

Heritability of three condition surrogates in the yellow dung fly

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Condition capture has been proposed as a general mechanism maintaining additive genetic variation, V_a , in sexually selected traits under directional selection. It relies on two main assumptions: condition-dependent trait expression and V_a in condition. Although there is evidence for the former, direct evidence that condition is heritable is scarce, although this is a requirement of most models of handicap sexual selection. We used a parent–offspring, full-sib, two-container laboratory breeding design in the yellow dung fly *Scathophaga stercoraria* to demonstrate the broad- and narrow-sense heritability of three surrogates of condition commonly used in sexual selection studies: lipid and glycogen reserves (i.e., physiological condition), body size, and fluctuating asymmetry. All three measures are nutrition dependent and have been linked to sexual selection in free-living yellow dung flies. While lipid reserves and body size were heritable, asymmetry and glycogen reserves were not. Moreover, the evolvability of physiological condition was higher than that of the other two traits. Of the three surrogates, physiological condition is most akin to the original definition, but all have their limitations. We conclude that condition is a useful heuristic concept in evolutionary ecology, but its practical value may be limited by the fact that it cannot be measured directly. *Key words*: body size, condition capture, energy reserves, fluctuating asymmetry, glycogen, lipids, *Scathophaga stercoraria*, sexual selection. [*Behav Ecol* 14:612–618 (2003)]

The maintenance of additive genetic variation (V_a) under persistent directional selection, such as typically found under sexual selection, is problematic because alleles coding for preferred traits should go to fixation (Charlesworth, 1987; Falconer, 1981; Fisher, 1930). This is the root of the lek paradox: females that receive only sperm from their partners should show little mate preference because the additive genetic variation in the preferred trait(s) should be exhausted (Kirkpatrick and Ryan, 1991). However, empirical evidence suggests that sexually selected traits have more rather than less genetic variance compared to traits thought to be under only natural selection (Pomiankowski and Møller, 1995), and meta-analyses have shown that genetic benefits typically conferred by mate choice are small but significant (Jennions et al., 2001; Møller and Alatalo, 1999).

Condition (or genic) capture has been proposed as a general mechanism maintaining V_a in traits under directional sexual selection (Rowe and Houle, 1996). With two key assumptions, condition-dependent trait expression and V_a in condition, this model will “lead inevitably to the capture of genetic variance into sexually selected traits concomitantly with the evolution of condition dependence” (Rowe and Houle, 1996: 1415). There is evidence for the former assumption of condition dependence in the sense that the environment, particularly nutrition, typically affects sexually selected trait expression (Andersson, 1994; e.g., David et al., 2000). In contrast, there is little direct evidence to date that condition is heritable (but see Bakker et al., 1999; David et al., 2000; Kotiaho et al., 2001; Merilä, 1996; Merilä et al., 2001), even though this is a critical assumption of Rowe and Houle’s (1996) model. Condition is a background trait that underlies and affects the phenotype’s fitness in all respects. Rowe and

Houle (1996) define it generally as the pool of resources that can be allocated to various traits. Condition will depend on genetic quality, for example, allowing females to evaluate the latter by means of the former (Andersson, 1986, 1994; Rowe and Houle, 1996). However, “condition” carries several meanings in the literature, and its operational definition remains elusive. Although Rowe and Houle’s (1996) definition of condition may best be described by residual reproductive potential, which cannot be measured directly (Kotiaho et al., 2001), physiological condition, or energy reserves, is probably the (measurable) trait most closely linked to it (Jakob et al., 1996). Nevertheless, while condition will reflect genetic quality and influence the expression of sexually selected traits, demonstrating V_a in condition is a prerequisite of most models of handicap sexual selection (Andersson, 1986; Iwasa et al., 1991; Nur and Hasson, 1984; Rowe and Houle, 1996), and in a recent review Bakker (1999) concluded that the study of V_a in condition is an area urgently in need of more attention. Here we investigated genetic variance in several surrogate measures of condition in the yellow dung fly *Scathophaga stercoraria*.

