Title: Selection for greater dispersal in early life leads to increased rate of age-dependent decline in locomotor activity and shorter lifespan

Authors: Ruchitha BG[1,2], Nishant Kumar[1], Chand Sura[1], Sudipta Tung[1]*

Affiliations:

1. Integrated Genetics and Evolution Laboratory (IGEL), Department of Biology, Ashoka University, Sonipat, Haryana, India, 131029.
2. Indian Institute of Science Education and Research (IISER) Pune, Pune, Maharashtra, India, 411008.

1. ruchitha.bg@students.iiserpune.ac.in
2. nishant.kumar@ashoka.edu.in
3. chand@ashoka.edu.in
4. sudipta.tung@ashoka.edu.in

Running title: Dispersal evolution accelerates functional senescence

Key words: Locomotor activity, *Drosophila melanogaster*, functional senescence, relaxed evolution, common garden, invasion risk

* **Name and address of the corresponding author:**

Sudipta Tung
DBT/Wellcome Trust India Alliance Early Career Fellow
Department of Biology, Ashoka University
Plot No. 2, Rajiv Gandhi Education City,
Post Office Rai, Near Rai Police Station,
Sonipat, Rai, Haryana, India 131029

Tel: +91-130 2300669
Email: sudipta.tung@ashoka.edu.in

Author contributions: RBG and ST formulated the study. RBG, NK, CS, and ST carried out the experiments. RBG and ST analyzed the data. ST and RBG wrote the manuscript with inputs from the other authors.

Acknowledgements
The authors thank Prof. Sutirth Dey from Indian Institute of Science Education and Research (IISER)-Pune for kindly providing us the experimental populations. The authors also thank Prof. Dey and Akhila Mudunuri for their valuable comments on an earlier version of the manuscript. RBG acknowledges the support from Kishore Vaigyanik Protsahan Yojana (KVPY) fellowship, NK and CS acknowledge the support of the Research and Development Office, Ashoka University. ST acknowledges the support of DBT/Wellcome Trust India Alliance Early Career Fellowship (#IA/E/18/1/504347) and Ashoka University. The authors declare no conflict of interest.

Abstract

Locomotor activity is one of the major traits that is affected by age. Greater locomotor activity is also known to evolve in the course of dispersal evolution. However, the manner in which dispersal evolution genetically alters the aging profile of locomotor activity, and whether the nature of this profile varies in the two sexes of sexually dimorphic organisms are largely unknown. Moreover, little is known regarding the fate of the evolved dispersal-associated traits, when the selection pressure for dispersal ceases to exist for several generations. We addressed these knowledge gaps using large outbred populations of Drosophila melanogaster, which evolved greater locomotor activity in their early life as a correlated response to early life selection for increased dispersal. For this, we maintained the selected and ancestry-matched control populations under identical conditions for nine generations in absence of dispersal selection. Subsequently, we tracked locomotor activity of individual flies of both sexes at regular intervals until a late age. Longevity of these flies was also recorded. Interestingly, we found that locomotor activity declines with age in general, but dispersal selected populations show a greater level of activity at all ages compared to the controls. More importantly, the rate of age-dependent decline in activity of the dispersal selected population was found to be much larger; while the two sexes perform similarly with respect to the ageing profile of activity. Dispersal selected populations were also found to have a shorter lifespan as compared to the control, a likely cost of elevated level of activity throughout their life. These results are crucial in the context of invasion biology as contemporary climate change, habitat degradation, and destruction provide congenial conditions for dispersal evolution. Such controlled and tractable studies investigating the ageing pattern of important functional traits are important in the field of biogerontology as well, which looks into improving the biological quality of life during late-life by postponing the onset of senescence.

Introduction

Dispersal is a central life-history trait (Bonte & Dahirel 2017). At an individual level, it can confer survival advantage against proximate environmental stresses (Studds *et al.* 2008), as well as reproductive advantage through a greater prospect of finding mates and suitable breeding grounds in case of sexually reproducing organisms (Greenwood & Harvey 1982; Studds *et al.* 2008). At the population level, it modulates the tempo and extent of adaptive dynamics by affecting the degree of gene flow between populations (Lenormand 2002; Garant *et al.* 2007). Dispersal also shapes local ecology by influencing processes such as, *inter alia*, territoriality, range expansion, species invasion, etc. (Hargreaves & Eckert 2014; Andrade-Restrepo *et al.* 2019).

It has been demonstrated both theoretically and empirically that the dispersal properties of individuals can evolve rather rapidly in the presence of suitable selection pressure (Alex Perkins *et al.* 2013; Huang *et al.* 2015; Ochocki & Miller 2017; Tung *et al.* 2018b). Notably, dispersal is known to have strong associations with a number of traits of an individual, such as locomotor activity, aggression, body size, boldness, etc. (Wahlström 1994; Michelangeli *et al.* 2017; Searcy *et al.* 2018; McGhee *et al.* 2021; Wu & Seebacher 2022), which are collectively known as dispersal syndrome. Consequently, these traits also often evolve as a result of dispersal evolution (Fjerdingstad *et al.* 2007; Tung *et al.* 2018a). Such changes in organismal trait distributions can lead to the evolution of organisms with combinations of dispersal and dispersal syndromic traits with significantly higher potential for range expansion and biological invasion, and thereby threaten local ecological stability (Lambrinos 2004; Alex Perkins *et al.* 2013; Renault *et al.* 2018). Thus, not surprisingly, investigating different aspects of dispersal evolution is a prime focus among contemporary ecologists, evolutionary biologists, and conservation biologists alike.

