doi: 10.1111/j.1420-9101.2006.01168.x

Male *Drosophila melanogaster* have higher mating success when adapted to their thermal environment

E. S. DOLGIN*† M. C. WHITLOCK* & A. F. AGRAWAL*‡

*Department of Zoology, University of British Columbia, Vancouver, BC, Canada
†Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, UK
‡Department of Zoology, University of Toronto, Toronto, ON, Canada

Keywords:

adaptation;
Drosophila;
sexual selection;
temperature.

Abstract

Adaptation to new environments is a well-documented phenomenon. Individuals from populations maintained in a particular environment for multiple generations tend to be better able to survive and/or reproduce in that environment than their ancestors or other individuals adapted to alternative environments. A third major component of fitness, mating success, has not been well studied in replicated populations under selection in divergent environments. In this study, we used mating trials to compare the mating success of male *Drosophila melanogaster* adapted for 10 years to two different temperatures, 18 and 25°C. In competition for female partners, males had significantly higher mating success at their adapted temperature compared with males adapted to a different temperature. These results are consistent with the notion that those mutations favoured by natural selection also tend to be favoured by sexual selection.

Introduction

Fitness traits such as survival and fecundity are expected to increase as a result of natural selection as a population adapts to a new environment. However, it is more difficult to make predictions about the evolution male mating success during adaptation to a new environment because it is not obvious how or if allelic effects on mating success change in a new environment. In contrast to the plethora of empirical data on adaptation with respect to survival and fecundity, there has been little effort to measure adaptation with respect to male mating success.

A simple prediction regarding the adaptation of male mating success is that males evolved in an environment should have higher mating success than competitors evolved in an alternative environment. This outcome is expected if mating success depends, at least partly, on the general condition of the males. Condition is expected to increase on average as populations accumulate alleles best suited to the new environment. Sexual selection is defined as the differential mating success among individuals of the same sex within a species. By this definition, sexual selection acts not only on ornaments and courtship behaviours, but any aspect that affects an organism's mating success, including overall condition. Sexual selection may then reinforce natural selection by promoting the evolution of greater condition.

It seems reasonable to hypothesize that, compared with low condition males, healthier males may be more likely to search for mates, more proficient in competition with other males, more able to vigorously pursue females, or appear more attractive to females. The sentiment that sexual and natural selection often act to reinforce one another has been expressed by numerous authors (e.g. Darwin, 1796; Darwin, 1871; Maynard Smith, 1956; Mayr, 1972; Koenig & Albano, 1986; Andersson, 1994). This perspective does not deny that natural and sexual selection may oppose each other for some genes (e.g. genes affecting expression of costly secondary sexual traits). However, it is likely that mutations at many, perhaps most, genes will affect condition but have little or no direct effect on any secondary sexual trait; such mutations are expected to be

Correspondence: Aneil F. Agrawal, Department of Zoology, University of Toronto, Toronto, ON, M5S 3G5, Canada.
Tel.: 1-416-946-5563; fax: 1-416-978-8532;
e-mail: afagrawal@zoo.utoronto.ca

selected in the same direction by both natural and sexual selection. For example, in a new thermal environment, alleles that allow an organism to function better at the new temperature may be favoured by both natural and sexual selection.

There are a variety of predictions that can be made to test this simple view of sexual selection, including: (1) New mutations should have positively correlated effects on male mating success and other fitness components (Hughes, 1995); (2) deleterious mutations introduced into the genome should reduce male mating success on average (Whitlock & Bourguet, 2000); (3) sexual selection should act to purge deleterious mutations from populations (Radwan, 2004); (4) populations subject to sexual selection should adapt faster than populations with monogamous no-choice matings (Partridge, 1980; Promislow *et al.*, 1998; but see Holland, 2002) and (5) adaptation should increase male mating success in the adaptive environment. Our experiment is a test of this final prediction.

