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Correlates of sexual dimorphism for dry weight and development time in five species of *Drosophila*

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Abstract

Pre-adult development time, dry weight at eclosion, and daily fecundity over the first 10 days of adult life were measured in five species of *Drosophila* from the *melanogaster* and *immigrans* species groups. Overall, the three species of the *melanogaster* group (*D. melanogaster, D. ananassae, D. malerkotliana*) developed faster, were lighter at eclosion, and produced more eggs per unit weight at eclosion than the two species of the *immigrans* group (*D. n. nasuta*, *D. sulfurigaster neonasuta*). The degree of sexual dimorphism in dry weight was greater than that in development time, but did not vary significantly among species, and was not correlated with fecundity, contrary to expectations that sexual selection for increased fecundity drives sexual size dimorphism in *Drosophila*. The degree of dimorphism in development time was significantly correlated with dry weight and fecundity, with lighter species tending to be more dimorphic for development time as well as more fecund, both in absolute terms and in terms of fecundity per unit weight. The results suggest that our understanding of the evolutionary forces maintaining sexual size dimorphism in *Drosophila* will probably benefit from more detailed studies on the correlates of sexual dimorphism within and among *Drosophila* species, and on the shape of reaction norms for the degree of sexual dimorphism across different levels of ecologically relevant environmental variables.

Key words: sexual dimorphism, dry weight, development time, fecundity, *Drosophila*

INTRODUCTION

Sexual dimorphism for traits expressed in both sexes poses interesting evolutionary questions about the genetics of the traits, and the nature of selection responsible for maintaining the dimorphism in the face of the mixing of genes in both sexes (Fisher, 1958; Lande, 1980; Rhen, 2000). Two life-history traits showing prominent sexual dimorphism in *D. melanogaster* are development time and body size/weight, with females typically being faster developing and also larger and heavier, thus implying an even stronger dimorphism in pre-adult rates of weight gain (Nunney, 1996; Chippindale *et al*., 1997). The greater development time of males is known to be the result of a longer pupal, rather than larval, duration in males (Bakker & Nelissen, 1963; Nunney, 1983), and it has been speculated that the reason for this is the time-consuming process of sperm maturation (Nunney, 1996). The degree of sexual dimorphism in development time in *D. melanogaster* is environment sensitive, and is more prominent at low or moderate larval density (Zwaan, Bijlsma & Hoekstra, 1995; Joshi, Do & Mueller, 1999). There is also evidence for the evolution of dimorphism in development time in *D. melanogaster* populations subjected to selection for faster development, with the difference between male and female development time being reduced from 4.5 h to 1.4 h over *c.* 70 generations of selection (Prasad *et al*., 2000). The ultimate cause of sexual dimorphism in development time in *D. melanogaster*, however, is as yet unknown and has been described as one of the 'mysteries of *Drosophila* biology' (Chippindale *et al*., 1997).

Body size dimorphism in *D. melanogaster* is thought to be driven by sexual selection for higher fecundity in females, and populations subjected to selection for greater fecundity have been seen to exhibit correlated increases in male–female differences in thorax length, thorax width and abdomen width (Reeve & Fairbairn, 1999). Yet, selection for increased or decreased thorax width in males only or females only did not result in the predicted correlated evolution of sexual size dimorphism (Reeve & Fairbairn, 1996). Unlike development time, it is not clear how larval density or body size affect

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sexual size dimorphism in *Drosophila*. Populations of *D. melanogaster* selected for faster development, which showed a 40% reduction in dry weight compared to controls, did not exhibit a correlated change in sexual dimorphism for dry weight at eclosion even after 170 generations of selection (N. G. Prasad, M. Shakarad & A. Joshi, pers. obs.), although dimorphism in development time in these populations decreased as selection proceeded (Prasad *et al*., 2000). Indeed, the per cent reduction in dry weight in these populations, over the first 70 generations of selection, was slightly greater in males than in females, suggesting that, if anything, sexual size dimorphism might be increasing with an overall reduction in size in both sexes (Prasad *et al*., 2000). Similarly, in another study carried out on related populations of *D. melanogaster*, the degree of sexual dimorphism in dry weight did not differ between treatments at high and low larval density, even though adult dry weights at eclosion were reduced by *c*. 20–33% in the high density treatment (Borash & Ho, 2001). A study on two strains of *D. melanogaster* that were completely unrelated to those used by Prasad *et al*. (2000) and Borash & Ho (2001), however, showed that reduced food levels per larva led to a reduction in both dry weight and sexual dimorphism for dry weight (Bakker, 1961). It is not possible to pinpoint the cause of the differences between the results from these studies.

Sexual size dimorphism in *D. melanogaster* may be owing to genes responsible for higher fecundity, that have female-limited expression, and cause correlated increases in size by affecting aspects of resource acquisition and accumulation in larvae (Prasad & Joshi, 2003). If there are relatively many more genes, or genes with larger effects, that affect body size in both sexes, this could explain why single-sex selection for size does not increase the degree of dimorphism (Prasad & Joshi, 2003). Reeve & Fairbairn (1996) also point out that predicting the relationship between development time and sexual size dimorphism in *Drosophila* may require a greater knowledge of how weight gain trajectories of males and females differ; constructing these trajectories empirically is, however, an extremely daunting task.

