

Zeitschrift: Alpine entomology : the journal of the Swiss Entomological Society
Herausgeber: Swiss Entomological Society
Band: 5 (2021)

Artikel: A fungal parasite selects against body size but not fluctuating asymmetry in Swiss subalpine yellow dung flies
Autor: Blanckenhorn, Wolf U.
DOI: <https://doi.org/10.5169/seals-966039>

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

Download PDF: 06.02.2026

ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>

A fungal parasite selects against body size but not fluctuating asymmetry in Swiss subalpine yellow dung flies

Wolf U. Blanckenhorn¹

¹ Department of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, CH-8057, Zürich, Switzerland

<http://zoobank.org/0D01A23B-D327-4F92-9726-93AAD929CAFD>

Corresponding author: Wolf U. Blanckenhorn (wolf.blanckenhorn@ieu.uzh.ch)

Academic editor: Patrick Rohner ♦ Received 8 March 2021 ♦ Accepted 25 May 2021 ♦ Published 11 June 2021

Abstract

Evidence for selective disadvantages of large body size remains scarce in general. Previous studies of the yellow dung fly *Scathophaga stercoraria* have demonstrated strong positive sexual and fecundity selection on male and female size. Nevertheless, the body size of flies from a Swiss study population has declined by ~10% 1993–2009. Given substantial heritability of body size, this negative evolutionary response of an evidently positively selected trait suggests important selective factors being missed. An episodic epidemic outbreak of the fungus *Entomophthora scatophagae* permitted assessment of natural selection exerted by this fatal parasite. Fungal infection varied over the season from ~50% in the cooler and more humid spring and autumn to almost 0% in summer. The probability of dying from fungal infection increased with adult fly body size. Females never laid any eggs after infection, so there was no fungus effect on female fecundity beyond its impact on mortality. Large males showed their typical mating advantage in the field, but this positive sexual selection was nullified by fungal infection. Mean fluctuating asymmetry of paired appendages (legs, wings) did not affect the viability, fecundity or mating success of yellow dung flies in the field. This study documents rare parasite-mediated disadvantages of large-sized flies in the field. Reduced ability to combat parasites such as *Entomophthora* may be an immunity cost of large body size in dung flies, although the hypothesized trade-off between fluctuating asymmetry, a presumed indicator of developmental instability and environmental stress, and immunocompetence was not found here.

Key Words

body size, developmental stability, *Entomophthora*, fecundity selection, fluctuating asymmetry, fungal parasite, insect immunity, *Scathophaga stercoraria*, sexual selection, trade-off, viability selection

Introduction

Systematic quantification of selection has become one of the hallmarks of modern biological research so as to acquire a thorough understanding of the process of natural selection and its evolutionary consequences. Standardized measures of selection have been available for some time (Lande and Arnold 1983; Arnold and Wade 1984a, b; Brodie et al. 1995) and have been applied to many species and situations to foster several comparative (meta-)analyses, which greatly enhanced our understanding of the action of natural selection in the wild (e.g. Endler 1986; Kingsolver et al. 2001; Kingsolver and Pfennig 2004; Cox and Calsbeek 2009). Phenomenological (i.e.

non-behavioural) investigations of selection also are the field method of choice to understand the evolution and population biology of single species and populations in an integrative manner, and to test hypotheses about the evolution of particular traits and patterns (e.g. sexual size dimorphism: Blanckenhorn 2007).

The widespread yellow dung fly *Scathophaga stercoraria* (Diptera: Scathophagidae) is a classic model species for studies of natural and particularly sexual selection (Parker 1979; Borgia 1982). The species prefers cooler climates and populates the entire northern hemisphere up to very high latitudes, being particularly common around cow pastures in north-central Europe, also at high altitudes (Sigurjónsdóttir and Snorrason 1995;

Blanckenhorn 1997; Bauerfeind et al. 2018; Blanckenhorn et al. 2018; Schäfer et al. 2018; <https://www.gbif.org/species/1556243>). In lowland central Europe, each year has a spring (March – June) and an autumn season (September – November), while during the hot midsummer (July and August) the flies largely disappear from the pastures due to their heat sensitivity (Blanckenhorn 2009). Phenomenological studies of our long-term field population in lowland Switzerland have documented temporally variable but on average very strong mating advantages of large males, as well as fecundity advantages of large females (cf. Honek 1993; Jann et al. 2000; Blanckenhorn et al. 2003). Strong sexual selection on male body size likely is the main driver of the untypical male-biased sexual size dimorphism of *S. stercoraria* (Fairbairn 1997; Kraushaar and Blanckenhorn 2002; Blanckenhorn 2007, 2009). Nevertheless, the body size of flies has declined by almost 10% over a 15-year period from 1993–2009, possibly related to our warming climate (Blanckenhorn 2015). Given generally substantial heritability of body size also in this species (Mousseau and Roff 1987; Blanckenhorn 2000), this negative evolutionary response of a trait that is measurably strongly positively selected suggests that we are missing important selective episodes or factors shaping the morphological evolution of yellow dung flies (Merilä et al. 2001; Blanckenhorn 2015; Gotanda et al. 2015). Evidence for selective disadvantages of large body size remains scarce in general, also for yellow dung flies (Blanckenhorn 2000, 2007).

One aspect not well studied in yellow dung flies is size-dependent survival in nature. This is generally the case for small-bodied invertebrates, for which longitudinal field studies are essentially impossible because individuals cannot be as easily marked and followed like larger vertebrates (Merilä and Hendry 2014; Schilthuizen and Kellermann 2014; Stoks et al. 2014; Blanckenhorn 2015). At the same time, laboratory longevity estimates (e.g. Blanckenhorn 1997; Reim et al. 2006b; Blanckenhorn et al. 2007) generally do not well reflect field mortality. We have acquired multiple field estimates of larval survivorship at various conditions suggesting some counter-selection against large body size mediated by their longer development (summarized in Blanckenhorn 2007). However, sex- and size-specific adult survivorship in the field was so far estimated only indirectly by Burkhard et al. (2002) using age-grading by wing injuries, with mixed results. We here add a study of natural selection on morphological traits by the fatal fungal parasite *Entomophthora* spp.

