Nutrition- and sex-dependent utilization of body resources in relation to reproduction in a scorpionfly

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Reproduction often comes at a cost of a reduction in body functions. In order to enhance their reproductive output, some insect species degenerate their thoracic muscles, typically resulting in reduced flight ability. From a life-history trade-off perspective, we expect the importance of body resource utilization to be amplified both with increased reproductive expenditure and with increased resource limitation. In this study, we measured age-related changes in thorax weight, as a measure of flight muscle size, during a major part of the adult lifespan in males and females of the scorpionfly *Panorpa vulgaris*. The aim of the study was twofold: first to investigate whether scorpionflies have the potential to degenerate their flight muscles; second, and more importantly, to determine whether the magnitude of flight muscle degeneration is a plastic response in relation to resource availability, and if it differs between the sexes. The results clearly demonstrate that food availability does influence investment in flight muscle development. The build-up of the thoracic muscles was strongly influenced by nutrient availability. Furthermore, the age-related decrease in thorax weight was significantly different for males and females. Only females showed a strong age-dependent decrease in thorax weight, indicative of muscle degeneration, yet no difference between food treatments was detected. For males, there was no significant directional change in thorax weight. Nevertheless, with increasing age, the difference in thorax weight between food treatments increased significantly. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **102**, 199–207.

ADDITIONAL KEYWORDS: flight muscles – insect flight – life history – nuptial gifts – oogenesis-flight syndrome – *Panorpa*.

INTRODUCTION

Reproduction is associated with considerable costs that animals have to cope with (Harshman & Zera, 2007). Following the search for mates and courtship costs, individuals will eventually mate and produce offspring, which bring about costs as a result of gamete production and possibly also parental care (Clutton-Brock, 1991; Andersson, 1994). During their lifetime individuals will have to trade off these costs against investment in somatic functions such as growth, metabolism, and maintenance (Stearns, 1992; Kirkwood & Austad, 2000). The resulting pattern of resource allocation characterizes typical life-history strategies. The level of reproductive investment and how this is partitioned to different components of reproduction and consecutive reproductive bouts can thus differ widely between different organisms (Roff, 1992; Stearns, 1992), and typically also differs between the sexes (Zuk & Stoehr, 2002; Wedell *et al.*, 2006; BondurianKsy *et al.*, 2008; Zajitschek *et al.*, 2009).

To cover the required energetic costs of reproduction, some species have evolved mechanisms to reallocate somatic resources into reproduction, such as resources from the immune system (Zuk & Stoehr, 2002), the nervous system (Julian & Gronenberg, 2002), and the skeletomuscular system (Zera & Denno, 1997). The flight muscles of insects are energetically expensive to build and maintain, and in many species they are variable in their size and function during an individual's life (Marden, 2000). A common phenomenon is a flight muscle histolysis resulting in severely reduced or even a complete loss

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of flight ability. Besides studies on the physiological mechanisms of flight muscle breakdown (e.g. Nair & Prabhu, 1985; Davis, Jones & Farmer, 1989; Tanaka, 1994; Socha & Sula, 2006; Oliver, Albury & Mousseau, 2007), there are a number of studies concerned with its ultimate function showing that in some species individuals can reallocate resources from their flight muscles to increase their reproductive potential, and through this achieve higher fecundity (e.g. Kaitala, 1988; Kaitala & Hulden, 1990; Tanaka, 1993; Tanaka & Suzuki, 1998; Stjernholm & Karlsson, 2000; Stjernholm, Karlsson & Boggs, 2005). The majority of studies focus on the trade-off between flight capability and reproduction in females, often referred to as the oogenesis-flight syndrome (e.g. Johnson, 1969; Edwards, 1970; Tanaka, 1993, 1994; Zera & Denno, 1997; Tanaka & Suzuki, 1998; Marden, 2000; Lorenz, 2007). Male reproduction is mostly not regarded in these studies, although a similar trade-off is likely to exist in males as well (Marden, 2000), for instance in mating systems that include some form of nuptial feeding (Vahed, 1998), where male reproductive success is highly resource dependent (Jia, Jiang & Sakaluk, 2000; Engqvist & Sauer, 2001; Engels & Sauer, 2006; Immonen *et al.*, 2009). Studies that show good evidence of a trade-off between flight ability and male reproductive investment have been performed mainly on wing dimorphic species (Fujisaki, 1992; Crnokrak & Roff, 1995; Sakaluk, 1997; Guerra & Pollack, 2007). However, there are a few studies on butterflies demonstrating that males might also be able to histolyse their flight muscles (Stjernholm & Karlsson, 2000; Norberg & Leimar, 2002), and that these resources can be used to increase their reproductive effort (Stjernholm *et al.*, 2005; Stjernholm & Karlsson, 2006). *Panorpa* scorpionflies (Insecta: Mecoptera) show several characteristics in their mating systems (see below) that make them particularly suitable for investigating resource reallocation, not only in females but also in males. Therefore, this species provides a good opportunity to increase the so far small number of studies on energy reallocation and male reproductive success, and to investigate sex differences in reproductive resource reallocation.

