Life history correlations and trade-offs resulting from selection for dispersal in *Tribolium castaneum*

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Abstract

Dispersal is an important facet of the life history of many organisms and is, therefore, subject to selective pressure but does not evolve in isolation. Across nature, there are examples of dispersal syndromes and life history strategies in which suites of traits coevolve and covary with dispersal in combinations that serve to maximize fitness in a given ecological context. The red rust flour beetle, *Tribolium castaneum*, is a model organism and globally significant post-harvest pest that relies on dispersal to reach new patches of ephemeral habitat. Dispersal behaviour in *Tribolium* has a strong genetic basis. However, a robust understanding of the relationship between dispersal and other life-history components, which could elucidate evolutionary processes and allow pest managers to control their spread and reduce the impact of infestation, is currently lacking. Here, we use highly replicated lines of *T. castaneum* previously artificially selected for divergent small-scale dispersal propensity to robustly test several important life history components: reproductive strategy, development time, and longevity. As predicted, we find that a suite of important changes as a result of our selection on dispersal: high dispersal propensity is associated with a lower number of longer mating attempts by males, lower investment in early life reproduction by females, slower development of later-laid offspring, and longer female life span. These findings indicate that correlated intraspecific variation in dispersal and related traits may represent alternative life history strategies in *T. castaneum*. We therefore suggest that pest management efforts to mitigate the species' agro-economic impact should consider the eco-evolutionary dynamics within multiple life histories. The benefits of doing so could be felt both through improved targeting of efforts to reduce spread and also in forecasting how the selection pressures applied through pest management are likely to affect pest evolution.

Keywords: dispersal, dispersal syndrome, emigration, experimental evolution, flour beetle, life history, *Tribolium*

Introduction

Dispersal is the movement of individuals with the potential to induce gene flow and, therefore, plays a crucial role in evolutionary ecology (Ronce, 2007). It is an important element of the life history of many organisms, with effects ranging from the individual level to the spatial dynamics of metapopulations (Matthysen, 2012; Benton & Bowler, 2012). A greater understanding of the ecology and evolution of dispersal will help in addressing several key problems in contemporary biology, including species' responses to climate change, spatial functioning of populations under habitat fragmentation, and the spread of invasive species (Travis et al., 2013; Renault et al., 2018).

Dispersal shows associations with many other traits across a broad range of taxa, and these suites of correlated phenotypes can be termed dispersal syndromes. Where there is individual variation in dispersal within species, high and low dispersal may represent different life history strategies (Clobert et al., 2012). As movement is energetically costly, it might be assumed that correlations between dispersal and other traits may be negative simply because the portion of any resource expended on dispersal is unavailable to be invested elsewhere. In reality, however, the picture is far more complex, and the presence, strength, and direction of

relationships, as well as the traits involved, are highly context dependent (Bonte & Dahirel, 2017) and vary even with the individual components of dispersal (Jervis et al., 2007). The concerted evolution of suites of traits serves to mitigate the significant costs of dispersal and maximize individual fitness within the specific ecology of different systems (Bonte et al., 2012). Dispersal syndromes, and the underlying correlations and trade-offs in phenotypes associated with dispersal, have attracted much attention (Ronce & Clobert, 2012) as they provide insight into the multivariate nature of selection on life history traits and the constraints on their evolution (Bonte et al., 2012; Clobert et al., 2012). Most notably, dispersal consistently shows a relationship between fecundity and survival across taxonomic orders; however, even these correlations are far from universal, depending on a range of factors, including locomotion strategy and mode of thermoregulation (Stevens et al., 2014). The majority of research has focussed on vertebrates where individual tracking is possible (e.g., Cote & Clobert, 2012) and on wing-dimorphic insects where the dispersal phenotypes are discontinuous (Zera & Denno, 1997; Guerra, 2011). Less has been done on wing-monomorphic insects where dispersal phenotypes are more difficult to quantify. Among these wing-monomorphic insects, the majority of studies are on species where flight is the major mode of

movement, and therefore, differences in energetic output between dispersal phenotypes are likely to be much more important than in systems where dispersal is by walking. Studies are required within more diverse systems to enable the recognition of more general patterns and to identify the extent to which causal factors and evolutionary consequences are dependent on the evolutionary ecology of the individual taxa (Bonte & Dahirel, 2017; Ronce & Clobert, 2012).

