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Comprehensive thermal performance curves for yellow dung fly life history traits and the temperature-size-rule

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ABSTRACT (239 WORDS)

Ambient temperature strongly determines the behaviour, physiology, and life history of all organisms. The technical assessment of organismal thermal niches in form of now so-called thermal performance curves (TPC) thus has a long tradition in biological research. Nevertheless, several traits do not display the idealized, intuitive dome-shaped TPC, and in practice assessments often do not cover the entire realistic or natural temperature range of an organism. We here illustrate this by presenting comprehensive sex-specific TPCs for the major (juvenile) life history traits of yellow dung flies (*Scathophaga stercoraria*; Diptera: Scathophagidae). This concerns estimation of prominent biogeographic rules, such as the temperature-size-rule (TSR), the common phenomenon in ectothermic organisms that body size decreases as temperature increases. *S. stercoraria* shows an untypical asymptotic TPC of continuous body size increase with decreasing temperature without a peak (optimum), thus following the TSR throughout their entire thermal range (unlike several other insects presented here). Egg-to-adult mortality (our best fitness estimator) also shows no intermediate maximum. Both may relate to this fly entering pupal winter diapause below 12 °C. While development time presents a negative exponential relationship with temperature, development rate and growth rate typify the classic TPC form for this fly. The hitherto largely unexplored close relative *S. suilla* with an even more arctic distribution showed very similar responses, demonstrating large overlap among two ecologically similar, coexisting dung fly species, thus implying limited utility of even complete TPCs for predicting species distribution and coexistence.

1. Introduction

Ambient temperature strongly determines the behaviour, physiology, life history and, ultimately, the distribution of all organisms (Levins, 1968; Hochachka and Somero, 2002; Angilletta, 2009; Diamond, 2018; Fox, 2018). The technical assessment of thermal tolerance in form of now so-called thermal performance curves (TPC) thus has a long tradition in biological research (Janisch, 1925; Prowser, 1935; Levins, 1968; Huey and Stevenson, 1979; Ratte, 1985; Danks, 1987; Huey and Kingsolver, 1989, 1993; Angilletta, 2009; Clusella-Trullas et al., 2011). Historically, TPCs are typically asymmetric, non-linear reaction norms between some aspect of organism performance and temperature (Janisch, 1925; Blanckenhorn, 1999): they usually feature a shallow incline from a critical lower temperature limit T_{min} (beyond which activity ceases) to a performance maximum (or optimum) T_{opt} followed by a steep decline towards a critical upper limit T_{max} (usually entailing death; see Fig. 1 in Huey and Stevenson, 1979; Huey and Kingsolver, 1989, 1993). 'Performance' in this context originally remained unspecified and in practice can refer to various life history or fitness traits, although some authors prefer more ultimate fitness measures as the primary reference of performance (Kozłowski et al., 2004; de Jong and van der Have, 2009; Walczyńska et al., 2016). The curve asymmetry intuitively follows from the nonlinear temperature-dependence of all chemical, enzymatic and metabolic reactions with temperature coefficients $Q_{10}>1$. Such TPC relationships (co-)define any organism's thermal performance breadth or

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fundamental niche (cf. Fig. 1), ultimately serving to separate species or differentiated populations. TPCs may further differ between life stages or the sexes (Chown and Nicolson, 2004; Bowler and Terblanche, 2008; e.g. Blanckenhorn et al., 2014), and for over a century have been assessed for various performance traits and organisms (Janisch 1925; Danks, 1987; Angilletta, 2009).

Nevertheless, several traits do not display the above-described idealized, intuitive shape so that TPCs may look substantially different (Angilletta, 2009; Walczyńska et al., 2016). Moreover, in practice TPCs are often incomplete in that they do not necessarily cover the entire realistic or natural temperature range of an organism (see Fig. 1 for examples). This regularly occurs on the one hand because especially at very low temperatures physiological processes (for instance development or growth rate) are slowed and at one point come to a halt, rendering assessments impractical if not impossible below a critical limit T_0 (which e.g. is ca. 9 °C for the sepsid fly *Sepsis cynipsea* and ca. 12 °C in *Drosophila melanogaster*; Blanckenhorn, 1999; cf. Fig. 1). Estimation of the lower critical limit nonetheless hinges on incorporating very low temperatures (Janisch 1925; Blanckenhorn, 1999). Furthermore, many insects enter winter diapause at low temperatures, which complicates matters (Danks, 1987; Blanckenhorn, 1998; Stålhandske et al., 2017; Khelifa et al., 2019; Zeender et al., 2019). Other studies from the start topically focus merely on one or the other end of the temperature spectrum, e.g. the upper thermal end in the context of climate warming, which at one point necessarily reaches the lethal limit of any organism (e.g. Berger et al., 2014; Khelifa et al., 2019). It should be obvious that description of nonlinear TPCs require at minimum 3 temperatures (however, best 7; de Jong and van der Have, 2009), even if there are many studies that assess merely 2 temperatures (typically for other purposes; cf. Angilletta and Dunham, 2003).

