Intraspecific variation in body size and the rate of reproduction in female insects – adaptive allometry or biophysical constraint?

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Summary

1. A high rate of reproduction may be costly if ecological factors limit immediate reproductive output as a fast metabolism compromises own future survival. Individuals with more reserves need more time and opportunity to realize their reproductive potential. Theory therefore predicts that the reproductive rate, defined as the investment in early reproduction in proportion to total potential, should decrease with body size within species.

2. However, metabolic constraints on body size- and temperature-dependent biological rates may impede biophysical adaptation. Furthermore, the sequential manner resources that are allocated to somatic vs. reproductive tissue during ontogeny may, when juveniles develop in unpredictable environments, further contribute to non-adaptive variation in adult reproductive rates.

3. With a model on female egg laying in insects, we demonstrate how variation in body reserves is predicted to affect reproductive rate under different ecological scenarios. Small females always have higher reproductive rates but shorter lifespans. However, incorporation of female host selectivity leads to more similar reproductive rates among female size classes, and oviposition behaviour is predicted to co-evolve with reproductive rate, resulting in small females being more selective in their choice and gaining relatively more from it.

4. We fed simulations with data on the butterfly *Pararge aegeria* to compare model predictions with reproductive rates of wild butterflies. However, simulated reproductive allometry was a poor predictor of that observed. Instead, reproductive rates were better explained as a product of metabolic constraints on rates of egg maturation, and an empirically derived positive allometry between reproductive potential and size. However, fitness is insensitive to moderate deviations in reproductive rate when oviposition behaviour is allowed to co-evolve in the simulations, suggesting that behavioural compensation may mitigate putative metabolic and developmental constraints.

5. More work is needed to understand how physiology and development together with compensatory behaviours interact in shaping reproductive allometry. Empirical studies should evaluate adaptive hypotheses against proper null hypotheses, including prediction from metabolic theory, preferentially by studying reproductive physiology in combination with behaviour. Conversely, inferences of constraint explanations on reproductive rates must take into consideration that adaptive scenarios may predict similar allometric exponents.

Key-words: behavioural compensation, body size, developmental constraints, Lepidoptera, metabolic rate, reproduction

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Introduction

One of the most important decisions facing an organism is at what rate it should devote energy to reproduction at the expense of own maintenance and future survival (Williams 1966; Bell 1980; Rosenheim 2011). Allocation patterns should closely track the expected opportunity for reproduction determined by the organism's energy budget and by ecological constraints imposed by the environment (Schaffer 1974; Jervis, Boggs & Ferns 2007; Rosenheim *et al.* 2008). The larger and more reproductively potent an individual gets the less likely it is that its reproductive output will be limited by its body reserves. Rather, the availability of nest and egg-laying sites, access to food or harsh climate limiting the time available for important activities related to parental investment are likely to determine the realized reproductive output in the wild (Leather 1988; Carroll & Quiring 1993; Jervis, Ferns & Heimpel 2003; Gotthard, Berger & Walters 2007). As limiting conditions for reproduction select for reduced reproductive effort and increased life span (Williams 1966; Schaffer 1974; Bell 1980), it is predicted that large individuals should invest a smaller proportion of their resources into reproduction per unit of time (e.g. Ellers & Jervis 2003). However, quantitative tests of such predictions are few because they rely on accurate fitness estimates associated with intraspecifc variation in life span and reproduction under natural conditions.