Three traits are commonly used as condition measures in sexual selection studies: body size, fluctuating asymmetry (FA; small random deviations from symmetry; Van Valen, 1962), and energy reserves or physiological condition. Body size is sexually selected (Andersson, 1994) and typically heritable in many species (Mousseau and Roff, 1987), including yellow dung flies (Blanckenhorn, 2002; Jann et al., 2000; Simmons and Ward, 1991). Also, adult size strongly depends on juvenile nutrition in most organisms, including yellow dung flies (Blanckenhorn, 1998), and this is why large size has been used as a trait indicating good condition in several sexual selection studies (e.g., Bjorksten et al., 2000a; David et al., 1998, 2000; Wilkinson and Taper, 1999). Likewise, FA is thought to be an indicator of developmental stability and genetic quality and hence condition (Møller and Swaddle, 1997; Palmer and Strobeck, 1986). As a result, FA has been prominently linked to good-genes models of sexual selection in recent years (Møller and Swaddle, 1997), although considerable

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Received 1 May 2002; revised 7 October 2002; accepted 7 October 2002.

controversy exists regarding its general heritability (Markow and Clark, 1997; Møller and Thornhill, 1997) and its causes (Lynch and Walsh, 1998; Roff, 1997). In yellow dung flies, FA in fore tibia length has been linked to sexual (Liggett et al., 1993) but also to natural selection (Swaddle, 1997), although variation in FA does not seem to carry fitness benefits, at least in terms of fecundity or fertility (Martin and Hosken, 2002). Energy (i.e., primarily lipid or body fat) content is a direct measure of an animal's (or genotype's) foraging and energy assimilation efficiency and its ability to cope with environmental stress. For these reasons it is a condition indicator used in many contexts (e.g., Bolger and Connolly, 1989; Milinski and Bakker, 1990; Otronen, 1995; Witter and Cuthill, 1993), including sexual selection (e.g., Kotiaho et al., 2001; Merilä et al., 2001; Saino et al., 1999; Weatherhead et al., 1999). In practice, energy reserves are rarely measured directly but instead estimated noninvasively as body mass corrected for size in various ways (Jakob et al., 1996; Kotiaho, 1999). In male yellow dung flies, both lipid and glycogen reserves, the latter being another labile, shorter term storage compound of sugars probably used primarily as the fuel for flight, have been shown to relate to mate acquisition in the field (Otronen, 1995; Sigurjónsdóttir and Snorrason, 1995).

In this study, we estimated the heritability of three commonly used condition surrogates, body size, FA, and energy reserves (i.e., lipid and glycogen) relative to body size, for the yellow dung fly *S. stercoraria* in a standard laboratory environment. Heritability estimates for physiological traits directly linked to reproductive success are essentially nonexistent in the literature (cf. Mousseau and Roff, 1987). All three measures have been reported to be sexually selected in free-living yellow dung flies (Jann et al., 2000; Liggett et al., 1993; Otronen, 1995). Although in this species sexual selection is primarily mediated by male–male competition (Parker, 1978), subtle forms of female choice also occur (Borgia, 1981; Reuter et al., 1998; Ward, 2000).

METHODS

We used a standard parent–offspring, full-sib, two-container laboratory breeding design (Roff, 1997) to assess both the narrow- and broad-sense heritabilities of three condition measures in *S. stercoraria*. To reduce maternal effects carried over from the field, the parents were the laboratory F_2 (and their offspring the F_3) of females originally caught at our field site in Fehraltorf near Zürich, Switzerland. From adult emergence, all flies were housed individually in 100-ml glass bottles and supplied with ad libitum water, sugar, and *Drosophila melanogaster* as prey at constant 19°C, 60% relative humidity, and 13-h photoperiod. We allowed F_2 females to copulate with one randomly chosen male and lay their first clutch about 14 days after emergence. From these full-sib clutches, approximately 15 eggs were allowed to develop in each of two containers with overabundant dung (>2 g/larva; Amano, 1983). This nested design controls for common environment effects, which confound broad-sense heritability estimates, by statistically removing them (Roff, 1997). Climatic conditions during offspring development were identical to the adult holding conditions.