Relative adaptation in male mating success can be measured by comparing the mating success of males in the environment to which they have adapted to their mating success in an alternative environment. To test for this type of adaptation, we made use of six long-term experimental lines of *Drosophila melanogaster*, three of which were adapted for almost 10 years to 18°C, whereas the remaining three were adapted to 25°C. Males from populations adapted to alternative thermal environments competed for females in common garden experiments at each of the two temperatures. In this design, males are not expected to have unconditionally good or bad genotypes. Rather, males from populations that have an evolutionary history at a specific temperature are expected to harbour genes that increase performance at that temperature. As predicted, the results indicate that males have greater mating success in their adaptive environments. We also discuss alternative interpretations of our results.

Materials and methods

We randomly paired each of three populations adapted to 25°C with one of the three populations adapted to 18°C. In mating cages, we allowed multiple males from paired populations to compete for females from a common stock population. We scored the number of males of each type found *in copula*. Experiments were conducted at both 18 and 25°C. For experiments at a given temperature, the males, as well as their parents, were reared at the experimental temperature to minimize any environmental differences between males from different populations. The females used in the mating trials were reared at 25°C to avoid effects of assortative mating by rearing temperature and transferred to the experimental temperature for habituation after eclosion but several days before the mating trials. These females came from a population that had been genetically isolated from each of the six male source populations for an equal amount of time. Thus, our results are not confounded by the possibility of male–female coevolution.

Study populations

The experiments were carried out using males from thermal selection lines, developed by Federico C. F. Calboli, Michael W. Reeve, Avis C. James and Linda Partridge at the University College London. These lines originated from a collection made in Dahomey (now Benin), West Africa, in 1970. The mass-bred stock was maintained in population cage culture at 25°C until 1994 when six cages were initiated from fly culture bottles containing large numbers of larvae. Three cages were randomly assigned to each of two thermal treatments with temperatures of 18 and 25°C. In 2003, large samples from each of these cages were transferred to Vancouver and maintained at their experimental temperature for approximately 1 year before conducting the present study. We randomly matched replicates from both the 18 and 25°C lines to create three independent paired mating competition experiments, referred to herein as 'sets'. Each set was reared and tested at both experimental temperatures. The females used in the mating experiments were also from the initial Dahomey stock population. This population has been maintained at 25°C but has been isolated from all six populations described above since 1994. All flies were maintained on corn meal medium, seeded with live yeast, with a 12 : 12 L : D diurnal cycle.

General methods

All the temperature-adapted lines were maintained at the experimental testing temperature for one generation prior to mating trials to minimize plastic and parental effect differences. Flies were then transferred using CO_2 anaesthesia to lay cups containing yeasted medium for an acclimation period of 24 h at low density before being transferred to fresh medium for egg collection, which lasted approximately 24 h at 18°C and 6 h at 25°C. First instar larvae were then collected after approximately 24 h at 18°C and 18 h at 25°C after the adult flies had been removed from the lay cups. Larvae were placed in vials containing medium in groups of 30. Emerging flies were collected every 24 h. Both sexes were maintained together post-eclosion for 4 days at 18°C and 2 days at 25°C to allow the males to gain sexual experience. Females were then discarded, and the males were isolated using CO_2 anaesthesia into vials of 15 flies each with any extra flies kept in vials at lower densities. Males were kept on normal media in the absence of females for 4 days at 18°C and 2 days at 25°C. To allow identification, males were subsequently

marked by transferring them to new vials containing red or blue food colouring added to the live yeast. If any flies escaped during transfer or had died before being moved to the vials containing food colouring, the excess flies were used to maintain vials of 15 males. Males were then kept on dyed media for an additional 4 days at 18°C and 2 days at 25°C before conducting the trials. Thus, mating trials were performed with males 11–13 days post-eclosion at 18°C and 6 days at 25°C. A balanced design was used to ensure that paired treatments within a set were reciprocally marked for half the treatments. Male colour had little or no effect on mating frequencies (51.8% matings with blue males, $P = 0.15$), consistent with previous studies (e.g. Rundle *et al.*, 1998). Note that all steps described above required about twice as long at 18°C relative to 25°C because development time is almost twice as long at 18°C compared with 25°C.

Females were reared from vials isolated from the caged Dahomey population at 25°C for both experimental temperatures, without precise control of density. Females were collected as virgins using CO_2 anaesthesia and placed into vials in groups of 10. For the 18°C treatment, females were transferred to the experimental temperature at 0–2 days post-eclosion. Mating trials were performed with females 4 days post-eclosion at 18°C and 2 days at 25°C.

