Testing Drosophila life-history in the field: local adaptation in body size, development time and starvation resistance

Linde, Kim van der

Citation

Linde, K. van der. (2005, January 12). *Testing Drosophila life-history in the field: local adaptation in body size, development time and starvation resistance*. Retrieved from https://hdl.handle.net/1887/572

Introduction

In the past decades, the life-history research on different *Drosophila* species has generated a wealth of knowledge. In this chapter, I review the relevant *Drosophila* literature concerning the three life-history traits I have investigated: body size, development time, and starvation resistance. I have organised the relevant literature with respect to the type of environmental variation influencing the different traits. These are gradients along latitudinal clines, temperature, and crowding effects.

Geographical variation in life-history traits is often observed, and this variation is sometimes clearly related to latitude (or altitude). These latitudinal clines provide insight into how natural selection shapes these traits, but different aspects of the environment change simultaneously and disentangling them is not always easy. One often mentioned environmental factor that could explain the geographical variation is temperature. Oversimplified, average temperature is highest in the tropics, and becomes lower with increasing latitude. Therefore, temperature could be the explanatory factor and I thus discuss the temperature-related relevant literature separately. The third environmental factor that I discuss is crowding. Although the actual crowding levels in nature are poorly documented, they do play a role in *Drosophila* (Sevenster 1992) and there are some indications that crowding does differ between patches (Atkinson 1979) or habitats and across seasons (Krijger 2000, Krijger & Sevenster 2001, Sevenster & van Alphen 1996). The final aspect I review in this chapter is the genetic correlations between these three traits.

Geographical variation in life-history traits

Geographical variation in life-history traits is commonly observed, and can provide valuable clues about which environmental factors could be responsible for the selection of the traits under natural conditions. An overview is given in Table 1.

BODY SIZE

Bergmann's rule states that "The smaller sized geographical races of a species are found in the warmest parts of the range, the largest races in the cooler districts" (cf. Mayr 1942). Body size within species of *Drosophila* usually show clear latitudinal clines with larger individuals at higher latitudes (Azevedo *et al.* 1996, Capy *et al.* 1993, Coyne & Beecham 1987, David & Bocquet 1975a, David & Bocquet 1975b, David & Kitagawa 1982, Hoffmann *et al.* 2001a, Hyytia *et al.* 1985, Imasheva *et al.* 1994, James *et al.* 1995, 1997, James & Partridge 1998, Karan *et al.* 1998c, Lemeunier *et al.* 1986, Misra & Reeve 1964, Parkash *et al.* 1998, Parkash & Munjal 1999, Parsons 1983, Prevosti 1955, Robinson *et al.* 2000, Stalker & Carson 1947, Tantawy & Mallah 1961, van 't Land *et al.* 1999, Watada *et al.* 1986). The North-American cline reported by Long & Singh (1995) for *Drosophila melanogaster* was non-monotonic in nature, with the largest flies at middle latitudes and smaller flies in the north and south. Detailed analysis of whether temperature might account for this non-monotonic cline showed that neither temperature, nor related aspects are likely to explain the observed cline. Hallas *et al.* (2002) found a non-linear cline for *D. serrata* with a sharp reduction in body size in the tropics. Clinal variation in *D. melanogaster* collected along the east coast of North America is maintained over a wide range of experimental developmental temperatures (Coyne & Beecham 1987, Tantawy & Mallah 1961) indicating that the differences along the cline is genetic. Hoffmann *et al.* (2001a) established iso-female lines from *D. melanogaster* flies collected at five locations in Queensland (tropical) and three locations in Tasmania (temperate), and scored the thorax length of 8 to 10 individuals from each iso-female line. The nested analysis of variance showed that the variation among iso-female lines within each collection site, and between geographic regions were significant, while the component of variation among the collecting locations within geographic region was not significant. The variation among iso-female lines, collection sites and geographic regions explained 13.5, 1.7 and 3.3 percent of the total variation, respectively. In general, the clinal patterns within the various *Drosophila* species are thus consistent with Bergmann's rule.

