

Bigger isn't always better: body size, developmental and parental temperature and male territorial success in *Drosophila melanogaster*

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Abstract. The effect of developmental temperature (18°C versus 25°C) on the body size and territorial success of male fruit flies, *Drosophila melanogaster*, in paired contests was examined. When tested at ambient temperatures of either 18°C or at 27°C, adult males raised at 25°C were relatively small in size but nevertheless had greater territorial success (control of a food/oviposition resource) than males raised at 18°C. This result negates a 'size-advantage hypothesis', which predicts that males raised at 18°C should be more successful at either contest temperature by virtue of their larger size. It also negates an 'acclimation-advantage hypothesis', which predicts that males raised at 18°C should be more successful than males raised at 25°C in contests at 18°C, but less successful at 27°C. The data are consistent, however, with an 'optimal developmental temperature hypothesis', which suggests that flies raised at 25°C, even though phenotypically small, are physiologically vigorous and will perform relatively well under diverse environmental circumstances. Thus, bigger isn't always better. In a small-scale experiment (territoriality scored only at 27°C) in which all males had the same developmental temperature (25°C) males whose parents developed at 25°C were more successful than were males whose parents developed at 18°C. These experiments demonstrate that developmental temperatures, both within and between generations, influence territorial success in male flies.

Body size has a major impact on reproductive success and fitness (Roff 1981; Barbault 1988). In both field and laboratory studies with several species of *Drosophila*, for example, large males typically dominate small males at oviposition sites, thereby gaining a substantial mating advantage (Ewing 1964; Partridge & Farquhar 1983; Hoffmann 1987a, b, 1988; Partridge et al. 1987; Wilkinson 1987; Markow 1988; Santos et al. 1988; but see Boake 1989; Hoffmann & Cacoyianni 1990; Markow & Sawka 1992). The size of a male is strongly influenced not only by its genes, but also by environmental conditions (e.g. larval density, nutrition, temperature) it experienced during development (Robertson 1963; David et al. 1983; Cavicchi et al. 1985; Hillesheim & Stearns 1991). For example, males raised at low temperature are phenotypically larger than males raised at high temperature (David et al. 1983; Scheiner & Lyman 1989). Consequently, the temperature at which a male fly develops might have a major impact on its territorial success as an adult.

Here we report experiments that involve manipulating the developmental (and parental) temperature of male flies (*D. melanogaster*) and then examining the consequences on body size and on territorial success. Territorial success is an important behavioural variable that can influence a male fly's feeding success (A. A. Hoffmann, personal communication) as well as his mating success (Dow & von Schilcher 1975; Hoffmann 1988; but see Partridge et al. 1987; Markow 1988; Hoffmann & Cacoyianni 1990). Our experiments were originally designed to discriminate between two hypotheses (not necessarily exclusive) concerning the effects of developmental temperature on territorial success. If large size in fact determines male dominance ('size-advantage hypothesis'; Huey et al. 1995), then males raised at low temperature (thus large) should be more successful than males raised at high temperature. Moreover, males raised at low temperatures should be more successful in contests at either high or low ambient temperatures. Alternatively, if development at one temperature later enhances performance of an adult at that same temperature ('acclimation-advantage hypothesis'; Leroi et al.

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1994; Huey et al. 1995), then a male raised at high temperature (thus small) will be more successful than a male raised at low temperature (thus large) only if both are tested at a high ambient temperature. Thus this second hypothesis proposes that the physiological advantage (at least with respect to territorial success) of acclimatization to a particular thermal environment outweighs size advantages of development at low temperature. Surprisingly, our data contradict both hypotheses. In paired contests at low or high temperature, males raised at high temperature (thus small) were usually dominant over males raised at low temperature. Interestingly, males whose parents were raised at high temperature were usually dominant over males whose parents were raised at low temperature. Thus, the temperature during development, both within and between generations, has a profound effect on adult vigour as well as on size (Crill 1991), with the result that bigger isn't always better.

METHODS

Populations of *D. melanogaster* were founded from a large outbred stock (collected in Brighton, U.K. in 1984) and maintained thereafter at 25°C (Huey et al. 1991). From 1984 until summer 1991, the flies were raised with overlapping generations in a large population cage (no control over adult or larval density) with 12 media bottles that were rotated on a 4-week schedule (see Huey et al. 1991). From summer 1991 until December 1991 (when the present experiments were conducted), flies were raised at low density (ca 50 eggs/vial; corn meal, molasses, agar, yeast, tegosept) with non-overlapping generations (ca 500 flies/generation).