Mating trials

Mating trials were conducted in small Plexiglas cages (*c.* $11 \times 11 \times 11$ cm), with a front opening covered in translucent nylon mesh, a transparent top and bottom, and white paper on the remaining sides so as to avoid any additional visual disturbance to the flies. Trials were conducted throughout the day at least 1 h after artificial daybreak. Mating trials were started with 10 females from the Dahomey population and 15 males from each temperature, reciprocally dyed. We ensured that there were 15 males upon transfer to vials with the food colouring and 10 females per vial upon virgin collection; however, there was some mortality in the vials over the days before the mating trials were performed. We ensured no trial ever had less than nine females. Furthermore, we documented the number of dead males for a subset of the mating trials (222 of 279 trials). Male mortality was low and randomly distributed between treatments, as there was no significant bias in the direction of mortality ($P = 0.59$). Flies were released sequentially (males first). For tests done at 25°C, each cage was checked only once, after 10 min, and all mating pairs were removed by aspiration. Due to the slower rate of mating in the 18°C tests, each cage was checked every 15 min for 1 h, and mating pairs were removed for identification of the male. Mating flies were only removed if they remained *in copula* during the disturbance of being slightly agitated by the aspirator.

Results

Mating trials were done in cages with groups of 15 males of each thermally-adapted type. The number of cages at a given temperature varied from 33 to 67 across all sets. The mean number of copulating pairs isolated from a given cage in each set ranged from 6.4 to 6.6 at the warm temperature, and 4.2 to 5.2 at the cold temperature (these numbers should not be viewed as comparable estimates of mating rate as mating trials lasted for a longer period at the cold temperature than at the warm temperature). Individual mating pairs in each cage were not independent of each other, as each copulating pair skewed the ratio of males available to unmated females. As a first step in the analysis, the proportions of successful males of each temperature type in each cage were compared by simulation to that expected by chance, assuming that the probability of the mating of a particular type of male was constant across all cages at a given temperature in each set. No evidence was found of a cage effect (P ranging from 0.63 to 0.96 across all six set by temperature combinations). In Table 1, we show the data pooled across cages for ease of presentation. To be conservative, the data were analysed using cages as the units of replication within each set. For each mating cage, the proportion of successfully mating males that originated from the 18°C treatment was arcsine-transformed, and the results were compared by Welch's t-tests.

Each pair of populations (what we have called a set) represents an independent experiment testing whether the mating environment interacts with adaptation to predict the line with the higher male mating success. In other words, does the relative mating success of a line increase in its adaptive environment relative to the alternative environment? Relative adaptation reveals evolutionary improvement with respect to the environment even in cases where males from the different populations have different intrinsic levels of mate acquisition ability. The number of matings obtained at each test temperature for each line is given in Table 1. In two of the three sets, males performed relatively better at their adapted temperatures compared with the alternate

Table 1 Males successfully mating from each temperature-adapted population.

Set	Experimental temperature	18°C Males	25°C Males	χ^2	Proportion matings by adapted males
1	Cold	188	93	17.29	0.60
	Warm	111	118		
2	Cold	148	152	2.25	0.53
	Warm	121	160		
3	Cold	145	63	27.88	0.63
	Warm	96	122		

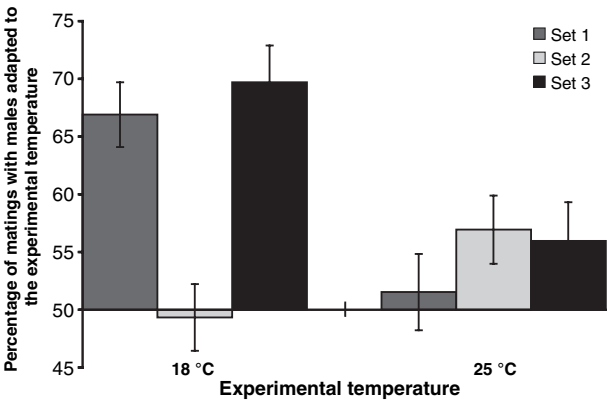

Fig. 1 Percentage of matings with the males from the population adapted to the experimental temperature at both test temperatures in each set. These results were calculated weighting by the number of matings per cage. The axis at 50% indicates no difference in mating success between males adapted to different temperatures. Error bars denote one standard error.

environment. In the other set, the relative mating success was nearly exactly the same. This difference was strongly statistically significant for sets 1 and 3 ($P = 7 \times 10^{-5}$, $P = 1.5 \times 10^{-5}$ respectively) but not set 2 ($P = 0.52$).