The negative allometry of reproductive rate (here defined as the number of offspring produced per time unit in relation to the female's total reproductive potential) parallels the general observation of a proportional decrease of biological rates with body size both within and between species (La Barbera 1989). However, the hypothesized negative allometry of reproductive rate within species has been inferred from optimality reasoning based on variation in ecological variables affecting reproduction (e.g. Leather 1988; Ellers & Jervis 2003; Jervis, Ferns & Heimpel 2003; Gotthard, Berger & Walters 2007). The explanation for the negative scaling of metabolic rate on the other hand is based on knowledge of how biochemical reactions that affect energy uptake, transport and conversion depend on physiological properties such as the fractal-like branching networks through which energy is transported and allocated to different body parts and functions (Kleiber 1947; Gillooly *et al.* 2001; Hochachka & Somero 2002). This physiological organization typically results in hypoallometry between organismal body mass and biological rates with an allometric exponent that averages 0·75 (Kleiber 1947; Brown *et al.* 2004). Deviations from this allometric-scaling pattern are common, indicating that ecological factors can be important in shaping species-specific variation in metabolic rate (Glazier 2005; Clarke 2006; Dell, Pawar & Savage 2011). Nevertheless, the negative allometry of metabolic rate has proven consistent in comparisons at the species level with many diverse taxonomic groups and has had great explanatory power of species-specific ecology

and demography (e.g. Kleiber 1947; La Barbera 1989; Brown *et al.* 2004; Savage *et al.* 2004). Given this predictability, it seems likely that intraspecific variation in metabolic rate is constrained by predefined features of organism physiology. Thus, without very detailed information on species ecology, it might be difficult to distinguish adaptive from non-adaptive allometry in the rate of reproduction.

In addition, patterns of allocation during growth typically follow certain rules in which energy necessarily first needs to be devoted to somatic growth and only thereafter to reproductive tissue – why (or how) build horns without having a head to put them on? Such allocation patterns can in part be explained by optimality models (e.g. Kozlowski 1992; Kodric-Brown, Sibly & Brown 2006) but may also represent developmental constraints (Glazier 2002; Ricklefs & Wikelski 2002; Davidowitz, D'Amico & Nijhout 2003; Tobler & Nijhout 2010). Either way, variation in growth conditions during the end of the juvenile period might have a disproportionally large effect on the energy allocated to reproductive tissue in comparison with the induced differences in overall body size. Theory would predict that in organisms often exposed to variation in food resource during development, adaptive plasticity would evolve to minimize such effects (Stevens, Hansell & Monaghan 2000; Boggs 2009). This prediction is also supported by the observation of highly orchestrated development of different body parts and organs in holometabolous insects developing under different food qualities (Shingleton *et al.* 2007; Tobler & Nijhout 2010). However, if variation in food resource is highly unpredictable, such adaptive plasticity is less likely to evolve if it bears costs (DeWitt, Sih & Wilson 1998). Thus, adaptive intraspecific allometry of life span and reproduction is expected when variation in body size is genetic or environmentally induced as long as there are reliable cues to be used enabling the organism to predict the variation in food resource, but to less extent when variation in growth conditions is unpredictable.

To determine to which extent the size allometry of reproductive rate is adaptive or mainly a result of physiological and/or developmental constraints, a better understanding of how individual performance (and fitness) is affected by variation in reproductive rate is needed. Here, we investigate how reproductive rate should scale with variation in female body size in insects. Biological rates scale deterministically with body mass both within and between species of insects (Hochachka & Somero 2002; Glazier 2005). Insect reproductive potential increases with body size (Honek 1993; Blanckenhorn 2000), and in most insects, environmentally induced body size variation can be substantial owing to variance in food abundance or quality. Furthermore, in most groups of holometabolous insects, all protein and fat reserves used by the adult are acquired during juvenile development, and investment into reproductive organs and body parts (e.g. genitals, secondary sexual traits and female ovaries) is disproportionally large during the latter stages of juvenile growth

(Wickman & Karlsson 1989; Hodin & Riddiford 2000; Davidowitz, D'Amico & Nijhout 2003; Nijhout 2003; Shingleton *et al.* 2007; Teder, Tammaru & Esperk 2008; Moczek 2009). Thus, food shortage or time constraints leading to an abrupt cessation of the juvenile growth period may cause large variation in the amount of resources available for adult reproduction. To investigate the link between intraspecific variation in body size and reproductive rate, we here:

1 Construct a general model of adult reproductive allocation to show how the rate of reproduction should scale with body size under different ecological scenarios.
2 Model behavioural and physiological coadaptation in terms of female host selectivity and reproductive rate and show how these traits are optimized in orchestration.
3 Illustrate the similarity between predictions from optimality models and metabolic theory (MT).
4 Compare adaptive and constraint explanations for reproductive rate allometry in an insect model species, the butterfly *Pararge aegeria*. We do this by analysing relationships between reproductive rate, life span, body size and environmental temperature to which we apply our simulation model to predict the optimal relationship between female body size and reproductive rate in the wild.
5 Discuss how developmental and metabolic properties may limit perfect adaptation and how coadaptation of several aspects of life history, physiology and behaviour may shape intraspecific variation in reproductive allometry.