The red flour beetle, *Tribolium castaneum*, is a globally significant post-harvest crop pest (El-Aziz, 2011) long used as a model system in evolutionary and population biology (Pointer et al., 2021). The species is long-lived for a small beetle, having a short egg, larval, and pupal stages (<5, <20, and <5 days, respectively, under near optimal conditions) followed by a long adult stage of up to 4 years (Good, 1936; Pointer et al., 2021). Historically, *Tribolium* were free-living, likely beneath the bark of trees or in rotting wood, where they were secondary colonizers characterized by rapid population growth, intense intraspecific competition, and ready dispersal (Dawson, 1977). At an unknown time in its history, the species switched to being predominantly human-commensal, infesting a wide variety of stored food products (Dawson, 1977). While they are capable of long-distance movement by flight, *Tribolium* beetles fly only in high temperatures (~>25 °C; Drury et al., 2016), and therefore, dispersal movements by flight are likely limited to outdoor movements in the tropics. In contrast, dispersals in the species' introduced, temperate range, or within artificially cooled food storage facilities, are likely to be predominantly by walking. Recent work in this system has shown variation in life history traits in natural populations (Matsumura et al., 2023), also that local dispersal (specifically emigration, but we keep the term dispersal for consistency with the existing literature) in *Tribolium* has a strong genetic basis, and that the architecture of the trait may be relatively simple (Pointer et al., 2023). Furthermore, dispersal propensity is correlated with several functionally dispersal-promoting traits (activity, movement pattern, affinity for the surface of the medium; Pointer et al. in review) related to activity and boldness, generally considered to be important dimensions of animal personality (Roche et al., 2016). As an established model system, the evolutionary ecology of *Tribolium* is relatively well understood (Pointer et al., 2020), yet despite the importance of dispersal to the species and to human pest management (Dawson, 1977; Jeger, 1999), little is known about a possible dispersal syndrome among life history traits. Such knowledge could help to predict the evolutionary consequences of management practices (Karlsson Green et al., 2020). The only previous studies used poorly replicated selection lines, selected under suboptimal conditions (Lavie & Ritte, 1978; Zirkle et al., 1988 using lines from Ritte & Lavie, 1977), or focused on correlations with walking motivation (distance walked by an individual in 30 min in the absence of food or conspecifics; e.g., Matsumura & Miyatake, 2019, using lines from Matsumura & Miyatake, 2015). As both the propensity to leave the fodder and directionality of movement are important aspects of walking dispersal in *Tribolium* (Korona, 1991; Pointer et al., in review), walking motivation is a single component of dispersal and a potential dispersal-enhancing trait, rather than dispersal per se, whereas the dispersal selection assay we employ explicitly captures all these components of dispersal behaviour.

Here, we use highly replicated lines of *T. castaneum* previously artificially selected for high and low levels of local dispersal propensity to investigate correlations between dispersal and several life history traits. The first trait we evaluate is male mating success. In wing-dimorphic insects, dispersal is known to show a negative association with mate acquisition traits (Guerra, 2011). Evidence for a similar trade-off in *Tribolium* has come from studying walking motivation lines (e.g., Matsumura et al., 2019). We expand on this previous work by using lines selected for a trait that better reflects dispersal and using mating assays within an ecologically realistic social environment, incorporating female choice and male–male competition, which are important aspects of reproductive biology in this system (Fedina & Lewis, 2008). If dispersal trades off with an investment in competitive ability, we expect to see highly dispersive males achieving fewer matings than less dispersive males.

We also evaluate female reproduction using a measure of fecundity. Fecundity is often seen to covary with dispersal, but the direction of the relationship is dependent on the cause (Stevens et al., 2014; Campos-Candela et al., 2019). The release from competition experienced by successful dispersers often means that they are able to invest more in reproduction (Burton et al. 2010). In contrast, the oogenesis-flight syndrome known from flying insects results from energetic constraint, meaning that dispersive individuals invest less in reproduction, particularly in early life (Johnson, 1969; Harshman & Zera, 2007; Tigreros & Davidowitz, 2019; Asplen, 2020). For this reason, we also include a temporal component, comparing fecundity before and after peak dispersal. Given the importance of intraspecific competition in *Tribolium* (Dawson, 1977), we expect population dynamic processes to dominate and, therefore, expect to observe increased female fecundity in highly dispersive lines, especially following the time of peak dispersal.

Another trait often seen to covary with dispersal is development time (Guerra, 2011). Associations between dispersal and development time in insects vary widely in strength and direction (Guerra, 2011), though these studies are overwhelmingly focussed on wing-dimorphic insects (but see Goodwyn & Fujisaki, 2007 in water-striders, Heteroptera: Gerridae). Such species are adapted to very different ecological conditions than the boom-bust cycles experienced by *Tribolium* populations, with bust phases characterized by cycles of very high intraspecific competition (including prolific larval and adult cannibalism of eggs and pupae [Stevens, 1989] and scarce resources [Dawson, 1977]). Under such conditions, a reversed dispersal-development pattern might be expected, in which a high-competition environment selects for rapid development to mitigate the risk of cannibalism by larvae to later-hatching eggs, with this pressure being relaxed among the offspring of dispersers in less competitive environments. Following this logic leads us to expect that a release from competition gained through dispersal will result in dispersive phenotypes being associated with slower development.

Finally, we examine longevity. As for fecundity, if energetic constraints influence life span, we might expect to see a negative relationship between dispersal and longevity. However, we expect high dispersal lines to have longer life spans, in line with the relationship observed among terrestrial animals, where greater longevity is thought to allow more time for a suitable reproductive habitat to be located (Stevens et al., 2014). This may be particularly strong considering the release from intense competition potentially afforded by successful dispersal in this system. Overall, if a dispersal syndrome

exists in this system, we expect to see significant correlations between dispersal phenotype and many of the studied traits. We discuss our results in the context of a dispersal syndrome in *T. castaneum*, the relevance to both the evolution of this and similar species, and pest management aiming to control this prolific pest.