The parasitic fungus *Entomophthora scatophagae* regularly infects yellow dung flies in Europe and North America (Hammer 1941; Steinkraus and Kramer 1988; Maitland 1994; Steenberg et al. 2001). Primarily at humid conditions infections can be occasionally (though unpredictably) epidemic (pers. obs.), in which case infected dead flies can be found prominently exposed near cow pastures on flowers, long grass or fences in a characteristic posture presumably effectively disseminating fungal

spores and/or attracting other flies (Møller 1993; Maitland 1994). Spore transmission may also occur via physical contact, e.g. during copulation (Møller 1993). This type of fungus is highly virulent and effective at infecting and killing insects within few days, and it can be manipulated such that *Entomophthora* species are being considered for biological control of insect pests (e.g. Steenberg et al. 2001; Nielsen and Hayek 2006). We took advantage of an unusually conspicuous fungus epidemic at our field population in Fehraltorf, Switzerland, in 2002.

I here assessed viability, fecundity and sexual selection acting on morphology and fluctuating asymmetry of field-collected yellow dung flies. Morphological traits reflecting body size are often evaluated in selection studies, documenting selective advantages of large size and corresponding evolutionary responses in many vertebrate and invertebrate species (Kingsolver et al. 2001; Kingsolver and Pfennig 2004; Blanckenhorn 2007; Gotanda et al. 2015). Body size is one of the most important quantitative traits of an organism, as it strongly affects most physiological and fitness traits (Calder 1984; Schmidt-Nielsen 1984; Roff 1992) and exhibits several prominent evolutionary patterns in many organisms (e.g. Rensch's Rule, Cope's Rule, or Bergmann clines; Rensch 1950; Fairbairn 1997; Blanckenhorn 2000; Blanckenhorn and Demont 2004; Kingsolver and Pfennig 2004). Depending on the taxon, diverse traits are typically used as surrogates of body size, which are usually highly correlated (i.e. integrated) within individuals due to pleiotropy, epistasis, or gene linkage. Nevertheless, for functional reasons selection on various body parts may vary (e.g. Preziosi and Fairbairn 2000), producing responses in correlated traits and thus generally requiring a multivariate approach (Lande and Arnold 1983). I focused on paired appendages (legs, wings), so I could also assess fluctuating asymmetry (FA; Palmer and Strobeck 1986). Small and random deviations from the a priori perfect symmetry in bilaterally symmetric organisms, i.e. FA, are presumed to reflect heritable developmental instability, such that individuals with good genes and/or living in good conditions can produce more symmetric bodies in the face of environmental or genetic stress, ultimately augmenting organismal fitness. Symmetric individuals consequently should have greater survival prospects (viability selection), or should be more successful at acquiring mates (sexual selection: Møller and Swaddle 1997). However, especially the latter notion, and the evidence, remain controversial (Møller and Thornhill 1997; Palmer 2000; Klingenberg 2003; Polak 2003; Van Dongen 2006; Knierim et al. 2007). In yellow dung flies, Liggett et al. (1993) and Swaddle (1997) found a negative relationship between FA and mating or foraging success, respectively, while Floate and Coughlin (2010) found no evidence for FA being a useful biomarker of environmental stress exerted by toxic livestock medications (ivermectin). Our own previous studies of this species revealed that FA is not heritable (Blanckenhorn and Hosken 2003), that it does not increase with inbreeding (or homozygosity: Hosken

et al. 2000), that it does not affect male mating success in the field while nevertheless being negatively related to energy reserves (Blanckenhorn et al. 2003), but that FA increases at stressfully high developmental temperatures (Hosken et al. 2000). Of central relevance for our study is the hypothesized link between FA and immunocompetence, postulating that more symmetric, but likely also larger individuals are expected to better fend off internal parasites such as *Entomophthora* (e.g. Rantala et al. 2000, 2004, 2007; Yourth et al. 2002, and references therein).

Materials and methods

Study species

Adult *S. stercoraria* are sit-and-wait predators of small flying insects, from which they extract protein to produce sperm and eggs (anaotogeny: Foster 1967). Females spend most of their time foraging for nectar and prey in the vegetation surrounding pastures. About once a week they visit fresh cattle (or other) dung to deposit a clutch of eggs. Larvae feed on and develop in the dung. Multiple males typically wait at fresh dung pats to mate with (stochastically) incoming females. Copulation usually takes place in the surrounding grass or on the dung pat; during the ensuing oviposition the male guards the female against other competitors (Parker 1970). Competition among males for females is strong as the operational sex ratio is highly male biased (Jann et al. 2000). Larvae face unpredictable spatio-temporal variation in local temperatures, dung (i.e. food) quality and quantity, intra- and inter-specific competition, and dung drying, all factors that ultimately largely determine their phenotypic adult body size. Towards the end of the season the flies have to reach the overwintering pupal stage before the first winter frost (Blanckenhorn 2009).

Fly sampling

I sampled our population in Fehraltorf near Zurich (47°52'N, 8°44'E) roughly once a month between April and November 2002 (8 seasonal samples; total of $N = 541$ flies). Fly densities permitting, we randomly selected one representative fresh dung pat, collecting all single and paired flies on and ca. 20 cm around the pat to bring them alive to the laboratory. (Else more than one pat were so sampled.) The group composition around any given fresh dung pat technically defines the relevant competitive situation for sexual selection (Arnold and Wade 1984a, b; elaborated below), and is as random as any random sample of flies from the entire pasture or population (Jann et al. 2000; Blanckenhorn et al. 2003). As virtually no unpaired females occur at the dung in the field because competition for mates is so intense, the number of pairs corresponds to the number of females present, and the proportion of paired males corresponds to the operational sex ratio (females / males).

Laboratory procedures

Although dead flies visibly infected with the fungus were occasionally found on and around the pasture, these were too rare and haphazard to be sampled systematically. Instead, all flies collected were kept alive in the laboratory in single 100 ml bottles with sugar and water for up to two weeks. Infected flies would develop the fungus within few days, first visible in the abdomen but eventually covering the entire fly (Fig. 1), and eventually die; non-infected, recovered or resistant flies, which for all practical purposes here were indistinguishable and hence subsumed as non-infected, would not. Once in the laboratory, all females received dung to oviposit one clutch of eggs, which was counted.