Male and female yellow dung flies are nutritionally anaerobic, requiring postemergence feeding to become sexually mature (Foster, 1967), so it is primarily adult foraging (as opposed to reserves gathered during the larval stage) that affects adult success in this species (see Blanckenhorn and Viele, 1999; Jann and Ward, 1999; Swaddle, 1997). Male and female maturation takes approximately 3–7 and 10–14 days, respectively, at the optimal laboratory conditions used here (Blanckenhorn and Hosken, personal observation). Adult

flies were thus killed with CO₂ 14 days after emergence, and abdominal lipid and glycogen content was measured using standard physiological methods (Van Handel, 1985a,b). We measured female offspring before they laid their first clutch, whereas we measured the mothers thereafter. The lipid and glycogen content of 20 eggs of each mother's clutch was therefore determined in the same manner, and the estimated amount of energy corresponding to her first clutch size added to that contained in her abdomen. Variation in lipid and glycogen content assessed in this study thus refers to variation in the end point of the trajectory describing the energy accumulated by individuals at day 14 of their adult life at nutritionally optimal (i.e., benign) laboratory conditions. Laboratory environments are often thought to inflate genetic estimates because the total phenotypic variance under such conditions may be reduced considerably relative to the typical field situation, but this is not necessarily so (Hoffmann and Merilä, 1999; Weigensberg and Roff, 1996).

FA is supposed to reflect overall developmental competence of an individual expected to be expressed in several traits within individuals, but it often turns out to be rather trait specific (Hoffmann and Woods, 2001; Leung and Forbes, 1997; Palmer and Strobeck, 1986; Watson and Thornhill, 1994; Whitlock, 1996). For all parents and offspring we therefore measured left and right wing length and width and hind, mid, and fore tibia length. All these paired morphological appendages were cut off and glued onto a piece of paper, in an orientation corresponding to their location on the live animal. All were then measured by one of three persons using a binocular microscope at 40× magnification, and all were measured a second time by the same person days to weeks later. The significance of asymmetry relative to measurement error was assessed for each trait using the side-by-individual interaction term as described in Palmer and Strobeck (1986), for both sexes together and with variance due to sex and measurer removed. This analysis additionally tests for directional as opposed to fluctuating asymmetry. We also computed repeatabilities of trait size and signed asymmetry (left-right) to quantify measurement error in another way (Falconer, 1981).

For each trait of each individual we computed the mean (left, L; right, R) and a number of asymmetry indices with slightly different meanings (Hoffmann and Woods, 2001; Palmer and Strobeck, 1986): (1) size-corrected signed asymmetry as $(L - R)/\text{mean}(L, R)$ in percent to document the expected normal distribution of FA with a mean of zero, independent of trait size; (2) size-corrected absolute asymmetry as $(|L - R|)/\text{mean}(L, R)$ in percent to document the absolute degree of FA independent of trait size; and (3) absolute asymmetry as $(|L - R|)$ in microns to document the raw data. We could additionally compute the mean for all five traits as our composite estimate of overall FA (see Hoffmann and Woods, 2001; Lens et al., 2002). Analogously, we extracted the first principal component, PC1, from the five measured morphological traits, reflecting overall body size. To avoid pseudoreplication, our conclusions are based on these overall measures. However, because asymmetry of different traits within individuals does not necessarily correlate (Leung and Forbes, 1997; Whitlock, 1996), and because different measures of FA are useful in different situations (Hoffmann and Woods, 2001), we present all data for all traits for the benefit of readers.

Because trait means and variances differed between the sexes for most traits, we estimated father–son, mother–daughter (i.e., narrow sense) and sex-specific full-sib (i.e., broad sense) heritabilities for mean trait size and size-corrected absolute asymmetry of all five paired morphological traits as well as lipid and glycogen content and supplied them