Materials and methods

Beetles and dispersal propensity

The *T. castaneum* beetles used in this study were from 44 experimental lines: 16 high dispersal lines, 16 low dispersal lines previously bred from an outbred stock population and 12 unselected control lines from the same original Krakow super-strain stock (Laskowski et al., 2015), maintained under the same conditions as the selection lines for five generations prior to experiments. High and low dispersal lines were bred under divergent artificial selection over five generations, using a dispersal assay in which each individual was given three opportunities to "disperse" from a mixed-sex group of 200 conspecifics (i.e., leave a patch of suitable habitat (120 mm × 120 mm × 200 mm container filled to 50 mm with a 9:1 mixture of organic wheat flour and brewer's yeast, and tops with oats for traction); cross a short distance of unsuitable habitat (150 mm of plastic tubing) and not return). Individuals that dispersed three times out of the three opportunities were considered to display a dispersive phenotype, and individuals that dispersed zero times from the three opportunities were considered to display a non-dispersive phenotype. Individuals of each of these extreme phenotypes were bred to produce the subsequent generation, while intermediate phenotypes were discarded. Further details of the selection experiment and of husbandry procedures can be found in Pointer et al. (2023). After a single generation of selection, mean dispersal phenotypes (measured as the mean number of dispersals per individual out of three opportunities) between the treatments were significantly different. After five generations of selection, dispersal phenotypes were strongly divergent, and the distributions of dispersal phenotypes between the two treatments were non-overlapping (Pointer et al., 2023). The lines were split into two temporal blocks to manage workload: block one consisted of high dispersal lines 1–8, low dispersal lines 1–8, and control lines 1–6, and block two consisted of high dispersal lines 9–16, low dispersal lines 9–16 and control lines 7–12. Individuals used for all experiments were taken from the same generation as those in which dispersal was quantified in Pointer et al. (in review), where dispersal was found to be still strongly divergent and non-overlapping between treatments (dispersals per individual out of a maximum of three, low dispersal lines = 0.70 ± 0.05; high dispersal lines = 2.44 ± 0.07). All experiments in this study used the 32 selected lines; in experiments where we were less constrained by limits imposed by experimental effort, we also incorporated 12 unselected control lines. Throughout all experiments, populations were kept on a fodder mix of 90% organic white bread flour and 10% brewer yeast; environmental conditions were maintained at 30 °C and 60% relative humidity—hereafter referred to as "standard conditions." This research consisted of non-invasive observations of the natural behaviour of insects, and no ethical approval was required in the United Kingdom. Nevertheless, all experiments were carried out according to good scientific and ethical practice.

Male mating behaviour

Mating behaviour was scored from 305 video recordings. Full details are given in Pointer et al. (in review), but briefly, test populations of 10 individuals at a 1:1 sex ratio were taken from the 44 experimental lines in 2 temporal blocks. Each assay consisted of recording one test population for 10 min within a 120 mm × 120 mm arena, which was smooth-sided to prevent climbing. The number of mountings and total duration of mounting within a 10-min window was scored for each replicate using event logging software BORIS (Friard & Gamba, 2016). It was impossible to entirely prevent escapes during recording; therefore, some replicates represent fewer beetles for part of the assay. To account for this, trait measures for each replicate were adjusted by the number of "beetle-seconds" described by that replicate (trait measure divided by the sum of the length of time each individual was present in the assay arena). This results in small values but represents the most accurate way to present the data.

Female reproductive output

The 32 dispersal selection lines were split into 2 temporal blocks. Twenty-two virgin adults of each sex were obtained per line by sexing as pupae and raising in single-sex groups of 20. Males were marked with a dot of paint on the dorsal thorax using a method that was shown not to affect reproductive output (Sales, 2018). Males and females were paired in vials for 48 hr of mating opportunity, after which the males were discarded. At 4 ± 2 days post-eclosion, females were transferred into pots to oviposit for 8 days, then transferred to a fresh pot for an additional 8 days of oviposition (hereafter termed oviposition periods). These timings were chosen to encompass the known dispersal peak of *T. castaneum*, which occurs at ~10 days post-eclosion (Ziegler, 1976). In the second temporal block of lines, the first 8 hr of oviposition were in a third pot to obtain individuals whose laying time was more precisely known to allow measurement of development time (below); however, offspring from the first 8 hr and the rest of the 8 days were combined in evaluating reproductive output. Oviposition pots were kept under standard conditions for 35 days after the removal of the female before being frozen until adult offspring could be counted. Offspring were allowed to develop in excess of fodder to eliminate any effect of density or resource limitation. A female's reproductive output was taken as the number of adult offspring resulting from a given period of oviposition. Replicates producing no offspring were removed from the analysis as they are far more likely to represent male reproductive failure rather than a lack of female fecundity, which is the variable of interest here. This is because rates of female infertility are extremely low in this system relative to those of males (Pai, 2001; Matsumura et al., 2023).

Development time

During the reproductive fitness assay, females from lines in the second temporal block (176 females from each dispersal regime) oviposited in a separate pot for the first 8 hr to obtain a cohort whose laying time was more precisely known. The offspring developing in these pots were observed every 24 hr, and each pupation day was recorded. We use pupation time as a measure of development to allow direct comparison with existing work (Zirkle et al., 1988).

Longevity

Within the 2 temporal blocks, 10 males and 10 females from each of 44 experimental lines were sexed as pupae and raised in single-sex sex groups until 6 ± 3 days post-eclosion. At this point, each virgin individual was placed into a separate vial with 3-ml fodder. Each individual was observed every 14 days until day 462, with the time of deaths recorded until all individuals were dead.

Statistical methods

All data wrangling and analyses were performed in R (ver.4.3.1; R Core Team, 2021). Mixed models were fitted using package "*lme4*" (Bates et al., 2015) with *p*-values added with "*lmerTest*" (Kuznetsova et al., 2017). Model validation used the check_model function from the "*performance*" package (Lüdecke et al., 2021) and/or simulated residuals with DHARMa (Hartig, 2022). Most experiments included temporal block as a control variable. This could not be modelled as a random factor in GLMMs as it has only two levels, and random effects with few levels are known to produce imprecise estimates (Hodges, 2013). We had no reason to believe that block would have any effect on the traits under study, and the study design balanced dispersal treatments across the two blocks. Therefore, to simplify the main models in each analysis, we first checked that temporal block was not a significant predictor of the dependent variable (see Supplementary Material) and did not include it in the main models.