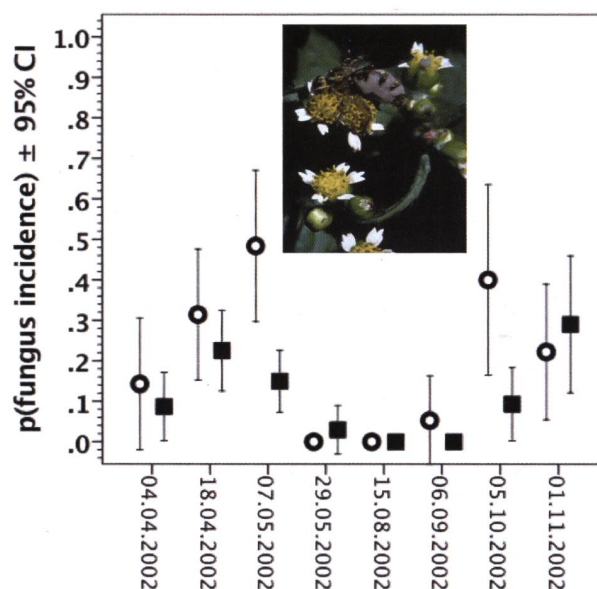


Figure 1. Proportion of male (filled squares) and female (open circles) flies infected by the fungus *Entomophthora* over the season 2002, with an infected specimen inset (photo Peter Jann).

After death, work study students measured left and right wing length as well as fore, mid and hind tibia length of each fly. Mean values for these paired traits were subsequently calculated, as well as signed FA as $(L - R)$, unsigned FA as $(|L - R|)$ (both in mm) and unsigned, size-corrected FA as $(|L - R|) / \text{mean}(L, R)$ in %, as recommended by Palmer and Strobeck (1986). Paired traits were measured twice blindly by the same person to estimate measurement error relative to fluctuating asymmetry (Palmer and Strobeck 1986), and to calculate the repeatability of all trait measurements (Becker 1992). All measurements were taken with a binocular microscope at 16× magnification.

Statistical analysis

For each monthly sample we calculated standardized viability selection differentials (= gradients) for both sexes

Table 1. Overall intensities ($\beta \pm 95\%$ CI) of female and male adult viability selection ($N_f = 171$ and $N_m = 370$) exerted by the fungus *Entomophthora*, female fecundity selection (clutch size; $N_f = 126$), and male sexual selection (pairing success; $N_m = 370$) for one Swiss population of yellow dung flies (*Scathophaga stercoraria*) over the season 2002. Significant coefficients are bold ($P < 0.05$).

Trait	Adult viability				Female fecundity		Male mating success	
	β_f	95% CI	β_m	95% CI	β	95% CI	β	95% CI
Hind tibia length	-0.158	0.305	-0.306	0.252	0.185	0.027	0.259	0.149
Mid tibia length	-0.089	0.310	-0.328	0.277	0.179	0.029	0.228	0.150
Fore tibia length	-0.196	0.304	-0.221	0.251	0.174	0.029	0.226	0.159
Wing length	-0.254	0.307	-0.324	0.248	0.179	0.029	0.267	0.147
Overall PC size	-0.099	0.292	-0.317	0.302	0.184	0.029	0.253	0.136
Hind tibia FA	-0.020	0.333	-0.086	0.258	-0.023	0.045	0.051	0.151
Mid tibia FA	0.204	0.231	0.003	0.219	-0.026	0.041	0.010	0.173
Fore tibia FA	-0.037	0.299	0.224	0.283	-0.024	0.045	0.040	0.180
Wing FA	-0.187	0.321	0.046	0.279	0.037	0.045	-0.041	0.168
Mean FA	0.035	0.284	0.097	0.327	-0.021	0.040	0.071	0.134

(binary variable: dead/alive = infected/uninfected), sexual selection differentials for males (binary: mated/unmated), and (continuous) fecundity selection gradients for females based on their clutch size using standard methods (Lande and Arnold 1983; Arnold and Wade 1984a, b; Brodie et al. 1995). It turned out that almost all females that developed the fungus and eventually died in the laboratory did not lay any eggs, so fecundity selection coefficients only refer to healthy (uninfected or resistant) females. We calculated female and male selection coefficients for each trait separately (4 morphological and 4 asymmetry traits), and additionally for the first principal component (PC) of all (mean) appendages signifying a compound index of body size.

Because the sizes of all appendages were highly positively correlated, and because FA and size are mathematically related (see formulae above), we calculated only univariate linear (β_{uni}) and corresponding non-linear (γ_{uni}) selection coefficients. To do so, for each seasonal sample we produced standardized z-scores for trait x by subtracting the sample mean from each value and dividing by the standard deviation: $z_i = (x_i - \text{mean}(X))/SD(X)$. In cases of low density, when more than one pat was sampled, pat identity was entered as random effect. Relative survival or male pairing success was computed as absolute survival or pairing success (1 or 0) divided by the sample proportion of survived flies or mated males, respectively (Brodie and Janzen 1996). We used the univariate model of relative fitness on standardized body size $w = c + \beta_{uni} \cdot z$ to estimate the linear selection intensities β_{uni} , and the corresponding quadratic model $w' = c + \beta_1 \cdot z + 0.5\gamma_{uni} \cdot z^2$ to estimate corresponding univariate non-linear selection coefficients γ_{uni} (note that $\beta_{uni} \neq b_1$). These linear coefficients (gradients) reflect the combined effects of direct and indirect selection on body size (Endler 1986). The overall weighted means presented in Table 1 were likewise derived from the overall model with all seasonal samples (and sex, where applicable) as fixed factor(s) and dung pat as random factor (plus any applicable covariates).

The difference of the regression coefficients from a slope of zero (the null hypothesis of no selection) was tested. For estimation of the coefficients least-squares regression was applied, but for tests of significance logistic

regression was used when our measures of success were binary (viability and mating success: Brodie et al. 1995). In general, binary variables were analysed with binomial errors, whereas normally distributed errors were analysed using normal errors, if necessary after (log- or square-root) transformation.

Results

Fungus prevalence (1/0) varied over the season and between the sexes. Infections (as high as 50%) were most common during the cooler and more humid periods at the beginning (spring) and the end of the season (autumn), whereas they were rare during the hotter summer (nearly 0%; significant season effect: $\chi^2 = 29.40$; $P < 0.001$). The sexes were overall affected similarly (main sex effect: $\chi^2 = 0.35$; $P = 0.553$), although a significant sex by season interaction indicates some differential susceptibility across the season ($\chi^2 = 34.04$; $P < 0.001$; Fig. 1). Adding potentially explaining variables, the probability of dying by fungal infection (i.e. fungal prevalence) was unaffected by mean FA (main effect of covariate: $\chi^2 = 1.99$; $P = 0.159$) but increased with fly body size (main effect of covariate: $\chi^2 = 12.56$; $P < 0.001$; Table 1), an effect that however varied among seasonal samples (size by season interaction: $\chi^2 = 12.55$; $P < 0.001$) but not the sexes (size by sex interaction: $\chi^2 = 0.27$; $P = 0.602$).

