Evol Ecol (2011) 25:875–884
DOI 10.1007/s10682-010-9442-x

ORIGINAL PAPER

# A cost of being large: genetically large yellow dung flies lose out in intra-specific food competition

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Received: 1 June 2010 / Accepted: 11 October 2010 / Published online: 22 October 2010


**Abstract** Most life history traits are positively influenced by body size, while disadvantages of large size are poorly documented. To investigate presumed intrinsic costs of large body size in yellow dung flies (*Scathophaga stercoraria*; Diptera: Scathophagidae), we allowed larvae from replicate lines artificially selected for small and large body size for 21 generations to compete directly with each other at 20°C (benign) and 25°C (stressful) and low and high food (dung) availability. Greater mortality of large line flies was evident at low food independent of temperature, suggesting a cost of fast growth and/or long development for genetically large flies during larval scramble competition under food limitation. Our results are congruent with a previous study assessing mortality when competing within body size lines, so no additional mechanisms affecting scramble or contest behavior of larvae need be invoked to explain the results obtained beyond the costs of longer development and faster growth. Thus, artificial selection producing larger yellow dung flies than occur in nature revealed some, albeit weak mortality costs of large body size that otherwise might have remained cryptic. We conclude, however, that these costs are insufficient to explain the evolutionary limits of large body size in this species given persistently strong fecundity and sexual selection favoring large size in both sexes.

**Keywords** Artificial selection · Body size · Food limitation · Juvenile mortality · *Scathophaga stercoraria* · Scramble competition · Temperature stress

## Introduction

In many organisms fecundity selection favors large females (Shine 1988; Roff 1992; Honek 1993) and sexual selection favors large males (Andersson 1994). In contrast, the counterbalancing forces favoring small body size, putatively mainly caused by viability selection at the juvenile or adult life stages (Schluter et al. 1991), remain poorly shown in

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general (Blanckenhorn 2000, 2005). Based on their publicly available database of selection studies (up to the year 1997: Kingsolver et al. 2001), Kingsolver and Pfennig (2004) have documented that fecundity, sexual and even viability selection coefficients for body size estimated in nature for 23 species are predominately positive, with only ca. 20% being negative. Assuming that estimates close to zero are not significant and consequently show no selection, these data imply that large body size primarily confers fitness advantages and rarely disadvantages. Fortunately in recent years more studies have specifically focused on this issue, revealing a number of cases documenting advantages of small body size (e.g. DiBattista et al. 2007; Carlson et al. 2008; Dufresne et al. 2009). Nevertheless, we need more such evidence in a wide variety of species to explain what limits body size in nature.

Adult body size is a highly plastic trait that is mediated by variation in juvenile growth and development, both of which strongly depend on environmental conditions such as temperature, food availability, photoperiod or predators encountered during development. To become larger, organisms must either grow faster or develop for longer time (Roff 1980, 1992; Sibly et al. 1985; Stearns and Koella 1986; Kozlowski 1992; Abrams et al. 1996; Arendt 1997; Dmitriew 2010). If development is prolonged, juveniles necessarily suffer a higher cumulative risk of death due to predation (e.g. Werner and Anholt 1993) or parasitism (e.g. Benrey and Denno 1997). Organisms developing in ephemeral habitats such as temporary ponds, water holes, dung, carcasses or rotting fruits further risk to die through habitat (and food) depletion (Newman 1992). Growing faster, on the other hand, is energetically, ecologically or physiologically costly. Faster growing individuals may have to forage and therefore move more, making them more conspicuous to predators or parasites (Werner and Anholt 1993; Bernays 1997; Munch and Conover 2003). More energy used for growth, especially when food is limited, reduces energy to be allocated to reproduction, maintenance, storage or repair mechanisms (Cody 1966; Partridge and Sibly 1991; Arendt 1997; Zera and Harshman 2001; Wikelski and Ricklefs 2001; Koella and Boëte 2002; Dmitriew 2010). Additionally, faster growth can have inherent costs of rapid mass accumulation or inefficient energy use (Higgins and Rankin 2001), resulting in greater mortality during or after food shortage (Dingle 1992; Gotthard et al. 1994; Blanckenhorn 1998). All these costs are invoked to play a role in limiting body size, but direct evidence for selective advantages of small body size remains limited (Blanckenhorn 2000, 2005; Kingsolver and Pfennig 2004; but see Carlson et al. 2008).