Overall, although it seems that sexual dimorphism for both development time and body size/weight in *Drosophila* can evolve in response to selection, it is not clear what selective forces are shaping sexual dimorphism in these traits. There are few studies that focus on both size dimorphism and development time dimorphism in *Drosophila*. Moreover, there do not seem to be any studies looking at correlates of dimorphism in these traits in species other than *D. melanogaster*. Here, results are reported from a study in which some of the correlates of sexual dimorphism for dry weight at eclosion and pre-adult development time were examined across five species of *Drosophila*, of which four were freshly wild caught, and one is a long-established laboratory strain, used here essentially as a comparative standard. Our aim was to assess whether sexual dimorphism in development time and dry weight at eclosion were correlated with one another, and particularly how the degree of dimorphism in these traits was correlated with other life-history traits such as male or female development time, dry weight and fecundity in early life.

MATERIALS AND METHODS

Experimental populations

One population each of 5 species of *Drosophila*, first described in Sharmila Bharathi *et al*. (2003), were used in this study. Three of the species belonged to the subgenus *Sophophora*, species group *melanogaster*, namely *D. melanogaster* (subgroup *melanogaster*), *D. ananassae* (subgroup *ananassae*, species complex *ananassae*), and *D. malerkotliana* (subgroup *ananassae*, species complex *bipectinata*). The other 2 species belonged to the subgenus *Drosophila*, species group *immigrans*, subgroup *nasuta*, namely *D. nasuta nasuta* (frontal sheen complex) and *D. sulfurigaster neonasuta* (orbital sheen complex). The *D. melanogaster* population was one of the JB populations (JB-1) previously described in detail (Sheeba, Madhyastha & Joshi, 1998) and has been in the laboratory for over 700 generations. The populations of *D. ananassae, D. malerkotliana* and *D. n. nasuta* were collected from orchards and domestic garbage dumps in different parts of Bangalore, whereas *D. s. neonasuta* was collected at both Bangalore and Mysore, India. At the time of this study, the *D. ananassae* population had been through 12 generations in the laboratory, whereas the populations of *D. malerkotliana, D. n. nasuta* and *D. s. neonasuta* had been in the laboratory for 2, 3 and 1 generation(s), respectively. The *D. ananassae* population was initiated from *c*. 300 inseminated females, collected during May–June 2001, while the other 3 populations were established from *c*. 70 inseminated females each, collected during October–November 2001. Collection of flies was achieved by a combination of banana traps and net sweeping, mostly during early morning and dusk.

Maintenance of flies

The *D. melanogaster* population has been in the laboratory for > 700 generations on a 21-day discrete generation cycle at 25 °C, under constant light and *c*. 90% relative humidity, on banana-jaggery food. The pre-adult stages were maintained at a moderate density of about 60–80 eggs per vial (9 × 2.4 cm). Eclosed adults were transferred to a Plexiglas cage (25 × 20 × 15 cm) on the 18th day from egg lay, and were given food medium supplemented with live yeast paste for *c*. 2.5 days before egg collection for the next generation. The populations of the other 4 species were also maintained in the laboratory under the same conditions, except that corn meal rather than banana-jaggery food was used, and the number of breeding adults was *c*. 1200 flies per population, compared to *c*. 1800 for the *D. melanogaster* population. Moreover, since the survival and fecundity of the wild-caught species was relatively low (see Results), these 4 populations were maintained on a discrete generation

of < 21 days. Adults were collected into cages as they eclosed, provided with corn meal food and live yeast paste, and eggs were collected *c.* 2 days after the last eclosions. There were logistical reasons, unrelated to the present study, for maintaining the 4 recently wild-caught species on corn meal food. In terms of gross nutritional quality, corn meal food does not seem to be different from banana-jaggery food, at least for our *D. melanogaster* populations, as rearing them on corn meal food does not significantly affect pre-adult development time and survivorship, weight at eclosion, adult lifespan or fecundity (N. Sharmila Bharathi, N. G. Prasad, M. Shakarad & A. Joshi, pers. obs.).

Development time and pre-adult survivorship assay

Eggs were collected from each species by placing a fresh food plate in the cage for 2–3 h. At the end of this interval, exactly 30 eggs were removed from the food plate and placed into vials containing 6 ml of corn meal food (banana-jaggery food for *D. melanogaster*). Eight such vials were set up for each species, and incubated at 25 °C, under constant light and *c.* 90% relative humidity. When the first larvae began to wander in the post-feeding phase, the vials were kept under regular observation every 2 h, and time of pupation of each individual was recorded. The 2-hourly observations were continued after eclosion began, until no flies eclosed for 2 consecutive days. These data, thus, yielded mean larval and pupal duration in each vial, although the larval and pupal duration could not be measured for each individual. Larval duration includes the egg duration which is *c.* 20 h and does not differ significantly among these species (N. Sharmila Bharathi, pers. obs.). Larval and pupal survivorship were also determined for each vial.

Dry weight assay

Freshly eclosed adults developing in vials set up at a density of *c.* 50 eggs per vial were collected, killed by freezing, dried for 36 h at 70 °C and weighed in batches of 5 males or 5 females. Five batches of males and females were weighed for each species. Each vial yielded 1 batch each of males and females, which were used for the estimation of degree of dimorphism (see Statistical analysis).

Fecundity assay

Vials were set up with a density of *c.* 50 eggs per vial and the adult flies from these vials were collected within 6 h of eclosion. For each species, 40 unyeasted vials were then set up, with each vial containing 1 male and 1 female. The flies were transferred to fresh unyeasted vials everyday, and the number of eggs laid by each female during the preceding 24 h was recorded. This assay was done for the first 10 days of adult life, and data from the few (< 5) vials in which the female did not survive the full 10 days were discarded.