Although in principle TPCs permit determination of the lower (T_0 or T_{min}; Janisch, 1925; Blanckenhorn, 1999) and upper critical temperature limits (T_{max}; e.g. Khelifa et al., 2019) of a species in addition to its performance maximum (T_{opt}, if only by extrapolation; Huey and Kingsolver, 1989, 1993; Angilletta, 2009), other methods have been developed that specifically assess organism tolerance to temperature extremes to empirically assess T_{min} or T_{max} (see Telemeco and Gangloff, 2021 for an extensive discussion). Heat or cold knockdown temperatures evaluate at which point an animal passes out, and heat or chill coma recovery times estimate how long they take to wake up again (if they did not die; e.g. Hoffmann et al., 2002, 2003; Klok et al., 2004; Angilletta, 2009; Esperk et al., 2016; Bauerfeind et al., 2018). Further approaches behaviourally assess the temperature preferences of live animals in various devices offering a temperature gradient (reviewed by Dillon

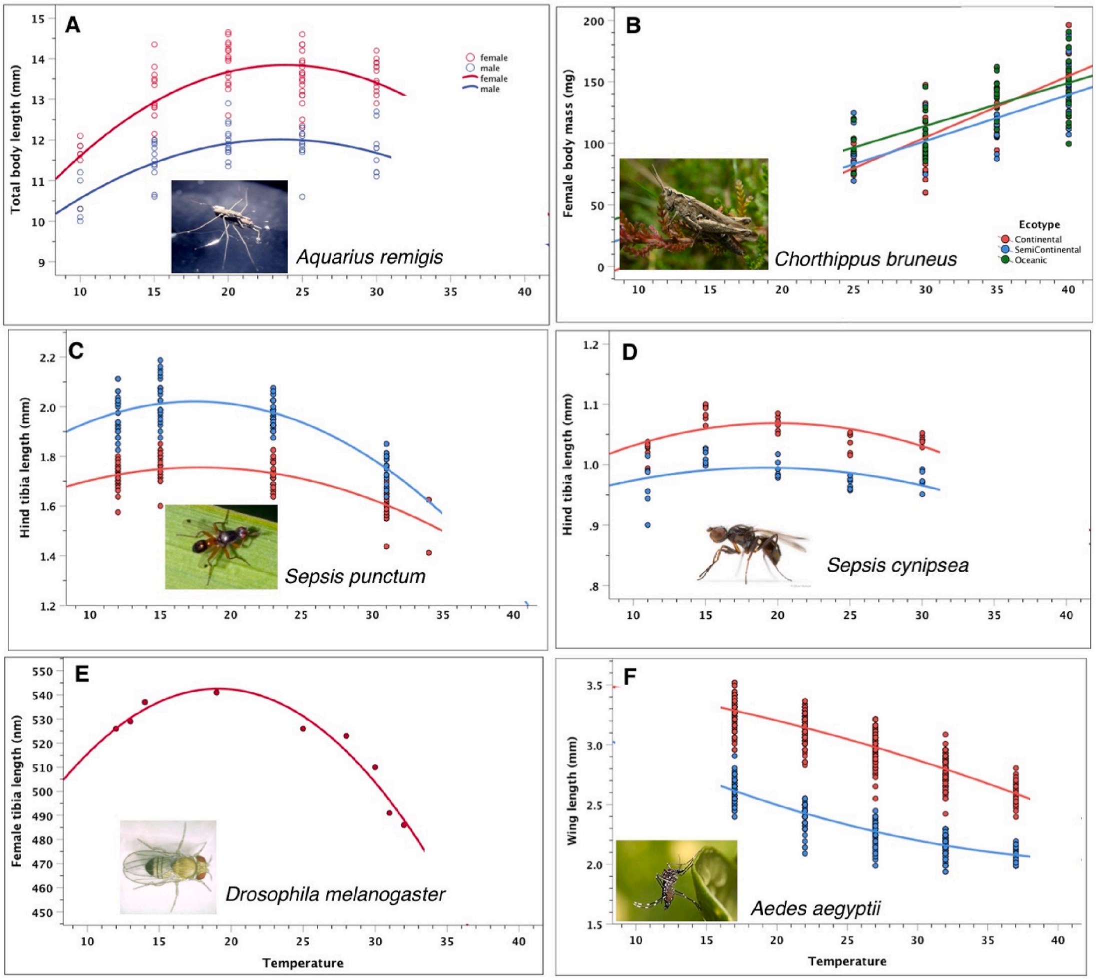

Fig. 1. Body size – temperature relationships (Thermal Performance Curves) for various terrestrial and aquatic insect species to demonstrate the variation typifying nature (sex-specific quadratic or linear (B) fits): (A) water strider *Aquarius remigis* (unpublished data from Blanckenhorn, 1991); (B) grasshopper *Chorthippus brunneus* (data from Walters and Hassall, 2006); the black scavenger flies (C) *Sepsis punctum* (unpublished data from Berger et al., 2014) and (D) *Sepsis cynipsea* (data from Blanckenhorn, 1997); (E) fruit fly *Drosophila melanogaster* (data from David and Clavel, 1967); (F) tropical mosquito *Aedes aegyptii* (W.U. Blanckenhorn, unpublished data). Only *Aedes aegyptii* shows a clean negative temperature-size relationship, although temperatures <17 °C were not assessed. Exclusion of 12 °C for *S. punctum*, 15 °C for *S. cynipsea*, and of temperatures <18 °C for *Drosophila melanogaster* also would have revealed linear negative relationships of body size with temperature following the temperature-size-rule.

et al., 2009). In all these methods, and regardless of the various devices applied, it has become clear that multiple environmental and physiological factors affect the estimates for any given species, population, or even individual (e.g. acclimation; Chown and Gaston, 1999; Huey et al., 1999; Addo-Bediako et al., 2000; Sinclair et al., 2003, 2012; Blanckenhorn and Demont, 2004; Dillon et al., 2009; Santos et al., 2011; Kellermann et al., 2012; Telemeco and Gangloff, 2021)