Looking at each temperature separately, the adapted males were significantly more likely to mate successfully than the less adapted males in all cases except for the warm temperature in set 1 and the cold temperature in set 2 (Fig. 1). In these cases, there was essentially no advantage for either type of male.

If we treat each set as an independent test of the null hypothesis that previous adaptation has no effect on environment-specific male mating success, then we have three separate tests. These tests can be combined to give an overall test of the effect of adaptation on male mating success, using the combined Z method (Whitlock, 2005). Doing so gives a combined *P*-value of $P = 4.5 \times 10^{-6}$.

If we prefer to view each set as a replicate, then we can ask whether the mean preference for locally adapted males is >0.5 by a *t*-test (see Table 1). The test performed this way has extremely low power, because there are only 2 d.f., but the locally adapted males are preferred significantly by a one-tailed test ($P = 0.0486$).

Discussion

Adaptation to temperature has been previously shown for *D. melanogaster* maintained in population cages at divergent temperatures (Partridge *et al.*, 1995). When tested at the experimental temperature at which they had evolved, flies of both sexes had greater lifespan and females showed higher fecundity and fertility than flies adapted to an alternate temperature. We have shown that male mating success also evolves in response to exposure to thermal environment. Males have higher mating success in the thermal environment in which they have evolved than they do in the alternative thermal environment.

To our knowledge, this is the only study in which relative male mating success, when measured independently from female preference evolution, has been shown to increase during adaptation to divergent environments. When pursuing different questions, previous authors have examined differences in mating behaviour between populations adapted to different environments using females from the same populations as the experimental males (e.g. Kilias *et al.*, 1980; Dodd, 1989; Klappert & Reinhold, 2005). However, such studies are not directly related to our question because they are confounded by the possibility of male–female coevolution. In our study, we used females that were not from any of the test populations and shared an equal evolutionary history with each test population. The ancestral population from which all the test populations were derived had been maintained at 25°C for over 20 years before the thermal selection regimes were established. The females used in this experiment were also from a population maintained at 25°C that had descended from the same stock as the selection lines. Thus, these females should provide a reasonable approximation to the ancestral state.

The power of our study was limited by the number of pre-existing temperature adapted lines; we hope that the study will be independently replicated. The overall test of whether adaptation affects mating success was highly significant; however, set 2 was not statistically significant on its own as there was essentially no advantage of male adaptation at the cold temperature. In contrast, in both sets 1 and 3 over two-thirds of matings at the colder temperature were with the cold-adapted males. It would be advantageous to have more replicates with which to create statistically independent sets to test the null hypothesis that adaptation has no effect on environment-specific male mating success. However, these populations were initially established for other purposes that required only a few replicates of each treatment. Despite this limitation, even when our results were analysed using a *t*-test with extremely low power, mating success was significantly positively correlated with evolutionary history.

It would be worth testing the prediction that adaptation enhances male mating success in the adaptive environment by using divergent replicated lines established from other sources of selection, such as relative humidity (e.g. Kennington *et al.*, 2003) or larval density (e.g. Joshi & Mueller, 1996). By testing directly for differential mating success among populations with different selective pressures, we should gain a more comprehensive picture of how male mating success adapts to new environments in general.