Both total reproductive output and timing of reproduction were modelled with LMMs (Table 1). To test the timing of reproduction, we initially modelled the difference in reproductive output between oviposition periods one and two; however, high overdispersion in these models prevented an adequate investigation. We therefore focussed on reproductive output in the first oviposition period, as early life reproduction is likely to be the most relevant for dispersal trade-offs (Zera & Denno, 1997).

Neither development time nor longevity data conformed to the proportional hazards assumption of Cox PH models. Seeing as the pupation rate among offspring in the development analysis was 100%, and no individuals needed to be censored from the dataset, we modelled time to pupation using a GLM with a Poisson error distribution (Table 1). Initially, we included female ID as a random factor to account for the fact that multiple individuals had the same mother; however, it was removed as it accounted for 0 variance in development time.

As Cox models were not appropriate, we modelled longevity using event history analysis (Keiding, 2014), which is qualitatively similar but without the assumption of proportional hazards. Rather than considering the time until some event (death), this approach considers the risk of an event occurring; hence, longevity is evaluated as a mortality risk. Accordingly, we modelled event (death) risk per time period using a binomial distribution; at each observation, individuals were assigned "0" if the event had not occurred and assigned "1" once the event took place. Repeated measures from each individual were included in the model via a random effect of individual ID. Line ID was initially included as a random effect but was removed as it added a large amount of complexity to the model structure without significantly improving model performance. Longevity models were also fitted for each sex independently, using the same structure but excluding sex as a fixed factor. The structure of GLMMs used to conduct these event history analyses is given in Table 1.

Results

Male mating behaviour

The number of mating attempts (mountings per individual per second, adjusted to account for escapes) observed in low dispersal lines (mean ± SE = 7.13e−4 ± 3.01e−5) was greater than that in either high dispersal (5.10e−4 ± 3.17e−5, GLMM: $\beta = 2.01e{-}4$, SE = 6.23e−5, $p < 0.01$; Figure 1Ai) or control lines (4.81e−4 ± 2.74e−5, GLMM: $\beta = 2.38e{-}4$, SE = 6.65e−5, $p < 0.001$). High dispersal lines did not differ from controls in their number of mating attempts ($\beta = 3.49e{-}5$, SE = 6.76e−5, $p = 0.61$). The total duration of mating (seconds per individual, adjusted to account for escapes) was not different between high dispersal lines (mean ± SE = 2.1e−2 ± 2.3e−3) and low dispersal lines (2.5e−2 ± 1.9e−3, GLMM: −3.9e−3, SE = 3.5e−3, $p = 0.27$; Figure 1Aii), between high dispersal lines and controls (2.0e−2 ± 2.2e−3, GLMM: $\beta = 9.2e{-}4$, SE = 3.8e−3, $p = 0.8$), or between low dispersal lines and controls (GLMM: $\beta = 4.8e{-}3$, SE = 3.7e−3, $p = 0.20$).

Reproductive output

Early life reproduction was significantly different between high and low selection lines, with high dispersal lines laying significantly fewer eggs in the first oviposition period (98.60 ± 1.74) than low dispersal lines (122.58 ± 2.08; LMM, $\beta = -23.89$, SE = 4.43, $p < 0.001$; Figure 1Bi). However, the total reproductive output across two oviposition periods did not differ between pairs from high (mean ± SE = 191.1 ± 3.9)

Table 1. Structure of models used to fit the effect of artificial selection for dispersal on several life history traits in replicate lines of *Tribolium castaneum*.

Trait	Dependent variable	Fixed factor/s	Random factor/s
Number of matings by males	Number of matings (per individual per second)	Dispersal regime	Line ID
Duration of mating by males	Mating duration (per individual per second)	Dispersal regime	Line ID
Total reproductive fitness	Total reproductive output	Dispersal regime	Line ID
Timing of reproductive fitness	Reproductive output in first oviposition period	Dispersal regime	Line ID
Development time	Pupation time	Dispersal regime × oviposition period	
Longevity	Alive (0)/dead (1)	Dispersal regime × sex	Individual ID, time