A general model

To illustrate how reproductive rate is predicted to scale with female body size and reproductive reserves, we develop a basic model of reproductive effort in insects. With the objective to keep our model as general and clear as possible, we define the case for a capital breeding, holometabolous insect that attains all its resources for adult reproduction at the juvenile stage. The organism also lays one single egg per host. The main qualitative predictions hold for cases where adult feeding is allowed or when females lay clutches instead of single eggs. The model could also easily be extended to incorporate several specific cases of insect life history and behaviour. We return to these topics in the discussion section.

The amount of tissue available for reproduction and maintenance increases in direct proportion to somatic size (Honek 1993). To reduce complexity, we assume that intrinsic adult life span is independent of body size *per se*. Egg maturation is known to be associated with increased rates of ageing and reduced life span in holometabolous insects (Papaj 2000; Jervis, Boggs & Ferns 2005). We assume that changes in the conversion rate of resources

into daily egg production (*R*), described as a proportion of total body reserves (*B*), render the same proportional decrease in life span (*L*) through an overall increase in metabolic rate and cell damage, which will accelerate senescence (Pearl 1928; Finkel & Holbrook 2000; Speakman 2005) and deplete body resources devoted to maintenance at a higher rate (Williams 1966; Monaghan, Metcalfe & Torres 2009). This trade-off function may be more or less appropriate when considering within-species variation as physiology will be shaped by previous selection and the trade-off can thus only take on values within a certain range. However, this trade-off structure is theoretically appealing and serves well to illustrate the evolutionary problem as it implies no weighted fitness advantage *a priori* of any ecological constraint – the reproductive potential can be realized either in a 'big bang' event or through several minor reproductive bouts, all scenarios with equal chance of success. This type of variation is at least present interspecifically within the Insecta, and even within orders like the Lepidoptera, exemplified by the long (>100 days) maximum adult reproductive life span and low daily fecundity of *Heliconius* butterflies (Boggs 1981) and the extreme strategy of females belonging to the moth genus *Orygia* that are wingless and lay their eggs on their cocoon during their first and only day of adult life (Tammaru, Esperk & Castellanos 2002). Even throughout the life of single individuals, the rate of reproduction and ageing can change markedly for some arthropods that switch from adult aestivation or diapause to reproduction (Carey 2001; Tatar & Yin 2001). Female survival can then be traded off against the rate of reproduction:

$$L = \frac{1}{R} \qquad \text{eqn 1}$$

where *L* is the average expected intrinsic adult life span and *R* is the daily investment in egg production expressed as a proportion of total body reserves at adult eclosion (*B*) counted in the currency of eggs (we here assume egg size to be constant and independent of body size). Thus, $0 \leq R \leq 1$. Assuming age-independent mortality risk, the daily intrinsic mortality rate (μ) is equal to $1/L$, and $\mu = R$. With unlimited access to hosts, a female will each day lay BR number of eggs and will need $1/R$ days in order to expend her egg supply. Thus, the lifetime reproductive success (LRS) is given by

$$\text{LRS} = \int_{x=0}^{x=\frac{1}{R}} \text{BR} * e^{-(R+P)x} \qquad \text{eqn 2}$$

where *P* is daily extrinsic mortality risk and *x* is female age. Without extrinsic mortality (*P* = 0), the solution to eqn 2 is independent of *R*, because a decrease in life span

is perfectly compensated by an increase in reproductive effort. If extrinsic mortality is incorporated, LRS in eqn 2 is maximized by maximizing R as this shortens the time period needed to expend egg supplies.