Experimental flies were raised from egg to adult at 18°C ('low-temperature males') or 25°C ('high-temperature males'). These developmental temperatures are well within the range experienced by flies in nature (Jones et al. 1987) and thus are ecologically relevant. Shortly after eclosion, males were briefly immobilized by chilling and marked on the top of the thorax with a tiny spot of red or white acrylic paint (Hoffmann 1987a). Colour was randomized across developmental temperature treatments. (Colour had no effect on dominance, see below.) Males were then isolated and maintained at their developmental temperature until

testing. To correct for the accelerating effects of high temperature on 'physiological age' (Long et al. 1980; Taylor 1981), we tested high-temperature males at an age of 3–4 days but low-temperature males at 6–7 days old. These ages were scaled to observed differences in development time in these lines. In any case, Hoffmann (1990) found that territorial success did not differ between 3- and 7-day-old males, even though territorial success of 1-day-old males was relatively low.

Territorial success was tested (modified from Hoffmann 1987a, b) after gently aspirating pairs of male flies (a high-temperature and a low-temperature male) into clear cylindrical cages (100 mm diameter, 40 mm high) with a disc of medium (20 mm diameter, 10 mm high, covered with a thin suspension of yeast paste) resting on a moistened tissue substrate. A mated female was immediately added to increase male territoriality (Hoffmann & Cacoyianni 1990). The disc of medium, which represents both food and a potential oviposition site (Markow 1988), served as a defendable resource (Hoffmann 1987a, b). Moreover, because mating in *D. melanogaster* occurs at the oviposition site (Markow 1988) and because such sites are patchily distributed in nature (Atkinson & Shorrocks 1977), a male that dominates the food disc should generally have high mating success (Dow & von Schilcher 1975; Hoffmann 1988).

Territorial success was tested at either 18 or 27°C. Males were given 2.5 h to establish territorial patterns (Hoffmann 1987a, b), and then we began scoring territorial success during spot censuses at 0.5-h intervals over the next 6 h (12 observations/pair). During each spot census we observed the males for 10 s and recorded which male(s) occupied the food/oviposition resource. If only one male occupied the oviposition site during all or part of the census, that male was designated as successful. If both males (or no male) were present during the census, we waited 40 s and then re-inspected the arena. If both males remained (or if no male was on the oviposition site), no male was designated as successful. After 12 spot censuses, we scored overall territorial success in two ways. First, we gave each male a numerical score based on the total number of censuses (range = 0–12) at which it alone had dominated the oviposition/food site. Second, we also assigned overall territorial success (categorical scale) to one

male if it alone occupied the food/oviposition site in at least two-thirds of all trials in which one male occupied the territory. Using this criterion we assigned territorial success in 27 of 38 pairs tested at 27°C and in 26 of 39 pairs at 18°C. The probability of making a territorial assignment was unaffected by test temperature (χ^2 test: $P=0.74$) or by the difference in body mass of the flies (ANOVA: $P=0.92$). Territorial success was not influenced by the colour of the paint spot ($P>0.3$). Flies were scored 'blind' with respect to developmental temperature, and a given male was used in only one trial. At the completion of the trials, all flies were removed, dried, and weighed on a microbalance.

An independent experiment demonstrates that our census technique, which directly scores only relative occupancy of the food/oviposition site, adequately indexes territorial success. We continuously followed focal pairs ($N=9$) in the above arenas for 1.5 h, and we recorded the cumulative time each male spent on the oviposition site and the number of chases (a dominance behaviour that correlates with overall dominance; see Hoffmann 1987a) by each male. Immediately thereafter, we conducted spot censuses (as above) of these pairs for an additional 6 h. In eight of nine trials, a definite winner (categorical criteria above) was assigned using data from the spot-census technique. In seven of these eight cases, the winner was also that male that spent more time on the food patch during the prior focal-pair observation period ($P=0.035$). For seven pairs, we also recorded the number of chases by each fly. Males assigned as successful based on their occupancy scores made significantly more chases per trial than did males assigned as unsuccessful (successful males = 8.1 ± 3.91 , unsuccessful males = 0.3 ± 0.18 ; Wilcoxon matched-pairs signed-ranks test: $P=0.046$). Thus relative occupancy of the food/oviposition site is an adequate proxy for direct observation of territorial success.