Table 1
Trait means, evolvability, and percent measurement error relative to asymmetry for all traits (offspring individuals)

| | Trait mean \pm SD | | Measurement error (%) | Evolvability ($\times 10^3$) | |
|------------------------|-----------------------|---------------------|-----------------------|--------------------------------|--------|
| | Females ($n = 152$) | Males ($n = 258$) | | Females | Males |
| Wing length (mm) | 3.74 \pm 0.13 | 4.34 \pm 0.13 | 51.8 | 3.48 | 6.89 |
| Wing width (mm) | 1.76 \pm 0.08 | 2.02 \pm 0.06 | 56.4 | -3.18 | 12.18 |
| Hind tibia length (mm) | 2.88 \pm 0.11 | 3.69 \pm 0.11 | 48.7 | 9.17 | 14.31 |
| Mid tibia length (mm) | 2.71 \pm 0.11 | 3.65 \pm 0.12 | 33.8 | 10.14 | 16.77 |
| Fore tibia length (mm) | 1.88 \pm 0.08 | 2.38 \pm 0.08 | 50.1 | -1.70 | 6.72 |
| Lipid content (mg) | 1.73 \pm 0.61 | 1.64 \pm 0.67 | — | 188.19 | 175.00 |
| Lipid content (%) | 4.91 \pm 1.93 | 3.34 \pm 1.44 | — | | |
| Glycogen content (mg) | 0.136 \pm 0.052 | 0.167 \pm 0.085 | — | 19.12 | 55.99 |
| Glycogen content (%) | 0.384 \pm 0.153 | 0.342 \pm 0.170 | — | | |

with approximate standard errors as described in Roff (1997). Following Roff (1997), we also calculated the (broad sense) genetic correlation between the left and right measurements of all five paired traits. Finally, we present the evolvability of all traits, defined by Houle (1992) as the additive genetic variance of the trait standardized by its standard deviation times its mean: $V_a/(SD \times \text{mean})$ (Lynch and Walsh, 1998). This is the same as the (narrow sense) heritability times the coefficient of variation of the trait (Roff, 1997): $h^2 \times (SD/\text{mean}) = h^2 \times CV$. To be conservative, we used the latter formula with our minimum h^2 estimate, theoretically and typically the narrow-sense parent-offspring estimate, but occasionally the broad-sense full-sib estimate.

RESULTS

In *S. stercoraria*, males are larger than females (Table 1). Lipid and glycogen content were therefore expressed in absolute (milligrams) as well as relative terms (percentage of wet body mass). Body mass was derived from hind tibia length using regression relationships established with laboratory animals: body mass = $\exp(0.880 + 0.817 \times \text{tibia length, in millimeters})$ for males, and body mass = $\exp(0.932 + 0.915 \times \text{tibia length, in millimeters})$ for females ($R^2 = .89$ and $n = 34$ for both sexes; Burkhard, 1999). Despite male-biased size dimorphism, females had more lipids (but not more glycogen), both in absolute and relative terms, probably related to production of eggs (Table 1).

Repeatabilities of signed asymmetry ranged from 0.56 (wing width) to 0.63 (mid tibia length), whereas those of trait size ranged from 0.89 (fore tibia length) to 0.98 (wing length). All distributions of signed asymmetry tended to be leptokurtic rather than platykurtic (i.e., exhibited positive kurtosis), so anti-symmetry could definitely be excluded (Leung and Forbes, 1997; Rowe et al., 1997). Asymmetry was significantly discernible from measurement error for all traits (side-by-side interaction: $F_{406,820} \geq 2.94$, $p < .001$; Palmer and Strobeck, 1986; Table 1). However, for all traits but fore tibia length, the same analysis yielded a significant, albeit small, side effect ($F_{1,820} \geq 3.03$, $p < .001$), a result also apparent for signed asymmetry of wing length and mid-tibia length when using one-sample t tests to test for differences from the expected mean of zero (Table 2). This would indicate slight directional rather than fluctuating asymmetry (Palmer and Strobeck, 1986). However, we have strong evidence that this is not a biological reality, but instead can be attributed to a known parallax measurement bias when using some binocular microscopes (discussed in Blanckenhorn et al., 1998). We have in the meantime changed our methods and

now definitely know we are dealing with fluctuating rather than directional asymmetry in this species. In any case, as FA, slight directional asymmetry may reflect some sort of (heritable) developmental instability as well (Graham et al., 1998), the heritability of which would be included in our estimates.