Statistical analyses

Data on mean development time of males and females in each vial, and on mean male and female dry weight at eclosion per fly in each batch weighed, were subjected to 2-way analysis of variance (ANOVA) treating species and sex as fixed factors. Larval, pupal and pre-adult survivorship data were subjected to 1-way ANOVAs, treating species as a fixed factor. Log transformation of development time data, and arcsine square-root transformation of survivorship data, did not qualitatively affect either the pattern of significance of ANOVA results or the distribution of errors and, therefore, only results on untransformed data are shown. Species was treated as a fixed factor in these analyses because this study was part of a larger long-term set of studies of the genetic architecture of life-history variation in *D. ananassae, D. malerkotliana, D. n. nasuta and D. s. neonasuta* (Sharmila Bharathi *et al*., 2003), and we are, consequently, specifically interested in these particular populations of these species.

The degree of dimorphism for development time and dry weight at eclosion was calculated in 2 ways: (1) the difference in trait value between the sexes was divided by the average trait value of both the sexes; (2) the trait value of the sex with the lower value was divided by the trait value of the sex with the higher value. Both measures of dimorphism yielded very similar outcomes on analysis, as also observed by David *et al*. (2003), and here only results based on the first measure are presented. Degree of dimorphism in development time and dry weight were calculated for each vial or batch of flies, respectively, and a 1-way ANOVA, treating species as a fixed factor, was carried out separately on the degree of dimorphism for development time and dry weight at eclosion. Data on mean daily fecundity per fly were subjected to a 1-way ANOVA with species as the fixed factor. All pairwise multiple comparisons were done using Tukey's honest significant difference test.

In addition to the ANOVAs, correlation coefficients were also estimated between the degree of dimorphism for development time and dry weight at eclosion and various other traits, both across species and within species. For the within-species analysis, the correlation between degree of dimorphism for a trait and the value of the trait in males and females was estimated, using vials or batches of flies weighed as the replicate observations. Separate analyses were done for development time and dry weight. For the among-species analysis, mean values of traits in each species were used, and all pairwise correlation coefficients were estimated between degree of dimorphism for development time, degree of dimorphism for dry weight at eclosion, male dry weight at eclosion, female dry weight at eclosion, male development time, female development time, male growth rate (dry weight at eclosion divided by development time), female growth rate, and degree of dimorphism in growth rate. Mean

growth rate estimated as dry weight at eclosion divided by development time was highly correlated with growth rate estimated as the dry weight at eclosion divided by larval duration ($r = 0.9554$, $P = 0.01$). Consequently, growth rate estimated as dry weight at eclosion divided by development time was used in all analyses, because this permits separate estimation of male and female growth rate. All analyses were implemented using STATISTICA for Windows Release 5.0 B (StatSoft, 1995).

RESULTS

Development time and pre-adult survivorship

Development time varied considerably across species, with *D. n. nasuta* taking the longest time to develop from egg to adult, followed by *D. s. neonasuta, D. ananassae, D. malerkotliana* and *D. melanogaster* (Fig. 1). The ANOVA revealed significant effects of species, sex, and the species × sex interaction (Table 1). All pairwise differences between species in mean development time (averaged across sex) were significant ($P < 0.025$), except between *D. n. nasuta* and *D. s. neonasuta* ($P = 0.53$).

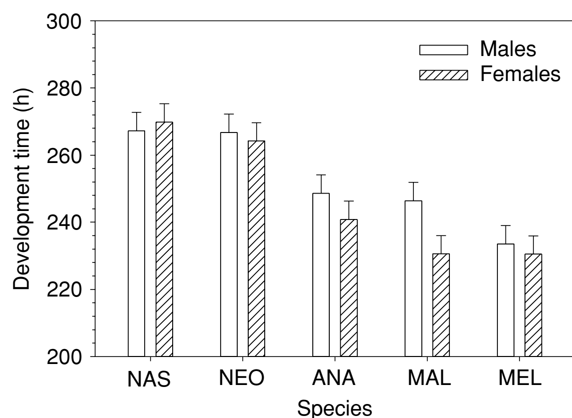

Fig. 1. Mean (± 95% CI) egg to eclosion development time of males and females in five *Drosophila* species. Confidence intervals are based on the mean square error term in the ANOVA. NAS, *D. n. nasuta*; NEO, *D. s. neonasuta*; ANA, *D. ananassae*; MAL, *D. malerkotliana*; MEL, *D. melanogaster*.

Table 1. Summary of results from two separate analyses of variance (ANOVA) carried out on egg to eclosion development time and dry weight at eclosion in five *Drosophila* species. d.f. error for development time and dry weight were 70 and 40, respectively

	Development time		Dry weight	
Effect (d.f.)	*F*	*P*	*F*	*P*
Species (4)	141.58	< 0.001	538.96	< 0.001
Sex (1)	18.85	< 0.001	368.64	< 0.001
Species × sex (4)	6.39	< 0.001	10.84	< 0.001