Lack of evidence disfavoring large body size also occurs in the yellow dung fly *Scathophaga stercoraria* (Diptera: Scathophagidae), a well-studied model organism in terms of behavior, ecology and evolution (Blanckenhorn 2009). These flies mate and lay their eggs on fresh cow dung, an ephemeral habitat and food source on which their larvae feed and which they thereby deplete (Parker 1978). Using flies from replicate lines artificially selected for small and large body size for 21 generations and thus having augmented (decreased) natural fly size by 11% (9.5%) relative to the original mean (and the unselected control; Table 1), Teuschl et al. (2007) found only slight (ca. 3%) mortality costs of large line relative to small line flies. While large line flies showed a correlated response of prolonged development times (ca. 2 days) and also faster growth rates at benign conditions (Table 1), mortality of flies of all lines was well buffered by their ability to plastically adjust growth, development and body size: at the lowest larval food limit possible, flies from all lines attained about similar minimum body sizes after roughly the same development time. Consequently, overall phenotypic plasticity strongly increased following selection for large body size (Teuschl et al. 2007). However, flies from the different lines were tested separately, i.e. not in direct (food) competition with each other. It is conceivable that in more realistic situations of direct contest or scramble competition

**Table 1** Linearized growth rate during the initial exponential phase, pupa length and adult head width of males and females of the large, control and small selection lines (replicates combined) at high and low food at generation 18 (data from Teuschl et al. 2007 and unpublished)

| Sex | Food | Line | Initial growth rate (mm/d) ± SE | Pupa length (mm) ± SE | Adult head width (mm) ± SE |
|---|---|---|---|---|---|
| Female | Low | Large | 0.567 ± 0.027 | 2.37 ± 0.03 | 1.65 ± 0.01 |
| | | Control | 0.552 ± 0.035 | 2.48 ± 0.03 | 1.61 ± 0.01 |
| | | Small | 0.630 ± 0.018 | 2.45 ± 0.04 | 1.56 ± 0.01 |
| | High | Large | 0.607 ± 0.016 | 3.36 ± 0.04 | 2.36 ± 0.01 |
| | | Control | 0.573 ± 0.018 | 3.20 ± 0.05 | 2.17 ± 0.01 |
| | | Small | 0.550 ± 0.017 | 2.90 ± 0.05 | 2.02 ± 0.01 |
| Male | Low | Large | 0.586 ± 0.023 | 2.58 ± 0.04 | 1.71 ± 0.01 |
| | | Control | 0.590 ± 0.042 | 2.65 ± 0.03 | 1.65 ± 0.01 |
| | | Small | 0.666 ± 0.022 | 2.62 ± 0.03 | 1.59 ± 0.01 |
| | High | Large | 0.687 ± 0.022 | 4.04 ± 0.03 | 2.70 ± 0.01 |
| | | Control | 0.639 ± 0.019 | 3.81 ± 0.03 | 2.51 ± 0.01 |
| | | Small | 0.627 ± 0.020 | 3.33 ± 0.04 | 2.31 ± 0.01 |

Control flies are roughly of original, natural size. Adult sizes stem from different flies than pupa lengths and growth rates

among larvae inhabiting the same dung pat, any correlated differences in competitive ability between the lines, caused e.g. by behavioral or physiological mechanisms affecting food assimilation or larval foraging success (e.g. Kause et al. 1999), would ultimately become manifest in differential survival.

