Artificial selection for increased dispersal results in lower fitness

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Abstract

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

Keywords: fitness-associated dispersal, dispersal syndromes, artificial selection, life-history theory, Caenorhabdtitis

Introduction

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

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

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

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

Using our experimental lines we tested predictions derived from life-history theory and two theoretical models discussed above. The predictions were as follows: 1) if the relationship between dispersal propensity and age-specific reproductive effort reflects the current versus future reproduction trade-off (Clark, 1994; Roff, 2002; Wolf, Doorn, Leimar, & Weissing, 2007), then the HD selection regime should consists of individuals selected at their reproductive peak. Reproductive peak of individuals from the LD regime should be observed at a different age, but their overall reproductive output should not be depressed; 2) if lower genetic quality is reflected in higher dispersal rates (Gueijman, Ayali, Ram, & Hadany, 2013; Hadany, Eshel, & Motro, 2004) then the HD selection regime should consist of individuals of lower overall quality, and their lower performance should be observed across different contexts. Finally, 3) if inherent, intrinsic costs of dispersal shape its relationship with life-history traits then the HD regime would be expected pay such costs in terms of reproduction and/or lifespan. Nonetheless, rather than being the best of a bad situation as in scenario 2), one would expect that under circumstances in which fitness benefits of dispersal can be acquired HD individuals would perform as good or better than LD individuals.

Materials and Methods

(a) General maintenance

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

(b) Selection

The experiment employed a bidirectional selection for increased and decreased dispersal propensity for 10 generations. The population density was kept roughly at 300-700 of worms per generation making inbreeding during the selection experiment unlikely. Four replicate lines for high (HD) and low (LD) dispersal were established. However, due to problems with cryopreservation of experimental lines, one line from each of the selection regimes was eventually lost, such that three replicate lines from each selection regime were used for experimental assays. For the first five rounds of selection, two replicate assay plates for each replicate line were established and after that only one assay plate for each replicate line was established. The assays were conducted on 150 mm Petri plates poured with NGM agar. Each assay plate had two patches of food (200 µl of *E. coli*) – one on each side of a plate. The distance between the centres of the two patches was 10 cm. Dispersal was operationally defined as a movement from one half of the plate to another half. While the scope of such movement was not big, in natural settings this should be enough to move between different microenvironmental patches allowing for gene flow. Before the beginning of the assays, worms (day 2 adults) were collected from 92 mm population plates by pipetting them in M9 buffer to 10 ml plastic tubes. After they settled at the bottom of a plastic tube, supernatant was removed, and worms were placed around one of the two food patches, which marked the beginning of the assay. During the assay, worms were free to move on the plates, which were monitored regularly to check if any worms reached the second food patch. Worms that reached the second bacterial patch were transferred onto a new 92 mm plate with food, until 50 males and 50 females were collected for each replicate line in HD regime. After that, 50 males and 50 females remaining around the first patch were picked haphazardly to establish LD replicate lines. The duration of the assays ranged from 7 to 10 hours. After selection worms that were collected mated overnight, and plates with eggs were bleached the following day. Once 10 generations of selection were completed worms were propagated for two more generations before being cryopreserved at -80 ^{o}C.

(c) Dispersal assays

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

(d) Fecundity and lifespan

To measure fecundity and lifespan of mated females (as males did not show response to selection, see Results) 34 females were isolated from each replicate line (giving 102 females per selection regime) on 35 mm Petri plates seeded with 100 µl of bacteria. The isolation was done at last (L4) larval stage and each female was subsequently paired with two standard males from the base SP8 population. Females and two accompanying males were transferred to new plates every day. Males that died were replaced. The number of progeny (larvae) was counted over the first seven days of adulthood. Previous findings indicate that in lab conditions *C. remanei* females lay about 93% of eggs during the first week of adulthood (Lind, Zwoinska, Meurling, Carlsson, & Maklakov, 2015; Zwoinska, Kolm, & Maklakov, 2013). Given this and that age-specific reproduction followed similar trajectories in both selection regimes (see Results and Supp. Fig. 1) we assumed that our measure accurately represents lifetime reproductive success for both selection regimes. After the first week of adulthood, females were transferred to the new plates every second day (because they largely stopped laying eggs) but deaths were scored daily. This continued until the last female died. In *Caenorhabditis* nematodes, females/hermaphrodites (genus consists of dioecious and androdioecious species) have two distinct causes of death. Mothers in poor condition often die by matricide when eggs hatch internally as triggered by stress, low nutrient availability or age-related degeneration of the egg-laying system (Pickett & Kornfeld, 2013). Mothers that do not commit matricide survive for longer and die in late ages from other age-related causes. We scored these two types of deaths separately.