We conducted an additional, but small-scale ($N=16$ pairs) experiment to test the possible effects of parental temperature on offspring territorial success. Parental temperature influences heat tolerance and adult body size in these flies (Crill 1991); and parental effects are often important in insects (Mousseau & Dingle 1991). We raised parental flies (egg to adult) at either 18 or 25°C, collected their eggs and raised them (egg to adult) at a common temperature of 25°C, and then

tested males whose parents were both raised at 18°C against males whose parents had been raised at 25°C. These tests were run only at an ambient temperature of 27°C.

Statistical analyses of territorial data are complicated by the non-independence of behavioural scores of individuals in a pair. To circumvent this problem, we developed two approaches. First, to determine whether developmental temperature influenced territoriality within a given test temperature, we used Wilcoxon matched-pairs signed-ranks tests, which evaluate the difference in territorial scores of paired individuals rather than the individual scores. Second, to consider simultaneously the effects of developmental temperature, test temperature, and body mass, we developed a general linear model of the following form

$$Y = a + T_{\text{test}} + \Delta_{\text{mass}} + (T_{\text{test}})(\Delta_{\text{mass}}) \quad (1)$$

where the dependent variable Y is the difference in territorial scores (specifically, score for the 25°C male minus score for the 18°C male), a is the intercept or grand mean, T_{test} is the test temperature, Δ_{mass} is the difference in dry body mass between the males (that is, $\text{mass}_{25} - \text{mass}_{18}$) and $(T_{\text{test}})(\Delta_{\text{mass}})$ is the interaction between test temperature and the difference in dry body mass (error term not shown). A significant and positive intercept would indicate that males reared at 25°C have a territorial advantage independent of test temperature and the difference in body mass. (Significance of the remaining terms is self-explanatory.)

RESULTS

Developmental Temperature, Body Size and Territorial Success

Developmental temperature had a significant effect on adult male size. Males that developed at low temperature were heavier on average (by 9.4%) in dry body mass (Wilcoxon matched-pairs signed-ranks test: $N=77$ pairs, $P<0.001$) than were males that developed at high temperature ($\bar{X}=0.267 \pm 0.003$ mg versus 0.244 ± 0.003 mg, respectively). Furthermore in 76.7% of all pairs, the heavier male had developed at low temperature.

Developmental temperature also affected male territorial success. We initially examined these

Table I. Mean (\pm SE) territorial scores (number of censuses at which a given male alone occupied the food/oviposition site) of *D. melanogaster* males raised at 18°C or at 25°C and then tested for territorial success at an ambient temperature of either 18 or 27°C

Male developmental temperature	Mean territorial score at different test temperatures	
	18°C (<i>N</i> =34)	27°C (<i>N</i> =38)
18°C	1.9 \pm 0.30	2.3 \pm 0.36
25°C	3.6 \pm 0.41	6.6 \pm 0.52
	(<i>P</i> =0.007*)	(<i>P</i> <0.001*)

N is the number of pairs in each sample.

**P*-values are two-tailed tests (Wilcoxon matched-pairs signed-ranks tests) of the probability that males with different developmental temperatures have equivalent territorial scores. By using this paired test, we circumvent the non-independence of territorial scores of individual males.

effects by comparing numerical territorial scores (number of censuses at which a male alone occupied the food/oviposition site) of the two males in each paired contest. Males raised at 25°C had significantly higher scores than did males raised at 18°C at both test temperatures (Table I; Wilcoxon matched-pairs signed-ranks tests: *P*=0.007 at 18°C, *P*<0.001 at 27°C).

We next checked the frequency of territorial success (categorical scale) of males from the two developmental temperatures. The larger of the competing males was infrequently the more successful male (only 19 of 53 trials, 36%). When tested at high ambient temperature (27°C), males raised at high temperature were almost always (85%, *N*=27) more likely to be classified as winners than were males raised at low temperature (*P*<0.001). When tested at low temperature, males raised at high temperature were again almost always more successful (81%, *N*=26, *P*<0.001). Based on categorical scores, the advantage of males raised at high temperatures was not significantly (χ^2 test: *P*=0.67) greater at high than at low test temperatures.