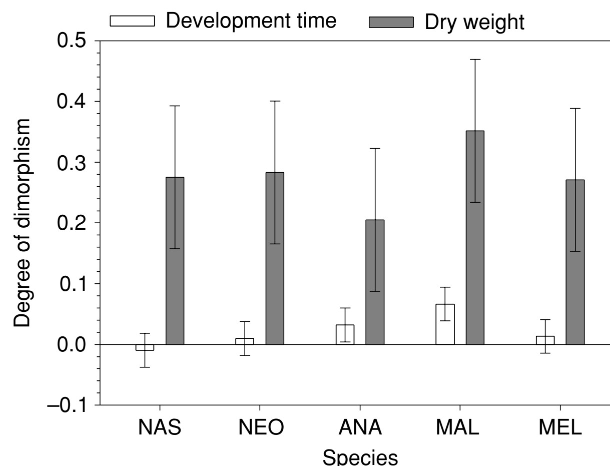

Fig. 2. Degree of sexual dimorphism for egg to eclosion development time and dry weight at eclosion in five *Drosophila* species. Confidence intervals are based on the respective mean square error terms in the ANOVAs. Degree of dimorphism is the trait difference between sexes scaled by the average trait value across sexes. Dimorphism for dry weight does not differ significantly among species. The only significant differences (0.01 level; Tukey's honest significant difference test) in dimorphism for development time are those between *D. malerkotliana* and *D. melanogaster*, *D. n. nasuta* and *D. s. neonasuta*, and between *D. ananassae* and *D. n. nasuta*. NAS, *D. n. nasuta*; NEO, *D. s. neonasuta*; ANA, *D. ananassae*; MAL, *D. malerkotliana*; MEL, *D. melanogaster*.

Overall, males took *c.* 5.3 h longer than females to develop, although the estimated degree of dimorphism for development time varied significantly across species (one-way ANOVA: $F_{4,35} = 8.73$, $P < 0.0001$). The greatest degree of dimorphism was seen in *D. malerkotliana*, with the male–female difference in development time being *c.* 3% of the female development time (Fig. 2). The next highest degree of dimorphism was seen in *D. ananassae*, and the degree of dimorphism for the other three species did not differ significantly from zero (Fig. 2).

Male and female development time across vials were strongly positively correlated in *D. melanogaster* and *D. s. neonasuta*, and not significantly correlated in *D. malerkotliana, D. ananassae* and *D. n. nasuta* (Table 2). As expected, the correlations between female development time and degree of dimorphism in development time were negative in all species. Male development time and degree of dimorphism in development time, on the other hand, were significantly ($P < 0.1$) correlated only in *D. n. nasuta* (Table 2), suggesting that variation in degree of dimorphism for development time is largely determined by variation in female development time in most of these species.

Larval and pupal duration were significantly negatively correlated across species ($r = -0.91$, $P = 0.03$), although the range of variation in larval duration was far greater than that in pupal duration, especially for the wild-caught species (Fig. 3). Not surprisingly, larval duration explained variation in total pre-adult duration time better

Table 2. Pairwise correlations between degree of dimorphism and trait value in males and females for egg to eclosion development (h) time within five *Drosophila* species. Correlation coefficients were calculated using vial means within each species. DD, dimorphism for development time; MD, male development time; FD, female development time

Species	Correlation between	*r*	*P*	*N*
D. malerkotliana	MD and FD	+ 0.2118	0.615	8
	MD and DD	+ 0.5932	0.121	8
	FD and DD	− 0.6611	0.074	8
D. melanogaster	MD and FD	+ 0.7569	0.030	8
	MD and DD	− 0.0183	0.966	8
	FD and DD	− 0.6672	0.071	8
D. ananassae	MD and FD	+ 0.2323	0.580	8
	MD and DD	+ 0.4250	0.294	8
	FD and DD	− 0.7817	0.022	8
D. n. nasuta	MD and FD	− 0.6171	0.103	8
	MD and DD	+ 0.8752	0.004	8
	FD and DD	− 0.9207	0.001	8
D. s. neonasuta	MD and FD	+ 0.7010	0.053	8
	MD and DD	+ 0.1937	0.646	8
	FD and DD	− 0.5639	0.145	8

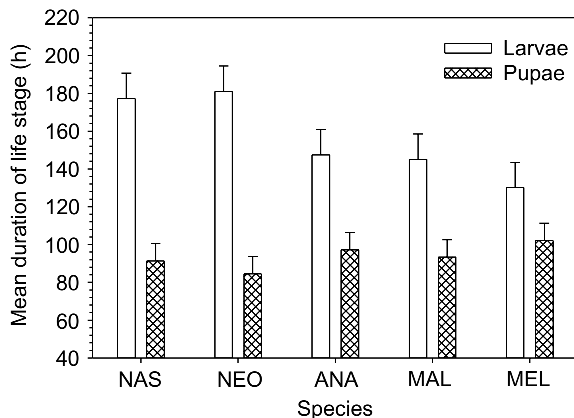

Fig. 3. Mean (± 95% CI) larval and pupal duration in five *Drosophila* species. Confidence intervals are based on the mean square error term in the ANOVA. Larval differences between *D. n. nasuta* and *D. s. neonasuta*, and those between *D. ananassae* and *D. malerkotliana* are not significant, nor are the pupal differences between *D. melanogaster* and *D. ananassae*, and those among *D. ananassae*, *D. malerkotliana* and *D. n. nasuta* (Tukey's honest significant difference test). NAS, *D. n. nasuta*; NEO, *D. s. neonasuta*; ANA, *D. ananassae*; MAL, *D. malerkotliana*; MEL, *D. melanogaster*.

than pupal duration, as all correlations between larval duration and male, female or mean development time were significantly positive ($P < 0.01$), whereas pupal duration was not significantly correlated with male, female or total development time. Overall, pre-adult survivorship varied significantly across species (one-way ANOVA: $F_{4,31} = 23.19$, $P < 0.001$), with *D. melanogaster* and *D. n. nasuta* showing the highest and least survivorship, respectively (Fig. 4). Differences among species in pre-adult