A prominent example of potentially incomplete TPCs concern investigations of the temperature-size-rule (TSR), the common phenomenon in ectothermic organisms that body size decreases as temperature increases (see Atkinson, 1994, for a compilation of early studies; Ray, 1960; Perrin, 1995; Atkinson and Sibly, 1997; Angilletta and Dunham, 2003; Forster et al., 2012; Hirst et al., 2015; Walczyńska et al., 2016). Fig. 1 illustrates the TPC variation that can be obtained when body size, a prominent performance trait, is plotted against typically constant laboratory rearing temperature. The semi-aquatic water strider *Aquarius remigis* (data from Blanckenhorn, 1991, Fig. 1A) presents the dome-shaped relationship most closely resembling the idealized TPC, whereas body size of the grasshopper *Chorthippus brunneus* keeps increasing with temperature throughout the temperature range tested (i.e. covers only the left part of the TPC before the modal T_{opt}; data from Walters and Hassall, 2006); thus, both these species do NOT follow the TSR. The two black scavenger flies *Sepsis punctum* and *S. cynipsea* (Fig. 1C and D; data from Blanckenhorn, 1997, and unpublished data from Berger et al., 2014; see also Rohner et al., 2019), and data from David and Clavel (1967) for *Drosophila melanogaster* (body size means only; Fig. 1E) present parts left, but mostly right of the performance maximum T_{opt} of the TPC (here occurring at ca. 15 °C for both sepsids and at 18 °C for *Drosophila*. (Compare Prowser's (1935) data for development rate of *D. melanogaster* in Blanckenhorn, 1999, for which the maximum (optimum), by contrast, occurs at 28 °C.) Data for the tropical mosquito *Aedes aegyptii,* with aquatic larvae, shows a decrease in resultant adult body size over the entire temperature range presented (i.e. only the right part of the TPC beyond its maximum, thus typifying the TSR; Fig. 1F); in this case this may well occur because temperatures lower than 15 °C were not tested. So: must a maximum necessarily exist for body size as the focal performance trait? And must it exist in general for any performance trait, or is this only specific to body size? This is important, because the selection and completeness of the temperature range tested (and reported) for any given species will have at least a quantitative effect on the estimate (slope) of the temperature-size-rule used in any meta-analysis, if not a qualitative effect (cf. Atkinson, 1994; Walczyńska et al., 2016).

By combining four separate data sets with overlapping temperature ranges from the same laboratory using similar methods, our main objective was to document sex-specific TPCs for the major yellow dung fly (*Scathophaga stercoraria*; Diptera: Scathophagidae) life history traits as completely as possible (in terms of temperature). *Scathophaga stercoraria* is a prominent widespread fly species that populates cow pastures throughout the northern hemisphere (reviewed in Blanckenhorn, 2009; Simmons et al., 2020). These unusually heat sensitive flies favour cooler climates with a distribution as far north as Alaska, Iceland and Spitzbergen (Sigurjónsdóttir and Snorrason, 1995), while in the southern, Mediterranean parts of their range they mainly occur at higher altitudes (Blanckenhorn, 2009; Schäfer et al., 2018 Fig. 2). One of our data sets included temperatures down to 5 °C, at which these flies typically enter pupal diapause in nature (Blanckenhorn, 1998) but may still be regularly active in the field (pers. obs.). Another data set assessed hot temperatures in half-degree intervals to precisely estimate these flies' critical upper limit supposed to lie around 27 °C (Parker, 1970; Ward and Simmons, 1990; Blanckenhorn et al., 2001, 2014). By encompassing a temperature range as wide as possible, we can evaluate the 'optimal thermal range' necessary for testing the TSR in this typical, very phenotypically plastic terrestrial insect (Blanckenhorn, 2009; Walczyńska et al., 2016). For direct comparison, and to examine the presumed species-specificity of TPCs, we additionally present not quite as encompassing data for the closely related and ecologically similar *Scathophaga suilla* (Gorodkov, 1984; Šifner, 2008; Bernasconi et al., 2001; Ball, 2014). As the prediction and explanation of animal distribution patterns in light of ever changing environments are a major goal of evolutionary ecology (Diamond, 2018; Fox, 2018), we considered GBIF distribution records suggesting that the center of distribution of the rarer *S. suilla* is more arctic than that of *S. stercoraria*, predicting a left-shifted TPC for the former relative to the latter species (https://www.gbif.org/species/1556370 vs. 1556243; Fig. 2).

2. Materials and methods

We combined four separate common garden laboratory data sets of *S. stercoraria* reared at various temperatures with identical methods at different times (temporal blocks; Blanckenhorn et al., 2010). In all cases, the parental flies had been originally collected on a farm in Fehraltorf, Switzerland (N47°23′, E8°44′), and their offspring were subsequently held for 2 to 4 generations in the laboratory using standardized methods (see Blanckenhorn et al., 2010; Schäfer et al., 2018 for more details). In general, full-sib offspring of laboratory-mated females were reared in groups of 5–15 flies in replicate plastic containers with overabundant (>2 g per larva) homogenized and previously frozen cow dung. The resulting traits thus reflect the maximal heritable survival, body size and development rate, largely unconstrained by inter- or intra-specific competition. While our designs often assessed quantitative genetic variation (Blanckenhorn, 1998, 2015; Schäfer et al., 2018), here we mainly treat all flies merely phenotypically (i.e. without reference to family belonging). One common garden rearing was performed at (always constant) 12 °C, 18 °C, 24 °C and 26 °C (Schäfer et al., 2018), another at 5 °C, 10 °C, 15 °C, 20 °C and 25 °C (Blanckenhorn, 1997;

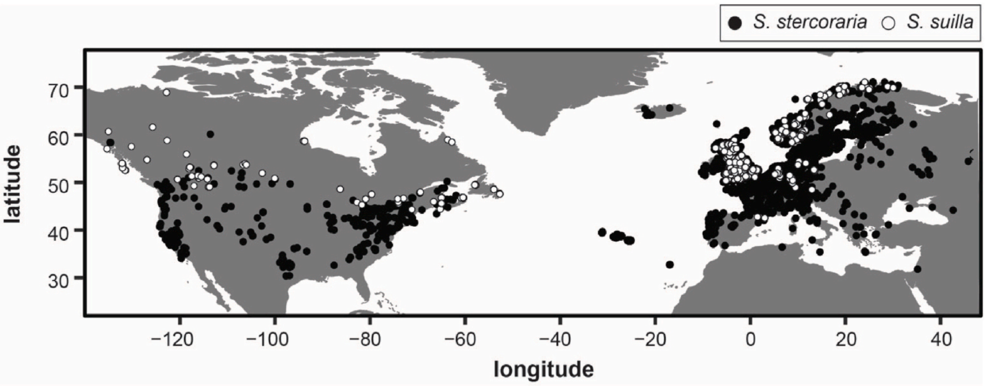

Fig. 2. Distribution of *Scathophaga stercoraria* and *S. suilla* according to GBIF records (data from https://www.gbif.org/species/1556370 vs. 1556243), indicating a more northern range of *S. suilla*.