HOST LIMITATION

In insects, parental care is often solely devoted to strategic placing of eggs during female oviposition, so the immediate availability of hosts and time for oviposition behaviour dictate the allocation to reproduction (Leather 1988; Papaj 2000; Awmack & Leather 2002). So, under natural conditions, the daily number of hosts encountered (H) sets the upper boundary for the number of eggs laid per day (E).

$$E = f(\text{BR}, H) = \begin{cases} \text{BR}, \text{BR} < H \\ H, \text{BR} \geq H \end{cases} \qquad \text{eqn 3}$$

Then, for a female to expend her egg supply, she needs to survive B/H days. Optimal reproductive rate is directly dependent on total body resources and the daily expected host encounter rate. This result is intuitive because increasing reproductive rate, BR > H offers no increase in daily reproductive output as only H hosts are available for oviposition, while it instead increases intrinsic mortality rate. On the other hand, decreasing reproductive rate, BR < H, infers unnecessary extrinsic mortality as the female needs to survive for a longer period in order to realize her fecundity. Thus, the optimal reproductive rate is equal to H/B, which implies that large, host-limited females will exhibit lower rates of reproductive investment in proportion to their total set of energy reserves (full lines Fig. 1a, b) but instead outlive smaller females, even though their daily reproductive investment (e.g. daily

egg loads) may be higher in absolute terms (full lines Fig. 1c, d).

STOCHASTICITY IN REPRODUCTIVE OPPORTUNITIES

Variation in host encounter rate (H_σ^2) is incorporated by randomly sampling a number of hosts per time step for each female from a uniform distribution with the range min = 0 and max = 2*mean. For each female size class, 100 000 individuals were simulated for different host abundances (five, 20 and 100 hosts per day) with and without stochastic variation in host encounter rates, under scenarios of high (0·20) and low (0·05) levels of daily extrinsic mortality risk. The optimal reproductive rate is given by finding the reproductive rate that maximizes LRS.

Stochastic variation will infer an imperfect match between the number of hosts encountered and the number of eggs matured, so in order not to miss out on oviposition opportunities, eggs need to be carried in surplus, but extra investment in reproduction decreases survival. The solution depends on the level of adult extrinsic mortality (see also Schaffer 1974; Rosenheim 2011): under low extrinsic mortality, lowering of reproductive rate ensures the female longer life, buffering against variability in host abundance (lost-out opportunities owing to egg limitation can be compensated later in life), but under high extrinsic mortality, the female stands a great risk of short life, independent of her reduced investment in eggs, and by investing more into egg production, the female may take advantage of days when oviposition opportunities are above average (compare dashed lines, Fig. 1a–d).

Stochasticity in reproductive opportunities also affects the reproductive allometry that becomes more negative (compare full and dashed lines, Fig. 1a, b). This is because at a given host density, an increase in reproductive rate will
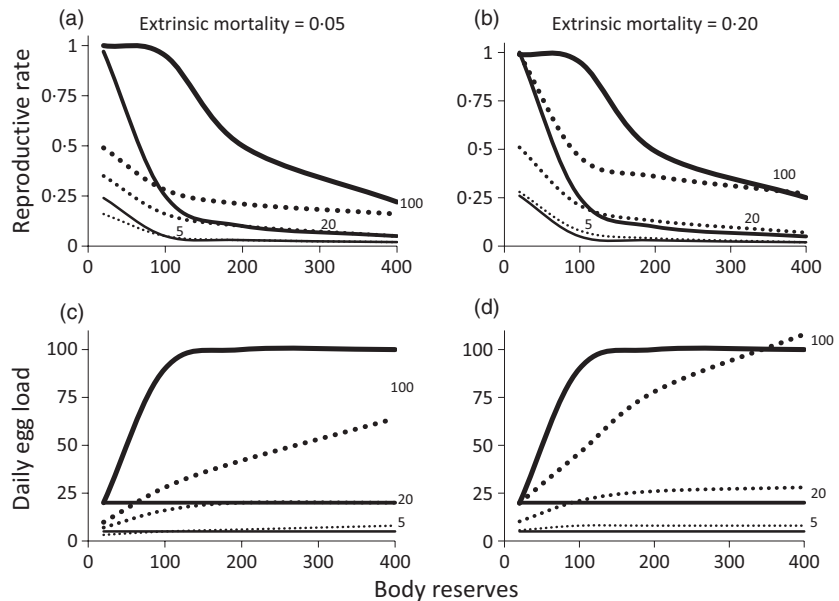