In our own study, we do not know what phenotypic changes have conferred thermal adaptation, but body size is one obvious phenotypic difference between lines

adapted to 18°C vs. 25°C. Temperature has been implicated as a major factor for the evolution of body size in *Drosophila* (e.g. Anderson, 1966, 1973; Cavicchi *et al.*, 1985, 1989; Partridge *et al.*, 1994), and body size tends to be a good indicator of male mating success (see review by Partridge, 1988). In particular, large males tend to court females more and have a higher lifetime mating success than do small males (Ewing, 1961; Partridge & Farquhar, 1983; Partridge *et al.*, 1987a,b). By manipulating body size through artificial selection, Reeve *et al.* (2000) compared the male reproductive success of large and small body-size selection lines tested at 18 and 25°C. They found large-line males to be fitter than small-size males or controls at both experimental temperatures, with the difference being greatest at the lower temperature. Of the populations used in the present study, males of the 18°C-adapted lines were larger when reared in either experimental temperature (F.C.F. Calboli, M.W. Reeve, A.C. James & L. Partridge, unpublished data). Our result that 18°C-adapted males generally performed better at the lower temperature is consistent with the observation that larger males have greater mating success. However, our results also show that when tested at the warmer temperature, the 25°C-adapted males had greater mating success, despite their smaller size. This supports the idea that mating success is directed by overall condition, rather than body size alone. However, body size may explain why mating success between thermally adapted males was generally reduced in the mating trials performed at the higher temperature (see Fig. 1).

Although our results pertain directly to the study of adaptation, they are also relevant to larger issues in population genetics. Recent theory shows that sexual selection can be important in eliminating deleterious alleles and fixing beneficial ones (Whitlock, 2000), and that sexual selection can result in sexual populations having a lower mutation load than asexual populations (Agrawal, 2001; Siller, 2001). The basic premise for these models is that most genes will have some effect on overall condition and that both natural and sexual selection should favour individuals in good condition. As predicted by this premise, males had higher mating success in the environment in which they had evolved. Thus, our results add to a growing body of evidence that most alleles favoured by natural selection are also favoured by sexual selection (Hughes, 1995; Whitlock & Bourguet, 2000; Radwan, 2004).

In this experiment we compare the states of different lines after independent evolution through a number of years. As the lines adapted to different environments, alleles which were on average beneficial would be fixed in the populations, although presumably different alleles would be fixed in the cold-adapted lines than in the warm-adapted lines. The patterns that we see in mating success reflect predominantly these fixed differences between lines, not the effects of genetic variation within lines. Within a population, the genetic variation that would be maintained would have been filtered by selection to include more alleles that had antagonistic effects on natural and sexual selection, whereas those alleles that had effects in the same direction for both kinds of selection would have largely fixed within populations. As a result, we expect a different pattern in this sort of study than in an experiment that measured the properties of standing variation within a population. Standing variation will show a biased sample of all mutations. Some studies using standing variation have found evidence of a positive relationship between natural and sexual selection (Petrie, 1994; Welch *et al.*, 1998; Drickamer *et al.*, 2000) whereas others have found the opposite (Chippindale *et al.*, 2001; Friberg & Arnqvist, 2003; Fedorka & Mousseau, 2004). The use of standing variation in these studies was appropriate for the questions these authors aimed to address. However, it is important to recognize that such studies do not provide a general or unbiased view of the relationship between natural and sexual selection acting on most mutations.

Our results are in accordance with previous studies that have shown a positive effect of mate choice on components of fitness in *D. melanogaster* (e.g. Partridge, 1980; Promislow *et al.*, 1998). However, it is interesting to contrast our results with those of Holland (2002). In his study, Holland allowed replicate populations to adapt to a novel thermal environment for up to 50 generations, either under enforced monogamy or by placing each female in a vial with four males. These treatments were intended to prevent or allow sexual selection respectively. Although substantial adaptation to the new thermal environment occurred, the difference in the rate of adaptation between the monogamous and polyandrous treatments was not significant. These results appear inconsistent with the idea that sexual selection typically reinforces natural selection. The relatively short time span of this experiment would mean that much of the response would be due to alleles that were reasonably common when the experiment began (i.e. alleles previously maintained by some form of balancing selection). As mentioned above, alleles maintained by balancing selection (including the opposition of sexual and natural selection), are a biased sample of all possible alleles. The selection lines we used had evolved for a much longer time period (hundreds of generations) so that alleles that were initially very rare (e.g. at mutation–selection balance) and new mutations may have contributed substantially to divergence. More studies would be needed to determine whether the relationship between sexual and natural selection is different for common alleles vs. rare alleles and/or new mutations.