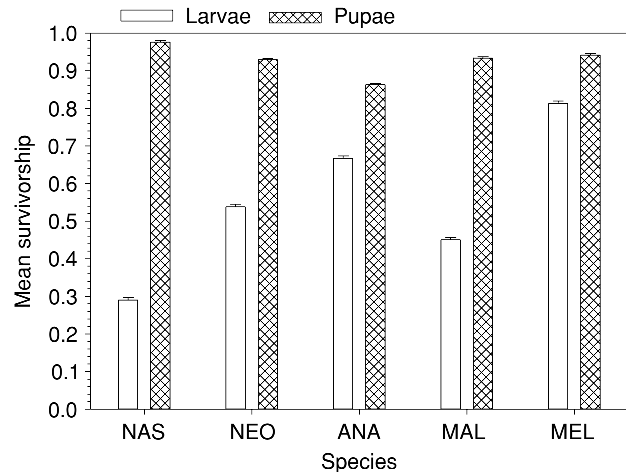

Fig. 4. Mean (± 95% CI) larval and pupal survivorship in five *Drosophila* species. Confidence intervals are based on the mean square error term in the ANOVA. None of the pupal differences in survivorship are significant, nor are larval differences between *D. ananassae* and *D. s. neonasuta*, and those between *D. malerkotliana* and *D. n. nasuta* (Tukey's honest significant difference test). NAS, *D. n. nasuta*; NEO, *D. s. neonasuta*; ANA, *D. ananassae*; MAL, *D. malerkotliana*; MEL, *D. melanogaster*.

survivorship were entirely the result of differences in larval survivorship (one-way ANOVA: $F_{4,31} = 30.87$, $P < 0.001$); pupal survivorship was generally high and did not vary significantly across species (one-way ANOVA: $F_{4,31} = 2.89$, $P = 0.081$). Overall, pre-adult survivorship was significantly higher in *D. melanogaster*, compared to the wild-caught species, which did, however, show significant differences among themselves (Fig. 4).

Dry weight at eclosion

Mean dry weight varied significantly across species with *D. s. neonasuta* having the highest dry weight per fly at eclosion, followed by *D. n. nasuta*, *D. melanogaster, D. ananassae and D. malerkotliana* (Fig. 5). The ANOVA revealed that significant effects of species, sex, and the species × sex interaction (Table 1). All pairwise comparisons between species were significant ($P < 0.01$). Overall, females were 32% heavier than males, and although the male–female difference varied across species (Fig. 5), the degree of dimorphism, though much higher than that for development time, did not differ significantly among species (one-way ANOVA: $F_{4,20} = 1.71$, $P = 0.187$).

Male and female dry weights were not significantly correlated ($P > 0.1$) in any of the species (Table 3). Both male and female dry weight were significantly ($P < 0.05$) correlated with degree of dimorphism in dry weight in *D. malerkotliana*, whereas only female dry weight was correlated with degree of dimorphism in *D. n. nasuta*, and only male dry weight was correlated with degree of dimorphism in *D. melanogaster*, unlike development time.

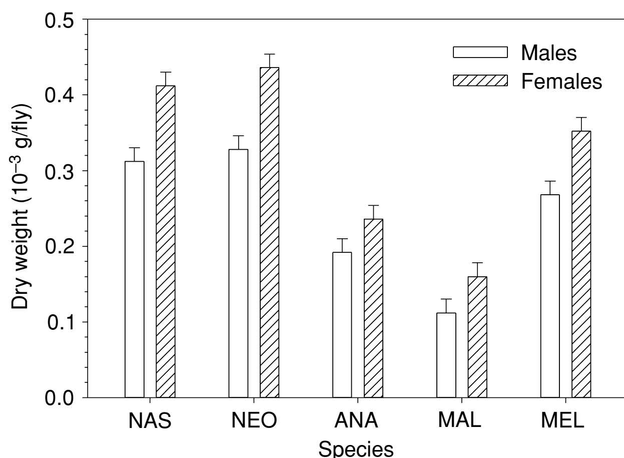

Fig. 5. Mean (± 95% CI) dry weight at eclosion of males and females in five *Drosophila* species. Confidence intervals are based on the mean square error term in the ANOVA (all differences between species for each sex are significant at the 0.01 level; Tukey's honest significant difference test). NAS, *D. n. nasuta*; NEO, *D. s. neonasuta*; ANA, *D. ananassae*; MAL, *D. malerkotliana*; MEL, *D. melanogaster*.

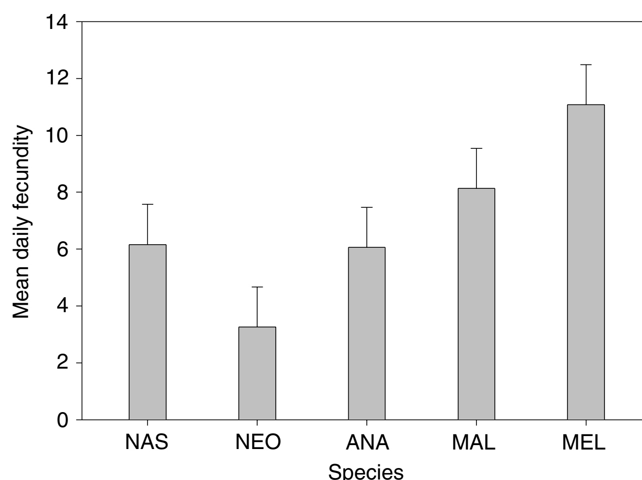

Fig. 6. Mean (± 95% CI) number of eggs laid by a female over the first 10 days post eclosion in five *Drosophila* species. Confidence intervals are based on variation among females as reflected in the mean square error term in the ANOVA (all differences between species except between *D. ananassae* and *D. n. nasuta* are significant at the 0.05 level; Tukey's honest significant difference test). NAS, *D. n. nasuta*; NEO, *D. s. neonasuta*; ANA, *D. ananassae*; MAL, *D. malerkotliana*; MEL, *D. melanogaster*.