Blanckenhorn et al., 2010). Two further, hitherto unpublished data sets reared flies at 15 °C and 23 °C, and in half-degree intervals from 24 °C to 26.5 °C (with no flies surviving beyond this temperature).

The data for *S. suilla*, another common but much less numerous fly around cow pastures that is more difficult to keep in the laboratory, were gathered in conjunction with our most recent studies at 12 °C–26 °C (Schäfer et al., 2018), to gauge this fly's upper critical temperature limit relative to that of *S. stercoraria*. *S. suilla* has been synonimised, i.e. confused by some authors with *S. taeniopa* (Ball, 2014). Next to nothing is known about the ecology of *S. suilla*, the range of which overlaps strongly with that of *S. stercoraria*, but is shifted more towards the arctic (Gorodkov, 1984; Šifner, 2008; Bernasconi et al., 2001, Fig. 2).

In all data sets, we scored the number of flies, of both sexes combined, that survived to adulthood (i.e. egg-to-adult survival per container) as our best fitness measure here, sex-specific egg-to-adult development time of all emerged flies, their corresponding development rate as the inverse of development time, and the length of one hind tibia as an index of their adult size. Integral growth rate was crudely calculated as hind tibia length divided by development time (cf. Tammaru et al., 2010; Rohner et al., 2017). Our final data set comprised roughly 2700 individual *S. stercoraria* across the entire temperature range from 5 °C to 26.5 °C, plus ca. 270 *S. suilla* individuals of both sexes combined.

No specific statistical tests were performed for the various trait-temperature relationships presented in Figs. 1–3, as the raw data were here merely described using various parametric or non-parametric fits. Experimental block adjustments proved unnecessary because the variation within temperatures and experiments was visibly large relative to blocking effects, and because the experimental temperatures were largely disjunct. The two *Scathophaga* species were statistically compared within the 12 °C–26 °C data set (Schäfer et al., 2018; cf. above) using linear models with temperature (and sex) as fixed factors and binomial errors for survival (Fig. 4) or normal errors for the other traits (Figs. 5 and 6).

3. Results

3.1. Comprehensive TPCs for yellow dung fly life history traits

For the yellow dung fly *Scathophaga stercoraria,* combination of various overlapping laboratory data sets generated over several years (without any experimental block adjustments) permitted assessment of complete TPCs, covering the full temperature range from 5 °C to 27 °C, for the main (juvenile) life history traits (Fig. 3). Body size (Fig. 3A) increased asymptotically with decreasing temperature towards the viable minimum of 5 °C (approximating the lower estimated temperature limit T_0 of this species: Blanckenhorn, 1998, 1999). That is, the yellow dung fly follows the TSR throughout its entire viable temperature range, thus showing an untypical TPC for this trait (cf. Fig. 1; Atkinson, 1994; Forster et al., 2012; Hirst et al., 2015; Walczyńska et al., 2016). Development time typically shows an exponentially decreasing reaction norm (i.e. TPC; see Fig. 1b in Marshall et al., 2020), while development rate and growth rate display the classic shape (Fig. 3C and D), as they are both rates and should therefore be driven by the temperature dependence of metabolism (Perrin, 1995; Atkinson and Sibly, 1997; de Jong and van der Have, 2009). Note that yellow dung flies are unusual in that males are the larger sex, which is achieved by males undergoing longer development (thus having a slower developmental rate: Fig. 3D) but faster growth than females (Fig. 3C; cf. Blanckenhorn et al., 2007; Esperk et al., 2007; Rohner et al., 2017).

3.2. Comparison of S. stercoraria with S. suilla

As *S. stercoraria, S. suilla* ranges widely across arctic habitats (Gorodkov, 1984; Bernasconi et al., 2001; Šifner, 2008, Fig. 2). Egg-to-adult survival in the laboratory was slightly higher for *S. suilla* across all tested temperatures (12 °C to 26 °C; Fig. 4; $\chi^2 = 9.69$; $P = 0.002$). *S. suilla*, which contrary to *S. stercoraria* is not sexually dimorphic nor