Although the causes, mechanisms, and proximate consequences of dispersal evolution are well researched, its long-term impacts on the evolved populations are poorly understood. For example, the selection for dispersal is not always going to be equally strong because of the changes of dispersal conditions. It is not clear what would be the fate of dispersal and its associated evolved traits when the selection pressure for greater dispersal weakens substantially or altogether ceases to exist over several generations. Intuitively, under relaxed selective pressure, an evolved trait will recede in magnitude if the expression of the trait is costly (Teotónio & Rose 2001). But it is demonstrated repeatedly both in natural populations (Lahti *et al.* 2009) and laboratory experiments (Bryant & Reed 1999; Dapper & Wade 2020) that the evolutionary trajectory of a trait can be complex when it loses its advantageous contribution to the organismal fitness. Moreover, the existing literature does not give us a clear and consistent idea of life-history trade-offs and energetic costs of dispersal and other dispersal syndromes (Ronce & Clobert 2012; Mishra *et al.* 2018). Thus, an a priori long-term prediction in this regard becomes counterproductive. Additionally, within the timescale of the lifespan of an organism, the rate of aging of relevant traits is critically important to realize invasive potential of the species. But, the impact of dispersal evolution on the age-dependent decline of functional status of individual traits, also known as functional senescence (Grotewiel *et al.* 2005), is rarely investigated. This is particularly important for situations, where the environmental selection pressure compels the organisms to disperse in their early-life.

Functional senescence can be characterized as a decrease in the physical and mental capabilities of an individual owing to an age-dependent decline in the performance of different organ systems and body functionalities, ultimately resulting in death (Grotewiel *et*

al. 2005). In the case of humans, one of the major challenges faced by aging individuals is the impairment of locomotor activity (McGibbon & Krebs 2004), which is a prominent dispersal syndromic trait that evolves as a correlated response to dispersal evolution. Although the performance of physical activity is known to deteriorate with age in humans, observations in model organisms are not as obvious. For example, senescence-accelerated mice (Miyamoto *et al.* 1986), and rabbits in open-field tests (Deyo *et al.* 1989), have both shown an increase in activity with age. In mice and rhesus monkeys, a decrease in activity with age has been observed (Dean *et al.* 1981; Emborg *et al.* 1998); whereas, no significant change has been seen in the age-dependent activity of cats (Nagahara & Handa 1997). In rats, both decline (Goodrick 1971) and no change (Levine *et al.* 1987) in locomotor activity across age has been reported. In the case of *Drosophila melanogaster*, Le Bourg (1987) has shown an age-dependent decrease in activity in females, and an increase in activity in males till 5 weeks of age followed by an activity decline. However, some studies have shown that such sexual dimorphism in the age-dependent activity of *Drosophila* is strongly influenced by the genotype of the flies used (van Dijken *et al.* 1979; Fernández *et al.* 1999). Thus, it is far from our understanding of how locomotor activity changes with age in sexually dimorphic organisms, and how that age-dependent patterns alters in individuals of populations that evolved greater locomotor activity as a by-product of selection for greater dispersal in their early life.

Here we have addressed this knowledge gap using a large, outbred, laboratory-maintained population of *Drosophila melanogaster* that was selected for greater dispersal in its early-life for about seven years (153 generations). Locomotor activity was found to have increased in response to selection for dispersal in these populations. To test the consequences of relaxation of selection pressure for dispersal on locomotor activity, we compared this trait between the evolved population and its ancestry matched control after maintaining both populations under identical maintenance regimes in absence of any selection for dispersal for nine generations *i.e.* about five months. Further, the aging profile of the evolved and the control populations were compared for males and females at five time-points across age to understand how functional senescence of locomotor activity in these flies is impacted by the evolution of dispersal. Moreover, we compared the longevity of the evolved and the control population to understand the impact of functional ageing of locomotor activity on their lifespan.

Methods

For this experiment, we used a large (n = ~2400), outbred, laboratory-maintained population of *Drosophila melanogaster* (VB_2) that was selected for greater dispersal propensity and ability for 153 generations (>6 years), and its ancestry-matched control (VBC_2) population. For the ease of readability, henceforth we shall denote the dispersal-selected VB_2 population as D and the corresponding control VBC_2 population as the C population. Details of the selection protocol and maintenance regime of these populations were reported previously (Tung *et al.* 2018b). Briefly, the D and C populations were maintained in 15-day discrete generation cycles on a standard banana-jaggery medium (following the recipe of Sheeba & Joshi 1998) at 25°C, with constant light. On the 12th day from the day of egg collection, the D population was subjected to a three-compartment source-path-destination dispersal selection setup, and only the most dispersive half of the population (the first 50% of the population reaching the destination) was allowed to lay eggs for the next generation. C population was not subjected to selection for dispersal, but the rest of the rearing conditions were identical to that of the D population.