Table 3. Pairwise correlations among degree of dimorphism and trait value in males and females for dry weight at eclosion ($\times 10^{-3}$ g) within five *Drosophila* species. Correlation coefficients were calculated using vial means within each species. DW, dimorphism for dry weight; MW, male dry weight; FW, female dry weight

Species	Correlation between	r	P	N
D. malerkotliana	MW and FW	− 0.6455	0.239	5
	MW and DW	− 0.9149	0.029	5
	FW and DW	+ 0.8977	0.039	5
D. melanogaster	MW and FW	− 0.1667	0.789	5
	MW and DW	− 0.8293	0.082	5
	FW and DW	+ 0.6892	0.198	5
D. ananassae	MW and FW	+ 0.3273	0.591	5
	MW and DW	− 0.4667	0.428	5
	FW and DW	+ 0.6826	0.204	5
D. n. nasuta	MW and FW	+ 0.4082	0.495	5
	MW and DW	− 0.1730	0.781	5
	FW and DW	+ 0.8285	0.083	5
D. s. neonasuta	MW and FW	+ 0.4082	0.495	5
	MW and DW	− 0.7933	0.109	5
	FW and DW	+ 0.2319	0.707	5

Overall, there did not seem to be any clear difference between female and male dry weight in terms of the extent to which they determine degree of dimorphism (Table 3).

Mean daily fecundity

Mean daily fecundity varied significantly among species (one-way ANOVA: $F_{4,180} = 35.82$, $P < 0.0001$), with *D. melanogaster* being the most fecund, followed by *D. malerkotliana, D. n. nasuta, D. ananassae* and *D. s. neonasuta* (Fig. 6). All differences between species were significant ($P < 0.05$), except that between *D. ananassae* and *D. n. nasuta*. However, the specific fecundity (daily fecundity divided by weight at eclosion) of *D. malerkotliana*, *D. melanogaster* and *D. ananassae* was higher than that of the two larger species, *D. n. nasuta* and *D. s. neonasuta* (Table 4).

Table 4. Mean specific fecundity of females, and growth rate of males and females of five *Drosophila* species. Specific fecundity is calculated as the mean daily fecundity divided by female dry weight for each species. Growth rate is calculated as the mean dry weight at eclosion divided by the mean development time for each sex × species combination

Species	Specific fecundity (eggs/d/10^{-3} g)	Male growth rate ($\times 10^{-6}$ g/h)	Female growth rate ($\times 10^{-6}$ g/h)
D. malerkotliana	50.87	0.454	0.694
D. melanogaster	31.48	1.148	1.527
D. ananassae	25.67	0.772	0.980
D. n. nasuta	14.96	1.168	1.527
D. s. neonasuta	7.49	1.229	1.650

Correlates of degree of dimorphism

For examining the correlates of degree of dimorphism, the degree of dimorphism in the mean growth rate (dry weight at eclosion divided by development time) was also estimated for the five species, and the results are, not surprisingly, similar to those for degree of dimorphism for dry weight. The greatest degree of dimorphism in growth rate was seen in *D. malerkotliana* (0.42), followed

Table 5. Correlations among species means for various traits ($n = 5$ species) in *Drosophila*. Entries are Pearson product moment correlation coefficients. DD, dimorphism for development time; DW, dimorphism for dry weight; DG, dimorphism for growth rate (growth rate = dry weight in mg/development time in h); MW, male dry weight; FW, female dry weight; MD, male development time; FD, female development time; MG, male growth rate; FG, female growth rate; SF, specific fecundity (eggs per day per mg dry weight). *, $0.10 > P > 0.05$; **, $0.05 > P$

	DD	DW	DG	MW	FW	MD	FD	MG	FG	SF
DD		+ 0.44	+ 0.74	– 0.95**	– 0.93**	– 0.47	– 0.74	– 0.94**	– 0.91**	+ 0.85*
DW			+ 0.93**	– 0.31	– 0.23	– 0.01	– 0.16	– 0.35	– 0.25	+ 0.51
DG				– 0.62	– 0.55	– 0.19	– 0.42	– 0.65	– 0.56	+ 0.73
MW					+ 0.99**	+ 0.53	+ 0.76	+ 0.98**	+ 0.98**	– 0.91**
FW						+ 0.54	+ 0.76	+ 0.98**	+ 0.98**	– 0.88**
MD							+ 0.94**	+ 0.37	+ 0.37	– 0.71
FD								+ 0.63	+ 0.62	– 0.86*
MG									+ 0.99**	– 0.84*
FG										– 0.82*

by *D. s. neonasuta* (0.29), *D. melanogaster* (0.28), *D. n. nasuta* (0.27) and *D. ananassae* (0.23). The results of the estimation of pairwise correlation coefficients among the degree of dimorphism and male and female trait values are shown in Table 5. Although the power to detect significant correlations is low because of small sample size ($n = 5$ species), the pattern of results is, nevertheless, instructive.