There were no sex differences in size-corrected absolute asymmetry for any trait (two-sample t tests; $p > .2$), nor for all traits combined (multivariate ANOVA; $p > .2$; Table 2). Size-corrected absolute asymmetry values were positively correlated among the five paired traits for males (9 of 10 correlations were positive; one-tailed binomial test, $p = .011$; mean \pm SE correlation, 0.088 ± 0.024), but not females (6 of 10 correlations were positive; $p = .377$; mean \pm SE correlation, 0.032 ± 0.031). However, this test has to be evaluated with caution because the pairwise data are not independent (Reusch and Blanckenhorn, 1998; Roff, 1995). It is interesting that size-corrected absolute asymmetry of fore tibia length, presumably a sexually and naturally selected trait (Liggett et al., 1996; Swaddle, 1997), was greater than that of all other traits for both males and females (repeated-measures planned contrasts: both $p < .001$; Table 2). Finally, phenotypic correlations among the three trait groups, morphology, asymmetry, and physiology, were low, inconsistent in sign, and rarely significant for all individual traits.

Heritabilities of three condition measures

There were 37 full-sib families with at least 2 but on average $k = 3.78$ daughters, and 46 families with at least 2 but on average $k = 5.52$ sons (both containers combined; Roff, 1997). Most morphological traits assessed, which are typically highly correlated with one another and with body size (Reusch and Blanckenhorn, 1998), were significantly heritable, at least in males (Table 3). The narrow-sense parent-offspring estimates, which contain only additive genetic variance (plus possibly some maternal effects), were on average smaller than the broad-sense full-sib estimates (as expected), which additionally contain dominance variance (however, variance due to common environment was removed here; Roff, 1997). The magnitude of the heritabilities agrees with other estimates for yellow dung flies (Blanckenhorn, 2002; Simmons and Ward, 1991). Heritabilities for males appear higher than for females, but this is not generally the case in this species (Blanckenhorn, 2002), so we think it relates here primarily to differences in sample sizes and hence power. Full-sib genetic correlations between the left and right trait were expectedly high, ranging from $r_g = 0.90$ – 0.99 for the five traits measures. This by itself predicts very low heritabilities for asymmetry (Roff, 1997; Windig and Nylin,

Table 2

Mean \pm SD percent size-corrected signed asymmetry (minimum, maximum), percent size-corrected absolute asymmetry (CV = SD/mean), and absolute asymmetry (evolvability = minimum $h^2 \times$ CV) for all offspring individuals measured

| Trait | Females ($n = 152$) | Males ($n = 258$) |
|---|----------------------------------|-----------------------------------|
| Size-corrected signed asymmetry (%; minimum, maximum) | | |
| Wing length | 0.36 \pm 0.68 (–1.65, 2.06)*** | 0.39 \pm 0.67 (–1.56, 2.53)*** |
| Wing width | 0.21 \pm 1.28 (–3.64, 3.77) | 0.13 \pm 1.31 (–4.58, 3.71) |
| Hind tibia length | –0.19 \pm 1.31 (–4.35, 2.68) | –0.14 \pm 1.19 (–3.56, 3.28) |
| Mid tibia length | –0.29 \pm 1.52 (–4.44, 3.76)* | –0.50 \pm 1.35 (–4.08, 3.79)*** |
| Fore tibia length | 0.08 \pm 1.82 (–4.46, 5.04) | 0.16 \pm 1.75 (–7.15, 7.79) |
| Size-corrected absolute asymmetry (%; CV) | | |
| Wing length | 0.62 \pm 0.50 (0.80) | 0.58 \pm 0.53 (0.90) |
| Wing width | 0.89 \pm 0.99 (1.12) | 0.94 \pm 0.95 (1.01) |
| Hind tibia length | 1.07 \pm 0.87 (0.82) | 0.94 \pm 0.78 (0.83) |
| Mid tibia length | 1.21 \pm 1.00 (0.82) | 1.15 \pm 0.88 (0.77) |
| Fore tibia length | 1.41 \pm 1.38 (0.98) | 1.27 \pm 1.24 (0.98) |
| Mean asymmetry | 1.02 \pm 0.45 (0.44) | 0.99 \pm 0.47 (0.48) |
| Absolute asymmetry (μ m; evolvability) | | |
| Wing length | 23.21 \pm 18.71 (–0.161) | 25.21 \pm 22.76 (–0.036) |
| Wing width | 15.63 \pm 17.30 (–0.332) | 19.03 \pm 19.15 (–0.050) |
| Hind tibia length | 30.68 \pm 24.79 (0.048) | 34.59 \pm 28.46 (0.041) |
| Mid tibia length | 32.95 \pm 27.34 (–0.075) | 41.67 \pm 31.76 (–0.038) |
| Fore tibia length | 26.83 \pm 26.82 (–0.100) | 30.09 \pm 29.33 (–0.127) |

Deviation from zero by one-sample t test: * $p < .05$; *** $p < .001$.