Fecundity selection (based on clutch size) on female body size was significantly positive, as is typical in this species (Jann et al. 2000; Kraushaar and Blanckenhorn 2002). The intensity of fecundity selection, i.e. the slope relating relative clutch size to standardized body size (PC), varied significantly but unsystematically over the season (Table 1; $F_{6,109} = 3.50$, $P = 0.03$). These estimates refer only to uninfected flies because all females infected with the fungus died before laying eggs, and therefore do not refer to fecundity selection exerted by the fungus beyond the parasite's effect on adult mortality.

As usual in yellow dung flies, larger males had a mating advantage (Jann et al. 2000; Kraushaar and Blanckenhorn 2002; Blanckenhorn et al. 2003; main effect of body size (PC): $\chi^2 = 14.23$; $P < 0.001$), while mean FA of

all paired appendages did not affect male mating success ($\chi^2 = 1.17$; $P = 0.279$; Table 1; Fig. 2). Except for one seasonal sample on 29 May, the large male advantage was consistent throughout the season such that sexual selection intensity did not significantly vary across the season (body size by season interaction: $\chi^2 = 0.11$; $P = 0.920$; Table 1; Fig. 2). Interestingly, this typical pattern of positive sexual selection did not hold for those 28 of a total of 47 infected males (of a total of 370 males, of which 148 had acquired a mate) that were found mating in the field and later succumbed to the fungus (main effect of fungal infection: $\chi^2 = 7.61$; $P = 0.006$; Fig. 3).

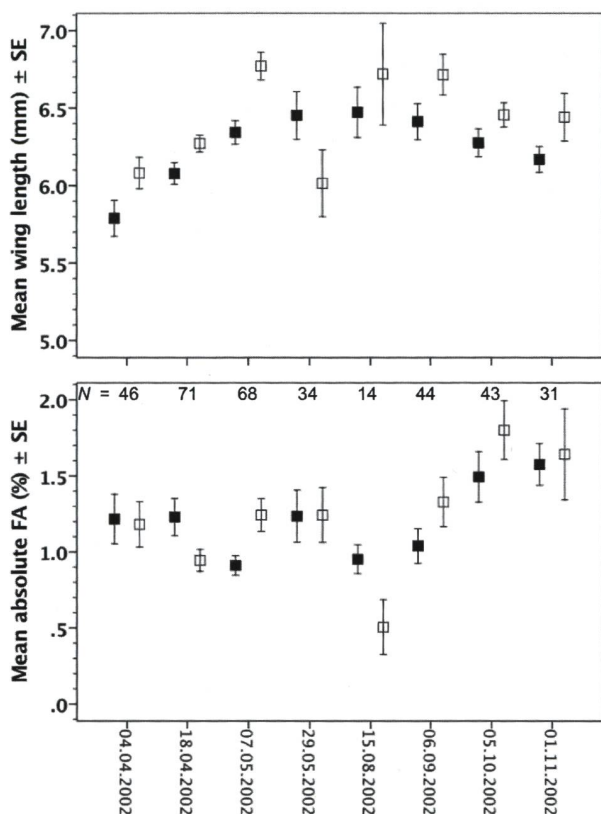


Figure 2. Body size (top; here exemplified by wing length) and mean percentage of fluctuating asymmetry (FA; bottom) of all traits for unpaired (filled squares) and paired males (open squares) over the season.

Table 1 presents weighted mean directional selection coefficients, β , for the entire data set. Corresponding non-linear (quadratic) selection coefficients, γ , were mostly low and not significant and are therefore not presented. The only exception was female fecundity selection on body size, for which $\gamma = 0.056 \pm 0.025$ was significantly positive overall, signifying accelerating selection (which has been reported before: Blanckenhorn 2007, 2009). Leg and wing lengths were expectedly highly correlated in both sexes (range of bivariate correlations: $r = 0.887$ to 0.972), whereas FA of the legs and wings were largely uncorrelated (range: $r = -0.024$ to $+0.215$). Measurement of all paired traits was generally repeatable using our methods ($R = 0.83$ – 0.97), which was also true for asymmetry

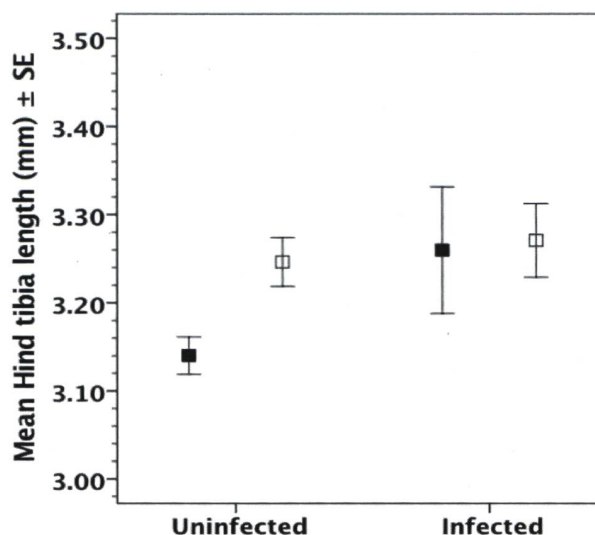


Figure 3. Body size (here exemplified by hind tibia length) of unpaired (filled squares) and paired males (open squares) when they were infected by the fungus or not (all seasonal samples combined).

($R = 0.53$ – 0.61), so that FA could indeed be discerned from measurement error (all side by individual interactions $P < 0.01$), fulfilling the criteria of proper FA assessment (Palmer and Strobeck 1986; Knierim et al. 2007).