Note. The first column gives the biological trait of interest to a part of the analysis, and the second column gives the measured included as the dependent variable in the model, including standardization or codings.
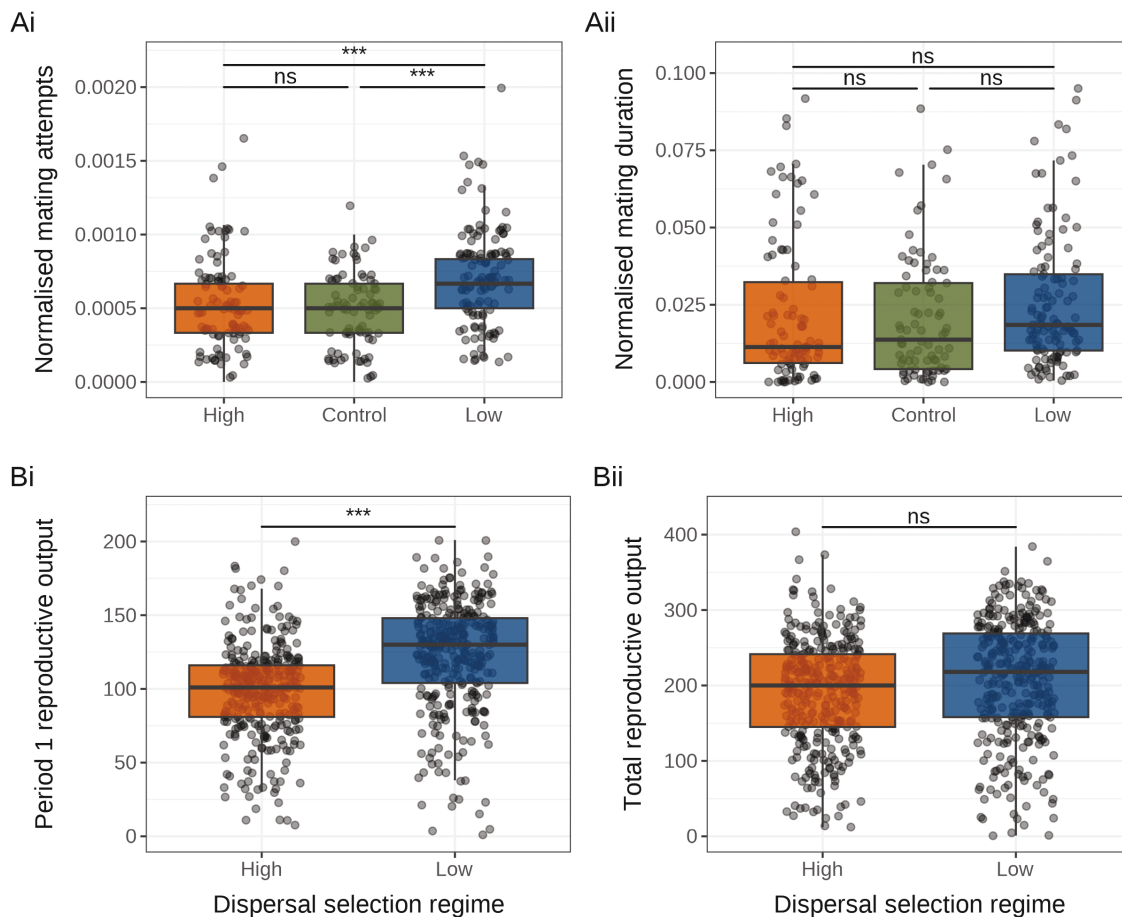
Figure 1. Reproductive traits in experimental lines of *Tribolium castaneum* selected for high or low dispersal behaviour and unselected controls. (A) Mating traits scored from 10-min video recordings of mixed-sex populations of ten individuals, showing (i) the number of mating attempts by males (normalized to be expressed per beetle per second) and (ii) the total mating duration (per beetle per second). These data are normalized by the number of "beetle-seconds" represented in replicate recordings to account for uneven representation due to escapes (trait measure divided by the sum of the number of seconds each beetle was present in the assay arena). (B) Reproductive output (number of adult offspring produced) of individual females, (i) in total across two 8-day periods of oviposition, roughly equating to before and after the peak of dispersal, and (ii) reproductive output in the first 8-day period of oviposition. Points are semi-transparent, so dark points indicate multiple overlapping points. ***A significance level of <0.001. "ns" indicates a non-significant difference.

and low dispersal lines (207.3 ± 4.4, GLMM: $\beta = 16.00$, SE = 8.73, $p = 0.077$; Figure 1Bii).

Development time

The pupation time of high dispersal lines (mean ± SE = 23.92 ± 0.08) was not significantly different from that of low dispersal lines (23.45 ± 0.08; Figure 2A; Table 2). Pupation time was significantly higher in the second oviposition period (24.44 ± 0.09) than the first (23.05 ± 0.07; Figure 2A; Table 2). There was also a significant interaction between the dispersal and oviposition period, with high dispersal lines in the second oviposition period having significantly lower pupation probability than expected from the additive effects of high dispersal and period 2 alone (Figure 2A; Table 2).

Longevity

High dispersal lines (median life span in days [mld] = 252) had significantly lower mortality risk than either low dispersal lines (mld = 224; Table 3) or controls (mld = 224; Table 3). Male mortality risk (mld = 294) was significantly lower than that of females (mld = 224; Table 3). There was a significant interaction between the dispersal regime and sex, with males from high dispersal and control regimes having greater

mortality risk than expected under the additive effects of sex and dispersal regime alone (Table 3). Low dispersal males had lower mortality risk than predicted by a purely additive model. Post hoc tests individually for each sex showed that the difference in mortality risk between dispersal phenotypes was absent in males, where high dispersers (mld = 308) did not have significantly longer life spans than either control (mld = 252; GLMM mortality risk, $\beta = 0.30$, SE = 0.23, $p = 0.186$; Figure 2Bi) or low dispersal lines (mld = 308; GLMM mortality risk, $\beta = -0.12$, SE = 0.16, $p = 0.433$; Figure 2Bi). Instead, the overall difference was driven by a significant difference in females, where high dispersers (mld = 252) had longer life spans than control (mld = 210; GLMM mortality risk, $\beta = 0.41$, SE = 0.20, $p = 0.043$; Figure 2Bii) and low dispersal lines (mld = 210; GLMM mortality risk, $\beta = 0.58$, SE = 0.14, $p < 0.001$; Figure 2Bii).