(e) Statistical analysis

All analyses were conducted in R software v. 3.2.2. To analyse dispersal beta-binomial models with a logit link function available in the package *glmmadmb* (Skaug, Fournier, Bolker, Magnusson, & Nielsen, 2015) were used, because our data were over-dispersed. Our response variable was a number of “successes” – worms that dispersed and “failures” – worms that did not disperse and remained on the same half of a plate they were placed on. Selection regime, total number of worms on plate, sex and their interactions were fitted as fixed predictors. The total number of worms on a plate refers to worms of both sexes. For our analysis, we decided to remove 2 assays with the highest number of worms (836 and 954 worms) because they both belonged to the HD treatment, and this number was well above the maximum number of worms observed in the LD treatment assays (maximum 707 worms). The conclusion about the significantly higher dispersal rates of HD females holds regardless of the treatment of these outliers. Replicate line (nested within selection regime) and day of assay were fitted as random factors. Males and females were also analysed in separate models.

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

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

Results

(a) Dispersal

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

(b) Reproduction

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

(c) Survival

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

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

Discussion

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

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

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

At this stage it is important to note that not all studies found a genetic correlation between dispersal and life-history traits. For example, a selection experiment on increased dispersal in *Drosophila melanogaster* (Tung et al., 2017) found increased aggression, exploratory tendency and locomotory activity in lines selected for dispersal but no relationship with life-history traits. While both in our experiment and in the *Drosophila* study life-history traits were measured in ad libitum conditions, the *Drosophila* study used a dispersal assay in which no food was provided in order to encourage dispersal. It would be interesting to investigate whether food conditions during the selection for dispersal can lead to different associations between life-history traits. Dispersal is a plastic trait and some individuals may disperse under one set of conditions but not under another set of conditions (e.g. density-dependent effects found in Shaffer et al. 2011). The absence of food can mobilize a higher proportion of individuals, with more diverse genetic backgrounds, to disperse.

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

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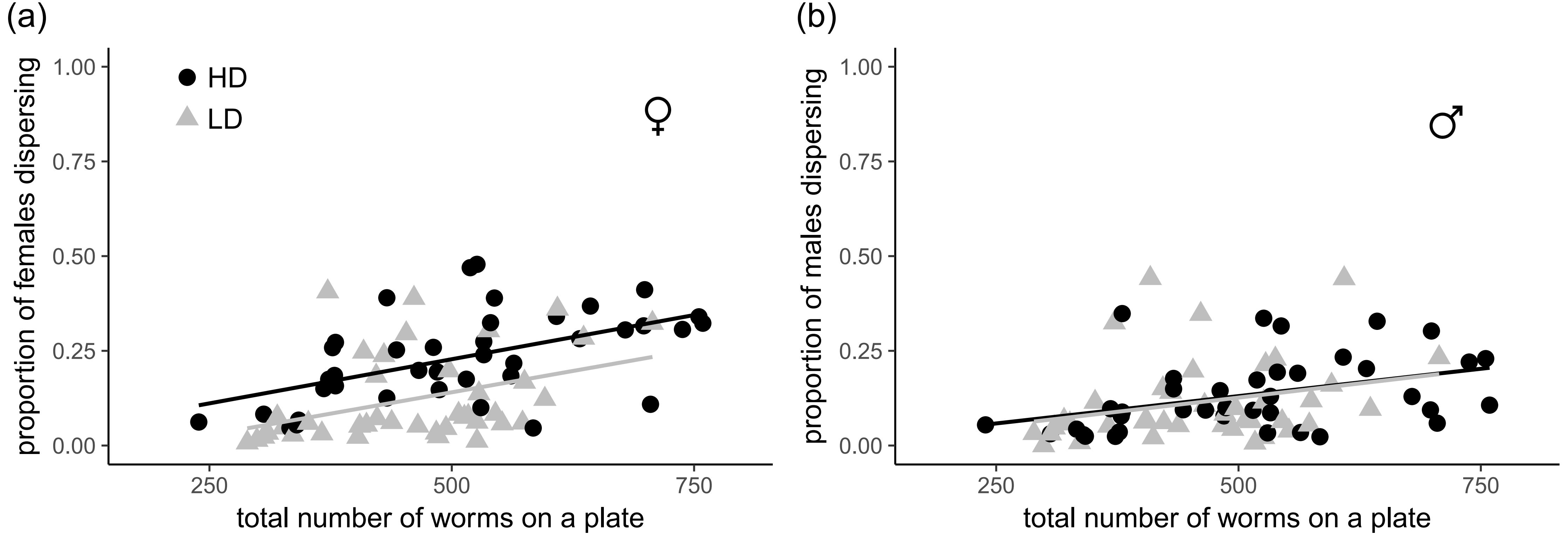
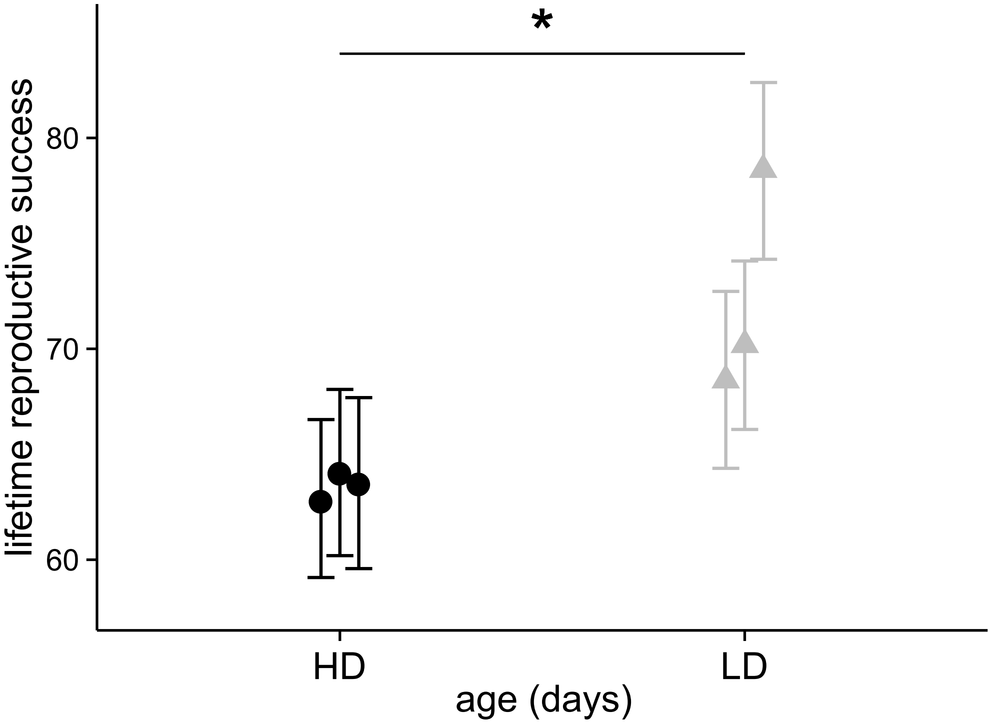
Figure 1. Dispersal propensity of worms selected for increased (HD) or decreased (LD) dispersal expressed as the number of males/females on a new "dispersal" half of a plate divided by the total number of males/females on a plate. (a) females and (b) males.