Prior to this experiment, selection pressure for dispersal was relaxed for nine generations, and D and C populations were maintained identically. In order to generate experimental flies for each population, ~300 eggs were collected in polypropylene drosophila-bottles (Laxbro® #FLBT20) containing 50mL banana-jaggery food. Three such replicates were made for each population. From the three bottles, 30 individuals of each sex were chosen at random during the P13-P15 stage of pupa and hosted individually in glass vials containing ~4mL of food and incubated at 25°C. On eclosion, these 120 virgin adult flies (*i.e.* 30 individuals per sex per population) were checked daily for their viability until death, and their age-dependent locomotor activity was tracked by measuring the trait at predetermined age-points. The flies were provided fresh food every alternate day, while strictly maintaining their vial identity.

We measured locomotor activity of these flies on the 12th, 26th, 33rd, 40th, and 47th day from the day of egg collection using Drosophila Activity Monitoring (DAM2) data collection system (Trikinetics Inc, Waltham, MA). Figure S1 shows a schematic diagram of the experimental design. On the specified days of activity measurement, flies were introduced into labeled, clean glass tubes (diameter: 5 mm, length: 8 cm), without CO_2 anesthesia. Each glass tubes contained 1.5% w/vol agar and sealed with parafilm on one end and secured with cotton plug on the other. Activity was recorded for the next 4h and 5mins. At the end of the recording, the flies were transferred back to the corresponding labelled glass vials with food. For the analysis, we excluded the activity data of the first 5mins and the subsequent 4h data was used to calculate per hour activity. Then this data was subjected to 2-way repeated measure ANOVA with Selection (D vs. C) and Sex (male vs. female) as fixed factors, and Age (12, 26, 33, 40, and 47) as the repeated measure.

We further estimated the slope of the age-dependent activity profile (*i.e*. activity vs age) of all the flies that lived at least until the second age-point using linear regression, and this data was statistically analysed using a full-factorial 2-way fixed factor ANOVA with Selection (D vs. C) and Sex (male vs. female) being the fixed factors.

As mentioned before, the viability of each fly was tracked until they died, and this lifespan data was subjected to a full-factorial 2-way fixed factor ANOVA with Selection (D vs. C) and Sex (male vs. female) being the fixed factors.

In further support of the outcome of the above experiment, we tracked locomotor activity of four independent but identically maintained, large, outbred, dispersal-selected populations VB_{1-4} across age and contrasted the same against their ancestry-matched control VBC_{1-4} populations (Tung *et al.* 2018b). Here we measured activity on the 12th, 26th, 40th, and 47th day from the day of egg collection following the similar procedure as above, except here on each day we randomly sampled 32 flies of each sex from each of these eight populations (~2400 adults on the 12th day in each population) for this measurement. For statistical analysis, mean population-level data obtained from this experiment were subjected to a 2-way repeated measure ANOVA with Selection (D vs. C) and Sex (male vs. female) as fixed factors, and Age (12, 26, 40, and 47) as the repeated measure. A detailed experimental protocol can be found in the online supplementary material Text S1.

Results and discussion

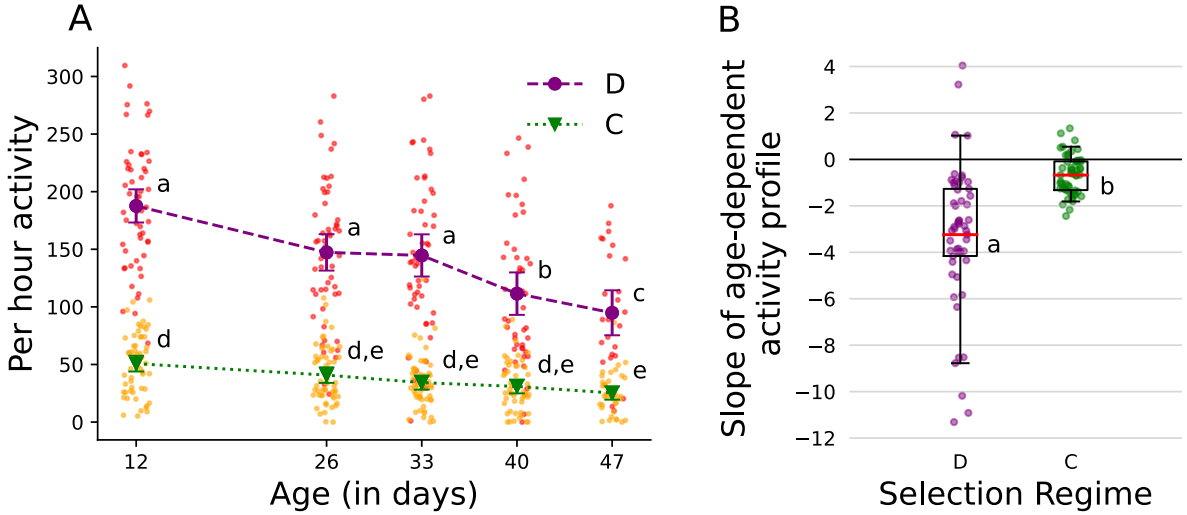


Figure 1. Age-dependent decline of locomotor activity. (A) Mean (±SEM) locomotor activity of individuals from dispersal selected D (purple circle) and its ancestry-matched control C (green inverted triangle) population are plotted against age, measured in days from the time of egg collection. Activity level of each individual at the tested age-point of D and C population are represented as red and yellow scatter points respectively. (B) Boxplot represents the slope of the linear regression of locomotor activity of each individual with age. The red line, lower and upper edge of the box, lower and upper end of the whiskers represent mean, 25th, 75th, 5th, 95th percentile of the locomotor activity data respectively. The scatter points denote slope of the regression line for each individual of the dispersal selected D (purple) and C (green) population. Different lower-case alphabets denote statistically significant differences ($p<0.05$).