Discussion

Our results show that aspects of mating behaviour, reproductive timing, development time, and longevity are covaried, with the tendency to initiate local dispersal by walking in *Tribolium castaneum*. Specifically, high dispersal propensity
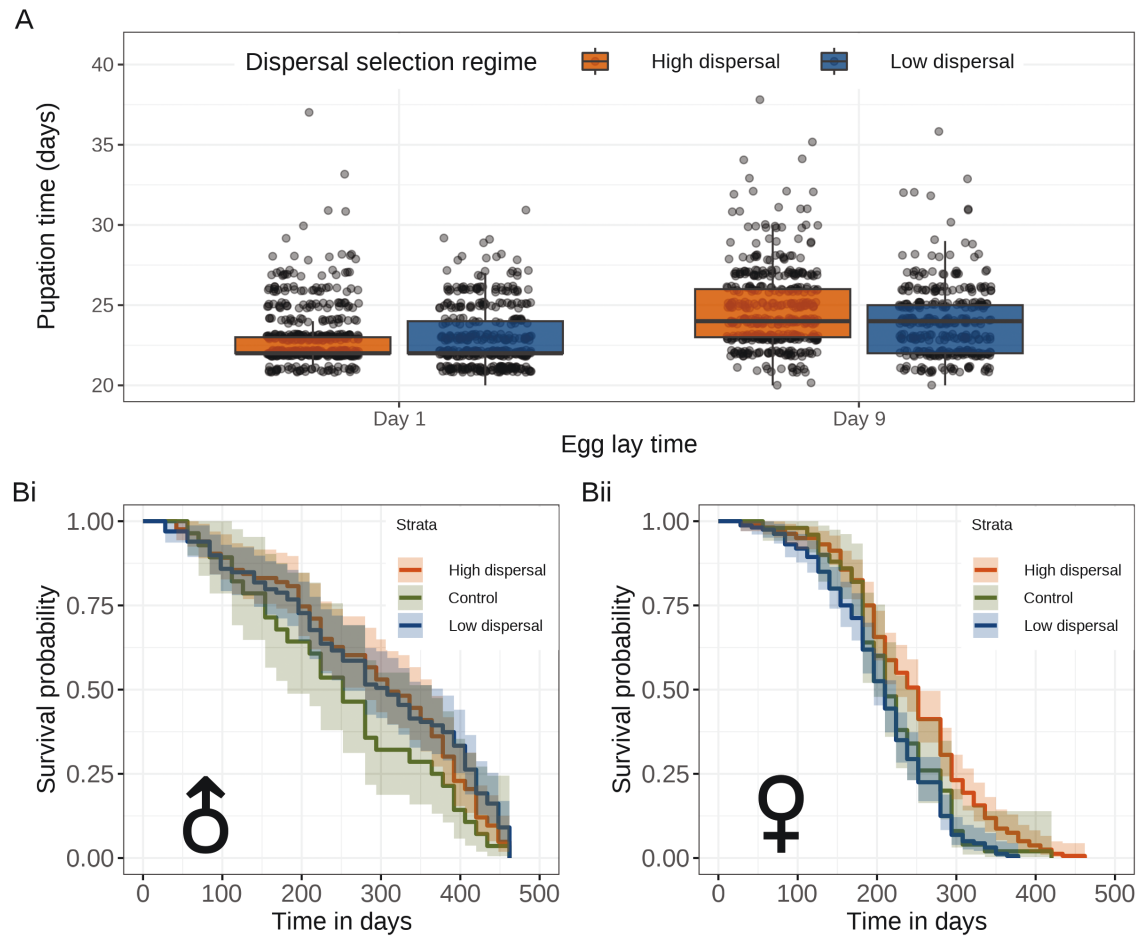
Figure 2. Life history traits in experimental lines of *Tribolium castaneum* selected for high or low dispersal behaviour. (A) Pupation time (days since the egg was laid) of offspring laid on either day 4 ± 2 or 13 ± 2 of adult life span (day 1 of oviposition period 1 and day 1 of oviposition period 2—these time points correspond to before and after the peak of dispersal in *Tribolium*), across dispersal regimes. (B) Survival probability across dispersal regimes for (i) males and (ii) females. Points are semi-transparent, so dark points indicate multiple overlapping points.

Table 2. GLM modelling the pupation time (days since the egg was laid) of offspring laid on either day 4 ± 2 or 13 ± 2 of adult life span across replicate lines selected for either high or low dispersal propensity.

	β	SE	*p*
Intercept	23.12	0.10	<0.001
Dispersal regime (low)	–0.14	0.15	0.34
Oviposition period (2)	1.66	0.15	<0.001
Dispersal regime (low): Period (2)	–0.64	0.22	0.004

Note. These time points correspond to day 1 of oviposition period 1 and day 1 of oviposition period 2, which are chosen to represent before and after the peak of dispersal in unselected *Tribolium* populations.

is significantly associated with fewer mating attempts, lower investment in early-life reproduction, slower development of later-laid offspring, and longer female life span.

Reproductive traits are commonly seen to vary with dispersal, and there are many possible reasons why mating behavior and dispersal might coevolve. For example, an individual might alter its reproductive environment through dispersal, changing the level of male–male competition or sexual antagonism it experiences. Alternatively, resources may need to be directed away from reproductive effort in preparation for

dispersal. Correlations in both directions exist between reproductive traits and dispersal among insects, e.g., mating frequency is higher for dispersive Glanville fritillary butterflies (*Melitaea cinxia*, Bonte and Saastamoinen 2012) but lower for more dispersive long-winged male crickets (*Velarifictorus* spp., Zeng & Zhu, 2012; Zhao et al., 2017). In *T. castaneum*, we observed fewer matings overall among the high dispersal phenotype. While total mating duration was equal across the high and low dispersal phenotypes, we observed fewer matings among the high dispersers, suggesting that each high dispersal line mating is of longer duration. There are a number of plausible explanations for this observation; similar patterns are seen in other beetle species, where the balance of mating duration and remating frequency is adjusted in response to investment in other physical or behavioural traits (Simmonds & Kotiaho, 2007; Yamane et al., 2010). More specifically, the longer mating duration could, for example, be driven by prolonged mate-guarding in these lines (Fedina & Lewis, 2008), potentially as a result of uncertainty about the mating environment in a post-dispersal habitat. Alternatively, greater investment in peri-copulatory mechanisms might compensate for poorer sperm competition of dispersers (Matsumura et al., 2019). This represents an interesting opportunity for further work to investigate questions such as whether sperm competitiveness differs with dispersal, whether the mating behaviour

Table 3. GLMM uses event history analysis to model longevity as mortality risk across time using a binomial distribution in lines of *Tribolium castaneum* artificially selected for dispersal propensity.