2000; see below). Evolvabilities of all morphological traits were approximately of the same magnitude (Table 1).

Asymmetry of the majority of traits, including mean asymmetry, was clearly not heritable in either sex, as most estimates were even negative (Table 3). Evolvabilities were correspondingly nil (or negative) as well (Table 2). Heritabilities were similar regardless of whether they were calculated using absolute asymmetry in microns, absolute asymmetry in microns with variance due to trait size removed by analysis of covariance (Møller and Thornhill, 1997), or absolute size-corrected asymmetry in percent (given in Table 3). Box-Cox transformations were not effective at normalizing the typically skewed, half-normal distribution of absolute asymmetry because of the frequent occurrence of zero asymmetry (Leung and Forbes, 1997; Møller and Thornhill, 1997; Rowe et al., 1997; Swaddle et al., 1994).

Relative lipid content was heritable for males and females based on full-sibs and for males based on father–son regression (Table 3; again, using absolute lipid content with PC1 as the covariate yielded similar results). The evolvability of lipid content is at least one order of magnitude greater than that of the morphological traits, largely due to greater phenotypic variance (Table 1). However, as discussed by Roff (1997), this measure is not necessarily scale independent, so comparison across traits is problematic (see Houle, 1992). In contrast, glycogen was largely not heritable, and its evolvability is consequently somewhat lower (Table 1).

DISCUSSION

Our results demonstrate consistent broad- and narrow-sense genetic variation in body size and lipid reserves, but not in asymmetry of paired morphological traits or glycogen reserves. All these traits have been used previously as surrogates for condition in a variety of species (see above) and have been linked to sexual selection in the yellow dung fly (Jann et al., 2000; Liggett et al., 1993; Otronen, 1995). We discuss the three groups of traits in turn.

Body size (i.e., hind tibia length) is under strong and consistent positive sexual selection in yellow dung flies, mainly through male–male competition (Jann et al., 2000). As expected (Blanckenhorn, 2002; Simmons and Ward, 1991), body size is heritable in this species. Body size also strongly depends on larval nutrition (Blanckenhorn, 1998), so the assumptions of Rowe and Houle's (1996) model are met for body size as a condition surrogate, which is why body size is often treated as such (e.g., Bjorksten et al., 2000a; Wilkinson and Taper, 1999). However, this demonstration is in some ways trivial because morphological traits are typically heritable (Mosseau and Roff, 1987). Furthermore, individuals may be large but yet in poor physiological condition (Jakob et al., 1996; see below), and we found no relationship between lipid content and body size here. Moreover, body size is far downstream from condition as defined as the resources available to be allocated among traits (Rowe and Houle, 1996), and therefore its assessment is subject to more (environmental) noise (see Price and Schluter, 1991). Therefore, we are not sure that body size per se is a meaningful condition surrogate.

Condition is frequently estimated as body mass corrected for size (Jakob et al., 1996; Kotiaho, 1999; e.g., Kotiaho et al., 2001; Merilä, 1996; Milinski and Bakker, 1990; Saino et al., 1999; Weatherhead et al., 1999). This indirect measure supposedly reflects an individual's energetic state or physiological condition (Jakob et al., 1996), even though body mass also depends considerably on water content and therefore can be unreliable. Of course, energy (primarily lipid and glycogen) reserves can also be measured directly, as done here. Energy reserves largely depend on nutrition but are also expected to be heritable, and they represent an easily measured trait that seems close to Rowe and Houle's (1996) definition of condition. However, fat reserves are subject to trade-offs and thus strategic decisions by individuals because they also carry costs (e.g., in terms of greater wing load), so the "best" (largest, fittest, dominant, etc.) individuals are not necessarily expected to have most energy stored at all times (McNamara and Houston, 1990; Witter and Cuthill, 1993).