Our result suggests that even after nine generations of relaxation of dispersal selection pressure, the dispersal-selected D population had a significantly elevated level of locomotor activity (Figure 1A, $F_{1,60} = 244.3$, $p < 0.00001$), which evolved as a correlated response to dispersal evolution (Tung *et al.* 2018a). This is consistent with an independent observation with these flies that the elevated level of locomotor activity persists even after 20 generations of relaxation of dispersal selection (unpublished data). These results suggest that once evolved, dispersal-associated traits such as locomotor activity can remain elevated even when the fitness advantage of dispersal phenotype no longer exists for several generations. This indicates that either the genetic variation for this trait has reduced to zero in course of selection, or maintaining the elevated level of this trait without an obvious selective advantage is not costly enough. The likelihood of the first possibility is less because even with negligible environmental variation under precisely controlled laboratory conditions we observed substantial phenotypic variation for locomotor activity of the individuals in the dispersal-selected population (Figure 1A and Figure S2), which can mostly be attributed to the genetic variation for this trait across individuals. This points toward the second possibility that under suitable environmental conditions, dispersal-associated traits such as locomotor activity can persist for a long time due to no apparent selective disadvantage against this trait. This is further supported by the fact that the dispersal-selected populations did not show any life history trade-off till the last published report (Tung *et al.* 2018a). This inference is important from a species-conservation point of view because locomotor activity has been implicated in the invasive potential of species (Llewelyn *et al.* 2010).

In terms of senescence of locomotor activity, we found that activity declines in these flies with age irrespective of the population they come from (Figure 1A). This is similar to the deterioration of performance of physical activity with age in humans (McGibbon & Krebs 2004; Kulmala *et al.* 2014), and also in accord with the observation in other model organisms such as mice and rhesus monkeys, where a decrease in activity with age has been observed (Dean *et al.* 1981; Emborg *et al.* 1998).

Interestingly, Figure 1A indicates that the rate of decline is steeper in the dispersal-selected population, which indeed led to a significant selection×age interaction ($F_{4,240}$ = 12.2, p <0.00001). To compare the rate of activity decline formally, we calculated the slope of locomotor activity of each individual of both the populations across age points. We found that the slopes of D individuals were significantly more negative than that of the C population ($F_{1,103}$ = 30.8, p <0.00001; Figure 1B), indicating accelerated functional senescence have evolved as a correlated response to dispersal evolution. This pattern is similar in males and females leading to the three-way selection×age×sex interaction being nonsignificant ($F_{4,240}$ = 0.8, p = 0.52). It is also worth noting that although locomotor activity senesces at an accelerated rate in the dispersal-selected population, these individuals have a higher absolute level of activity compared to the controls at all the measured age-points (Tukey p for D vs. C at all age points = 0.00001; Figure 1A). These broad trends remain consistent when age-dependent locomotor activity levels of flies from four independent dispersal-selected populations were compared with their ancestry-matched controls at the population level (Figure S2). Further, it is noteworthy that the selected population also had a shorter lifespan as compared to the control (Figure 2).

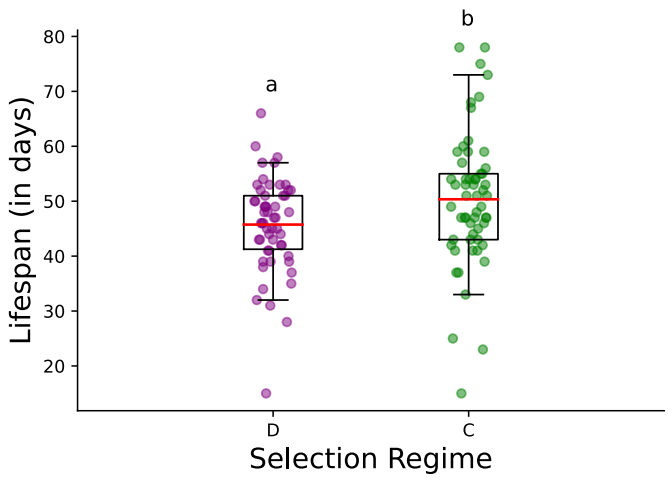


Figure 2. Lifespan of dispersal selected and control population. In the box plot, the red line, lower and upper edge of the box, lower and upper end of the whiskers represent mean, 25th, 75th, 5th, 95th percentile of the longevity data respectively. The scatter points denote longevity of each individual of the dispersal selected D (purple) and C (green) population. Different lower-case alphabets denote statistically significant differences (p<0.05).