	Log odds	SE	z	Pr(>|z|)
(Intercept)	–2.58	0.37	–6.89	<0.001
Low dispersal	0.51	0.12	4.13	<0.001
Unselected dispersal control	0.35	0.17	1.98	0.047
Male	–0.72	0.15	–4.77	<0.001
Unselected dispersal control: Male	0.03	0.29	0.12	0.908
Low dispersal: Male	–0.63	0.20	3.09	0.002
(Intercept)	–2.07	0.38	–5.46	<0.001
High dispersal	–0.50	0.13	–3.91	<0.001
Unselected dispersal control	–0.16	0.18	–0.85	0.369
High dispersal: Male	0.63	0.20	3.10	<0.01
Unselected dispersal control: Male	0.69	0.30	2.33	0.024

Note. Data above the dashed line are from a model in which "high dispersal" was the reference category, below the dashed line "low dispersal" was the reference.

of males differs before and after the age of peak dispersal, and whether there is an effect of social environment on each reproductive strategy.

With regard to the reproductive output of females, in the present study, we saw no overall difference in the number of eggs laid between dispersal phenotypes, which aligns with the finding that reproductive output did not differ in *Tribolium* lines divergently selected specifically for walking distance (Matsumura & Miyatake, 2018). However, that study did not have a temporal component, whereas in the present study, we saw less investment in early reproduction in high dispersal lines. "Early" and "late" here, while both relatively early in the long lifetime of *Tribolium*, roughly coincide with before and after the age of peak dispersal, which occurs at ~10 days post-eclosion (Ziegler, 1976). Two possible, though not mutually exclusive, explanations for this observation are that (i) high investment in movement early in life reduces reproductive investment through energy constraint, and (ii) dispersers delay reproductive investment until after dispersal "in expectation" of finding a more favourable environment. Existing examples of delay in reproduction appear to be limited to flying insects and are attributed to energetic constraints (e.g., Zera & Zhao, 2006). However, in this case, the fact that total reproductive output is equal over both oviposition periods seems to lend support to the latter explanation. Similar findings have come from rhesus macaques (*Macaca mulatta*), where reproductive timing and dispersal are associated with the serotonin transporter gene genotype (Trefilov et al., 2000). This gene has been linked to aggressive behaviour and risk-taking, traits commonly seen as important elements of animal personality and behavioural syndromes (Roche et al., 2016). More research is required to uncover whether either i, ii, or both of these causes are driving reproductive timing differences between dispersal phenotypes, as well as the genetic and physiological mechanisms.

In our experiments focussed on development time, we observed no average difference in development time with dispersal phenotype over the whole laying period, in contrast to a previous study using *Tribolium*, which showed slower development of dispersers (Lavie & Ritte, 1978). However,

we found that eggs laid later developed more slowly, and this effect was strongest in high dispersal lines. It is likely that this pattern is driven by the effects of cannibalism acting at different strengths across different temporal and spatial scenarios. Evidence is provided by a study in which populations selected for increased population size also showed increased cannibalism and shorter development times (Wade, 1979). A similar pattern has been seen in invasive cane toad populations (*Rhinella marina*), where tadpoles in high-density populations evolved cannibalistic feeding behaviour and, in response, reduced development time (DeVore et al., 2021). However, while these examples are suggestive, the situation in *Tribolium* is very complex, and to confirm a causative role of cannibalism, more information is needed on the relative strengths of different types of cannibalism (larvae eating eggs, larvae eating pupae, adults eating eggs, adults eating pupae) in different dispersal contexts. Interestingly, our results show some agreement with an experimental evolution study in *Tribolium*, where dispersal and other traits were allowed to coevolve as a population expanded across a landscape of connected habitat patches (Weiss-Lehman et al., 2017). Here, populations at the range front evolved high dispersal and low intrinsic growth rates. Our finding is that development time increases post-dispersal in dispersive lines, which might contribute to low growth rates in range-front populations.

We found that highly dispersive females had greater longevity than females from low dispersal lines but saw no difference among males. This result was opposite to that found in the only previous comparable study (Lavie, 1981; further discussed below). Among insects, most data on dispersal and longevity suggests that highly dispersive individuals have shorter life spans (Hanski et al., 2006; Gu et al., 2006). However, as with other traits, those studies on insects overwhelmingly focus on species where flight is the major mode of movement and differences in energetic output between dispersal phenotypes are likely to be much more important than in *Tribolium*. Indeed, the *Tribolium* dispersal phenotype has been shown previously to lack any association with a higher metabolic rate (Arnold et al., 2017), which might be expected to lead to early mortality (Lints, 1989). Our own experimental lines show differences in dispersal-enhancing traits that would not be expected to require higher metabolic output, such as straightness of movement and disinclination to burrow (Pointer et al., in review). Rather, our findings fit better with the most common relationship between these traits more broadly across terrestrial animals, where longevity is higher in dispersers, potentially allowing a longer time in which to locate a suitable habitat patch (Stevens et al., 2014). This may be additionally explained by competitive pressures in *Tribolium*, where the particularly intense competition experienced by residents selects for competitive ability over the life span, and escape from this competition could allow longer life in dispersers. In other systems, highly competitive environments are shown to select for higher metabolic rates (Hack, 1997; Pettersen et al., 2020). That the effect is seen only in females is interesting. Male *T. castaneum* ordinarily live far longer than females, so the observed effect served to equalize the life span of the sexes in high dispersal lines. Possibly, female longevity is suppressed more than male longevity under high competition, for example, by the known effect of male harassment (e.g., Attia et al., 2023), and release from competition allows them to approach the greater life span of males.