Although our result is consistent with the idea that sexual and natural selection typically act in the same direction, there are potential alternative explanations. The most reasonable alternative explanation would be that female preference is environmentally plastic such

that females prefer different male characteristics in cool environments than in warm environments. For example, Grace & Shaw (2004) suggest that female Hawaiian crickets reared in warmer temperatures prefer male calls with a faster pulse rate than is preferred by females reared at a cooler temperature. If female preference is plastic, then sexual selection on males will be divergent across environments because males will be selected to produce the phenotype preferred by females in that environment. Under this scenario males are expected to have higher mating success in the environments in which they have evolved even if there are no differences in natural selection between environments. This alternative explanation would require that preference is plastic specifically with respect to test temperature rather than rearing temperature, because we always reared females at 25°C.

In sum, our study provides evidence for adaptation of male mating success. We expect the pattern we observed is not unique to these lines. More data from other selection regimes and other species will be required to determine the generality of the result reported here. Assuming a similar pattern does hold, a larger challenge will be determining which of the two possible explanations we discuss best explains such results.

Acknowledgments

We are grateful to L. Partridge, S. Otto, L. Rowe, B. Charlesworth, E. Cunningham, A. Cutter and A. Hall for very useful comments on the manuscript. We are very grateful to Linda Partridge for providing the temperature-adapted flies used in this study. Funding was generously provided by the Natural Sciences and Engineering Research Council, Canada.

References

Agrawal, A.F. 2001. Sexual selection and the maintenance of sexual reproduction. *Nature* **411**: 692–695.

Anderson, W.W. 1966. Genetic divergence in M. Vetukhiv's experimental populations of *Drosophila pseudoobscura*. III. Divergence in body size. *Genet. Res.* **7**: 255–266.

Anderson, W.W. 1973. Genetic divergence in body size among experimental populations of *Drosophila pseudoobscura* kept at different temperatures. *Evolution* **27**: 278–284.

Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, NJ.

Cavicchi, S., Guerra, D., Giorgi, G. & Pezzoli, C. 1985. Temperature-related divergence in experimental populations of *Drosophila melanogaster*. I. Genetic and developmental basis of wing size and shape variation. *Genetics* **109**: 665–689.

Cavicchi, S., Guerra, D., Natali, V., Pezzoli, C. & Giorgi, G. 1989. Temperature-related divergence in experimental populations of *Drosophila melanogaster*. II. Correlation between fitness and body dimensions. *J. Evol. Biol.* **2**: 235–251.

Chippindale, A.K., Gibson, J.R. & Rice, W.R. 2001. Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in *Drosophila*. *Proc. Nat. Acad. Sci. USA* **98**: 1671–1675.

Darwin, E. 1796. *Zoonomia; or, the Laws of Organic Life*. J. Johnson, London.

Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. Murray, London.

Dodd, D.M.B. 1989. Reproductive isolation as a consequence of adaptive divergence in *Drosophila pseudoobscura*. *Evolution* **43**: 1308–1311.

Drickamer, L.C., Gowaty, G.A. & Holmes, C.M. 2000. Free female mate choice in house mice affects reproductive success and offspring viability and performance. *Anim. Behav.* **59**: 371–378.

Ewing, A.W. 1961. Body size and courtship behaviour in *Drosophila melanogaster*. *Anim. Behav.* **9**: 93–99.

Fedorka, K.M. & Mousseau, T.A. 2004. Female mating bias results in conflicting sex-specific offspring fitness. *Nature* **429**: 65–67.

Friberg, U. & Arnqvist, G. 2003. Fitness effects of female mate choice: preferred males are detrimental for *Drosophila melanogaster* females. *Evolution* **16**: 797–811.

Grace, J.L. & Shaw, K.L. 2004. Effects of developmental environment on signal-preference coupling in a Hawaiian cricket. *Evolution* **58**: 1627–1633.

Holland, B. 2002. Sexual selection fails to promote adaptation to a new environment. *Evolution* **56**: 721–730.

Hughes, K.A. 1995. The evolutionary genetics of male life-history characters in *Drosophila melanogaster*. *Evolution* **49**: 521–537.

Joshi, A. & Mueller, L.D. 1996. Density-dependent natural selection in *Drosophila*: trade-offs between larval food acquisition and utilization. *Evol. Ecol.* **10**: 463–474.