DEVELOPMENT TIME

Latitudinal clines in *Drosophila* for development time have been reported for Australia and South America, with egg-to-pupae and egg-to-adult development times (James & Partridge 1995, 1998) and egg-to-adult development times (van 't Land *et al.* 1999) that are longer at lower latitudes. However, the South-American cline is very shallow, explaining only 0.1 percent of the measured variation, while the variation between sites independent of latitude is considerable. The significant effect in the Australian cline depends heavily on one low-latitude population (A.C. James, personal communication in van 't Land *et al.* 1999), and only one of the two correlations between latitude and pupation time remained significant after removal of this single data point out of 13. Van der Linde & Sevenster (chapter 2) measured egg-to-adult development times of *Drosophila* species from the Philippines in a common environment. They found that there were significant differences between populations of five out of eight species on a short transect covering four different habitats ranging from grassland to secondary forest. All but one species displayed a similar pattern in development times among habitats, giving a highly regular response to the underlying differences between the collection sites. However, the pattern was not related to habitat-ranking as based on microclimates and vegetation.

STARVATION RESISTANCE

Hoffmann & Harshman (1999) showed in their review of all available studies, that tropical populations of the various *Drosophila* species had a better starvation resistance than temperate populations (Da Lage *et al.* 1990, Karan *et al.* 1998a, Karan & Parkash 1998, Parkash *et al.* 1994, Parkash & Vandna 1994, Shamina *et al.* 1993). In more recent studies, Robinson *et al.* (2000) and Hallas *et al.* (2002) did not find such a latitudinal cline in South-America or Australia. Robinson *et al.* (2000)

Table 1: Overview of the results as reported in the literature for the three life-history traits. Effects of temperature and crowding are each partitioned into phenotypic and genetic effects. For references, see the text.

Trait	Geographical variation	Temperature variation: selection experiments	Temperature variation: environmental effects	Crowding effect: phenotypic	Crowding effect: genetic
Body size	Lower latitudes -> smaller; Sometimes inverted U-shape with smaller at both ends; iso-female variation much larger than geographical or population	higher -> smaller	higher -> smaller; Sometimes inverted U-shape with smaller at both ends	increased -> smaller, sex difference increased	The two studies contradict each other
Development time	Lower latitudes -> longer	higher -> longer	higher -> shorter	increased -> longer, sex difference often decreased	increased -> shorter
Starvation resistance	Inconsistent, but most tropical>temperate, some no effect; iso-female variation much larger than geographical or population	-	Inverted U-shape, shorter at both ends	15-28 days after emerging: Increased -> longer; 0 days after emerging: Increased -> shorter; sex differences increased	increased: 0 days -> longer

suggest that the Indian latitudinal cline (Karan *et al.* 1998a) is due to the specific Indian climatic situation and exclude the possibility of rapid laboratory selection in the South-American lines because other traits had not undergone laboratory adaptation since collection (Azevedo *et al.* 1996, van 't Land *et al.* 1999). However, Hoffmann *et al.* (2001b) and Matos *et al.* (2002) found rapid loss of starvation resistance in the laboratory within short periods after establishing the stocks. This is supported by the rapid responses to laboratory selection regimes (Borash & Ho 2001, Chippindale *et al.* 1996, Harshman & Schmid 1998, Hoffmann & Parsons 1989, Service *et al.* 1988). Hoffmann *et al.* (2001a) measured the variation in starvation resistance among iso-female strains. The females were collected at several localities in Tasmania and Queensland (Australia). Geographic region had a significant impact on the realised starvation resistance confirming earlier results (Queensland populations having a higher starvation resistance), but it explained only a small fraction of the variation (2.7%). Most variation (over 40%) was attributable to the strain effect. Van der Linde & Sevenster (chapter 2) found that two out of eight species from the Philippines showed significant genetic variation between populations from different habitats, but found no systematic correlation with habitat. Parkash & Munjal (1999) found that higher starvation tolerance was positively correlated with minimum temperatures, higher metabolic stress in relation with smaller body size, and higher population density and competition.

SUMMARY

Development time and body size both show clear and repeatable responses to latitude, while a generalised pattern for starvation resistance is less obvious. Studies show either that tropical populations have a longer starvation resistance, or that there is no relation with latitude. The genetic variation within populations is generally very wide for body size and development time, compared to the geographical variation. This abundant genetic variation could facilitate local adaptation to environmental differences.