The above analyses compare territorial success of males raised at different temperatures, but do not simultaneously consider possible effects of (or interactions between) test temperature or differences in dry body mass. However, a general linear model (Methods) with all these effects indicates that the only significant term was the intercept. In

other words, males raised at 25°C had relatively high territorial success (*P*<0.001) that was independent of test temperature (*P*=0.145), of the difference in mass between tested individuals (*P*=0.947) and of the interaction between test temperature and the difference in mass (*P*=0.566).

Parental Temperature and Territorial Success

We conducted a small-scale test (*N*=16 pairs) to determine whether parental temperature regime might influence the territorial success of their male offspring (at 27°C), where all tested males were raised only at 25°C. Indeed, males whose parents were raised at 25°C had significantly higher territorial scores (6.5 \pm 0.058) than did males whose parents were raised at 18°C (3.8 \pm 0.62; Wilcoxon matched-pairs signed-ranks test: two-tailed *P*=0.046).

DISCUSSION

Our experiments demonstrate that males raised at 25°C were successful in paired territorial contests with males raised at 18°C (*P*<0.001). This pattern was independent of test temperature (18 or 27°C, *P*=0.145), of the difference in body mass of the individuals being tested (*P*=0.947), or of the interaction of these variables (*P*=0.566). As argued below, these patterns contradict both the size-advantage hypothesis and the acclimation-advantage hypothesis.

The 'size-advantage hypothesis' predicted that low-temperature males, by virtue of their larger size, would be successful in territorial contests at both high and low ambient temperature. In our experiments, however, low-temperature males were infrequently successful and had relatively low territorial scores at either temperature (Table I). Clearly, bigger isn't always better, contrary to the impression given by the literature (see references in Introduction). Consequently, whether large size is or is not associated with male territorial success may depend on the particular developmental and genetic factors responsible for large adult size. For example, large males may well be successful if their large size reflects development under uncrowded conditions (Hoffmann 1987b), but not if it reflects development at low temperature (herein). (This pattern suggests that the large-size advantage documented in field studies

(Partridge et al. 1987; Markow 1988; Santos 1988) may be due to something other than developmental temperature (L. Partridge, personal communication). Interestingly, a recent analysis (Thomas 1993) suggests that within-season variation in body size in *D. buzzatii* is determined primarily by variation in nutrition not in developmental temperature.) Moreover, following selection for male territorial success, selected males had enhanced aggression and territorial success but were not larger in size (Hoffmann 1988). Thus, size per se may be a 'red herring' with respect to territorial success.

The acclimation-advantage hypothesis (Leroi et al. 1994; Huey et al. 1995) predicted that (1) males raised at high temperature would win contests at high ambient temperature, which they did and (2) that they would lose at low temperature, which they did not. Thus, development in a particular environment does not guarantee enhanced performance (or at least territorial success) in that same environment. However, the territorial advantage of males raised at 25°C was slightly but not significantly ($P=0.145$) reduced in contests at 18°C relative to those at 27°C (see Table I). It would be interesting to determine whether development at 25°C might become a disadvantage at test temperatures lower than 18°C, consistent with the acclimation-advantage hypothesis.

The observed patterns can be interpreted in two ways. First, smaller might be better with regard to male territoriality. After all, 25°C males, which were generally small, did have relatively high territorial success at both test temperatures. However, this suggestion is strongly contraindicated by many laboratory and field studies (references above) with *Drosophila*. More to the point, the difference in mass between paired males had no effect on territorial success ($P=0.947$). Second, development at 25°C might be physiologically advantageous relative to development at 18°C (Cohet & David 1978; Huey et al. 1995), such that males raised at 25°C, though small in size, might be sufficiently vigorous to more than compensate for being small. By extension, perhaps an 'optimal' developmental temperature exists for flies (Cohet & David 1978; Huey et al. 1995), such that flies raised at their optimal temperature might have relatively high fitness independent of the environment they experience as adults. This optimal developmental temperature hypothesis is potentially testable by comparing dominance of

males raised at a series of temperatures, not just at two. Especially interesting will be the relative territoriality of males raised at very high temperature (ca 29°C). These males will be smaller than males raised at 25°C (David et al. 1983). If smaller is better, males raised at 29°C should have high territorial success at 18, 25, or 29°C. If, however, 25°C represents an optimal developmental temperature (Cohet & David 1978; Huey et al. 1995), then male flies raised at 25°C should have greater territorial success than those raised at 29°C (or 18°C) at all three test temperatures.