Kennington, W.J., Killeen, J.R., Goldstein, J.B. & Partridge, L. 2003. Rapid laboratory evolution of adult wing area in *Drosophila melanogaster* in response to humidity. *Evolution* **57**: 932–936.

Kilias, G., Alahiotus, S.N. & Pelecanos, M. 1980. A multifactorial genetic investigation of speciation theory using *Drosophila melanogaster*. *Evolution* **34**: 730–737.

Klappert, K. & Reinhold, K. 2005. Local adaptation and sexual selection: a reciprocal transfer experiment with the grasshopper *Chorthippus biguttulus*. *Behav. Ecol. Sociobiol.* **58**: 36–43.

Koenig, W.D. & Albano, S.S. 1986. On the measurement of sexual selection. *Am. Nat.* **127**: 403–409.

Maynard Smith, J. 1956. Fertility, mating behaviour and sexual selection in *Drosophila subobscura*. *J. Genet.* **54**: 261–279.

Mayr, E. 1972. Sexual selection and natural selection. In: *Sexual Selection and the Descent of Man 1871–1971* (B. G. Campbell, ed.), pp. 87–104. Aldine Publishing Co., Chicago.

Partridge, L. 1980. Mate choice increases a component of offspring fitness in fruit flies. *Nature* **283**: 290–291.

Partridge, L. 1988. Lifetime reproductive success in *Drosophila*. In: *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (T. H. Clutton-Brock, ed.), pp. 11–23. University of Chicago Press, Chicago.

Partridge, L. & Farquhar, M. 1983. Lifetime mating success of male fruit flies (*Drosophila melanogaster*) is related to their size. *Anim. Behav.* **31**: 871–877.

Partridge, L., Ewing, A. & Chandler, A. 1987a. Male size and mating success in *Drosophila melanogaster*: the roles of male and female behaviour. *Anim. Behav.* **35**: 555–562.

Partridge, L., Hoffman, A. & Jones, J.S. 1987b. Male size and mating success in *Drosophila melanogaster* and *Drosophila pseudoobscura* under field conditions. *Anim. Behav.* **35**: 468–476.

Partridge, L., Barrie, B., Fowler, K. & French, V. 1994. Evolution and development of body-size and cell-size in *Drosophila melanogaster* in response to temperature. *Evolution* **48**: 1269–1276.

Partridge, L., Barrie, B., Barton, N.H., Fowler, K. & French. V. 1995. Rapid laboratory evolution of adult life history traits in *Drosophila melanogaster* in response to temperature. *Evolution* **49**: 538–544.

Petrie, M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* **371**: 598–599.

Promislow, D.L., Smith, E.A. & Pearse, L. 1998. Adult fitness consequences of sexual selection in *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. USA* **95**: 10687–10692.

Radwan, J. 2004. Effectiveness of sexual selection in removing mutations induced with ionizing radiation. *Ecol. Letters* **7**: 1149–1154.

Reeve, M.W., Fowler, K. & Partridge, L. 2000. Increased body size confers greater fitness at lower experimental temperature in male *Drosophila melanogaster*. *J. Evol. Biol.* **13**: 836–844.

Rundle, H.D., Mooers, A.Ø. & Whitlock, M.C. 1998. Single founder-flush events and the evolution of reproductive isolation. *Evolution* **52**: 1850–1855.

Siller, S. 2001. Sexual selection and the maintenance of sex. *Nature* **411**: 689–692.

Welch, A.M., Semlitsch, R.D. & Gerhardt, H.C. 1998. Call duration as an indicator of genetic quality in male gray tree frogs. *Science* **280**: 1928–1930.

Whitlock, M.C. 2000. Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles, and sexual selection. *Evolution* **54**: 1855–1861.

Whitlock, M.C. 2005. Combining probability from independent test: the weighted Z method is superior to Fisher's approach. *Journal of Evolutionary Biology* **18**: 1368–1373.

Whitlock, M.C. & Bourguet, D. 2000. Factors affecting the genetic load in *Drosophila*: synergistic epistasis and correlations among fitness components. *Evolution* **54**: 1654–1660.

Received 13 April 2006; revised 28 April 2006; accepted 5 May 2006