The impact of temperature on life-history traits

Temperature is one of the variables that covaries with latitude, but other variables, including additional climatic factors, also covary with latitude. In addition, changes in vegetation alter the daily temperature pattern (Walter 1984). Temperature is often suggested as a key factor explaining latitudinal cline variation in life-history traits. For that reason, the effect of temperature on life-history evolution has been tested in the laboratory. However, it is crucial to keep in mind that those experiments are conducted under constant temperatures while the temperatures in the field fluctuate greatly. Therefore, the laboratory results are not necessarily related to the latitudinal cline patterns. The effects of the temperature are divided into two categories: genetic and environmental effects. An overview is given in Table 1.

BODY SIZE

Temperature-mediated artificial selection results in relatively larger adult body size for lines selected at lower temperatures (Anderson 1966, 1973, Cavicchi *et al.* 1985, Neat *et al.* 1995, Partridge *et al.* 1994a, Powell 1974). Besides shaping the genetics, temperature also has a direct environmental effect on body size resulting in smaller individuals at higher temperatures (Alpatov & Pearl 1929, Atkinson & Sibly 1997, Azevedo *et al.* 1996, Eigenbrodt 1930, Imai, 1933 #908, Imai 1937, James *et al.* 1997, James & Partridge 1998, Karan *et al.* 1998c, Karan *et al.* 1998b, Noach *et al.* 1996, Ray 1960). The response to temperature resembles an inverted U-shaped curve, with a sharp reduction in size at the lower end (David & Clavel 1967, David *et al.* 1983, David *et al.* 1990, David *et al.* 1994, de Moed *et al.* 1997a, Morin *et al.* 1996, Morin *et al.* 1997, de Moed, 1997 #3051).

DEVELOPMENT TIME

Temperature selection on development time shows that low temperatures lines have a shorter larval (Partridge *et al.* 1994b) or egg-to-adult (Anderson 1973, James & Partridge 1995) developmental time compared to the high temperature lines when measured at the same temperature. Pupal development time is less predictable with no difference at lower temperatures but low temperature lines had longer development times at higher rearing temperatures (Partridge *et al.* 1994b). Besides the evolutionary effect, lower temperatures directly result in increased development times (Azevedo *et al.* 1996, James *et al.* 1997, Zwaan *et al.* 1992).

STARVATION RESISTANCE

Several authors (Da Lage *et al.* 1989, Karan & David 2000) have studied the starvation resistance of different *Drosophila* species under different temperatures. All species showed a biphasic response curve at all temperatures measured, with a reduction in resistance to either end of the temperature range. The optimum differed among species, ranging between 4.76 and 14.55 ºC. A comparison of *D. melanogaster* individuals grown at different temperatures showed that flies reared at lower temperatures have a lower optimum than flies reared at higher temperatures (range: 6.2 - 7.5 ºC) but the differences in survival at the higher temperatures are minimal between flies from the different growth temperatures (Karan & David 2000).

SUMMARY

Selection experiments showed that the high temperature selected lines are smaller and have a longer development time. This is in line with the latitudinal cline patterns. The rearing temperature has a similar effect on body size, but development times become shorter with increasing temperatures. Starvation resistance seems to have an optimum temperature, with lower starvation resistances at either end. Habitat change leads to changes in the daily temperature regime, and this could partially explain the variation between habitats in the realised life-history traits.

The impact of crowding on life-history traits

Crowding can play a role in studies when the experimental densities are not controlled for. Moreover, food abundance varies between habitats, but also within habitats, both at a spatial and temporal scale. These differences in food abundance can result in different levels of crowding. Krijger (2000) found that the mean resource abundance was higher in the three disturbed habitats than the three forest habitats in his study in Panama. Furthermore, the temporal heterogeneity was less in the disturbed habitats. Sevenster (1992, Sevenster & van Alphen 1993a) found that the food availability varied widely during the year, but also at a spatial scale. An overview is given in Table 1.

BODY SIZE

Several authors (Bakker 1961, Borash & Ho 2001, Chiang & Hodson 1950, de Moed *et al.* 1997b, Grimaldi & Jaenike 1984, James & Partridge 1998, Karan *et al.* 1998c, Perez & Garcia 2002, Robinson *et al.* 2000, Santos 1996, Sevenster 1992, Wilkinson 1987, Zwaan *et al.* 1991) have found a phenotypic response in which body size at eclosion is severely reduced with increased crowding. This reduction in body weight at eclosion can be up to 80% of the maximum weight at eclosion. Van 't Land (1997) found that crowding increased the difference between the sexes. *Drosophila* flies from wild populations are generally more variable for body size than their laboratory reared relatives (Coyne & Beecham 1987, David *et al.* 1980, Gibert *et al.* 1998, Imasheva *et al.* 1994, Moreteau *et al.* 1995). This is often explained as an effect of variation in crowding (Prout & Barker 1989, Santos 1996). Perez & Garcia (2002) found that high-density selected lines had smaller body-sizes when measured at the same density in the common garden experiment, while in a similar experiment Borash & Ho (2001) found the opposite, namely that high-density selected flies were heavier. It is unclear how such a difference can be accounted for.