Discussion

At our Swiss study population, the entomophagous fungal parasite *Entomophthora scatophagae*, which has previously been described as a specific parasite of adult yellow dung flies at several sites in Europe and North America (Hammer 1941; Steinkraus and Kramer 1988; Maitland 1994; Steenberg et al. 2001), showed high and generally fatal infection rates of up to 50% during the cooler and more humid periods of the year 2002. Although the fungus is likely present most years, 2002 was a year of extraordinary high fungal prevalence, which before we had experienced only once before in the mid 1990s. I could document that this fungus exerts relatively strong and consistent negative viability selection on female and male adult body size in *S. stercoraria* (Table 1). Fungal infection further nullified the usual large male mating advantage in this fly (Borgia 1982; Jann et al. 2000; Blanckenhorn et al. 2003; Fig. 3), but did not affect female fecundity beyond its impact on mortality. This represents the first evidence demonstrating viability disadvantages of large yellow dung flies mediated by a parasite, which is generally rare in animals and particularly invertebrates (Blanckenhorn 2000, 2005; Kingsolver and Pfennig 2004; Gotanda et al. 2015). These results complement previous evidence of viability disadvantages of large flies at the juvenile stage, and lend further credence to the notion that the male-biased sexual size dimorphism of yellow dung flies is indeed at evolutionary equilibrium (Blanckenhorn 2007).

This study is merely phenomenological, so I could not assess underlying mechanisms. Nonetheless, I speculate

that the reduced parasite resistance of larger flies signifies a trade-off between body size and immunity (Rantala and Roff 2005; Schwarzenbach and Ward 2006; Cotter et al. 2008). Based on age grading by wing injuries, Burkhard et al. (2002) found that adult age (i.e. longevity) of yellow dung flies in the field tends to be positively related to body size at least during part of the season. Energy reserves also scale positively with body size (Reim et al. 2006a; Blanckenhorn et al. 2007) and positively influence mating success (Blanckenhorn et al. 2003). Adult longevity under most environmental circumstances, including complete starvation, can therefore generally be expected to increase with body size on physiological grounds (Reim et al. 2006b). One possible mechanism selecting against large body size is (positively) size-selective predation and/or parasitism (Blanckenhorn 2000). However, beyond expectations of a general positive correlation between predator and prey size (Brose et al. 2006; Vucic-Pestic et al. 2010), evidence for systematic size-selectivity of predators is generally weak at best, also for yellow dung flies (Blanckenhorn 2000; Busso and Blanckenhorn 2018; Blanckenhorn et al. 2021). Size-selective parasitism has been reported for some parasitoids because larger hosts result in larger parasite offspring (e.g. McGregor and Roitberg 2000), but otherwise few data exist (Zuk and Kolluru 1998; Blanckenhorn 2000). Rather than invoking increased infection rates of larger flies with the parasite, for whatever reasons, I rather suspect that the ability of larger flies to combat the parasite is compromised due to their generally greater absolute energy demands in stressful environments (trade-off hypothesis: Rantala and Roff 2005; Reim et al. 2006a, b; Schwarzenbach and Ward 2006, 2007; Cotter et al. 2008). Females were infected more by the parasite at least in spring (Fig. 1), possibly related to their generally greater reproductive burden (i.e. the cost of producing expensive eggs rather than cheap sperm; cf. Nunn et al. 2009, but see e.g. Rantala et al. 2007 for opposite results). Nevertheless, the standard sex differences in reproductive (energetic) costs should be somewhat offset by the male-biased sexual size dimorphism of yellow dung flies, which implies relatively greater costs of producing and maintaining the larger, condition-dependent male size (Blanckenhorn 2000, 2007), and might explain why size-dependent viability selection here turned out to be stronger in males (Table 1). Yellow dung fly females indeed produce higher heritable levels of phenoloxidase than males (Schwarzenbach et al. 2005), one of the central mediators of insect immunity (Schmid-Hempel 2005; Rolff and Reynolds 2009; González-Santoyo and Córdoba-Aguilar 2012), and higher phenoloxidase levels decrease adult longevity in this species, demonstrating a trade-off (Schwarzenbach and Ward 2006). However, higher phenoloxidase levels did not lead to greater resistance against mites or another fungus (Schwarzenbach and Ward 2007), and phenoloxidase is also unrelated to body size in *S. stercoraria* (Schwarzenbach et al. 2005). Overall, therefore, the evidence in favour of immunity

mediating the higher mortality of large-bodied dung flies documented here remains rather limited.

In contrast to body size, fluctuating asymmetry (FA) of legs and wings influenced none of the fitness components investigated here (contrary to Liggett et al. 1993, but confirming an earlier sexual selection study by Blanckenhorn et al. 2003). Based on evidence in other animals (Rantala et al. 2000, 2004), I had expected that low FA would be a signal of greater immunocompetence augmenting resistance against parasites, but this was not found. It is not unlikely that FA is a bad indicator of developmental stability in general, as various reviews have revealed no clear verdict based on the available evidence on this question, so the entire concept remains controversial (Møller and Swaddle 1997; Møller and Thornhill 1997; Palmer 2000; see various articles in Polak 2003; Van Dongen 2006; Knierim et al. 2007). In yellow dung flies, beyond Liggett et al. (1993) there is no evidence for a role of FA in sexual selection is (Blanckenhorn et al. 2003; Blanckenhorn and Hosken 2003; this study). What remains is that FA reliably indicates at least hot temperature stress in this species (Hosken et al. 2000).

Conclusions

I here took advantage of an unusually intense epidemic outbreak of the species-specific entomophagous fungus *Entomophthora scatophagae* in our experimental Swiss field population of yellow dung flies to assess natural selection exerted by this fatal parasite. Overall, the survival of flies of both sexes infected with the fungus was negatively related to fly size, thus exerting negative size selection, but not the fluctuating asymmetry of their wings and legs. Whereas reduced ability to combat parasites such as *Entomophthora* may be an immunity cost of large body size in dung flies explaining the selection patterns presented, I conclude that fluctuating asymmetry is no good indicator of immunocompetence in yellow dung flies (cf. Rantala et al. 2000, 2004, 2007; Yourth et al. 2002; Rantala and Roff 2005; Schwarzenbach and Ward 2006; Cotter et al. 2008).

Acknowledgements

I thank the University of Zurich and the Swiss National Fund for financial support over the years, and Ana, Lukas, Nils and Patricia for doing the measurements.