A variety of independent data support the suggestion that development of *D. melanogaster* at 21–25°C may be physiologically advantageous relative to development at lower or higher temperature (Cohet & David 1978). Flies raised at 25°C have much higher maze-running success than do flies raised at 13°C (Cohet 1974). Males raised at 25°C run faster at a variety of temperatures than do males raised at 18°C (Gilchrist 1993). Furthermore, females raised at 21 or 25°C had greater maximal daily egg production as well as higher lifetime egg production than did flies raised at lower ($\leq 17^\circ\text{C}$) or higher ($\geq 28^\circ\text{C}$) temperatures, when tested at 25°C (Cohet & David 1978). However, the thermal sensitivity of similar traits was less pronounced in two parallel studies (McKenzie 1978).

Our cross-generational experiment was small scale, but it nevertheless suggests that males whose parents are raised at 25°C had greater territorial success than did males whose parents are raised at 18°C, at least when tested at 27°C. Cross-generational effects of temperature are also known for adult dry mass and heat tolerance (Crill 1991) and fecundity in *D. melanogaster* (Huey et al. 1995), and now for territorial success as well. Cross-generational effects of many other factors have been documented in insects (Mousseau & Dingle 1991).

The above patterns generally suggest that flies raised at 25°C (and whose parents are raised at 25°C) are more vigorous as adults than are flies raised at 18°C (or whose parents are raised at 18°C). Interestingly, female *D. melanogaster* preferentially lay their eggs at 23–25°C in a laboratory thermal gradient (Fogleman 1979). If selection has favoured females that select oviposition sites with physiologically suitable temperatures (in other words, 'mother knows best'), then these behavioural results are also consistent

with the idea that an optimal developmental (parental) temperature exists and is near 25°C. One possible exception is, however, an experiment in which males raised at 18°C had faster mating speeds than did males raised at 26°C (Ewing 1964). However, these experiments were non-competitive. Moreover, experiments involving artificial selection for male territorial success suggest that mating speed has limited relevance to mating success (Hoffmann 1988): relative to control males, the selected males had enhanced territorial success and enhanced mating success but nevertheless had similar mating speeds (Hoffmann 1988). Thus mating speed may be weakly related to mating success when territories are present.

We raise three caveats concerning our interpretations. First, our results might be dependent on the particular stocks we used, given that these flies had been evolving at 25°C for over 7 years. Indeed, these flies are known to differ in the thermal sensitivity of development time from lines evolving for the same period at 16.5°C (Huey et al. 1991). However, testing a California stock of *D. melanogaster* that had been at 25°C for less than 1 year, Gilchrist (1993) found that male flies raised at 25°C also ran faster than flies raised at 18°C. This, plus evidence from a variety of other stocks (above), suggest that the differences we observed are robust. Of course, this issue must ultimately be resolved either by testing flies that were more recently collected from nature, or by testing flies that have been evolving for several years at different temperatures (e.g. Cavicchi et al. 1985; Huey et al. 1991).

Second, although we have interpreted our findings in terms of the effects of developmental temperature on the physiological vigour and the size of adults, we recognize that developmental temperatures may influence male territorial success in ways that are independent of physiological vigour or body size. For example, developmental temperatures influence mating success in some *Drosophila* via effects on epicuticular hydrocarbons (Markow & Toolson 1990). Conceivably, those hydrocarbons might influence male territorial success as well.

Third, results of previous studies (see references in Introduction) suggest that males raised at 25°C will not only have high territorial success, but also high reproductive success relative to males raised at 18°C. However, this hypothesis should be tested directly in separate experiments.

The concept of an optimal developmental temperature (Cohet & David 1978; Huey et al. 1995), and perhaps even that of an optimal parental temperature, has significant applied implications. If the physiological and behavioural vigour of an adult insect ('quality control', Boller & Chambers 1977) is strongly influenced by developmental and parental temperatures, then the impact of insect-release programmes (e.g. sterile male, biocontrol) may be enhanced by raising insects at temperatures that maximize offspring performance and vigour.

In conclusion, developmental and parental temperatures have profound effects on male territorial success in *D. melanogaster*. The developmental effect is independent both of the temperature at which territorial success is tested and also of difference in body size between males. Consequently, studies attempting to address the impact of body size on fitness may be clarified by recognizing that mapping of size on fitness may not be simple: whether large size confers an advantage may depend strongly on the particular developmental and genetic factors that are responsible for large size.

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