Several important insights can be inferred from the above observations. Firstly, here we found a clear life-history trade-off of dispersal evolution in terms of reduced lifespan. This result is in line with the observation in neotropical butterflies, where a higher dispersal rate was associated with decreased longevity (Tufto *et al.* 2012). But, one may expect that this

dispersal-longevity trade-off should lead to a rapid decline of dispersal and dispersal associated traits such as locomotor activity upon relaxation of selection for greater dispersal. Contrary to this expectation, greater locomotor activity persists even after nine generations of relaxation of dispersal selection. This apparent discrepancy resolves by noting that these experimental flies are maintained in a 15-day discrete-generation lifecycle, and therefore, the dispersal-selected flies never realize their entire lifespan in this laboratory condition. However, understandably, the consequences of this trade-off can be different in natural settings, where they can reproduce and pass on their genes throughout their lifespan.

Secondly, it is worth noting that in a previous study on the same populations (Tung *et al.* 2018b), the difference between the selected and control populations in terms of dispersal ability and propensity was apparent as early as after 10 generations of selection. However, the lifespan of the dispersal-selected and control populations were not significantly different, although there was a trend (Figure 3C in ref Tung *et al.* 2018a). Whereas, the same trade-off became apparent after 153 generations of dispersal selection. This is an excellent demonstration of the fact that the rate of evolution of the correlated traits can differ drastically compared to the traits which are under direct selection. Further, it also highlights that the trait correlations observed in the short-term can change over a longer evolutionary timescale.

Thirdly, although the dispersal-selected individuals die early, their level of locomotor activity is much higher than the controls at all measured age-points. This indicates that the metabolic remodelling due to dispersal evolution has led to constitutively elevated expression of locomotor activity in the selected flies throughout their life. This pattern is identical for males and females. From prior research it is known that higher locomotor activity promotes mating success due to an elevated courtship behaviour (Kyriacou 1981; Cobb *et al.* 1987) and aids females to find suitable oviposition sites (Ferguson *et al.* 2015). Thus, taken together, all else being equal, elevated locomotor activity in the dispersal-selected populations should enable them to achieve a greater lifelong reproductive success in natural settings.

Finally, the evolution of accelerated senescence because of selection for dispersal in the early life, and the concomitant shortening of lifespan are rather intriguing. Although we do not have direct evidence for a mechanistic explanation behind these observations, here we provide three likely mechanisms that could have led to this observation. Firstly, the dispersal-selected flies were reported to have evolved an elevated level of metabolite 3-HK (Tung *et al.* 2018a), which is associated with age-dependent neural degeneration in *Drosophila* (Savvateeva *et al.* 2000) and hence the greater rate of neuromuscular impairment, leading to deterioration of locomotor activity and overall reduced lifespan. Secondly, the selected files were found to have a greater level of cellular respiration resulting in an elevated level of ATP in these flies (Tung *et al.* 2018a). It is also known that free radicals are produced during ATP production via oxidative phosphorylation in mitochondria (Cadenas & Davies 2000). Thus, the accelerated rate of ageing could be a result of increased oxidative stress due to an elevated rate of accumulation of reactive free radicals in dispersal-selected flies. Thirdly, *Drosophila* insulin-TOR signalling pathways are known to affect cardiac functional aging, and thereby shorten lifespan (Wessells *et al.* 2009). Systemic glucose level is reported to be higher in dispersal-selected flies (Tung *et al.* 2018a), which can lead to relatively greater activation of insulin-TOR signalling pathways in these flies resulting in faster senescence. Further targeted experiments are needed to dissect which of these mechanisms or if a combination of all are applicable here.

To summarize, evolutionary history affects age-dependent locomotor activity in flies. We see that a correlated increase in locomotor activity due to dispersal selection does not disappear even after nine generations of removal of selection pressure. Additionally, the increased locomotor activity remains higher than that of the control population until rather late ages. Moreover, we found that the dispersal-selected flies have a shorter lifespan. However, whether this shortening of lifespan is a cost of increased locomotor activity, or a consequence of metabolic remodelling due to dispersal evolution remains to be determined. Age-dependent decline of life-history and behavioural traits in the context of dispersal evolution will have serious implications in terms of species invasion, range expansion, disease spread and population stability. A thorough understanding of this is pertinent in the current setting, where rampant habitat degradation and destruction, and rapid climate change provide a distinct evolutionary advantage to better dispersers.

References

Alex Perkins, T., Phillips, B.L., Baskett, M.L. & Hastings, A. (2013). Evolution of dispersal and life history interact to drive accelerating spread of an invasive species. *Ecol. Lett.*, 16, 1079–1087.

Andrade-Restrepo, M., Champagnat, N. & Ferrière, R. (2019). Local adaptation, dispersal evolution, and the spatial eco-evolutionary dynamics of invasion. *Ecol. Lett.*, 22, 767–777.

Bonte, D. & Dahirel, M. (2017). Dispersal: a central and independent trait in life history. *Oikos*, 126, 472–479.

Bryant, E.H. & Reed, D.H. (1999). Fitness Decline under Relaxed Selection in Captive Populations. *Conserv. Biol.*, 13, 665–669.

Cadenas, E. & Davies, K.J. (2000). Mitochondrial free radical generation, oxidative stress, and aging. *Free Radic. Biol. Med.*, 29, 222–230.

Cobb, M., Connolly, K. & Burnet, B. (1987). The relationship between locomotor activity and courtship in the melanogaster species sub-group of Drosophila. *Anim. Behav.*, 35, 705–713.

Dapper, A.L. & Wade, M.J. (2020). Relaxed Selection and the Rapid Evolution of Reproductive Genes. *Trends Genet.*, 36, 640–649.