Fig. 1. The theoretical optima of reproductive rate (R) and daily egg load (reproductive rate (R) * body reserves (B)) as a function of host abundance (H), body reserves (B) and extrinsic mortality (P). In fig a and c, extrinsic mortality $P = 0.05$, and in b and d, $P = 0.20$. Three different host encounter rates (five, 20, 100 hosts per day) are depicted (thin to thick lines) under constant (full lines) and variable (hatched lines) host encounter rates. In general, females with large reserves are predicted to invest a smaller proportion of energy in reproduction per unit of time (a and b) but still invest more in egg production in absolute terms (c and d) (see text for details).

for larger females (that have low reproductive rates and long life spans) render a relatively small decrease in life span and a large relative increase in reproduction. For small females (with higher reproductive rates and short life spans) on the other hand, an increase in reproductive rate will cause a relatively large decrease in life span and a relatively small increase in reproduction (see also Ellers, Sevenster & Driessen 2000).

BEHAVIOURAL AND BIOPHYSICAL COADAPTATION — FEMALE HOST SELECTIVITY

Finally, we consider a potentially crucial fitness parameter: the opportunity for females to be able to choose between hosts of different quality (Damman & Feeney 1988; Minkenberg, Tatar & Rosenheim 1992; Papaj 2000; Doak, Kareiva & Kingsolver 2006). We evaluate whether i) this strategy should depend on the reproductive reserves carried by the female and specifically ii) how host selectivity may co-evolve with reproductive rate. To maintain simplicity, we assumed that females encounter 100 hosts each day. Variance in host quality (q_σ^2) was allowed to range between 0·01 (reflecting little variation in quality with fitness roughly between 0·8 and 1·2 for different hosts) and 0·16 (reflecting more variation with fitness varying roughly between 0 and 2). We allowed selectivity (s) to range between 0 (meaning that the female accepts all encountered hosts) and 0·9 (meaning she accepts only the upper 10%), which is directly related to the threshold value for the host quality (q_{crit}) that a female is willing to accept, thus generating the trade-off between accepting lower-quality hosts enabling a higher oviposition rate and choosing only high-quality hosts limiting the number of egg-laying opportunities. The proportion of hosts accepted is equal to the area of a standardized cumulative density function with a total area of 1, in a range defined by host qualities equal and above the q_{crit}:

$$S = \int_{q_{crit}}^{\infty} f(q)\mathrm{d}q \qquad \text{eqn 4}$$

The optimal reproductive rate (R) and selectivity (s) for females with different reproductive reserves (B) were found by maximizing LRS under different scenarios of extrinsic mortality (P) and variation in host quality (q_σ^2) using computer simulation.

When reproductive rate and female host plant selectivity are allowed to be co-optimized, the main predictions are that small, egg-limited females will benefit from becoming selective in their host plant choice whereas large, host-limited females are predicted to show much less restrictiveness in their choice (Fig. 2c, d). Importantly, reproductive rate allometry co-evolves with female selectivity so that small females may benefit from lowering their reproductive rates, living longer and only laying their eggs on the few hosts of highest quality (Fig. 2a, b) (see also: Rausher 1985). Logically, therefore, small females also benefit more in terms of relative fitness from this behaviour (Fig. 2c, d). The effect, and the benefit, of being selective is naturally also most pronounced when there is more variation in fitness associated with host choice (results for low variation in host quality not shown) and when extrinsic mortality is low, allowing pay-offs of postponing reproduction (compare Fig. 2c, d).