Development time

Flies reared under crowding conditions have a longer egg-to-adult development time than those reared under non-crowding conditions (Borash & Ho 2001, Chiang & Hodson 1950, Perez & Garcia 2002, van 't Land 1997, Zwaan *et al.* 1991). It is also interesting that some studies report that the sex difference disappears with increased crowding because the development time of females increases more rapidly with crowding than males (Santos *et al.* 1994, van 't Land 1997). However, other studies fail to find such a differential response between the sexes (Roper *et al.* 1996). Perez & Garcia (2002) found that the additive genetic variation and the heritabilities for development time varied with the selection density. Selection on density leads to a decrease in the development time (Borash & Ho 2001, Perez & Garcia 2002).

STARVATION RESISTANCE

Starvation resistance can be measured at different ages of a fly, and the results should be interpreted accordingly. Zwaan *et al.* (1991) measured starvation resistance in non-selected *Drosophila melanogaster* reared at different densities at ages of 15 and 28 days old and found a crowding-related increase in starvation resistance. Baldal *et al.* (in press), using unselected stocks and rearing at different densities, measured flies at eclosion and found that starvation resistance decreased with crowding in *Drosophila melanogaster*, *D. equinoxialis,* and *D. ananassae*. This result matches those of Borash & Ho (2001) for freshly emerged *D. melanogaster* flies of both the uncrowded and crowded selection lines. Several authors (Borash & Ho 2001, Mueller *et al.* 1993) found that selection under high crowding conditions leads to an increase of the starvation resistance. Females reared under crowding conditions generally have a higher starvation resistance, while males reared under crowding conditions seem to have similar starvation resistances or even somewhat lower values (Service *et al.* 1985, Service 1987, van 't Land 1997, Zwaan *et al.* 1991, 1995b).

SUMMARY

Crowding results in smaller adults with longer development times. Starvation resistance is increased at higher age but decreases directly after eclosion. The increased crowding results in increased differences between the sexes in body size and starvation resistance, but those differences decrease for development time. Selection in response to increased crowding results in flies that have shorter development times and increased starvation resistances. The effect of crowding selection on body size is unclear as the two studies contradict each other. Due to the effects of density on the life histories of the flies, it will be important for the data I collect to initially examine the effect of density. Furthermore, resource abundance varies between habitats, but also within habitats, both in time and space. When this leads to habitat specific differences in selection, this could lead to locally adapted populations.

Genetic and phenotypic correlations among traits

Genetic correlations between traits may limit the response to selection when opposite selection pressures work on the two traits. In this section, I not only review the literature for genetic correlations within species, but also explore the interspecific correlations between traits. An overview is given in Table 2.

BODY SIZE AND DEVELOPMENT TIME

Selection experiments for larger body size or longer development time in *D. melanogaster* showed that larger body sizes were associated with longer pre-adult development times (Cortese *et al.* 2002, Gu & Barker 1995, Nunney 1996b, Partridge & Fowler 1993, Partridge *et al.* 1999, Reeve 1954, Robertson 1957, 1960a, b, 1963, Roper *et al.* 1996, Santos *et al.* 1992, 1994, Zwaan *et al.* 1995a). However, in some experiments, the opposite selection for smaller flies did not result in a decrease in development time as expected (Nunney 1996b, Partridge & Fowler 1993, Partridge *et al.* 1999). Betran *et al.* (1998) and Gu & Barker (1995) found positive phenotypic and genetic correlations between the two traits. Van 't Land *et al.* (1999) found a significant negative correlation between latitudes and development time and a significant positive correlation between latitude and wing size. The correlation between the two traits was, however, non-significant. A similar pattern is observed for the Australian cline (James & Partridge 1995). Perez & Garcia (2002) did not find significant genetic or phenotypic correlations between these two traits in their base population, but the sign of the correlations was in all but one case, negative. Their explanation was that the effect was caused by the medium they used. This did not allow yeast growth and may thus have limited the available food versus the situation in which yeast growth offers a continuous fresh supply of food (cf. Bakker 1961). Bakker (1969) found indeed that fast developing individuals were the heaviest. Other authors found that this genetic correlation is dependent on the diet of the flies (Robertson 1963) and that the presumed trade-off between the traits disappeared under non-crowding conditions (Cortese *et al.* 2002), or even changes sign completely with change of the environment (Gebhardt & Stearns 1988).