Here we report an experiment in which we allowed larvae from the small and large selection lines to compete directly with each other in stressful (food limited and hot) vs. benign environments (cf. Teuschl et al. 2007). The general logic behind using flies artificially selected to be larger than in nature was that this could reveal costs of large size that might otherwise remain cryptic in the wild. Selection against large size can remain undetected because large individuals that die early during development are not part of the natural size distribution of adults, or because the function linking fitness to body size can be primarily flat with steep decreases in fitness occurring only at the very ends of the size distribution (Blanckenhorn 2000). Moreover, putative trade-offs often become unmasked or more visible only in stressful environments because individuals can invest maximally in all traits when environmental conditions are optimal (van Noordwijk and de Jong 1986; Alatalo et al. 1990; Schluter et al. 1991; Rowe and Houle 1996). We therefore predicted that large line flies would survive less well in direct competition with small line flies particularly at limited food, if only because they might not be able to complete development by the time food is depleted (Blanckenhorn 1998; Teuschl et al. 2007). On the other hand, large line flies may compensate by means of faster growth, presumably mediated by higher larval food intake and food processing rates, or by behavioral or physiological competitive advantages. Any disadvantage of large line flies should be further exacerbated at high temperatures, which are generally stressful for yellow dung flies and further accelerate dung depletion. We only assessed mortality here, as we already knew the corresponding effects on body size, development times and growth rate (Teuschl et al. 2007). However, we provide mean body sizes and growth rates for the selection lines (plus the control) at generation 18 in Table 1.

## Methods

### Selection lines

We maintained two independent replicates (A and B) each of small (S), large (L) and control (C) body size selection lines for 21 generations. At generation 21, flies from the two replicates within each selection line were crossed to offset potential inbreeding effects, and these crossed S, L and C flies were further propagated without selection for two more generations. To propagate the flies, every generation head widths (a practical surrogate for body size) of 150 males (if possible three from each family) were measured, and the 50 smallest (S) or largest (L) or 50 randomly chosen (C) males were allowed to reproduce with 50 randomly chosen females of the same line. We thus exerted (strong) directional truncation selection on male body size only, of a magnitude of roughly 0.06 mm adult male head width per generation, corresponding to a standardized selection differential of ca. 1 standard deviation unit (calculated as the ($z$-score standardized) difference between the mean of the selected and all measured individuals: Brodie et al. 1995). To produce the next generation, 20–25 eggs of each clutch were transferred into 50 ml plastic containers with 80 g dung, as more than 2 g dung/larva can be considered unlimited larval food conditions (Amano 1983). The containers were kept at constant 20°C and 60% humidity until offspring emerged after 18–24 days. Adult flies were kept singly in 100 ml vials until sexually mature at 20°C, 60% humidity and at 12 h photoperiod with water, sugar and *Drosophila melanogaster* ad libitum as prey (see Teuschl et al. 2007 for more details).

### Experimental design

For our competition experiment with the 21st (original replicates A and B) or the 23rd (crossed replicates) generation, we randomly paired males and females to produce full-sib offspring families within each of the S and L line replicates as well as within the crossed S and L lines (C lines were ignored for this experiment), as described above. Separately for each data set (A, B, crossed), 10 larvae from a random family of the S line were then allowed to compete against 10 larvae from a random family of the respective L line to produce three disjunct larval competition data sets. Ca. $N = 15$–$30$ such replicate dung containers with competing larvae per treatment combination and data set were originally set up. These containers were randomly allocated to two temperatures, 20°C (benign) and 25°C (stressful), and two food (dung) levels, limited (low) and unlimited (high), and subsequently reared to adulthood in laboratory climate chambers (60% humidity in all cases). Based on previous experience with similar experiments, unlimited food was 10 L larvae plus 10 S larvae in 60 g cow dung, and limited food was 10 L larvae plus 10 S larvae in 10 g cow dung (cf. Amano 1983; Teuschl et al. 2007). All emerged adults were collected and frozen for subsequent microsatellite analysis to assign the flies to either the S or the L line.

### Microsatellite analysis

We used microsatellite markers developed for this species to discriminate flies of the competing L and S lines (Garner et al. 2000). We scored 4–6 polymorphic loci until one or more loci were found that unequivocally identified the parents, which were genotyped as well, and hence the selection line (S or L) of all surviving adult offspring that emerged

alive from each competition container in each treatment combination. Relative survivorship was scored as the number of flies emerged from the L line minus the number of flies emerged from the S line, yielding the null expectation of zero if offspring of both lines survived equally well.