To obtain matings and increase copulation duration, male *Panorpa vulgaris* offer females nuptial gifts, usually several protein-rich salivary secretions, during copulation (Sauer *et al.*, 1998). Saliva is produced and stored inside the males' salivary glands (Grell, 1938; Sauer *et al.*, 1998). Sperm is transferred continuously during copulation so that long copulations lead to high numbers of transferred sperm and high fertilization success (Sauer *et al.*, 1999). Saliva production has been shown to be highly resource dependent in terms of requiring more or less perma-

nent nutritional supply, at least to replenish saliva once it is depleted (Engels & Sauer, 2006). Surprisingly, in a previous study, starving male *P. vulgaris* showed a significant decrease in body mass, whereas their salivary glands were still growing (Engels & Sauer, 2008). Moreover, with increasing age males and females seem to suffer a reduction in flight ability (L. Engqvist, pers. observ.), and show an ongoing degeneration of the flight muscle when ageing (Collatz & Collatz, 1981). Based on these findings we conducted an experiment testing whether male and female *P. vulgaris* are able to histolyse their flight muscles in order to use these resources for reproduction, i.e. for saliva production in males and for egg production in females. To confirm our hypothesis we would expect to find an age-related decrease in thorax mass (as an estimate for flight muscle mass).

However, a loss of flight ability is presumably costly in terms of a reduced ability to search for food and mates, as well as in predator avoidance (Marden & Chai, 1991; Marden, 2000). Allocation processes are also associated with costs resulting from energy waste, as transformations are never 100% effective (Boggs, 2009). We therefore expected muscle histolysis to be more pronounced with lower food quality (Boggs, 2009). To test this assumption, experiments were performed with two different food regimes. The use of thoracic resources is also expected to relate to reproductive expenditure (Stjernholm & Karlsson, 2006). As females and males usually differ in reproductive investment (Trivers, 1972; Clutton-Brock, 1991), we also expect them to differ in the use of body resources. Hitherto, the only data of sex differences in flight muscle degeneration patterns come from studies on butterflies, which have generally shown that muscle breakdown is more pronounced in females (Karlsson, 1994; Stjernholm & Karlsson, 2000; Norberg & Leimar, 2002; Stjernholm *et al.*, 2005). A further aim of this study is therefore to increase our limited knowledge on sex differences in the use of body resources for reproduction, and test the hypothesis that female *P. vulgaris*, which typically invest more in reproduction than males (Engqvist & Sauer, 2001; Engqvist, 2007b), also show a more distinct age-related decline in thoracic mass.

MATERIAL AND METHODS
BREEDING

We used F_1 offspring of the second annual generation of *P. vulgaris* of 2005. Animals of the parental generation were collected from a field population near Freiburg im Breisgau, Germany, and were transferred to a laboratory in Bonn for breeding. They were kept in male–female pairs in plastic boxes ($10 \times 10 \times 7$ cm)

Table 1. Sample sizes of the different treatment groups for males and females

Age (days)	0	6		12		18		24	
Food regime	/	LF	HF	LF	HF	LF	HF	LF	HF
Males	15	15	15	14	15	8	15	5	13
Females	15	14	15	10	15	1	11	3	13

HF, high food availability; LF, low food availability.

containing moist tissue paper, food ad libitum, and a small Petri dish filled with moist peat for oviposition. F_1 larvae were reared under a 12-h light/12-h dark cycle at 18 °C on moist tissue paper with ad libitum food consisting of small cut pieces of last-instar mealworm (*Tenebrio molitor*) at a maximum density of 20 larvae per Petri dish (12 cm in diameter). Third-instar larvae were transferred into soil-filled, open-bottomed plastic cylinders (40 cm in diameter) placed outdoors in the ground. Here they entered diapause, before emerging in April–May 2006.