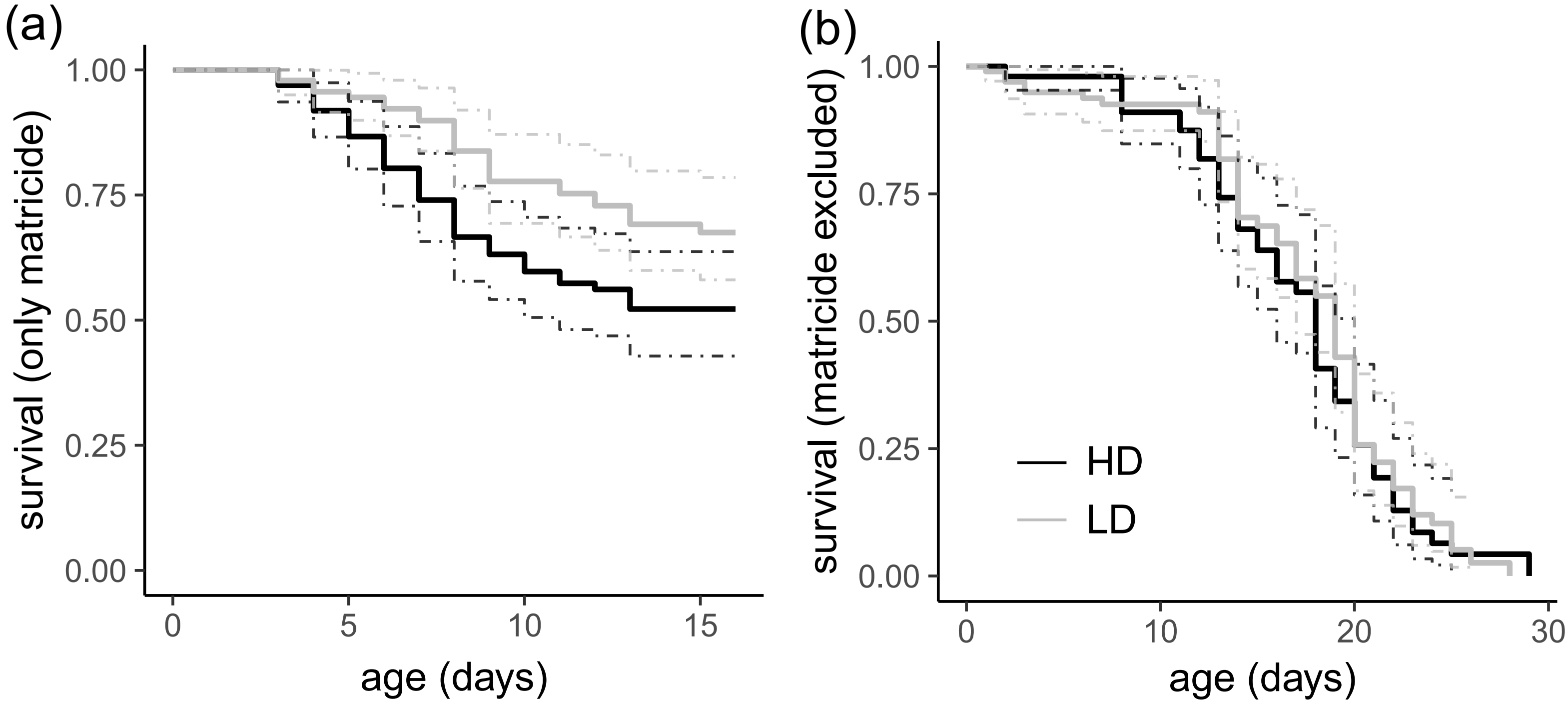
Figure 2. Lifetime reproductive success of females coming from HD and LD regimes expressed as a mean of each replicate line ± SEM.