DNA was extracted as described in the QIAamp® DNA Mini Kit (Qiagen) using the fly's head and part of the thorax. PCRs were performed using the following conditions. The total reaction volume was 10 µl containing 50–300 ng of template DNA, 0.5 U Taq Polymerase (Qbiogene), 10 mM Tris–HCL, pH 9.0, 50 mM KCL, 1.5 mM $MgCl_2$, 0.1% TritonX100, 0.2 mg BSA (Qbiogene), 100 µM of each dNTP (Roche Diagnostics GmbH) and 0.5 µM of both forward and reverse primer. PCRs were carried out on a Techne Flexigene or Genius thermocycler (Techne Ltd) using an initial denaturation step (3.5 min at 94°C), 26–31 cycles consisting of 1 min denaturation at 94°C, 1 min annealing (see Garner et al. 2000 for locus-specific annealing temperatures), and 1 min elongation at 72°C followed by a final elongation step at 72°C for 2 min. Products were electrophoresed on Spreadex EL-300 S-100 or, in the case of SsCa1- and SsCa21-products, EL-600 S-50 gels (Elchrom Scientific AG, Switzerland). For electrophoresis, the SEA 2000 advanced submerged gel electrophoresis apparatus (Elchrom Scientific AG, Switzerland) was used. Gels were run at 100 V for 90–110 min, depending upon the length of the amplified fragment and on gel type. Gels were then stained with SYBR Gold nucleic acid stain (Molecular Probes, Inc.) and scored against the M3 Marker ladder (Elchrom Scientific AG, Switzerland). Fragment sizes were scored using the TotalLab v2.01 software (Nonlinear Dynamics, UK).

## Results

Analysis of variance with the difference in number of emerged (i.e. survived) adults between the L and S lines (L–S) as the dependent variable and replicate line (A, B, or crossed), food (dung) level (low vs. high) and temperature (20°C vs. 25°C) as fixed factors only yielded a significant main effect of food level (which after dropping all non-significant interactions from the model changed to $F_{1,128} = 5.81$, $P = 0.017$; Table 2): small line flies overall survived better at low but not at high food (Fig. 1). Analogous analysis of the overall emergence success (percent survival) showed that, independent of selection line, flies survived much worse at the high temperature and in the original (uncrossed) selection line replicates A and B, the latter indicating some inbreeding effects following artificial selection (Fig. 1; Table 2). Overall, small line flies survived about 3.5% better in our experiment than large line flies (44.7% vs. 41.3%), which is very similar to the difference of about 3% obtained by Teuschl et al. (2007). All containers with 100% mortality were excluded from the analysis because they are uninformative regarding the questions.

## Discussion

Direct scramble competition for food (dung) between larvae stemming from large (L) and small (S) body size selection lines resulted in greater mortality of L line flies at limited (low) but not at unlimited (high) food, irrespective of temperature. This difference in survivorship between the S and L lines at limited food was small, however, averaging only about one individual of ten (Fig. 1) or 3% overall mortality, roughly corresponding to a

**Table 2** Analysis of variance for the difference in number of emerged (i.e. survived) adults between the L and S lines (L–S) and the percentage of emerged adults (overall survival) as a function of selection line (A, B, or crossed), food (dung) level (low vs. high) and temperature (20°C vs. 25°C)

| Source | *df* | Difference (L–S) | | | Overall survival | | |
|---|---|---|---|---|---|---|---|
| | | MS | F | *P* | MS | F | *P* |
| Intercept | 1 | 26.46 | 4.72 | 0.032 | 139,310.4 | 620.52 | **<0.001** |
| Replicate line | 2 | 3.40 | 0.61 | 0.547 | 2,817.7 | 12.55 | **<0.001** |
| Food level | 1 | 27.66 | 4.93 | **0.028** | 564.2 | 2.51 | 0.115 |
| Temperature | 1 | 0.03 | 0.01 | 0.94 | 49,377.4 | 219.94 | **<0.001** |
| Replicate×food | 2 | 4.63 | 0.83 | 0.44 | 73.3 | 0.33 | 0.722 |
| Replicate×temperature | 2 | 3.86 | 0.69 | 0.504 | 105.2 | 0.47 | 0.627 |
| Food×temperature | 1 | 0.01 | 0.00 | 0.969 | 114.8 | 0.51 | 0.476 |
| Replicate×food×temperature | 2 | 0.51 | 0.09 | 0.912 | 627.6 | 2.59 | 0.095 |
| Error | 122 | 5.607 | | | 224.5 | | |
| Total | 134 | | | | | | |