Table 3

Heritabilities $h^2 \pm \text{SE}$ of asymmetry (lightface) and trait size (boldface) of five morphological traits, a composite, and of lipid and glycogen content, with the associated full-sib variance components

| | Full-sib h^2 | | $V_{\text{fam}}; V_{\text{container}}; V_{\text{error}}$ | | Parent-offspring h^2 | |
|-------------------|---------------------|------------------------|--|-------------------------|-----------------------------------|-----------------------|
| | Females | Males | Females | Males | Females | Males |
| Wing length | -0.20 ± 0.30 | 0.00 ± 0.17 | -0.23; 0.21; 2.28 | 0.00; -0.06; 2.74 | -0.01 ± 0.26 | -0.04 ± 0.13 |
| | -0.36 ± 0.28 | +0.49 ± 0.18** | 2.67; 6.69; 5.44 | 3.48; 3.5; 7.07 | 0.10 ± 0.30 | -0.23 ± 0.17 |
| Wing width | -0.30 ± 0.29 | -0.21 ± 0.16 | -1.55; 4.54; 7.44 | -0.87; 1.19; 7.96 | +0.30 ± 0.17 ^(*) | -0.05 ± 0.10 |
| | +0.34 ± 0.27 | +0.53 ± 0.18** | 0.93; 2.09; 2.28 | 0.89; 0.54; 1.93 | -0.07 ± 0.34 | -0.41 ± 0.19* |
| Hind tibia length | +0.18 ± 0.28 | +0.11 ± 0.18 | 0.13; -0.81; 7.32 | 0.32; 0.05; 5.46 | +0.06 ± 0.12 | -0.05 ± 0.06 |
| | +0.24 ± 0.28 | +0.64 ± 0.18*** | 1.47; 5.40; 5.26 | 3.80; 1.55; 6.44 | +0.37 ± 0.22^(*) | -0.48 ± 0.19* |
| Mid tibia length | -0.09 ± 0.29 | -0.05 ± 0.17 | -0.42; 0.58; 9.34 | -0.17; 0.40; 6.37 | +0.04 ± 0.18 | 0.02 ± 0.14 |
| | +0.25 ± 0.28 | +0.51 ± 0.18** | 1.52; 5.54; 5.14 | 3.31; 2.97; 6.82 | +0.33 ± 0.25 | +0.51 ± 0.17** |
| Fore tibia length | -0.10 ± 0.29 | -0.05 ± 0.17 | -0.96; 4.04; 16.15 | -0.36; -0.13; 14.51 | -0.07 ± 0.18 | -0.13 ± 0.13 |
| | +0.19 ± 0.28 | +0.39 ± 0.18* | 0.46; 1.96; 2.55 | 1.05; 1.05; 3.21 | -0.04 ± 0.22 | +0.20 ± 0.20 |
| Mean asymmetry | -0.28 ± 0.29 | -0.07 ± 0.16 | -0.27; 0.81; 1.43 | -0.06; 0.19; 1.60 | -0.02 ± 0.11 | -0.13 ± 0.10 |
| PCI (size) | +0.27 ± 0.27 | +0.52 ± 0.18** | 0.47; 1.48; 1.48 | 0.90; 0.78; 1.80 | +0.26 ± 0.25 | +0.40 ± 0.19* |
| Lipid content | +0.53 ± 0.26* | +0.43 ± 0.18** | 1.10; 0.70; 2.34 | 1.00; 0.93; 2.68 | +1.02 ± 0.64 | +0.68 ± 0.33* |
| Glycogen content | +0.05 ± 0.29 | +0.33 ± 0.16* | 0.09; 0.80; 2.05 | 1.19; -0.23; 6.22 | +0.07 ± 0.14 | +0.11 ± 0.18 |

Effect of body size removed for asymmetry and lipid content; $n = 37$ and 46 full-sib families for females and males, respectively.

(*) $p < .10$, * $p < .05$, ** $p < .01$; *** $p < .001$.