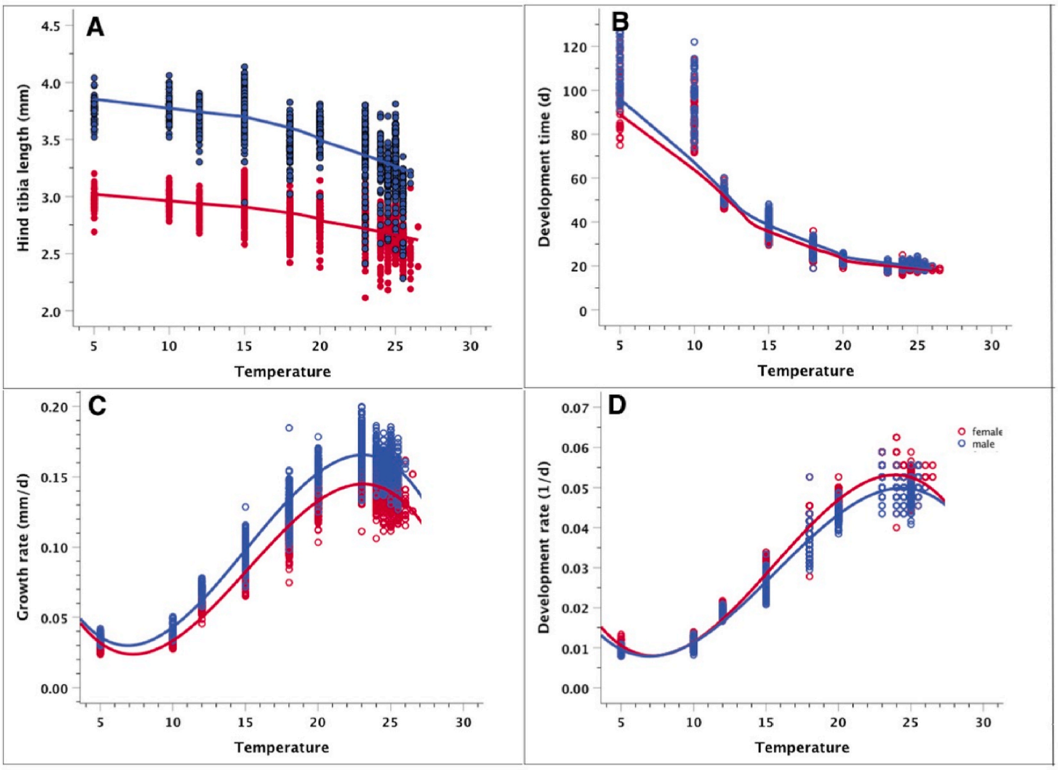

Fig. 3. Comprehensive Thermal Performance Curves (TPC) for female (red) and male (blue) (A) hind tibia length, (B) development time, (C) integral growth rate (calculated as hind tibia length/development time), and (D) development rate (1/development time) of *Scathophaga stercoraria* from 5 °C to 26.5 °C (all flies died beyond 27 °C). Sex-specific non-parametric spline (A,B) or third-order polynomial fits (C,D) are depicted.

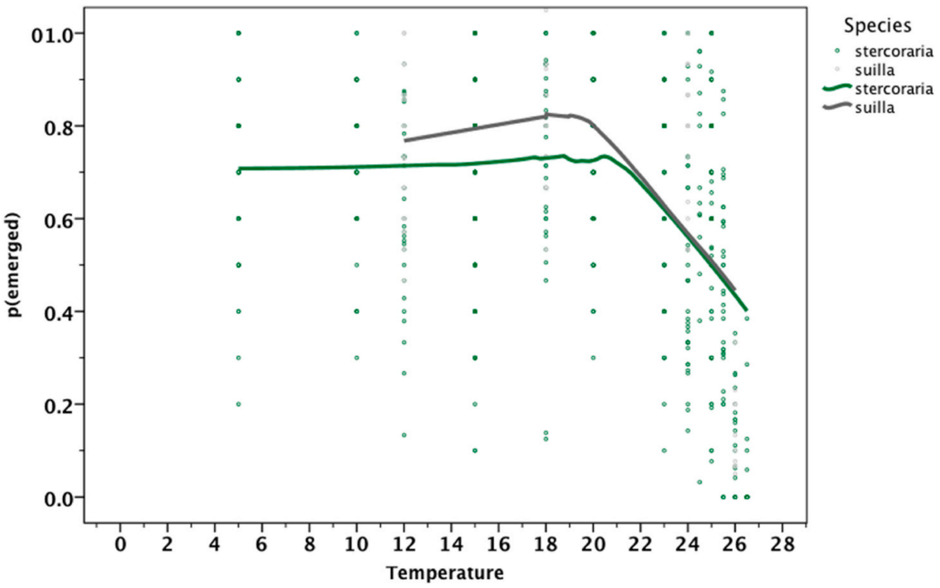

Fig. 4. Temperature-dependent egg-to-adult survival of both sexes for *Scathophaga stercoraria* and *S. suilla* (flies enter winter pupal diapause below 12 °C; non-parametric spline fits). Maximal survivorship (fitness) occurs around 19 °C ('T_{opt}').