Dean, R.L., Scozzafava, J., Goas, J.A., Regan, B., Beer, B. & Bartus, R.T. (1981). Age-related differences in behavior across the life span of the C57BL/6J mouse. *Exp. Aging Res.*, 7, 427–451.

Deyo, R.A., Straube, K.T., Moyer, J.R. & Disterhoft, J.F. (1989). Nimodipine ameliorates aging-related changes in open-field behaviors of the rabbit. *Exp. Aging Res.*, 15, 169–175.

van Dijken, F.R., van Sambeek, M.P.J.W. & Scharloo, W. (1979). Divergent selection on locomotor activity in Drosophila melanogaster. III. Genetic analysis. *Behav. Genet.*, 9, 563–570.

Emborg, M.E., Ma, S.Y., Mufson, E.J., Levey, A.I., Taylor, M.D., Brown, W.D., *et al.* (1998). Age-related declines in nigral neuronal function correlate with motor impairments in rhesus monkeys. *J. Comp. Neurol.*, 401, 253–265.

Ferguson, C.T.J., O'Neill, T.L., Audsley, N. & Isaac, R.E. (2015). The sexually dimorphic behaviour of adult Drosophila suzukii: elevated female locomotor activity and loss of siesta is a post-mating response. *J. Exp. Biol.*, 218, 3855–3861.

Fernández, J.R., Grant, M.D., Tulli, N.M., Karkowski, L.M. & McClearn, G.E. (1999). Differences in locomotor activity across the lifespan of Drosophila melanogaster☆. *Exp. Gerontol.*, 34, 621–631.

Fjerdingstad, E.J., Schtickzelle, N., Manhes, P., Gutierrez, A. & Clobert, J. (2007). Evolution of dispersal and life history strategies – Tetrahymena ciliates. *BMC Evol. Biol.*, 7, 133.

Garant, D., Forde, S.E. & Hendry, A.P. (2007). The Multifarious Effects of Dispersal and Gene Flow on Contemporary Adaptation. *Funct. Ecol.*, 21, 434–443.

Goodrick, C.L. (1971). Free Exploration and Adaptation Within an Open Field as a Function of Trials and Between-Trial-Interval for Mature-Young, Mature-Old, and Senescent Wistar Rats. *J. Gerontol.*, 26, 58–62.

Greenwood, P.J. & Harvey, P.H. (1982). The Natal and Breeding Dispersal of Birds. *Annu. Rev. Ecol. Syst.*, 13, 1–21.

Grotewiel, M.S., Martin, I., Bhandari, P. & Cook-Wiens, E. (2005). Functional senescence in Drosophila melanogaster. *Ageing Res. Rev.*, 4, 372–397.

Hargreaves, A.L. & Eckert, C.G. (2014). Evolution of dispersal and mating systems along geographic gradients: implications for shifting ranges. *Funct. Ecol.*, 28, 5–21.

Huang, F., Peng, S., Chen, B., Liao, H., Huang, Q., Lin, Z., *et al.* (2015). Rapid evolution of dispersal-related traits during range expansion of an invasive vine Mikania micrantha. *Oikos*, 124, 1023–1030.

Kulmala, J.-P., Korhonen, M.T., Kuitunen, S., Suominen, H., Heinonen, A., Mikkola, A., *et al.* (2014). Which muscles compromise human locomotor performance with age? *J. R. Soc. Interface*, 11, 20140858.

Kyriacou, C.P. (1981). The relationship between locomotor activity and sexual behaviour in ebony strains of Drosophila melanogaster. *Anim. Behav.*, 29, 462–471.

Lahti, D.C., Johnson, N.A., Ajie, B.C., Otto, S.P., Hendry, A.P., Blumstein, D.T., *et al.* (2009). Relaxed selection in the wild. *Trends Ecol. Evol.*, 24, 487–496.

Lambrinos, J.G. (2004). How Interactions Between Ecology and Evolution Influence Contemporary Invasion Dynamics. *Ecology*, 85, 2061–2070.

Le Bourg, E. (1987). The rate of living theory. Spontaneous locomotor activity, aging and longevity in Drosophila melanogaster. *Exp. Gerontol.*, 22, 359–369.

Lenormand, T. (2002). Gene flow and the limits to natural selection. *Trends Ecol. Evol.*, 17, 183–189.

Levine, M.S., Lloyd, R.L., Fisher, R.S., Hull, C.D. & Buchwald, N.A. (1987). Sensory, motor and cognitive alterations in aged cats. *Neurobiol. Aging*, 8, 253–263.

Llewelyn, J., Phillips, B.L., Alford, R.A., Schwarzkopf, L. & Shine, R. (2010). Locomotor performance in an invasive species: cane toads from the invasion front have greater endurance, but not speed, compared to conspecifics from a long-colonised area. *Oecologia*, 162, 343–348.

McGhee, K.E., Barbosa, A.J., Bissell, K., Darby, N.A. & Foshee, S. (2021). Maternal stress during pregnancy affects activity, exploration and potential dispersal of daughters in an invasive fish. *Anim. Behav.*, 171, 41–50.

McGibbon, C.A. & Krebs, D.E. (2004). Discriminating age and disability effects in locomotion: neuromuscular adaptations in musculoskeletal pathology. *J. Appl. Physiol.*, 96, 149–160.