EXPERIMENTAL TREATMENT AND SAMPLE SIZES

Emerging males and females were each assigned to one of two food regimes. They all received food directly after emergence and every sixth day from then on. Food-deprived individuals were provided with one segment piece of last-instar *T. molitor* per feeding event (low food, LF); well-fed individuals received two pieces (high food, HF). These different food levels are distinctively different, signified also by the difference in starvation rate (see Table 1). A fraction of animals in each group (LF males, HF males, LF females, and HF females) was killed and dissected on days 6, 12, 18, and 24 after emergence. All experimental groups were scheduled to consist of 15 individuals. However, we had some losses as a result of starvation in some of the groups. Actual sample sizes for the different treatments are listed in Table 1.

DISSECTION OF ANIMALS AND MEASURED PARAMETERS

The salivary glands of males were dissected and dried using standard protocols (see Engqvist & Sauer, 2001; Engels & Sauer, 2006). After drying they were weighed with a Mettler Toledo precision balance (model XS 205 Dual Range). To measure female reproductive potential, females were anesthetized using CO_2 and then killed in 70% ethanol. Their abdomen was opened laterally with small dissection scissors and the number of fully developed eggs inside was counted.

Thoraces of males and females were cut off from the rest of the body, and remaining parts of the digestive tract were removed. They were then dried until they were of constant weight, and weighed as an estimate for flight muscle mass (Mettler Toledo precision balance, model: XS 205 Dual Range).

STATISTICAL ANALYSES

Linear models were used to analyse changes in thorax weight with increasing age. Throughout the analyses adult hatch weight was used as a covariate. Additionally, sex and food regime were entered as categorical variables. Thus, in these analyses, a significant age × food regime interaction or age × sex interaction, for instance, would indicate different age-related changes in thorax weight for the different food regimes or sexes. All analyses were performed in R 2.10.1 (R Development Core Team, 2009). Initially, all interactions were included in a full model. However, non-significant higher order interactions were stepwise excluded until the final model only contained the main effects and significant interactions (cf. Engqvist, 2005).

RESULTS

THORAX WEIGHT

We first analysed changes in thorax weight from the age of 6 days onwards for both sexes together. After controlling for hatch weight ($F_{1,176} = 96.8$, $P < 0.0001$) and food regime ($F_{1,176} = 87.3$, $P < 0.0001$), we found a significant age × sex interaction ($F_{1,176} = 7.17$, $P = 0.008$), indicating different age-related changes in thorax weight for males and females. The decline in thorax weight with increasing age was thus significantly stronger for females (Fig. 1). Subsequently, we analysed the changes in thorax weight for both sexes separately.

For males there was a significant age × food regime interaction ($F_{1,95} = 4.35$, $P = 0.04$) on thorax weight after controlling for the effect of hatch weight ($F_{1,95} = 103.9$, $P < 0.0001$). As predicted, the age-related decrease in thorax weight was different in the different food regimes, and was stronger for males in the LF treatment (Fig. 1A). Nevertheless, neither the decrease in thorax weight for males in the LF treatment nor the thorax weight increase for males in the
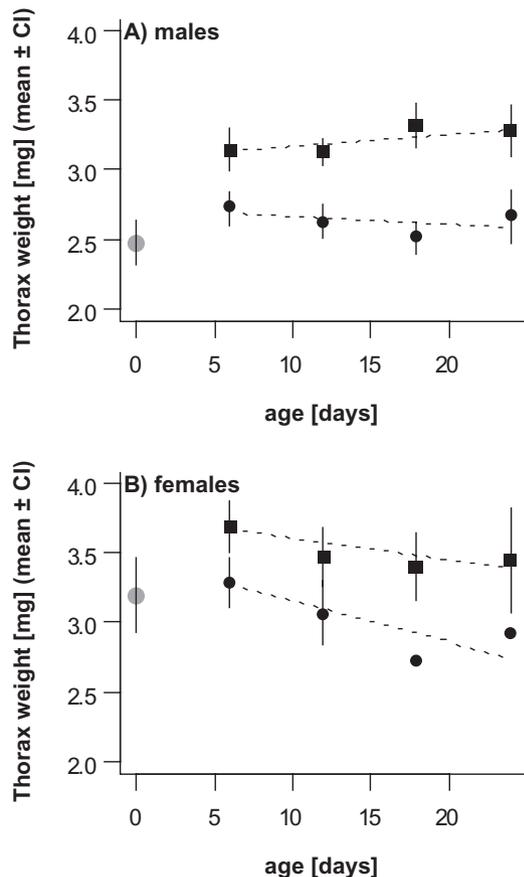
Figure 1. The effect of food regime and age on the thorax weight of (A) males and (B) females. Adjusted means are shown controlling for the strong effect of hatch weight. Values are thus given for individuals with an average hatch weight (■, high food treatment; ●, low food treatment; ●, animals that were dissected directly after hatching; CI, confidence interval).