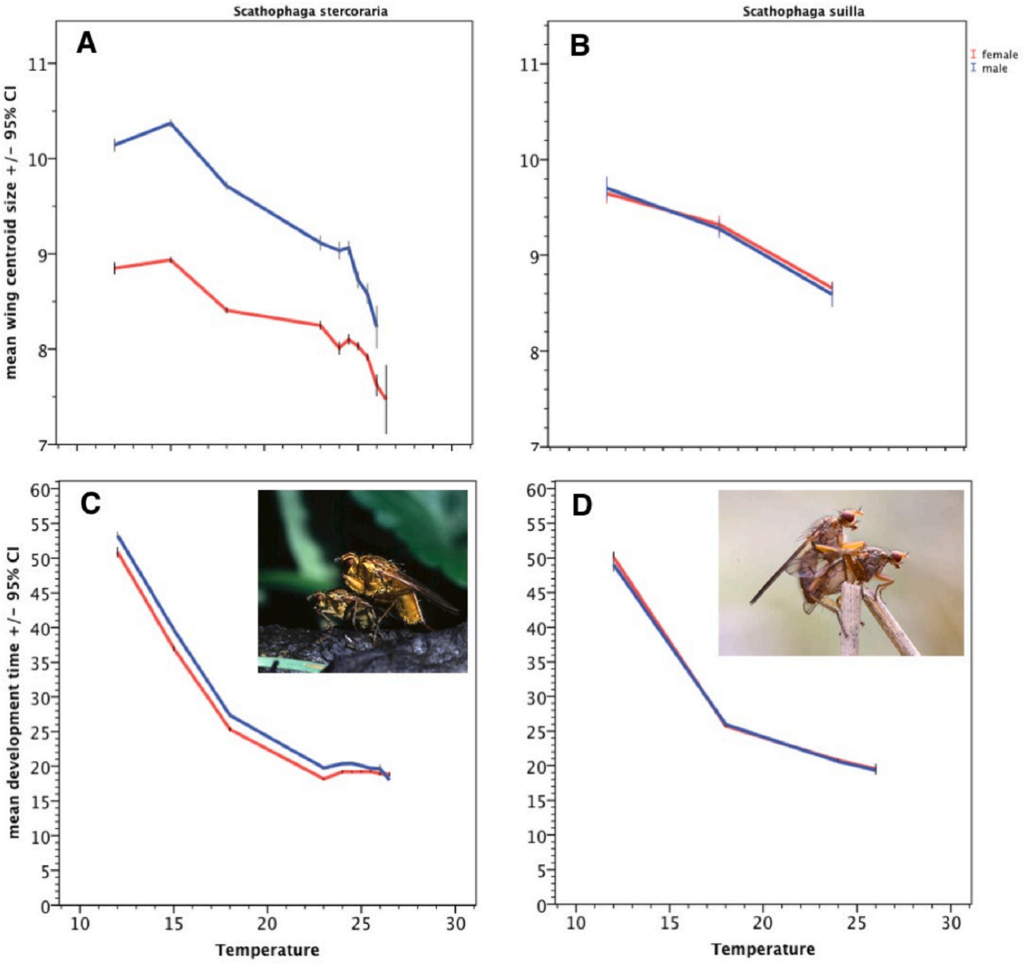

Fig. 5. Comparison of wing centroid size (A,B; top) and development time (C,D; bottom) of male (blue) and female (red) *Scathophaga stercoraria* (left; males are larger than females) and *S. suilla* (right; no sexual dimorphism) from 12 °C to 26 °C (simple line fits).

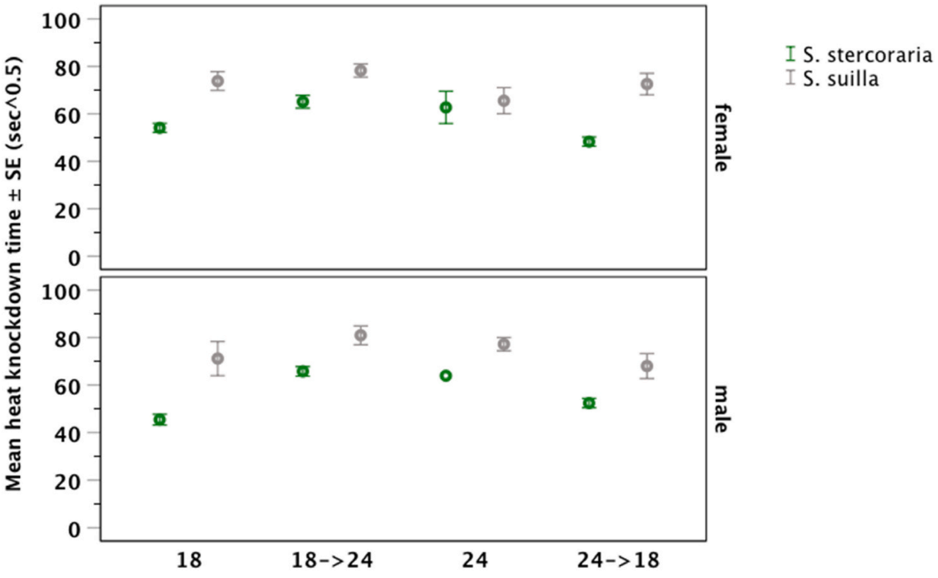

Fig. 6. Heat knockdown time comparison in a 35 °C water bath of female and male *S. stercoraria* (green) and *S. suilla* (grey). Flies were reared in 18 °C or 24 °C, including a switching treatment where temperature was ramped up (18->24) or down (24-<18) over 30 days, thus additionally testing for acclimation effects (irrelevant here).

dichromatic (Fig. 5), is a bit smaller but also develops somewhat faster (species differences are nevertheless significant at $P < 0.01$). *S. suilla* (61.7±6.2 (SE), $N = 16$) lays slightly larger first clutches (fecundity) than *S. stercoraria* (51.4±3.0, $N = 23$; $P = 0.064$) at 18 °C, while only ca. 7% (1 and 2, respectively) of all females produced (typically smaller) clutches at 24 °C (not evaluated statistically). A heat knockdown assessment in a 35 °C water bath indicated greater heat resistance of *S. suilla* than *S. stercoraria* adults of both sexes (Fig. 6; species effect: $F_{1,103} = 9.69$; $P = 0.003$).

4. Discussion

Scathophaga stercoraria shows an untypical asymptotic thermal performance curve (TPC) with a continuous body size increase as temperature decreases (Fig. 3A), i.e. no clear temperature optimum T_{opt}, unlike other ecologically similar or dissimilar insects (compare Fig. 1), thus according with the temperature-size-rule throughout their entire viable thermal niche (Atkinson, 1994; Blanckenhorn, 1999; Forster et al., 2012; Hirst et al., 2015; Walczyńska et al., 2016). Egg-to-adult mortality also shows no marked intermediate maximum (Fig. 4); if anywhere, the survival (fitness) maximum lies around 19 °C (Fig. 4; cf. Walczyńska et al., 2016). These results may relate to this fly regularly entering pupal winter diapause below 12 °C, thus escaping winter mortality (Blanckenhorn, 1998; Demont and Blanckenhorn 2008). While development time hardly ever displays the classic TPC form but rather a negative exponential shape (de Jong and van der Have, 2009; Marshall et al., 2020, Fig. 3B), development and growth rate do also for this fly (Fig. 3C and D). Overall, the hitherto largely unexplored close relative *S. suilla* showed very similar responses (Figs. 4–6), demonstrating almost complete thermal niche overlap of these two coexisting and ecologically similar dung fly species (see also e.g. Khelifa et al., 2019, for similar development rate data of sepsid flies). If anything, the more arctic *S. suilla* (Fig. 2) shows greater heat resistance than *S. stercoraria* (Fig. 6), contrary to expectation. This suggests limited utility of TPCs for predicting species coexistence and distribution (cf. Hoffmann et al., 2003; Clusella-Trullas et al., 2011; Kellermann et al., 2012; Payne et al., 2016).