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

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


(a)
(b)
HD
LD
♀
♂
proportion of females dispersing
proportion of males dispersing
1.00
0.75
0.50
0.25
0.00
250
500
750
total number of worms on a plate


*
lifetime reproductive success
80
70
60
HD
LD
age (days)


(a)
survival (only matricide)
1.00
0.75
0.50
0.25
0.00
0
5
10
15
age (days)
(b)
survival (matricide excluded)
1.00
0.75
0.50
0.25
0.00
0
10
20
30
age (days)
HD
LD

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:

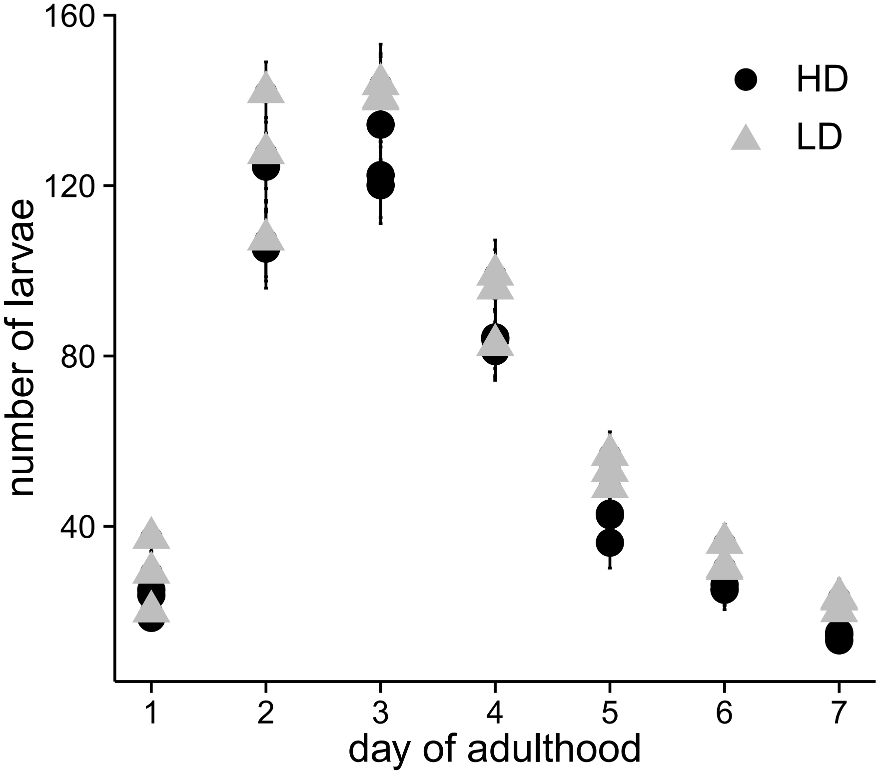
	Variance	Std. Dev
Replicate line	0.0084	0.092

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


160
120
80
40
number of larvae
1
2
3
4
5
6
7
day of adulthood
● HD
▲ LD