Nevertheless, we demonstrated here a heritable component to lipid content, the primary long-term energy storage compound in most animals. In contrast, glycogen content was not heritable, perhaps because it is a physiologically more labile, short-term storage compound. The heritability of condition has also been reported by Kotiaho et al. (2001) and Merilä (1996), although they did not measure physiological compounds but instead used a morphological condition index. We also found that the evolvability of physiological condition (i.e., lipids and glycogen) was much greater than that of our other condition surrogates, primarily due to increased phenotypic variance; however, direct comparisons among traits are complicated by the possible scale dependence even of evolvability (Roff, 1997).

Otronen (1995) previously showed that copulating male yellow dung flies have higher glycogen content and that males on the dung pat, where most mating occurs, have higher lipid reserves than those in the surrounding grass. In addition, Sigurjónsdóttir and Snorrason (1995) showed that males on the pat have greater mating success. We have also performed a sexual selection field study showing greater lipid and glucose (but not glycogen) reserves of paired males (Blanckenhorn et al., in press). Energy reserves thus positively correlate with mate acquisition of male yellow dung flies in the field, although a direct causal link to sexual selection has yet to be experimentally demonstrated.

Fluctuating, and probably also directional, asymmetry has been argued to be an indicator of developmental stability and genetic quality, and hence condition, in a sexual selection context (e.g., Graham et al., 1998; Hosken, 2001; Møller and Swaddle, 1997). FA is also typically affected by various environmental stresses, including nutritional stress (Bjorksten et al., 2000b; Hoffmann and Parsons, 1991; Hosken et al., 2000; Palmer and Strobeck, 1986; Woods et al., 1999). However, we found asymmetry not to be heritable here, as expected from the very strong genetic correlation between each pair of limbs (Roff, 1997; Windig and Nylin, 2000). With the possible exception of asymmetry in hind tibia length, which was consistently positive and may perhaps become significant at larger sample sizes (Table 1), the heritabilities of asymmetry of all traits were consistently nil. (We consider the nearly significant parent-offspring estimate for female wing

width spurious, as the broad-sense full-sib estimate was negative.) Perhaps most crucially, the heritability of mean asymmetry was nil. This occurred despite the fact that asymmetry of the five traits was slightly positively correlated within males. This lack of additive genetic variation is unlikely to be due to low statistical power because our sample sizes were reasonable and most estimates were negative, rendering power analysis pointless. Our study is therefore one of a growing number that have failed to find evidence for a heritable component to asymmetry (e.g., Blanckenhorn et al., 1998; Bjorksten et al., 2000a; David et al., 1998; Møller et al., 1996; Tomkins and Simmons, 1999; see also Clark, 1998; Palmer, 1999; Simmons et al., 1999).

In conclusion, Rowe and Houle (1996) explicitly stated that their model requires condition dependence of sexually selected traits and (high) genetic variance in condition. We have assessed and compared, in the yellow dung fly, the heritability of three condition surrogates commonly used in the literature to which Rowe and Houle's (1996) prerequisites have been argued to generally apply. Our study demonstrates that lipid reserves (i.e., physiological condition) as well as body size, but not asymmetry, have additive genetic components. While all condition surrogates investigated typically reflect various environmental factors (see above), V_a in condition does not hold, at least not for asymmetry. Moreover, the evolvability of lipid reserves is much greater than that of the other traits (Rowe and Houle, 1996). It is possible that our genetic estimates are somewhat inflated because the animals were held in a benign laboratory environment, but this question is far from being settled in general (Hoffmann and Merilä, 1999; Weigensberg and Roff, 1996). Of the three surrogates, we prefer physiological condition, as it is most akin to Rowe and Houle's (1996) definition of condition, although all measures have their limitations as discussed above. Unfortunately, although condition is a useful heuristic concept in evolutionary ecology (Pomiankowski and Møller, 1995; Rowe and Houle, 1996), a practical measure that closely approximates it appears to be lacking. It is important that all researchers using any condition surrogate be aware that the theoretical concept and what they are measuring are not the same thing.

We thank M. Greeff, L. Pennanen, and M. Schulze for measuring flies, A. Haigis for conducting the physiological analyses, D. Roff and J. Kotiaho for comments and statistical advice, and the Swiss National Fund for financial support.

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