Michelangeli, M., Smith, C.R., Wong, B.B.M. & Chapple, D.G. (2017). Aggression mediates dispersal tendency in an invasive lizard. *Anim. Behav.*, 133, 29–34.

Mishra, A., Tung, S., Shreenidhi, P.M., Aamir Sadiq, M., Shree Sruti, V.R., Chakraborty, P.P., *et al.* (2018). Sex differences in dispersal syndrome are modulated by environment and evolution. *Philos. Trans. R. Soc. B Biol. Sci.*, 373, 20170428.

Miyamoto, M., Kiyota, Y., Yamazaki, N., Nagaoka, A., Matsuo, T., Nagawa, Y., *et al.* (1986). Age-related changes in learning and memory in the senescence-accelerated mouse (SAM). *Physiol. Behav.*, 38, 399–406.

Nagahara, A.H. & Handa, R.J. (1997). Age-related changes in c-fos mRNA induction after open-field exposure in the rat brain. *Neurobiol. Aging*, 18, 45–55.

Ochocki, B.M. & Miller, T.E.X. (2017). Rapid evolution of dispersal ability makes biological invasions faster and more variable. *Nat. Commun.*, 8, 14315.

Renault, D., Laparie, M., McCauley, S.J. & Bonte, D. (2018). Environmental Adaptations, Ecological Filtering, and Dispersal Central to Insect Invasions. *Annu. Rev. Entomol.*, 63, 345–368.

Ronce, O. & Clobert, J. (2012). Dispersal syndromes. In: *Dispersal Ecology and Evolution* (eds. Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M.). Oxford University Press, pp. 119–138.

Savvateeva, E., Popov, A., Kamyshev, N., Bragina, J., Heisenberg, M., Senitz, D., *et al.* (2000). Age-dependent memory loss, synaptic pathology and altered brain plasticity in the Drosophila mutant cardinal accumulating 3-hydroxykynurenine. *J. Neural Transm.*, 107, 581–601.

Searcy, C.A., Gilbert, B., Krkošek, M., Rowe, L. & McCauley, S.J. (2018). Positive correlation between dispersal and body size in Green Frogs (Rana clamitans) naturally colonizing an experimental landscape. *Can. J. Zool.*, 96, 1378–1384.

Sheeba, V. & Joshi, A. (1998). A test of simple models of population growth using data from very small populations of Drosophila melanogaster. *Curr. Sci.*, 75, 1406–1410.

Studds, C.E., Kyser, T.K. & Marra, P.P. (2008). Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. *Proc. Natl. Acad. Sci.*, 105, 2929–2933.

Teotónio, H. & Rose, M.R. (2001). Perspective: Reverse Evolution. *Evolution*, 55, 653–660.

Tufto, J., Lande, R., Ringsby, T.-H., Engen, S., Sæther, B.-E., Walla, T.R., *et al.* (2012). Estimating Brownian motion dispersal rate, longevity and population density from spatially explicit mark–recapture data on tropical butterflies. *J. Anim. Ecol.*, 81, 756–769.

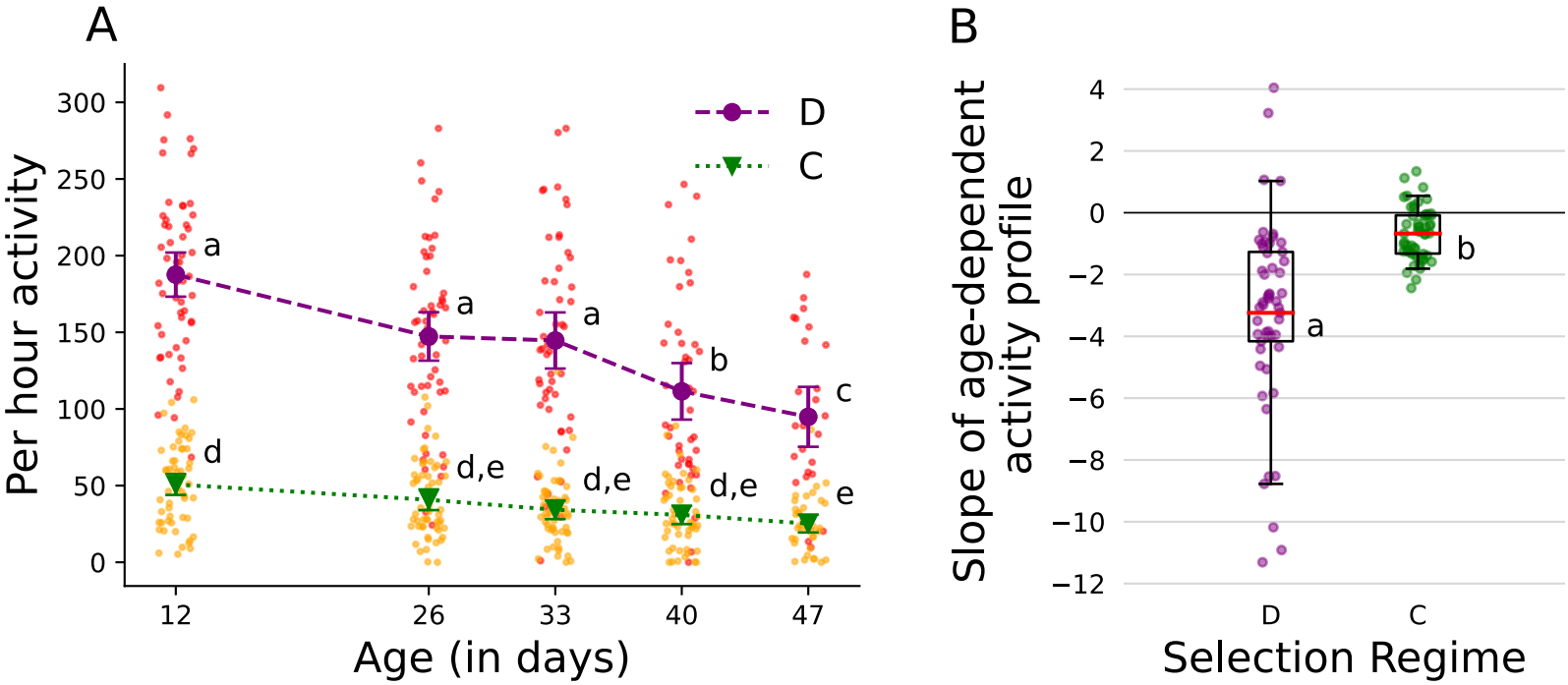
Tung, S., Mishra, A., Gogna, N., Aamir Sadiq, M., Shreenidhi, P.M., Shree Sruti, V.R., *et al.* (2018a). Evolution of dispersal syndrome and its corresponding metabolomic changes. *Evolution*, 72, 1890–1903.