References

- Arnold SJ, Wade MJ (1984a) On the measurement of natural and sexual selection: applications. *Evolution* 38: 720–734. <https://doi.org/10.1111/j.1558-5646.1984.tb00345.x>
- Arnold SJ, Wade MJ (1984b) On the measurement of natural and sexual selection: theory. *Evolution* 38: 709–719. <https://doi.org/10.1111/j.1558-5646.1984.tb00344.x>

- Bauerfeind SS, Schäfer MA, Berger D, Blanckenhorn WU, Fox CW (2018) Replicated latitudinal clines in reproductive traits of European and North American yellow dung flies. *Oikos* 127: 1619–1632. <https://doi.org/10.1111/oik.05421>
- Becker WA (1992) *Manual of Quantitative Genetics* (5th edn.). Academic Enterprises, Pullman.
- Blanckenhorn WU (1997) Altitudinal life history variation in the dung flies *Scathophaga stercoraria* and *Sepsis cynipsea*. *Oecologia* 109: 342–352. <https://doi.org/10.1007/s004420050092>
- Blanckenhorn WU (2000) The evolution of body size: what keeps organisms small? *Quarterly Review of Biology* 75: 385–407. <https://doi.org/10.1086/393620>
- Blanckenhorn WU (2007) Case studies of the differential equilibrium hypothesis of sexual size dimorphism in dung flies. In: Fairbairn DJ, Blanckenhorn WU, Székely T (Eds) *Sex, Size and Gender Roles. Evolutionary Studies of Sexual Size Dimorphism*. Oxford University Press, Oxford, 106–114. <https://doi.org/10.1093/acprof:oso/9780199208784.003.0012>
- Blanckenhorn WU (2009) Causes and consequences of phenotypic plasticity in body size: the case of the yellow dung fly (Diptera: Scathophagidae). In: Whitman DW, Ananthakrishnan TN (Eds) *Phenotypic Plasticity of Insects: Mechanisms and Consequences*. Science Publishers, Strixton, 313–366. <https://doi.org/10.1201/b10201-11>
- Blanckenhorn WU (2015) Yellow dung fly body size evolution in the field: response to climate change? *Evolution* 69: 2227–2234. <https://doi.org/10.1111/evo.12726>
- Blanckenhorn WU, Demont M (2004) Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integrative and Comparative Biology* 44: 413–424. <https://doi.org/10.1093/icb/44.6.413>
- Blanckenhorn WU, Kraushaar U, Reim C (2003) Sexual selection on morphological and physiological traits and fluctuating asymmetry in the yellow dung fly. *Journal of Evolutionary Biology* 16: 903–913. <https://doi.org/10.1046/j.1420-9101.2003.00587.x>
- Blanckenhorn WU, Fanti J, Reim C (2007) Size-dependent energy reserves, energy utilization and longevity in the yellow dung fly. *Physiological Entomology* 32: 372–381. <https://doi.org/10.1111/j.1365-3032.2007.00589.x>
- Blanckenhorn WU, Hosken DJ (2003) The heritability of three condition measures in the yellow dung fly. *Behavioral Ecology* 14: 612–618. <https://doi.org/10.1093/beheco/arg052>
- Blanckenhorn WU, Bauerfeind SS, Berger D, Davidowitz G, Fox CW, Guillaume F, Nakamura S, Nishimura K, Sasaki H, Stillwell CR, Tachi T, Schäfer MA (2018) Life history traits, but not body size, vary systematically along latitudinal gradients on three continents in the widespread yellow dung fly. *Ecography* 41: 2080–2091. <https://doi.org/10.1111/ecog.03752>
- Blanckenhorn WU, Cozzi G, Jäggl G, Busso JP (2021) Size- and sex-specific predation on dung flies by amphibian and arthropod predators. *Israel Journal of Ecology & Evolution*, in press. <https://doi.org/10.1163/22244662-bja10026>
- Borgia G (1982) Experimental changes in resource structure and male density: size-related differences in mating success among male *Scathophaga stercoraria*. *Evolution* 36: 307–315. <https://doi.org/10.1111/j.1558-5646.1982.tb05046.x>
- Brodie III ED, Janzen FJ (1996) On the assignment of fitness values in statistical analyses of selection. *Evolution* 50: 437–442. <https://doi.org/10.1111/j.1558-5646.1996.tb04505.x>
- Brodie III ED, Moore AJ, Janzen FJ (1995) Visualizing and quantifying natural selection. *Trends in Ecology & Evolution* 10: 313–318. [https://doi.org/10.1016/S0169-5347\(00\)89117-X](https://doi.org/10.1016/S0169-5347(00)89117-X)
- Brose U, Jonsson T, Berlow EL, Warren P, Banasek-Richter C, Bersier L-F, Blanchard JL, Brey T, Carpenter SR, Cattin Blandenier M-F, Cushing L, Dawah HA, Dell T, Edwards F, Harper-Smith S, Jacob U, Ledger ME, Martinez ND, Memmott J, Mintenbeck K, Pinnegar JK, Rall BC, Rayner TS, Reuman DC, Ruess L, Ulrich W, Williams RJ, Woodward G, Cohen JE (2006) Consumer-resource body-size relationships in common food webs. *Ecology* 87(10): 2411–2417. [https://doi.org/10.1890/0012-9658\(2006\)87\[2411:CBRINF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2)
- Burkhard DU, Ward PI, Blanckenhorn WU (2002) Using age-grading by wing injuries to estimate size-dependent adult survivorship in the field: a case study of the yellow dung fly *Scathophaga stercoraria*. *Ecological Entomology* 27: 514–520. <https://doi.org/10.1046/j.1365-2311.2002.00453.x>
- Busso JP, Blanckenhorn WU (2018) Viability selection by invertebrate predators in the polyphenic black scavenger fly *Sepsis thoracica* (Diptera: Sepsidae). *Behavioral Ecology* 29: 992–1000. <https://doi.org/10.1093/beheco/ary039>
- Calder WA (1984) *Size, Function, and Life History*. Harvard University Press, Cambridge.
- Cotter S, Myatt J, Benskin C, Wilson K (2008) Selection for cuticular melanism reveals immune function and life-history trade-offs in *Spodoptera littoralis*. *Journal of Evolutionary Biology* 21: 1744–1754. <https://doi.org/10.1111/j.1420-9101.2008.01587.x>
- Cox RM, Calsbeek R (2009) Sexually antagonistic selection, sexual dimorphism and the resolution of intralocus sexual conflict. *American Naturalist* 173: 176–187. <https://doi.org/10.1086/595841>
- Endler JA (1986) *Natural Selection in the Wild*. Princeton University Press, Princeton.
- Fairbairn DJ (1997) Allometry for sexual size dimorphism: Pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology, Evolution & Systematics* 28: 659–687. <https://doi.org/10.1146/annurev.ecolsys.28.1.659>
- Floate KD, Coghlin P (2010) No support for fluctuating asymmetry as a biomarker of chemical residues in livestock dung. *Canadian Entomology* 152: 354–368. <https://doi.org/10.4039/n10-014>
- Foster W (1967) Hormone-mediated nutritional control of sexual behavior in male dung flies. *Science* 158: 1596–1597. <https://doi.org/10.1126/science.158.3808.1596>
- González-Santoyo I, Córdoba-Aguilar A (2012) Phenoloxidase: a key component of the insect immune system. *Entomologia Experimentalis et Applicata* 142: 1–16. <https://doi.org/10.1111/j.1570-7458.2011.01187.x>
- Gotanda K, Correa C, Turcotte MM, Rolshausen G, Hendry AP (2015) Linking macro-trends and micro-rates: re-evaluating micro-evolutionary support for Cope's rule. *Evolution* 69: 1345–1354. <https://doi.org/10.1111/evo.12653>
- Hammer O (1941) Biological and ecological investigations on flies associated with pasturing cattle and their excrement. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 105: 140–393.
- Honek A (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66: 483–492. <https://doi.org/10.2307/3544943>
- Hosken DJ, Blanckenhorn WU, Ward PI (2000) Developmental stability in the yellow dung fly (*Scathophaga stercoraria*): fluctuating asymmetry, heterozygosity and environmental stress. *Journal of Evolutionary Biology* 13: 919–926. <https://doi.org/10.1046/j.1420-9101.2000.00239.x>