The classic shape of TPCs described in the Introduction can be intuitively expected for all metabolic rate-limited physiological traits, including developmental and growth rate in Fig. 3C and D (Atkinson and Sibly, 1997; Jarošík et al., 2002; 2004; Angilletta, 2009), but not necessarily for all relevant life history traits that signal organismal performance, as demonstrated here for survival, development time, or body size of the yellow dung fly. Development time typically decreases quasi-exponentially with temperature in most ectothermic organisms because temperature speeds up growth and development (Jarošík et al., 2002, 2004; de Jong and van der Have, 2009; Marshall et al., 2020), whereas its inverse, development rate, indeed follows the classic TPC shape (Fig. 3B,D). The same holds for growth rate, at least when crudely calculated integrally by simply dividing body size by development time, as done here (Fig. 3C). It likely also holds true when growth is more precisely assessed instantaneously based on the typically sigmoid growth trajectories (Teuschl et al., 2007; Berner and Blanckenhorn, 2007; Tammaru and Esperk, 2007; Tammaru et al., 2010), although this must remain speculative because developmental mechanisms involve critical weight threshold mechanisms (Nijhout, 2003; Rohner et al., 2017). By contrast, body size may indeed diminish again towards colder temperatures beyond an optimum (see Fig. 1), which can also happen for survival (cf. Fig. 4). This might occur due to an allocation trade-off, if at (too) cold temperatures limited energy may have to be invested disproportionately in maintenance rather than growth or survival. We suspect that, for the yellow dung fly, a body size and survival decline in the cold was offset by entering pupal winter dormancy, indicated in Fig. 3B by similar diapause development times >80 days at 5 °C and 10 °C. Diapause is a classic strategy to circumvent environmental extremes (here cold temperatures: Danks, 1987; Blanckenhorn, 1998; Demont and Blanckenhorn 2008). Whether this is the only reason for obtaining such unusual reaction norms remains doubtful. The actual shape of the body size (and survival) TPC in practice will depend on the specific life history of the organism in question (see the variation displayed in Fig. 1). Given the typically experimental nature of such data, it is always possible that the temperature range tested is incomplete, especially at the (cold or hot) extremes. As argued above, including very low temperatures is experimentally cumbersome, and including very high temperatures will necessarily at one point lead to death of the tested organisms (as happened here beyond 26 °C), so both extremes may lead to unreliable data (as argued below). Assessing TPCs with fluctuating temperatures, as is definitely more natural and therefore probably superior in terms of predictive power, will however be less predictable or repeatable and may (or not) considerably change the overall shape of the TPC, including the critical limits T_{min}, T_{max} and the performance optimum T_{opt} (e.g. Fischer et al., 2011; Kjærsgaard et al., 2013).

Temperature effects on morphology following the temperature-size rule (smaller when warmer) have long been well documented for yellow dung flies (Blanckenhorn, 1997, 1998) and many other species, as have been a minor but overall not ignorable percentage of species that definitely do not follow the temperature-size rule (Atkinson, 1994), such as the water striders and grasshoppers in Fig. 1A and B. Regardless, incomplete TPCs are commonplace for many species, to the extent that they may bias comparative assessments of the temperature-size-rule (TSR; Atkinson, 1994; Angilletta and Dunham, 2003; Forster et al., 2012; Hirst et al., 2015; Walczyńska et al., 2016). The TSR refers to the part of the body size reaction norm to the right of its optimum (or maximum), where body size decreases (again) as temperatures warm (cf. Fig. 1). In such assessments it can always be that especially low temperatures, but also extreme high temperatures, remain untested (as was the case for e.g. *Aedes aegyptii* in Fig. 1F). This likely quantitatively if not qualitatively affects the TSR slope estimate. For instance, *Sepsis punctum* (and also *S. cynipsea*) in Fig. 1 *would* strictly follow the TSR if 12 °C were excluded, but not otherwise. We note in this context that T_{min} for *S. cynipsea*, and probably also *S. punctum*, is roughly at 9 °C (Blanckenhorn, 1999), i.e. considerably lower (cf. Walczyńska et al., 2016). Furthermore, no *S. punctum* males emerged at 34 °C whereas at least some females survived that temperature, suggesting sex differences in upper critical temperature (Fig. 1C; cf. Hirst et al., 2015). Little can be done beyond requiring researchers to be as thorough and encompassing as possible to avoid incomplete TPC assessments, which ideally should be undertaken based on sensible criteria (see Walczyńska et al., 2016; see below). In practice however, many if not most studies that formed the basis for the meta analyses by Atkinson and colleagues (op. cit.) probably were originally performed for other purposes, thus not providing full information (cf. Angilletta and Dunham, 2003).

How, then, can researchers judge which of the many published TPCs are reasonably complete; and/or which temperatures are actually naturally relevant for any given species so as to be part of any realistic evaluation of, e.g. here, the temperature-size-rule? Walczyńska et al. (2016) suggested a practical criterion for the optimal temperature range of each species to be considered. Their suggestion is that only body size values generated under reasonably ‘optimal’, well canalized thermal conditions should be included, while all suboptimal values (under extreme temperatures) constrain juvenile growth and therefore should be discarded *a priori* (or at least *a posteriori*). Optimal growth conditions should be defined by the TPC of the best fitness measure available for any given species. Working with small aquatic invertebrates (rotifers and oligochaete worms) and protists, Walczyńska et al. (2016) used the population growth rate *r*, an ideal population-based fitness measure that however is not easily obtained for many larger species. According to their logic, all temperatures between $T_{min}(r)$ with $r > 0$ (positive population growth rate) and $T_{opt}(r)$, where *r* is maximal, should generate valid body sizes to be considered for the TSR, whereas all hot temperatures beyond $T_{opt}(r)$, when *r* decreases again (while still potentially being positive) should be discarded (because population growth obviously suffers, hence likely also the resulting adult body sizes; see Fig. 2 in Walczyńska et al., 2016). Although it is not entirely clear why temperatures beyond $T_{opt}(r)$ with positive population growth values should be excluded *a priori*, this reasonable criterion requires an independent TPC for fitness, which is no trivial empirical task for many species (or researchers). For most larger (terrestrial) animals, including insects, temperature-dependent estimates of population growth will not be available, nor assessable, but one could instead, for instance, use survival, which is our best proxy for fitness here.