Other than trivially obvious results, such as that male and female development time, or male and female dry weight, tend to be significantly positively correlated across species, attention is drawn to the following few points. First, the degrees of dimorphism for different traits are not correlated across species, except for a significant positive correlation between degree of dimorphism for growth rate and degree of dimorphism for dry weight at eclosion. This suggests that the dimorphism in growth rate, which is a function of both dry weight and development time, is being driven largely by the dimorphism in dry weight. Second, the degree of dimorphism in dry weight is not even marginally significantly correlated across species with female weight or specific fecundity. Third, at least across these five species, female dry weight at eclosion is significantly negatively correlated with specific fecundity, as is female development time, and, not surprisingly, female growth rate. Fourth, the degree of dimorphism in development time is significantly negatively correlated with male and female dry weight and growth rate and marginally ($P < 0.1$) significantly correlated with specific fecundity. The overall picture emerging is that, at least among the five species studied, lighter species are more dimorphic in development time and tend to produce more eggs per unit weight at eclosion over the first 10 days of life, compared to heavier species.

DISCUSSION

Trait values

In terms of major components of fitness, the long-term laboratory population of *D. melanogaster* seems to be clearly superior under laboratory conditions to the four recently wild-caught species. *Drosophila melanogaster* flies develop faster and are more fecund than the other four species (Figs 1 & 6), and also have superior pre-adult survivorship (Fig. 4). This is not surprising given that the *D. melanogaster* population studied has been in the laboratory for several hundred generations, and is presumably well adapted to the conditions in the laboratory. One of the reasons the *D. melanogaster* population was included in this study was to have a point of reference from a well-characterized population, to act as a backdrop against which the four wild-caught species could be compared.

More interesting than the superiority of *D. melanogaster* is the observation that among the recently wild-caught species, the two *melanogaster* group species seem to be superior to the *immigrans* group species in the fitness traits studied. *Drosophila ananassae* and *D. malerkotliana* take *c*. 20 h less than *D. n. nasuta* and *D. s. neonasuta* to complete development (Fig. 1). This could, in principle, be explained by the fact that *D. n. nasuta* and *D. s. neonasuta* are substantially heavier at eclosion than the two wild-caught *melanogaster* group species (Fig. 5). In fact, not only do the two *melanogaster* group species weigh less at eclosion, their average rate of weight gain till eclosion is also less than that of the two *immigrans* group species, whereas that of *D. melanogaster* is about the same as *D. n. nasuta* and *D. s. neonasuta* (Table 4). Yet, the average daily fecundity over the first 10 days of adult life in *D. malerkotliana* and *D. ananassae* is greater than or equal to that of *D. n. nasuta* and *D. s. neonasuta* (Fig. 6), and the fecundity per unit dry weight at eclosion is substantially greater (Table 4). Adult lifespan and total lifetime fecundity of *D. malerkotliana* and *D. ananassae* is also greater than *D. n. nasuta* and *D. s. neonasuta* (Sharmila Bharathi *et al*., 2003). Although *D. n. nasuta* and *D. s. neonasuta* lay eggs that are slightly larger than those of *D. malerkotliana* and *D. ananassae* (N. Sharmila Bharathi, pers. obs.), the difference in egg size is not of an order that could render fecundity per unit dry weight at eclosion commensurate across species once egg weight is taken into account.

Why the two *melanogaster* group species seem to be superior to the two *immigrans* group species under

laboratory conditions is not clear at this time. It may be that these *melanogaster* group species are in a sense pre-adapted to a laboratory environment optimized for *D. melanogaster*, a species to which they are closely related. It may also be that oviposition preferences differ among these four species and, thus, fecundity differences reflect behavioural aversion rather than physiological differences among species. Yet, the superiority of *D. ananassae* and *D. malerkotliana* in the laboratory does not seem to translate into greater abundance in the wild. In our collections, it was found that *D. n. nasuta* and *D. ananassae*, together with *Zaprionus indianus*, were the most abundant drosophilids, with *D. ananassae* being restricted largely to the insides of houses, and *D. n. nasuta* to domestic garbage dumps, where it coexisted with, and greatly outnumbered, *D. malerkotliana*. Therefore, the possibility that the *immigrans* group species are superior or similar in performance to the *melanogaster* group species in their natural habitat, especially with regard to adult traits, cannot be ruled out. This possibility is supported by the observation that *D. n. nasuta* and *D. s. neonasuta* are clearly more starvation and desiccation tolerant than *D. ananassae* or *D. malerkotliana* (Sharmila Bharathi *et al*., 2003).

Sexual dimorphism

There are two general results about sexual dimorphism from this study that merit attention. First, the degree of dimorphism for dry weight is not significantly correlated with either fecundity (data not shown), specific fecundity, or male and female dry weight (Table 5) across species. This is surprising given that sexual size dimorphism in *D. melanogaster* is thought to be driven by sexual selection for greater fecundity (Reeve & Fairbairn, 1999). The fecundity differences across the species span a factor of four (Fig. 5), yet the degree of dimorphism for dry weight at eclosion does not vary significantly across species. Although, across-species and within-species correlations can differ greatly in magnitude and even sign, the result still suggests that further studies on a variety of *Drosophila* species may be required to assess the role of sexual selection in promoting larger females in this genus.

Second, the degree of dimorphism in pre-adult development time is significantly negatively correlated with male and female dry weight, and significantly positively correlated with specific fecundity (Table 5). Thus, across these five species, the trend is for the lighter and smaller species to have higher fecundity per unit dry weight at eclosion, and to be more dimorphic for development time. The dimorphism in development time, moreover, seems to be driven more by variation in female rather than male development time (Table 2). In *D. melanogaster*, males take longer to develop because their pupal duration is longer than that of females; the larval periods do not differ between sexes (Bakker & Nelissen, 1963; Nunney, 1983). If this is also true for other *Drosophila* species, perhaps female development time is more variable than male development time because male development time is under stabilizing selection for some optimal pupal duration required for sperm maturation. Such a difference in the variation in male and female development time could explain why female development time seems to explain dimorphism in development time better than male development time (Table 2). We stress that our results on the correlates of dimorphism are essentially conservative. The major findings are of several unexpected significant correlations between dimorphism and other traits, and these correlation coefficients are of a large magnitude (Table 5), and hence significant even in an analysis with low power resulting from small sample size ($n = 5$).