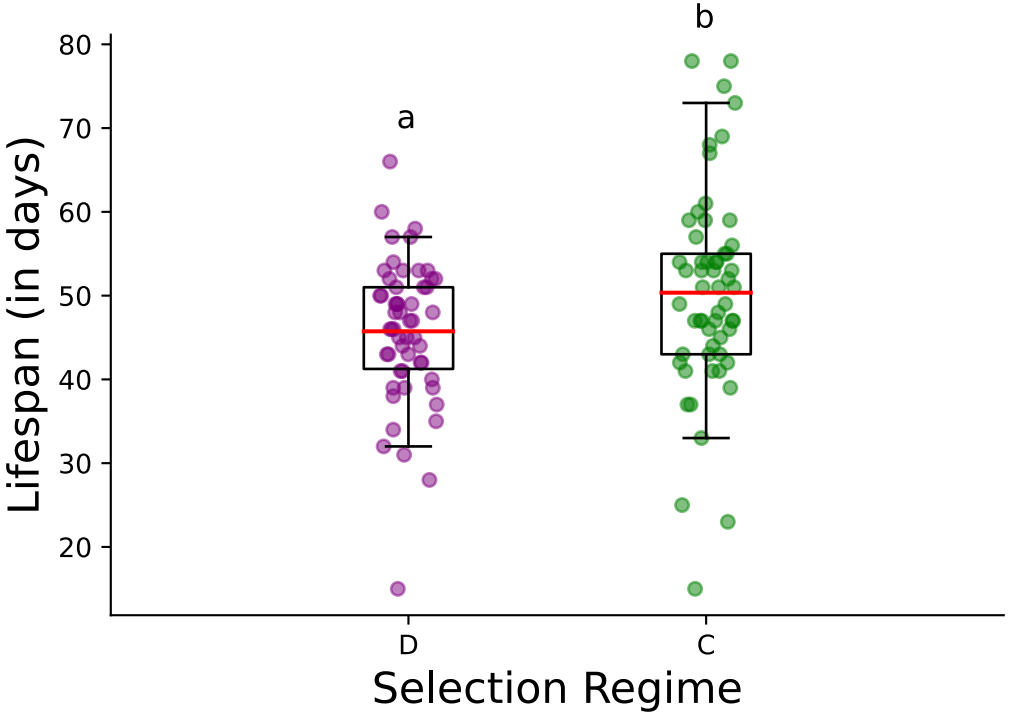
Tung, S., Mishra, A., Shreenidhi, P.M., Sadiq, M.A., Joshi, S., Sruti, V.R.S., *et al.* (2018b). Simultaneous evolution of multiple dispersal components and kernel. *Oikos*, 127, 34–44.

Wahlström, L.K. (1994). The significance of male-male aggression for yearling dispersal in roe deer (Capreolus capreolus). *Behav. Ecol. Sociobiol.*, 35, 409–412.

Wessells, R., Fitzgerald, E., Piazza, N., Ocorr, K., Morley, S., Davies, C., *et al*. (2009). d4eBP acts downstream of both dTOR and dFoxo to modulate cardiac functional aging in Drosophila. *Aging Cell*, 8, 542–552.

Wu, N.C. & Seebacher, F. (2022). Physiology can predict animal activity, exploration, and dispersal. *Commun. Biol.*, 5, 1–11.


A
Per hour activity
300
250
200
150
100
50
0
D
C
a
a
a
b
c
d
d,e
d,e
d,e
e
12
26
33
40
47
Age (in days)
B
Slope of age-dependent activity profile
4
2
0
−2
−4
−6
−8
−10
−12
a
b
D
C
Selection Regime


b
a
80
70
60
50
40
30
20
Lifespan (in days)
D
C
Selection Regime