HF treatment was statistically significant (LF, -8.00 ± 5.85 µg day^{-1}, $F_{1,39} = 1.87$, $P = 0.18$; HF, 10.1 ± 5.92 µg day^{-1}, $F_{1,55} = 2.96$, $P = 0.091$). Adult food regime also had an overall effect on thorax weight. At 6 days of age, the difference in thorax weight between HF and LF males was already significant (mean ± SE difference: 0.409 ± 0.103 mg, $F_{1,27} = 15.8$, $P = 0.0004$), and this difference increased later on (see above; Fig. 1). During the first 6 days following adult hatch, there was a significant increase in thorax weight for males in both treatments (HF, 0.668 ± 0.095 mg, $F_{1,27} = 48.9$, $P < 0.0001$; LF, 0.262 ± 0.083 mg, $F_{1,27} = 10.1$, $P = 0.004$; Fig. 1).

For females, we could not verify a significant age × food regime interaction ($F_{1,76} = 0.26$, $P = 0.61$). Instead, the age-related decrease in thorax weight was homogenous across both food regimes, and was statistically significant (-15.8 ± 7.18 µg day^{-1},

$F_{1,78} = 4.84$, $P = 0.03$; Fig. 1B). Additionally, there was a significant overall effect of food regime on thorax weight: from day 6 onwards, the thorax weight of females in the HF treatment was significantly larger than for females in the LF treatment (mean ± SE difference: 0.453 ± 0.102 $F_{1,78} = 19.8$, $P < 0.0001$).

In contrast to males, thorax weight increased significantly during the first 6 days post-hatch only for females in the HF treatment (0.458 ± 0.110 mg, $F_{1,27} = 17.3$, $P = 0.0002$; Fig. 1), whereas the thorax for females in the LF treatment remained relatively constant during the first 6 days (0.138 ± 0.127 mg, $F_{1,26} = 1.18$, $P = 0.29$; Fig. 1).

SALIVARY GLAND

We found a significant age × food regime interaction on salivary gland size ($F_{1,95} = 34.3$, $P = 0.0001$). Hence the age-related increase of the salivary gland is food regime dependent, and is stronger in the HF treatment than in the LF treatment (LF, 121 ± 7.2 µg day^{-1}, $F_{1,38} = 284.8$, $P < 0.0001$; HF, 231 ± 13.7 µg day^{-1}, $F_{1,55} = 282.8$, $P < 0.0001$; Fig. 2A). For males in the HF treatment, hatch weight had no significant influence on salivary gland development ($F_{1,55} = 1.12$, $P = 0.29$), yet hatch weight affected salivary gland development for males in the LF treatment, as demonstrated by a significant age × hatch weight interaction on salivary gland size ($F_{1,39} = 5.75$, $P = 0.02$). The nature of this interaction is that the increase of salivary gland weight with age is stronger for males with a larger hatch weight (Fig. 3A).

