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SHORT COMMUNICATION

Local adaptation does not always predict high mating success

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Abstract

The hypothesis that adaptation to local environments can increase mating success was tested using ten replicate lines of *Drosophila melanogaster* adapted either to 16 °C or to 25 °C. Competitive mating trials at both temperatures were performed with males taken from a pair of lines, one adapted to each temperature. There was no average increase in mating success for males adapted to the local environment. Although one pair of lines showed the expected pattern, another pair showed the reverse pattern. More data are needed on this hypothesis, preferably with lines that have more strongly adapted to local environments.

Introduction

Natural selection and sexual selection have the potential to interact in many ways. Sexual selection can impede natural selection, by causing antagonistic demands on phenotypes. Sexual selection can also create conflict between the sexes, which in return can constrain either or both sexes from their optimum fitness (Arnqvist & Rowe, 2005). However, sexual selection also has the potential to reinforce natural selection. Sexual selection can increase the effective selection against deleterious alleles or for adaptive alleles (Kodric-Brown & Brown, 1987; Whitlock, 2000; Agrawal, 2001; see reviews by Candolin & Heuschele, 2008 and Whitlock & Agrawal, 2009). Numerous experiments have either found support for this claim (Partridge, 1980; Promislow *et al.*, 1998; Whitlock & Bourguet, 2000; Radwan, 2004; Pischedda & Chippindale, 2005; Stewart *et al.*, 2005; Fricke & Arnqvist, 2007; Sharp & Agrawal, 2008; Hollis *et al.*, 2009) or not (Holland & Rice, 1999; Holland, 2002; Martin & Hosken, 2003; Radwan *et al.*, 2004; Rundle *et al.*, 2006; Tilszer *et al.*, 2006). Part of the difficulty in interpreting these experiments is that sexual selection also allows the potential for load because of sexual conflict, which can reduce fitness at the same time that fitness may be enhanced at other loci by sexual selection.

Conversely, natural selection has the potential to affect the mating success of individuals. Rowe & Houle (1996) suggested that sexual selection would often be condition-dependent. They provided a review of evidence that males in better condition are often more successful at attracting mates, which is supported by a larger meta-analysis (Jennions *et al.*, 2001). If males in better condition are better at attracting mates, then we might predict that the mating success of a male ought to depend on the match between his phenotype and the local environment. Males that are better adapted to the local environment should be better at attracting mates in that environment, compared to males that are adapted to other environments. To our knowledge, only one test of this prediction has been made by Dolgin *et al.* (2006). In that experiment, three lines of *Drosophila melanogaster* that had been adapted to colder environment were compared with three lines that had been adapted to warmer environments. Males adapted to warmer environments did relatively better when assayed in competitive mating trials in the warm, compared to mating trials at the colder temperature.

Given that this interesting prediction has only been tested once, and in that test there were only three replicates available, we decided to test this prediction again using five new pairs of lines of *Drosophila* adapted to warm and cold temperature. Unlike Dolgin *et al.* (2006), where the flies had adapted to their temperature environments for about 10 years; in this experiment, the adaptation has occurred only over a 2-year period and may be less complete. However, these lines show weak but statistically significant adaptation to temperature, as shown by an interaction between adaptive temperature and assay temperature for fecundity (S. Yeaman, Y. Chen

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and M. C. Whitlock, unpublished data). We followed the procedures of Dolgin *et al.* (2006) in testing relative mating success by matching one line that was adapted to a colder environment with another line adapted to a warmer environment and doing competitive mate choice trials at both temperatures.

Methods

Experimental evolution and assay lines

A large breeding population was created from a collection of wild-caught flies and used to establish two groups of five replicate populations, which were evolved in cages at constant 16 °C (the cold treatment, c) or 25 °C (the hot treatment, h). These populations were then maintained under a discrete generation schedule for 116 weeks, which corresponds to 29 generations for the c treatment or 58 generations for the h treatment (S. Yeaman, Y. Chen and M. C. Whitlock, unpublished data). Following this period of laboratory adaptation, subsamples from the five replicates of each treatment were reared under both assay temperatures (16 and 25 °C) at controlled densities (30–36 eggs per vial for 10 replicate vials). The adults from this generation were released into cages at the assay temperature to mate freely, and a second generation of controlled density vials was established, with the males from this generation used in the mating trials. These generations at the assay temperature ensured that flies were acclimated to the test temperature, so any differences in mating success can be ascribed to differences in genetic adaptation.

To obtain females for the mating trial, another subline was established from a different population, which had been maintained during the evolution phase of the experiment with half of the population at 25 °C and half at 16 °C, fully mixed every 4 weeks; as earlier, this subline was reared under controlled density at each assay temperature. Rearing and manipulation of the lines were blocked by day, such that a single pair of one c and one h population was established each day.