BODY SIZE AND STARVATION RESISTANCE

Parkash & Munjal (1999) found a negative correlation between body size and starvation resistance within six species of Drosophilids collected along a climatic cline in India. This negative correlation also appears to be present in the data from Hoffmann *et al.* (2001a) who found in the laboratory that Tasmanian populations were larger and had a shorter starvation time than the Queensland populations (estimation from their figure 2: $R^2 = 0.55$, $p = 0.058$). The selection experiment of Hoffmann & Parsons (1993) on both *D. melanogaster* and *D. simulans* did not result in a correlated response for body size, while later experiments showed that lines of *Drosophila melanogaster* selected for higher starvation resistance became larger (Chippindale *et al.* 1996, Harshman *et al.* 1999). Zwaan *et al.* (1991) found no phenotypic correlation between body size and starvation resistance in flies 15 or 28 days after eclosion. Hallas *et al.* (2002) in their study did not find differences in starvation resistance between populations of the cline, but did find a non-linear cline for development time. Toda & Kimura (1997) found a positive interspecific correlation for mycophagous Drosophilids of Japan.

DEVELOPMENT TIME AND STARVATION RESISTANCE

Several authors have shown that lines of *Drosophila melanogaster* selected in the laboratory for starvation resistance had a longer development time (Chippindale *et al.* 1996, Harshman *et al.* 1999). Zwaan *et al.* (1991) found no phenotypic correlation between development time and starvation resistance in flies 15 or 28 days after eclosion, nor did they (Zwaan *et al.* 1995a) find a correlated response for starvation resistance in their upward or downward selection lines for development time. Robinson *et al.* (2000) found no corresponding cline for the South American cline, which does show a slight cline for development time. Sevenster & van Alphen (1993a) have described a positive interspecific correlation between development time and starvation resistance for Panamanian *Drosophila*, while Toda & Kimura (1997) found a negative interspecific correlation for mycophagous Drosophilids of Japan. Van der Linde & Sevenster (chapter 2) in their study on *Drosophila* from the Philippines found that the two traits had completely different patterns and the correlations were either absent or negative, both suggesting that there is no underlying genetic correlation or that differential selection on the two traits is obscuring such a correlation.

SUMMARY

Table 2 is an attempt to provide an overview of the research to date. Despite the large volume of articles on *Drosophila* life-history traits, several cells of the table remain empty, as I could not find any relevant data. Furthermore, many studies report no correlated responses or results varied between similar studies.

Table 2: Overview of estimated correlations among the three traits. First two columns describe genetic correlations, the second pair phenotypic, and the last, interspecific. For references, see text.

	Selection experiments	Other methods	Phenotypic	Latitudinal	Interspecific
Body size - development time	Positive response, sometimes no response in selection for smaller flies	Non-significant negative, variable	Positive	Negative	
Body size - starvation resistance	Absent or positive		Absent	Absent	Positive
Development time - starvation resistance	Absent or positive	Absent		Absent	Positive or absent

Concluding remarks

Since the mid 20th-century, many studies concerning *Drosophila* life-history traits have been published. In this chapter, I reviewed the literature concerning three life-history traits: body size, development time and starvation resistance. Specifically, I reviewed four different topics: latitudinal clines, temperature effects, crowding effect, and genetic correlations among the three traits.

This overview provides a useful starting point to understand how environmental cues can shape life-history traits. In **Chapter 4**, I will present a field-based study in which I examine the effect of habitat differences on the realised life-history traits. In **Chapter 5**, I present a laboratory-based study in which I examine the existence and magnitude of genetic correlations between these three traits. These studies can shed more light on how life-history evolution takes place under field conditions, and whether genetic correlations can slow adaptation to a new environment.