EGG NUMBER

In analogy to the results for males, we found a significant age × food regime interaction on egg number ($F_{1,78} = 10.0$, $P = 0.002$). The age-related increase in egg number is thus food regime dependent, and is stronger in the HF treatment than in the LF treatment (LF, 0.384 ± 0.175 eggs day^{-1}, $F_{1,24} = 4.83$, $P = 0.04$; HF, 2.67 ± 0.37 eggs day^{-1}, $F_{1,51} = 52.5$, $P < 0.0001$; Fig. 2B). For females in the HF treatment, the weight at adult hatch had no significant influence on subsequent egg production ($F_{1,51} = 0.58$, $P = 0.56$). Similar to males, there was a significant age × hatch weight interaction on egg number for females in the LF treatment only ($F_{1,24} = 18.9$, $P = 0.0002$). The shape of this interaction signifies that when adult food availability is scarce, ovarian development is influenced by female hatch weight (Fig. 3B).

DISCUSSION

Our results demonstrate an age-dependent change in thorax weight in males and females of the scorpionfly
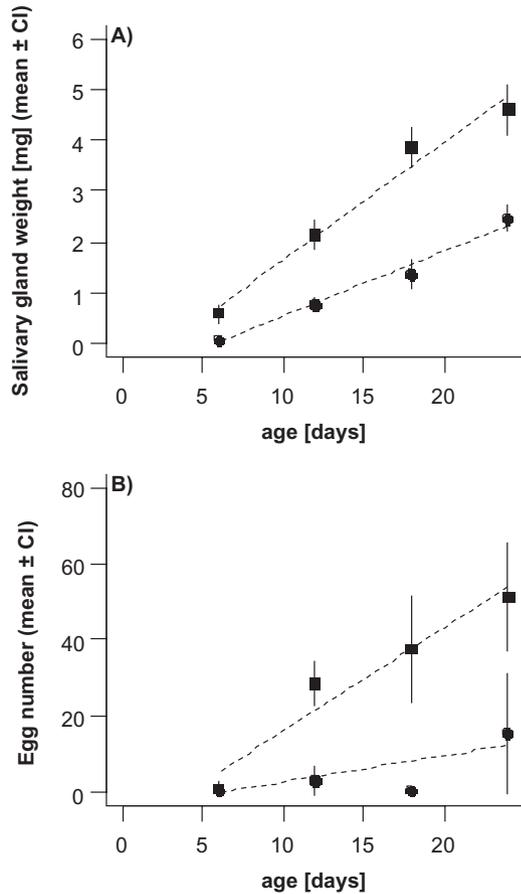
Figure 2. The effect of food regime and age on (A) the salivary gland weight of males and (B) the egg number of females. As in Figure 1, adjusted means are shown controlling for the effect of hatch weight. Values are given for individuals with an average hatch weight (■, high food treatment; ●, low food treatment; CI, confidence interval).