- Jann P, Blanckenhorn WU, Ward PI (2000) Temporal and microspatial variation in the intensities of natural and sexual selection in the yellow dung fly *Scathophaga stercoraria*. *Journal of Evolutionary Biology* 13: 927–938. <https://doi.org/10.1046/j.1420-9101.2000.00230.x>
- Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gibert P, Beerli P (2001) The strength of phenotypic selection in natural populations. *American Naturalist* 157: 245–261. <https://doi.org/10.1086/319193>
- Kingsolver JG, Pfennig DW (2004) Individual-level selection as a cause of Cope's rule of phyletic size increase. *Evolution* 58: 1608–1612. <https://doi.org/10.1111/j.0014-3820.2004.tb01740.x>
- Knierim U, Van Dongen S, Forkman B, Tuytens FAM, Špinka M, Campo JL, Weissengruber GE (2007) Fluctuating asymmetry as an animal welfare indicator – A review of methodology and validity. *Physiology & Behaviour* 92: 398–421. <https://doi.org/10.1016/j.physbeh.2007.02.014>
- Kraushaar U, Blanckenhorn WU (2002) Population variation in sexual selection and its effect on body size allometry in two species of flies with contrasting sexual size dimorphism. *Evolution* 56: 307–321. <https://doi.org/10.1111/j.0014-3820.2002.tb01341.x>
- Lande R, Arnold SJ (1983) The measurement of selection on correlated characters. *Evolution* 37: 1210–1226. <https://doi.org/10.1111/j.1558-5646.1983.tb00236.x>
- Liggett AC, Harvey IF, Manning JT (1993) Fluctuating asymmetry in *Scathophaga stercoraria* L.: successful males are more symmetrical. *Animal Behaviour* 45: 1041–1043. <https://doi.org/10.1006/anbe.1993.1126>
- Maitland DP (1994) A parasitic fungus infecting yellow dungflies manipulates host perching behaviour. *Proceedings of the Royal Society London B* 258: 187–193. <https://doi.org/10.1098/rspb.1994.0161>
- McGregor RR, Roitberg BD (2000) Size-selective oviposition by parasitoids and the evolution of life-history timing in hosts: Fixed preferences vs. frequency-dependent host selection. *Oikos* 89: 305–312. <https://doi.org/10.1034/j.1600-0706.2000.890212.x>
- Merilä J, Hendry AP (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evolutionary Applications* 7: 1–14. <https://doi.org/10.1111/eva.12137>
- Merilä J, Sheldon BC, Kruuk LEB (2001) Explaining stasis: microevolutionary studies in natural populations. *Genetica* 112–113: 199–222. <https://doi.org/10.1023/A:1013391806317>
- Møller AP (1993) A fungus infecting domestic flies manipulates sexual behaviour of its host. *Behavioural Ecology & Sociobiology* 33: 403–407. <https://doi.org/10.1007/BF00170255>
- Møller AP, Swaddle JP (1997) *Asymmetry, Developmental Stability and Evolution*. Oxford University Press, Oxford.
- Møller AP, Thornhill R (1997) A meta-analysis of the heritability of developmental stability. *Journal of Evolutionary Biology* 10: 1–16. <https://doi.org/10.1007/s000360050001>
- Mousseau TA, Roff DA (1987) Natural selection and the heritability of fitness components. *Heredity* 59: 181–197. <https://doi.org/10.1038/hdy.1987.113>
- Nielsen C, Hayek AE (2006) Diurnal pattern of death and sporulation in *Entomophaga maimaiga*-infected *Lymantria dispar*. *Entomologia Experimentalis et Applicata* 118: 237–243. <https://doi.org/10.1111/j.1570-7458.2006.00382.x>
- Nunn CL, Lindenfors P, Pursall ER, Rolff J (2009) On sexual dimorphism in immune function. *Philosophical Transactions of the Royal Society London B* 364: 61–69. <https://doi.org/10.1098/rstb.2008.0148>
- Palmer A (2000) Quasi-replication and the contract of error: lessons from sex ratios, heritabilities and fluctuating asymmetry. *Annual Review of Ecology, Evolution & Systematics* 31: 441–480. <https://doi.org/10.1146/annurev.ecolsys.31.1.441>
- Palmer AR, Strobeck C (1986) Fluctuating asymmetry: measurement, analysis, patterns. *Annual Review of Ecology, Evolution & Systematics* 17: 391–421. <https://doi.org/10.1146/annurev.es.17.110186.002135>
- Parker GA (1970) The reproductive behaviour and the nature of sexual selection in *Scathophaga stercoraria* L. (Diptera: Scathophagidae) II. The fertilization rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. *Journal of Animal Ecology* 39: 205–228. <https://doi.org/10.2307/2896>
- Parker GA (1979) Sexual selection and sexual conflict. In: Blum NS, Blum NA (Eds) *Sexual Selection and Reproductive Competition in Insects*. Academic Press, New York, 123–166. <https://doi.org/10.1016/B978-0-12-108750-0.50010-0>
- Preziosi RF, Fairbairn DJ (2000) Lifetime selection on adult body size and components of body size in a waterstrider: opposing selection and maintenance of sexual size dimorphism. *Evolution* 54: 558–566. <https://doi.org/10.1111/j.0014-3820.2000.tb00058.x>
- Polak M [Ed.] (2003) *Developmental instability. Causes and consequences*. Oxford University Press, Oxford.
- Rantala MJ, Roff DA (2005) An analysis of trade-offs in immune function, body size and development time in the Mediterranean field cricket, *Gryllus bimaculatus*. *Functional Ecology* 19: 323–330. <https://doi.org/10.1111/j.1365-2435.2005.00979.x>
- Rantala MJ, Koskimäki J, Taskinen J, Tynkkynen K, Suhonen J (2000) Immunocompetence, developmental stability and wing spot size in the damselfly *Calopteryx splendens* L. *Proceedings of the Royal Society London B* 267: 2453–2457. <https://doi.org/10.1098/rspb.2000.1305>
- Rantala MJ, Ahtiainen JJ, Suhonen J (2004) Fluctuating asymmetry and immune function in a field cricket. *Oikos* 109: 479–484. <https://doi.org/10.1111/j.0030-1299.2004.12776.x>
- Rantala MJ, Roff DA, Rantala LM (2007) Forceps size and immune function in the earwig *Forficula auricularia*. *Biological Journal of the Linnean Society* 90: 509–516. <https://doi.org/10.1111/j.1095-8312.2007.00741.x>
- Reim C, Teuschl Y, Blanckenhorn WU (2006a) Size-dependent effects of larval and adult food availability on reproductive energy allocation in the yellow dung fly. *Functional Ecology* 20: 1012–1021. <https://doi.org/10.1111/j.1365-2435.2006.01173.x>
- Reim C, Teuschl Y, Blanckenhorn WU (2006b) Size-dependent effects of temperature and food stress on energy reserves and starvation resistance in yellow dung flies. *Evolutionary Ecology Research* 8: 1215–1234.
- Rensch B (1950) Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße. *Bonner Zoologische Beiträge* 1: 58–69.
- Roff DA (1992) *The Evolution of Life Histories*. Chapman and Hall, New York.
- Rolff J, Reynolds S (2009) *Insect Infection and Immunity: Evolution, Ecology, and Mechanisms*. Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199551354.001.0001>
- Schäfer MA, Berger D, Rohner PT, Kjærsgaard A, Bauerfeind SS, Guillaume F, Fox CW, Blanckenhorn WU (2018) Geographic clines in wing morphology relate to biogeographic history in New World but not Old World populations of dung flies. *Evolution* 72: 1629–1644. <https://doi.org/10.1111/evo.13517>