Male flies used in the mating trials were maintained in their natal vials for at least 4 days following eclosion (2 days in the warm assay) to allow them to gain sexual experience. Following this period, females on the natal vials were discarded, and males were transferred to vials with yeast paste that was coloured with either red or blue food colouring in groups of 15 using CO_2 anaesthesia. Males were kept isolated from females in these vials for at least 4 days before the mating trials (2 days in the warm assay). Virgin females for the mating trials were collected from the s vials < 20 h following eclosion (10 h in the warm assay) using CO_2 anaesthesia and transferred to yeasted vials in groups of 10. In all cases, mating trials in the cold assay were conducted with males that were 15–18 days post-eclosion (7–8 days in the warm assay) and on females that were 11–13 days post-eclosion (3–4 days in the warm assay).

Mating trials

Each line from the c-adapted replicates was paired with one unique line from the h-adapted lines for mating trials. Thus, we have five independent replicates of the effects of differential adaptation on mating success in adaptive environments. Fresh coloured yeast paste was added to the male vials approximately 1 h before beginning of the mating trials to assure easy identification of the treatment of origin of the males. (Males eat the coloured yeast, and then their vial of origin can be determined under a microscope by examining their digestive tract.) Males from each treatment were released without anaesthesia in groups of 15 into 10 × 10 × 10 cm cages that were enclosed on all sides by clear plastic, except for one side, which had a nylon covering. Virgin females were then released in the mating cages without anaesthesia in groups of 10, at which point the timing of the mating trial began. Mating trials were run for 1 h in the cold assay, with mating pairs counted and removed by aspiration at 15 min intervals. Mating trials in the warm assay were run for 10 min, with mating pairs counted and removed at the end of this period. Only mating pairs that remained in copulation at the end of an interval were removed; and in all cases, males were anaesthetized and examined under a dissecting microscope immediately following the trial to identify their treatment of origin. *Drosophila melanogaster* typically mate for about 15 min at 25 °C and longer at colder temperatures, so we are unlikely to miss many matings with this procedure. The colour of yeast paste used to identify the treatments (red or blue) was alternated between the treatments each day. Between 35–39 mating trials were run in the warm assays, and 35–49 assays were run for the cold assays, with an average of 264 matings per replicate pair in the warm assays and 293 matings in the cold assays.

Results

We used each mating trial as a replicate and quantified the proportion of matings in a trial made by the male that was adapted to the warmer temperature. For each line, we used a two-sample *t*-test to compare the relative mating success of warm-adapted males in warm or cold assay environment (Table 1). Three of the pairs of lines show no significant difference in the relative mating success of h-adapted males between the assay environments. For one pair of lines, replicate 2, there is a strong difference in mating success where warm-adapted males do better in the warm environment compared to their relative mating success in the cold ($P = 0.0008$). However, for the remaining pair of lines (replicate 4), mating success was marginally better for warm-adapted males when assayed in the cold environment ($P = 0.032$).

Using each pair as a replicate and calculating for each pair, the difference in the proportion of h-adapted male

Table 1 Proportion of matings by H-adapted males as a function of assay environment.

Pair	Proportion H-adapted matings in H-assay (SE)	Proportion H-adapted matings in C-assay (SE)	*t* (d.f.)	*P*
1	0.553 (0.047)	0.543 (0.044)	0.15 (70)	0.88
2	0.613 (0.032)	0.450 (0.034)	3.5 (76)	0.0008
3	0.519 (0.021)	0.506 (0.025)	0.4 (84)	0.69
4	0.468 (0.025)	0.548 (0.027)	–2.2 (80)	0.032
5	0.566 (0.026)	0.585 (0.024)	–0.5 (76)	0.60

matings in H or C assays, we find that on average there is no significant difference from zero (Welch's paired *t*-test, $t_4 = 0.51$, $P = 0.64$). Overall, these data offer no support for the idea that adaptation to the local environment affect mating success.

In both hot and cold assays, the hot-adapted males achieved more matings than the cold in four of the five replicates, but this was not statistically different from equality in either environment.

Discussion

Mating success was enhanced by local adaptation in only one of the five replicates in our study; and in another replicate, the opposite pattern was found. Overall, this study gives little support for the hypothesis that local adaptation enhances mating success.

The lines used in this study were adapted for 2 years to the assay temperatures, but this may not have allowed much effective adaptation. The cold-adapted lines have a fecundity that is approximately 14% higher than the warm-adapted lines at 16 °C, but the warm-adapted lines do not have a significantly higher fecundity than the cold-adapted lines at 25 °C (S. Yeaman, Y. Chen and M. C. Whitlock, unpublished data). As a result, the pattern of local adaptation may have been too subtle to detect mating success differences. We strongly suggest that similar studies be conduced in the future, preferably with lines that have more strongly adapted to the local environments than these lines used here.

Having said that these lines do show significant local adaptation but in general do not show higher mating success for locally adapted individuals. This demonstrates that the relationship between mating success and local adaptation is not so strong that adaptation always leads to predictable strong changes in mating success. In a total of eight pairs of temperature-adapted lines [combining this study with Dolgin *et al.* (2006)], three show significant evidence of mating success associated with local adaptation, one shows the opposite, and the other four show no statistically significant deviation from the null expectation. More work of this sort will be necessary to fully resolve the relative importance of local adaptation to mating success.

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