P. vulgaris. Most importantly, females show a considerable decrease in thorax weight in concert with intense egg production (Fig. 1B). This indicates that individuals seem to be able to histolyse flight muscles, making energy resources available that they need for the increase in reproductive output. Collatz & Collatz (1981) found evidence of muscle degeneration in ageing *P. vulgaris*. Thus this study reinforces their results, but also shows that the degeneration of thoracic muscles already begins a few days after adult emergence. The ability to histolyse flight muscles and reallocate these resources into reproduction seems common across insect orders, and has been referred to as the oogenesis-flight syndrome (Johnson, 1969; Zera & Denno, 1997; Marden, 2000). However, most commonly flight muscle histolysis is associated with a change in dispersal and migratory ability (i.e. Heteroptera and Orthoptera: Johnson, 1969; Edwards, 1970; Kaitala & Hulden, 1990; Zera & Denno, 1997;
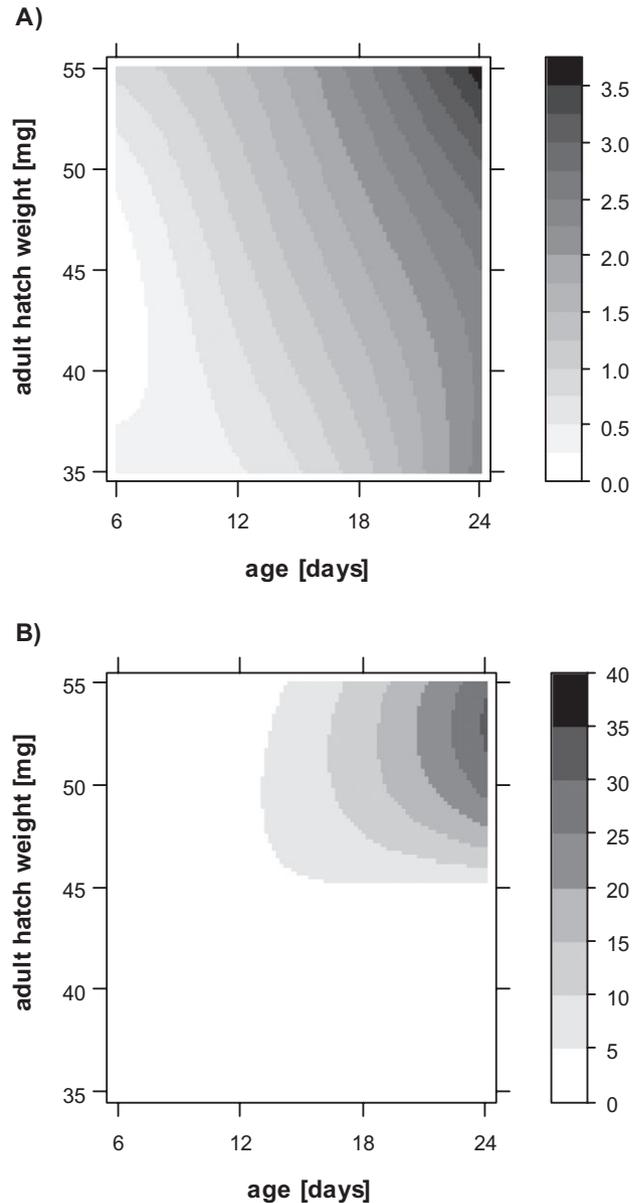
Figure 3. Illustration of the effect of adult hatch weight on (A) salivary gland and (B) ovarian development for individuals reared under severe adult food limitation. Shown are the predicted values from a model incorporating quadratic terms of hatch weight and age (males, $r^2 = 91.9$ %; females, $r^2 = 78.2$ %). The colour key to the right provides the predicted values for salivary gland size (mg) and egg number, respectively. For males the hatch weight ranged from 34.1 to 51.1 mg (mean: 41.4 mg), and in females from 30.3 to 54.2 mg (mean: 44.7 mg).

Marden, 2000; Lorenz, 2007), or with a food quality change from a nutrient-rich larval diet to a poorer and typically nitrogenous-deficient adult diet (i.e. Lepidoptera: Karlsson, 1994; Stjernholm & Karlsson, 2000; Stjernholm *et al.*, 2005). Scorpionflies are an

exception, because they are non-stationary foragers and hence are dependent on flight. Furthermore, throughout their life they are scavengers, and thus have access to protein-rich food resources. Then again, in comparison with other studies, the magnitude of the decline in thorax weight is relatively small, and is evident only in females (Fig. 1). This fits rather well within a life-history framework expecting flight muscle degeneration to be associated with lower food quality (Boggs, 2009). For instance, in butterflies the histolysis of flight muscles has been shown to be more pronounced in species where adults feed on a poor-quality nectar diet than in species feeding on a more rich pollen diet (Karlsson, 1994). Also the observed stronger age-dependent decline in the thorax weight of females might be expected from existing life-history allocation trade-offs, as female scorpionflies will have a greater expenditure of resources in eggs than males will have in salivary glands (Engqvist & Sauer, 2001; Engqvist, 2007b), similar to the pattern that has been found in butterflies (Karlsson, 1994; Stjernholm & Karlsson, 2000; Norberg & Leimar, 2002). Another explanation for the observed sex differences is different benefits of flight ability. Decreased mobility will affect both sexes to some extent. Both males and females are highly dependent on their foraging success to gain resources for ovarian and salivary gland development (Fig. 2, Bockwinkel & Sauer, 1994; Sauer, Vermeulen & Aumann, 2003; Engels & Sauer, 2006), and males and females continue to forage throughout their lives. The reproductive lifespan in the wild is approximately of the same magnitude as the length of the experiment presented here (20–35 days). Thus, the observed effects of age, sex, and nutrition on thorax weight seen here is likely to be of importance for an individual's ability to search for food. However, it is at least possible that males depend more on flight than females in order, for instance, to find mating partners, and therefore the cost of flight muscle degeneration would be higher in males.