Previous investigations into life history correlations with dispersal in *Tribolium* have either utilized poorly replicated selection lines generated under potentially unreliable methodologies (Ritte & Lavie, 1977; Lavie & Ritte, 1978; Lavie, 1981; Zirkle et al., 1988) or tested for associations with walking motivation as a proxy for dispersal, rather than dispersal per se (Matsumura & Miyatake, 2015, 2018). As well as serving as a robust, explicit test of a dispersal syndrome in *Tribolium*, we can compare the results of this study to previous work to assess the consistency of effects across independent studies using this system. Overall, our results conflict with those of earlier tests of life history traits using dispersal lines derived from Ritte and Lavie (1977), which found greater fecundity, faster development, and shorter life span among dispersers (Lavie & Ritte, 1978; Lavie, 1981; Zirkle et al., 1988). Some issues in the original selection experiment may contribute to these differences, as sample sizes were small (3 replicates per treatment vs. 16 in the present study), dispersal assays were conducted on groups of full siblings, and the strength of selection was highly inconsistent between generations (Ritte & Lavie, 1977). Nevertheless, it seems surprising that these methodological differences could flip the direction of relationships between traits. The present study finds greater agreement with work on lines selected for walking motivation by Matsumura and Miyatake (2015), who have subsequently shown that individuals with higher walking motivation have shorter matings and equal fecundity to those with lower walking motivation (Matsumura & Miyatake, 2018; Matsumura et al., 2019). In combination, data from these studies indicate that life history correlations in *Tribolium* are not necessarily robust to variations in methods used to generate and measure dispersal phenotypes. Consequently, the effects of all possible contributing factors must be considered when designing artificial selection regimes. We consider this study the most rigorous effort to date addressing these questions in the *Tribolium* system.

Taken together, our results suggest that correlations between life history traits and dispersal in *Tribolium* are qualitatively different from insects whose principal dispersal mode is by flight, where bioenergetic constraints are responsible for trade-offs. Instead, we suggest that the coevolution of life history and dispersal in *Tribolium* is shaped by dispersal, facilitating escape from intense intraspecific competition that characterizes the species' ecology (Dawson, 1977). It is important to note here that our investigations focus on emigration and walking movement as the mode of travel likely most relevant within temperature-controlled food storage facilities. It is possible that experimental selection on flight might uncover a set of correlations and trade-offs more akin to those seen in flying insects, but this is beyond the scope of the current study.

The observation of associations between traits inevitably raises questions about the mechanistic basis of such patterns. Genetic correlations between life history traits may be due to linkage-disequilibrium between causal loci or because of pleiotropy with key genes underlying multiple traits. Characterizing correlations in our *T. castaneum* lines opens up the potential for investigating the links between traits using molecular genomics. Current theory suggests that the genetic basis of *Tribolium* dispersal is relatively simple (Ritte & Lavie, 1977; Pointer et al., 2023) or at least involves only a few genes of large effect. Major effect loci implicated in dispersal and life history variation in insects are known

(Saastamoinen et al., 2018), the best-studied example being the Pgi locus in the Glanville Fritillary butterfly (Klemme & Hanski, 2009; Niitepõld & Saastamoinen, 2017). However, the most comprehensive studies are in *Drosophila* and have identified hundreds of genes differentially expressed in common between lines independently artificially selected for aggression, mating behaviour and locomotor activity (Jordan et al., 2007). Resolving the genetic basis of dispersal and its association with life history variation may be highly instructive in considering how these traits evolve and how they may be managed.

Overall, our findings suggest that correlated intraspecific variation in local dispersal and related traits may represent alternative life history strategies in *T. castaneum*. We therefore suggest that pest management efforts to mitigate the species' agro-economic impact should consider the eco-evolutionary dynamics within multiple life histories. The benefits of doing so could be felt both through improved targeting of efforts to reduce spread and also in forecasting how the selection pressures applied through pest management are likely to affect pest evolution.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

Raw data files used in this study can be found on Dryad 10.5061/dryad.j6q573nn8 Representative image files can be found on Zenodo at https://doi.org/10.5281/zenodo.10852855.

Author contributions

Michael Pointer (Conceptualization [equal], Formal analysis [lead], Investigation [lead], Methodology [lead], Project administration [equal], Validation [equal], Visualization [lead], Writing—original draft [lead], Writing—review & editing [lead]), Lewis Spurgin (Conceptualization [equal], Investigation [supporting], Supervision [supporting], Writing—review & editing [supporting]), Mark McMullan (Conceptualization [supporting], Supervision [supporting], Writing—review & editing [supporting]), Simon Butler (Conceptualization [supporting], Supervision [supporting], Writing—review & editing [supporting]), and David Richardson (Conceptualization [supporting], Formal analysis [supporting], Investigation [supporting], Project administration [equal], Supervision [lead], Writing—review & editing [equal])

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None declared.

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