Significant terms are in bold

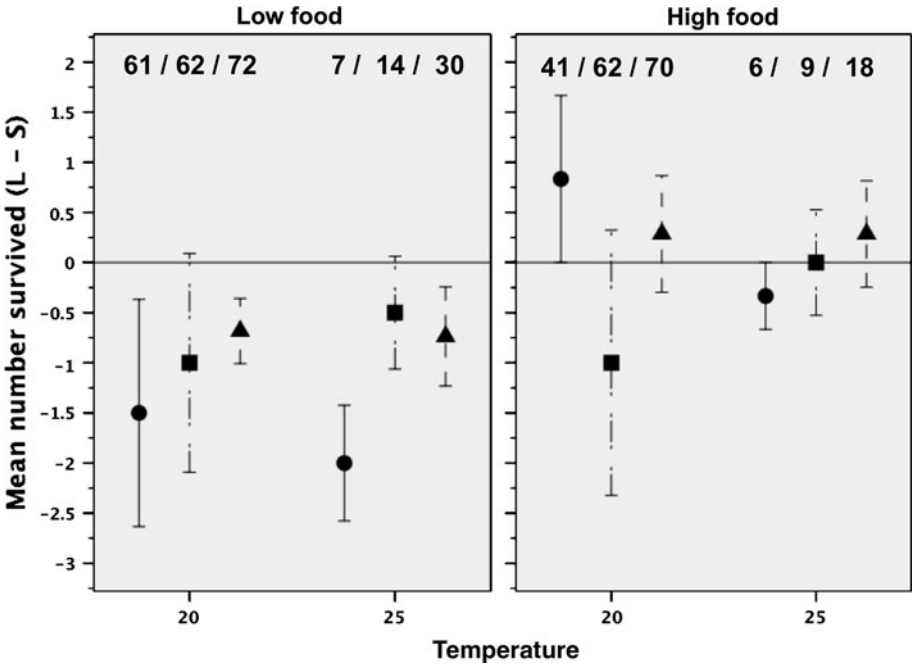


**Fig. 1** Mean difference (±SE) in the number of flies from the large body size selection line minus the number of flies from the small body size selection line that survived to adulthood in a given dung container at two temperatures (20°C = benign and 25°C = stressful) and two food (dung) treatments (low and high) for three selection line replicates (A (*circles*) B (*squares*) Crossed (*triangles*)). The *numbers* refer to the overall survivorship (in %) at the various treatment combinations (final $N = 6$–9 for replicate A; $N = 7$–9 for B; $N = 18$–21 for the Crossed replicate; all replicates with 100% mortality excluded; 10 larvae per selection line entered each replicate)

very modest standardized phenotypic selection differential of $S = -0.05$, similar to the values obtained by Teuschl et al. (2007; their Table 1). Note that overall survivorship was between 41 and 72% at 20°C but only 6–30% at the stressful 25°C, with no differences in overall survivorship between the food treatments (Fig. 1; Table 2). Similarly, Teuschl et al. (2007) found that juvenile mortality decreased substantially, but equally for all selection lines, at hot temperatures (25°C) when larvae competed within lines, whereas dung limitation only slightly increased juvenile mortality, but more so for L line than for S line individuals. Yellow dung flies are known to respond well to food shortage and dung drying, but not so well to hot temperatures (Blanckenhorn 1998, 1999; Teuschl et al. 2007). Dingle (1992) also found that milkweed bugs selected for large size showed higher larval mortality when raised under food restriction. Here we have shown a similar effect when flies from the S and L lines directly competed with each other, using microsatellite markers to distinguish the line provenance of the surviving competitors. Thus L line flies show some mortality cost of large body size, at least at some stressful, here limited food conditions (cf. Blanckenhorn 2000). We had expected the strongest competitive disadvantage of L line flies in the treatment combining low food and hot temperature, however this interactive effect did not occur.

