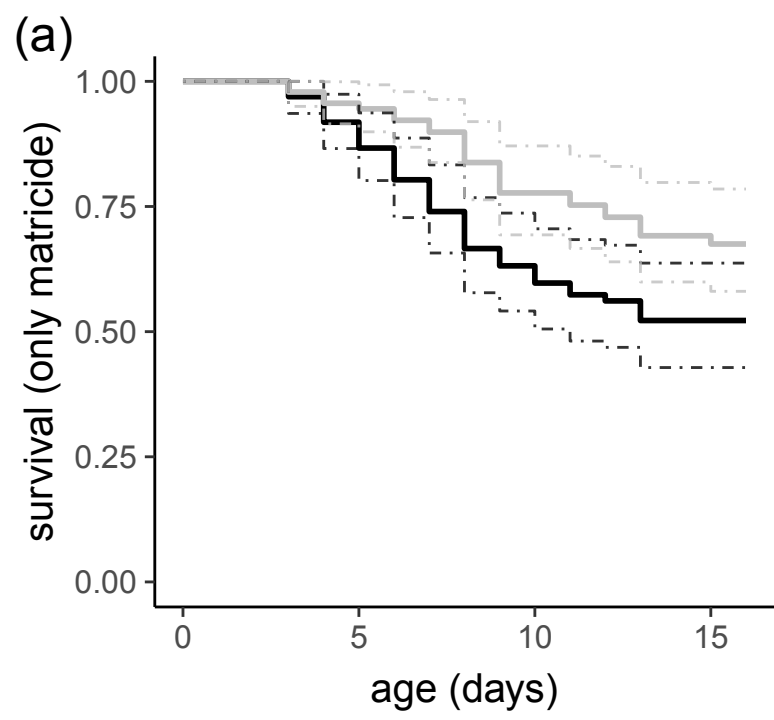
(a)



(b)







Dispersal assays

Generalised beta-binomial models (logit link function)

Response: Proportion dispersing (both sexes)

	Estimate	Std. Error	z value	P
Intercept [HD regime, Female sex]	-2.43	0.34	-7.04	< 0.001
Selection regime	-1.33	0.62	-2.15	0.032
Sex	-0.70	0.14	-4.79	< 0.001
Total number of worms	0.0022	0.00054	4.04	< 0.001
Selection × Sex	0.61	0.22	2.76	0.0057
Selection × Total number of worms	0.0014	0.0012	1.21	0.23

Random effects:

	Variance	Std. Dev
Replicate line	0.076	0.28
Day of assay	0.0079	0.089

Response: Proportion dispersing (females)

	Estimate	Std. Error	z value	P
Intercept [HD regime]	-2.46	0.42	-5.85	< 0.001
Selection regime	-1.74	0.81	-2.16	0.031
Total number of worms	0.0022	0.00069	3.24	0.0012
Selection × Total number of worms	0.0023	0.0016	1.47	0.14

Random effects:

	Variance	Std. Dev
Replicate line	0.10	0.32
Day of assay	0.0076	0.087

Response: Proportion dispersing (males)

	Estimate	Std. Error	z value	P
Intercept [HD regime]	-2.99	0.47	-6.39	< 0.001
Selection regime	-0.49	0.78	-0.64	0.52
Total number of worms	0.0022	0.00084	2.59	0.010
Selection × Total number of worms	0.00080	0.0015	0.52	0.60

Random effects:

	Variance	Std. Dev
Replicate line	0.014	0.12
Day of assay	0.042	0.205

Female lifetime reproductive success

Generalised negative binomial model

Response: Number of larvae

	Estimate	Std. Error	z value	P
Intercept [HD regime]	4.13	0.054	77.25	< 0.001
Selection regime	0.17	0.070	2.43	0.015

Random effects:

	Variance	Std. Dev
Replicate line	0.0038	0.062

Female age-specific reproduction

Generalised negative binomial model

Response: Number of larvae

	Estimate	Std. Error	z value	P
Intercept [HD regime]	0.78	0.24	3.20	< 0.001
Selection regime	0.59	0.33	1.80	0.072
Age	3.38	0.23	14.72	< 0.001
Age ²	-0.86	0.066	-13.13	< 0.001
Age ³	0.060	0.0056	10.93	< 0.001
Selection × Age	-0.37	0.31	-1.17	0.24
Selection × Age ²	0.084	0.90	0.95	0.34
Selection × Age ³	-0.0054	0.0080	-0.71	0.48

Random effects:

	Variance	Std. Dev
	0.0063	0.079

Female survival

Cox proportional hazards models with Gaussian random effects

Response: Age at death (all causes)

	Estimate	Std. Error	z value	P
Selection regime	-0.29	0.15	-1.94	0.052

Random effects:

	Variance	Std. Dev
Replicate line	0.00040	0.020

Response: Age at matricide

	Estimate	Std. Error	z value	P
Selection regime	-0.58	0.26	-2.26	0.024

Random effects:

	Variance	Std. Dev
Replicate line	0.0084	0.092

Response: Age at death (matricide censored)

	Estimate	Std. Error	z value	P
Selection regime	-0.10	0.19	-0.54	0.59

Random effects:

	Variance	Std. Dev
Replicate line	0.000083	0.0091