Why small size seems to go together with greater development time dimorphism and specific fecundity is not clear at this time; it may be an artefact of the confounding of large size with species of the *immigrans* species group, and of small size with those of the *melanogaster* species group, in our study. It is possible that these two groups of species differ in their ecology, and have evolved different life-history strategies with *D. n. nasuta and D. s. neonasuta* compensating for their low specific fecundity and lifespan (under laboratory conditions) by greater tolerance to stresses such as starvation, desiccation and pathogens (Sharmila Bharathi *et al*., 2003). Unfortunately, little is known about the ecology and life history of these species in the wild, and it is therefore difficult to do much more than speculate at this time. It would also be desirable to have data on multiple populations of each of these species, such that within- and among-species differences could be studied in more detail. Life-history variation and dimorphism in Indian species of *Drosophila*, unfortunately, has not been much studied and this study is viewed as a beginning in that direction. Our results, albeit of a preliminary and suggestive nature, are believed to underscore the importance of extending studies of sexual dimorphism in *Drosophila* to a wider range of species, preferably spanning a range of sizes and development times within species groups, and also of examining the various pre-adult and adult life-history correlates of sexual dimorphism, both within and among species. Another hitherto neglected area of fruitful investigation could be to examine the reaction norms of degree of dimorphism for size and development time across ecologically relevant environmental variables.

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REFERENCES

Bakker, K. (1961). An analysis of factors which determine success in competition for food among larvae of *Drosophila melanogaster. Arch. Néerl. Zool*. **14**: 200–281.

Bakker, K. & Nelissen, F. X. (1963). On the relations between the duration of the larval and pupal period, weight and diurnal rhythm in emergence in *Drosophila melanogaster. Entomol. Exp. Appl*. **6**: 37–52.

Borash, D. J. & Ho, G. T. (2001). Patterns of selection: stress resistance and energy storage in density-dependent populations of *Drosophila melanogaster. J. Insect Physiol*. **47**: 1349–1356.

Chippindale, A. K., Alipaz, J. A., Chen, H.-W. & Rose, M. R. (1997). Experimental evolution of accelerated development in *Drosophila*. 1. Developmental speed and larval survival. *Evolution* **51**: 1536–1551.

David, J. R., Gibert, P., Mignon-Grasteau, S., Legout H., Petavy, G., Beaumont, C. & Moreteau, B. (2003). Genetic variability of sexual size dimorphism in a natural population of *Drosophila melanogaster*: an isofemale line approach. *J. Genet*. **82**: 79–88.

Fisher, R. A. (1958). *The genetical theory of natural selection*. Oxford: Oxford University Press.

Joshi, A., Do, M. H. & Mueller, L. D. (1999). Poisson distribution of male mating success in laboratory populations of *Drosophila melanogaster. Genet. Res*. **73**: 239–249.

Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34**: 292–305.

Nunney, L. (1983). Sex differences in larval competition in *Drosophila melanogaster*: the testing of a competition model and its relevance to frequency-dependent selection. *Am. Nat*. **121**: 67–93.

Nunney, L. (1996). The response to selection for fast larval development in *Drosophila melanogaster* and its effect on adult weight: an example of a fitness trade-off. *Evolution* **50**: 1193–1204.

Prasad, N. G. & Joshi, A. (2003). What have two decades of laboratory life-history evolution studies on *Drosophila melanogaster* taught us? *J. Genet*. **82**: 45–76.

Prasad, N. G., Shakarad, M., Gohil, V. M., Sheeba, V., Rajamani, M. & Joshi, A. (2000). Evolution of reduced pre-adult viability and larval growth rate in laboratory populations of *Drosophila melanogaster* selected for shorter development time. *Genet. Res*. **76**: 249–259.

Reeve, J. P. & Fairbairn, D. J. (1996). Sexual size dimorphism as a correlated response to selection on body size: an empirical test of the quantitative genetic model. *Evolution* **50**: 1927–1938.

Reeve, J. P. & Fairbairn, D. J. (1999). Change in sexual size dimorphism as a correlated response to selection on fecundity. *Heredity* **83**: 697–706.

Rhen, T. (2000). Sex-limited mutations and the evolution of sexual dimorphism. *Evolution* **54**: 37–43.

Sharmila Bharathi, N., Prasad, N. G., Shakarad, M. & Joshi, A. (2003). Variation in adult life-history and stress resistance across five species of *Drosophila. J. Genet*. **82**: 191–205.

Sheeba, V., Madhyastha, N. A. A. & Joshi, A. (1998). Oviposition preference for novel *vs* normal food resources in laboratory populations of *Drosophila melanogaster. J. Biosci*. **23**: 93–100.

StatSoft Inc. (1995). *STATISTICA*^{TM} **I**, *General conventions and statistics I*. Tulsa, OK: StatSoft.

Zwaan, B. J., Bijlsma, R. & Hoekstra, R. F. (1995). Artificial selection for development time in *Drosophila melanogaster* in relation to the evolution of aging: direct and correlated responses. *Evolution* **49**: 635–648.