As larval feeding behavior is difficult to observe in dung, it remains unclear how the competitive advantage of S line individuals is realized. The easiest explanation is that large line flies might not have completed development by the time the dung was depleted (time constraint), which was found to be the case with regard to winter survival by Teuschl et al. (2007; see also Blanckenhorn 1998). Another rather general potential explanation is that large (line) individuals pay some physiological cost of growing fast and/or large (cf. Table 1). It could be that large line flies have greater mass-specific metabolic requirements, less efficient energy use, or weaker food assimilation capacity and therefore ultimately lower foraging success and higher intrinsic morality (e.g. Kause et al. 1999; Reim et al. 2006). It is also conceivable that differences in scramble or contest competitive ability, i.e. in foraging behavior, between the S and L lines are partially responsible for the higher mortality of large line flies found here under direct competition. If this were the case, we would have expected a greater effect size here than found by Teuschl et al. (2007) when larvae were competing within body size lines as opposed to between lines (this study). However, the results of both studies are largely congruent. We therefore conclude that no additional behavioral of physiological mechanisms need be invoked to explain our results beyond the costs of longer development and faster growth shown by Teuschl et al. (2007) and Blanckenhorn (1998). In this sense we are reporting largely negative results here, although this was and could not have been anticipated a priori.

It is possible that our restricted laboratory assessment underestimates viability costs of large size in nature, although Blanckenhorn's (1998) comparable study was conducted in the field, albeit excluding predators, parasites and parasitoids. While a number of egg, larval and pupal predators and parasites have been identified in and around dung (Laurence 1954; Skidmore 1991), quantitative assessment of juvenile or adult size-dependent mortality due to predation or parasitism in yellow dung flies remains difficult but could indeed substantially contribute to costs of becoming and being large (Blanckenhorn 2000). Contrary to the simple situation of scramble competition for food investigated here, we would expect correlated behavioral differences between small and large (line) dung fly larvae to crucially affect their predation risk, unless predation is a mere function of prey body size (cf. Berger et al. 2006).

In summary, artificial selection used to produce larger yellow dung flies than occur in nature have revealed some, albeit overall weak mortality costs of large body size in yellow

dung flies that otherwise might have remained cryptic. Compatible with an earlier field study (Blanckenhorn 1998), we found a genetically correlated juvenile mortality increase that apparently trades off with large body size, in addition to mortality costs of prolonged development time before winter (i.e. a seasonal time constraint: Teuschl et al. 2007). These mortality costs of large body size were, however, only evident in situations of food stress (cf. van Noordwijk and de Jong 1986; Alatalo et al. 1990; Schluter et al. 1991), testifying to the strong buffering effect of growth plasticity of this species (Blanckenhorn 1998, 1999, 2009). We therefore conclude that these mortality costs of producing a larger body are insufficient to explain the evolutionary limits of large body size in yellow dung flies given persistently strong fecundity and sexual selection favoring larger body size in both sexes, a problem also in other species and highlighted by a general paucity of data on juvenile viability selection on body size (Blanckenhorn 2000; Kingsolver and Pfennig 2004; Teuschl et al. 2007; but see e.g. DiBattista et al. 2007; Carlson et al. 2008; Dufresne et al. 2009). We also readily admit that, in retrospect, our use of selection lines did not augment effect sizes to the extent originally envisaged (see Introduction). This is perhaps surprising because artificial selection worked well, showing no sign of an asymptote after 20+ generations (see Fig. 1 in Teuschl et al. 2007), depleting additive genetic variation only to a limited extent (unpublished data) with few signs of inbreeding evident, which could be entirely offset by crossing the replicate lines (Teuschl et al. 2007; this study). Further, although our artificial selection for large size (in males only) increased growth rate and development time as a correlated response (Table 1), individuals were not necessarily selected for fast growth because the flies were not reared in the stressful (food or time limited and hot) conditions they were later tested. Thus in principle the use of artificial selection to augment the natural range of body sizes remains a viable strategy in cases where selection against large size cannot be readily demonstrated in nature, for whatever reasons.

**Acknowledgments** We thank the Swiss National Fund for financial support.

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