- Schilthuizen M, Kellermann V (2014) Contemporary climate change and terrestrial invertebrates: evolutionary versus plastic changes. *Evolutionary Applications* 7: 56–67. <https://doi.org/10.1111/eva.12116>
- Schmid-Hempel P (2005) Evolutionary ecology of insect immune defenses. *Annual Review of Entomology* 50: 529–551. <https://doi.org/10.1146/annurev.ento.50.071803.130420>
- Schwarzenbach GA, Hosken DJ, Ward PI (2005) Sex and immunity in the yellow dung fly *Scatophaga stercoraria*. *Journal of Evolutionary Biology* 18: 455–463. <https://doi.org/10.1111/j.1420-9101.2004.00820.x>
- Schwarzenbach GA, Ward PI (2006) Responses to selection on phenoloxidase activity in yellow dung flies. *Evolution* 60: 1612–1621. <https://doi.org/10.1111/j.0014-3820.2006.tb00506.x>
- Schwarzenbach GA, Ward PI (2007) Phenoloxidase activity and pathogen resistance in the yellow dung fly *Scatophaga stercoraria*. *Journal of Evolutionary Biology* 20: 2192–2199. <https://doi.org/10.1111/j.1420-9101.2007.01430.x>
- Schmidt-Nielsen K (1984) *Scaling. Why is Animal Size so Important?* Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9781139167826>
- Sigurjónsdóttir H, Snorrason SS (1995) Distribution of male yellow dungflies around oviposition sites: the effect of body size. *Ecological Entomology* 20: 84–90. <https://doi.org/10.1111/j.1365-2311.1995.tb00432.x>
- Steenberg T, Jespersen JB, Jensen KMV, Nielsen BO, Humber RA (2001) Entomopathogenic fungi in flies associated with pastured cattle in Denmark. *Journal of Invertebrate Pathology* 77: 186–197. <https://doi.org/10.1006/jipa.2001.5021>
- Steinkraus DC, Kramer JP (1988) *Entomophthora scatophagae*, a fungal pathogen of the yellow dung fly, *Scatophaga stercoraria*. *Mycotaxon* 32: 105–113.
- Stoks R, Geerts AN, de Meester L (2014) Evolutionary and plastic responses of freshwater invertebrates to climate change: realized patterns and future potential. *Evolutionary Applications* 7: 42–55. <https://doi.org/10.1111/eva.12108>
- Swaddle JP (1997) Developmental stability and predation success in an insect predator-prey system. *Behavioral Ecology* 8: 433–436. <https://doi.org/10.1093/beheco/8.4.433>
- Van Dongen S (2006) Fluctuating asymmetry and developmental instability in evolutionary biology: past, present and future. *Journal of Evolutionary Biology* 19: 1727–1743. <https://doi.org/10.1111/j.1420-9101.2006.01175.x>
- Vucic-Pestic O, Rall BC, Kalinkat G, Brose U (2010) Allometric functional response model: Body masses constrain interaction strengths. *Journal of Animal Ecology* 79: 249–256. <https://doi.org/10.1111/j.1365-2656.2009.01622.x>
- Yourth CP, Forbes M, Smith BP (2002) Immune expression in a damselfly is related to time of season, not to fluctuating asymmetry or host size. *Ecological Entomology* 27: 123–128. <https://doi.org/10.1046/j.1365-2311.2002.0376a.x>
- Zuk M, Kolluru GR (1998) Exploitation of sexual signals by predators and parasitoids. *Quarterly Review of Biology* 73: 415–438. <https://doi.org/10.1086/420412>

Supplementary material 1

Table S1

Author: Wolf U. Blanckenhorn

Data type: species data

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/alpento.5.65653.suppl1>