Our survival Fig. 4 does not present a clear mode (T_{opt}), which may be unusual (as argued above) but could be conjectured to lie around 19 °C. Given the corresponding temperature plasticity (TPC) of body size in Figs. 3A and 5A,B, however, 19 °C seems an arbitrary cut-off for Scathophagids. Walcznyńska et al.'s (2016) own data (in their Fig. 2) also indicate that some warmer temperatures beyond $T_{opt}(r)$ still generate reasonable body sizes in line with the TSR for the worm and the protist (but not the rotifer). As empirical TPCs for fitness will be hard to come by for many larger organisms, it appears from our results that the TPC of growth and/or development rate (Fig. 3C and D) may actually provide a more practical, encompassing criterion for temperature inclusion based on the logic of Walczyńska et al. (2016): accepting all temperatures that generate positive growth and development between T_{min} (ca. 7 °C in Fig. 3C and D) and T_{opt} (ca. 24 °C) maximises the range of useable body sizes in Fig. 3A to estimate the TSR in yellow dung flies. T_{opt} for growth and development rate typically lies considerably to the right (i.e. towards warmer temperatures) of that for body size (see Blanckenhorn, 1991, for data on water striders, and Blanckenhorn, 1999, for data on *Scathophaga, Sepsis,* and *Drosophila*; cf. Fig. 1). Any growth or development at hot temperatures beyond T_{opt}(growth rate) definitely can be judged as indicating suboptimal conditions (and consequently body sizes). Using growth and development as the basis for defining the optimally canalized body size range of a given species directly acknowledges the underlying physiological mechanisms (Nijhout, 2003; de Jong and van der Have, 2009; Rohner et al., 2017). Regardless of the trait used, any such method or criterion hinges on relevant, best independent TPC data, either for some encompassing fitness measure or for growth/development rate, being available in the first place, not merely body size data generated at multiple arbitrary temperatures, as minimally required for any meta-analyses as those by Atkinson (1994); Forster et al. (2012) or Hirst et al. (2015). Otherwise the logic of an *a priori* inclusion criterion, and the data, would be somewhat circular, because development, growth rate and body size are naturally connected (Blanckenhorn, 1999; de Jong and van der Have, 2009). In addition, the temperature range employed in any such experimental assessments must consider the natural situation of the species in question: besides the problem of (artificial) constant vs. (more natural) variable temperatures mentioned above, the temperature range encountered in a species' or population's natural habitat should guide the choice of temperatures applied in any laboratory rearing. After all, at least terrestrial animals can avoid extreme temperatures in the field by microhabitat choice, which is not possible for plants and many aquatic organisms. For example, the tropical mosquito *Aedes aegyptii* (Fig. 1F) may well hardly ever face temperatures <17 °C in nature, hence there might be no point in confronting this species with lower temperatures in the lab, only to find that they cannot cope with them and produce crippled (or no) adults (cf. Verhulst et al., 2020). Again however, any such criteria can only be set and experienced after the fact of having reared the species in the laboratory to begin with, i.e. post-hoc.

The inclusion of *S. suilla* as comparison here was haphazard from an experimental perspective, as we by chance had this species in the lab when we conducted one of our major *S. stercoraria* rearing experiments (Schäfer et al., 2018). This also explains why we did not assess the full temperature range for this species. Any other congener would have been equally useful for comparison (Bernasconi et al., 2001; Ball, 2014). *S. suilla* is closely related and very similar to the yellow dung fly morphologically and ecologically, and the species occurs in the same habitat, although not throughout the season, as *S. stercoraria* numerically dominates many cattle pastures in the northern hemisphere (Blanckenhorn et al., 2010). Other than *S. stercoraria,* related scathophagids proved difficult to maintain in our laboratory (on cow dung) over the years, for unclear reasons. Overall, *S. suilla's* distribution range is even more arctic based on GBIF observation records in Fig. 2, suggesting even greater heat sensitivity than *S. stercoraria.* The main objective guiding our very limited species comparison here was to investigate whether coexisting related species are differentiated thermally, i.e. visibly in their TPC, as ecological niche theory would predict (cf. Payne et al., 2016, for salmonid fish). Our comparison did not support this based on thermal life history performance (Figs. 4 and 5); if anything, the heat knockdown data indicated greater heat resistance of the more arctic *S. suilla* (Fig. 6). It may of course be that *S. suilla* occupies other microhabitats than *S. stercoraria* in the same landscape, thus on average encountering different temperatures. It could also be that *S. suilla* is competitively inferior to the rather aggressive *S. stercoraria* (Simmons et al., 2020), which could lead to a shift in their distribution further northward into enemy-free space. Khelifa et al.'s (2019) study also revealed merely minor differentiation in developmental rates along the thermal gradient of five closely related, coexisting sepsid fly species. Thus, large fundamental niche (i.e. TPC) overlap does not necessarily imply no differences in optimal temperature or critical limits, ultimately co-defining species distributions (Payne et al., 2016; Blanckenhorn et al., 2014; Khelifa et al., 2019); it merely means that thermal performance may be somewhat phylogenetically constrained (Kellermann et al., 2012), which may be compensated by differential microhabitat choice of different species. Therefore, in the end TPCs might still serve to some extent for distinguishing species and populations after all.

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