For individuals reared with less benign food conditions, we predicted the decrease in flight muscle weight to be more distinct. The rationale for this prediction is that individuals with low nutrient supply might have a stronger need to reallocate somatic resources to cover the immediate costs of reproduction (Zera & Harshman, 2001; Zuk & Stoehr, 2002; Boggs, 2009). We found mixed support for this prediction. First, there was no evidence of differences in the age-dependent decline of thorax weight in females (Fig. 1B). Yet for males we found different patterns of age-related changes in thorax weight consistent with our predictions: the difference in thorax weight between HF and LF males increased with age (Fig. 1A). However, we found weak support for any

decline in thorax weight in males. Thus, we cannot say for sure that the histolysis of flight muscles is more pronounced under food limitation. The lack of a clear effect of food treatment on flight muscle degeneration is most likely the result of a much more prominent effect, namely a food-dependent increase in thorax weight during the first days of post-eclosion (Fig. 1). Thus, depending on food availability, we observe differential allocation of resources for the building up of thoracic muscles, but they are less differentially histolysed. A similar build-up of flight muscles early in adult life and a later breakdown accompanied by ovary development and reproduction has also been observed in other insects (Marden, 1989, 2000; Lorenz, 2007; Socha & Sula, 2008). Our interpretation of these results is that relatively large flight muscles are initially beneficial, yet seem costly to develop. Hence an increased allocation to thoracic muscle development is only possible with high food, especially protein, availability. Later on it is more beneficial, at least for females, to reallocate these resources into reproduction. We also want to point out that because we observed mortality (mainly as a result of starvation) during the experiment, our sampled individuals, especially of the later age classes, do not represent a random sample. This has possibly resulted in a weaker observed decrease in thorax weight, as starved individuals are likely to have been individuals with a particularly rapid body condition decline, including a decrease in thorax weight. Thus, our comparisons between nutritional treatments are likely to have been conservative, as starvation was much more severe in the LF treatment.

In addition to the effect on flight muscle weight, food regime also had a strong effect on individual reproductive output. Both female egg production and male salivary gland development was strongly influenced by adult food availability (Fig. 2). Previous studies on *P. vulgaris* and other scorpionflies have established that reproduction is strongly dependent on the resources acquired during adult life (Bockwinkel & Sauer, 1994; Engqvist & Sauer, 2003). *Panorpa vulgaris* have therefore been characterized as typical income breeders (Engqvist, 2007c), as opposed to capital breeders depending more strongly on larval nutrition (e.g. nectar-feeding butterflies, Boggs, 1981; Karlsson, 1994, 1995; Stjernholm *et al.*, 2005). Not only female egg production and other reproductive parameters (Engqvist & Sauer, 2001, 2003), but also male salivary gland weight (Engels & Sauer, 2007, 2008), and thus ability to produce plentiful saliva during copulation (Engqvist & Sauer, 2002; Engels & Sauer, 2006), has been shown to be strongly condition dependent and influenced by adult nutrition. This present study confirms

these findings and also suggests that *P. vulgaris*, at least to some extent, cover their reproductive demands by differential allocation and reallocation of resources to and from thoracic flight muscles. However, an interesting by-product of the present study is the finding that hatch weight has an effect on both egg production and salivary gland development, but only under conditions of food limitation (Fig. 3). Hatch weight is affected by larval nutrition and growth (Engels & Sauer, 2007; Engqvist, 2007a), and thus represents resources acquired during larval development. The results thus indicate that for *P. vulgaris*, larval conditions are important, but only when adult resources (income) are limited. In their study, Engels & Sauer (2007) found a comparable effect for males. Here, we verify this and simultaneously demonstrate a much stronger effect of hatch weight on females (Fig. 3), confirming the notion that for females, reproduction is more resource constrained than for males.

In conclusion, we have demonstrated age-related variation in the thoracic muscles of *P. vulgaris*, and these changes are condition- and sex-dependent. An initial increase in thorax weight during the first days of adult life is followed by a decrease, especially in females, implying flight muscle histolysis. As predicted, food-limited individuals showed a different resource allocation pattern than less food-constrained individuals, but this was mainly manifested in a differential build-up, and not in the histolysis of flight muscles. These results suggest that *P. vulgaris*, at least females of the species, sacrifice flight ability in order to increase reproductive effort.

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