ADAPTIVE ALLOMETRY OR BIOPHYSICAL CONSTRAINT?

In conclusion, reproductive rate is predicted to decrease with increased body reserves carried by the female owing to the incidence of host limitation. However, the incorporation of ecological realism, such as stochasticity in reproductive opportunities, or allowing female behavioural plasticity to co-evolve with reproductive rate can significantly weaken the relationship. The resulting allometries resemble neutral
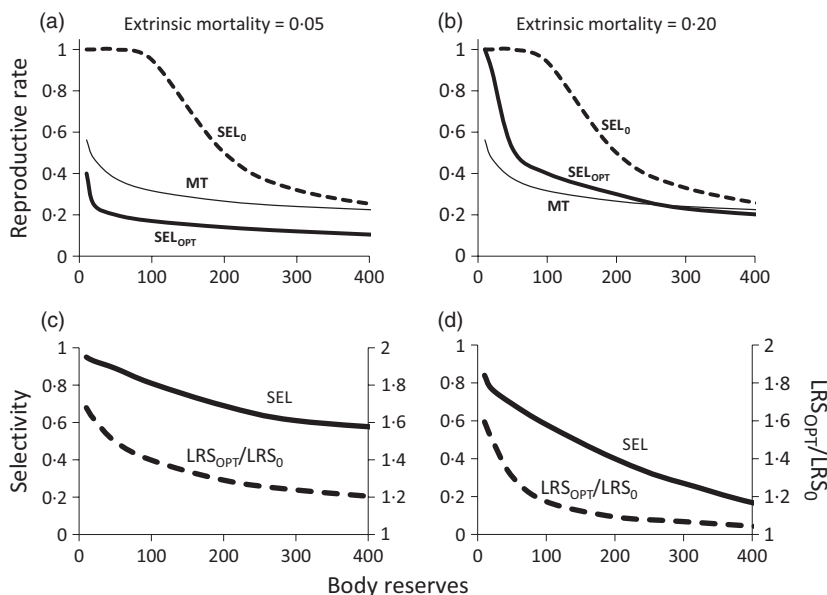

Fig. 2. (a) and (b) Optimal reproductive rate allometry for females accepting all potential host plants (SEL_0) and when female host plant selectivity is allowed to be optimized in coordination with reproductive rate (SEL_{OPT}) compared to neutral expectations based on metabolic scaling (MT). (c) and (d) Optimal selectivity (SEL_{OPT}) and the relative fitness benefit (LRS_{OPT}/LRS_0) of being selective as compared to the scenario when females accept all host plants. Host quality mean (q) = 1 and variance (q_σ^2) = 0·16, host abundance (H) = 100.

predictions from MT. This theory predicts that physiological constraints on important processes such as oxygen and nutrient diffusion, transport and uptake (Hochachka & Somero 2002) will cause biological rates to scale to body mass with an exponent close to 0·75 in absolute terms or −0·25 in relative terms (Gillooly *et al.* 2001; Brown *et al.* 2004). In Fig. 2a, b for comparison, the prediction of relative reproductive rate from MT is depicted as MT = c mass$^{-0.25}$, where c is the normalization constant converting mass into eggs (here, arbitrarily set to 1 in both cases). The similarity between predictions illustrates a potential difficulty with differentiating between adaptive and neutral hypotheses concerning reproductive allometry. Below, we explore how well theoretical predictions from optimality models vs. explanations based on metabolic and developmental constraints agree with empirically derived estimates of reproductive rates for a real case by applying a simulation model to data on the butterfly *P. aegeria*.

Reproductive allometry in *Pararge aegeria*

The butterfly *P. aegeria* is widespread throughout Europe (Tolman 1997). Females emerge without any mature eggs (Berger, Walter & Gotthard 2008) and their life span may vary widely (5–40 days) depending on temperature conditions (e.g. Karlsson & Wiklund 2005; Berger, Walter & Gotthard 2008). Fecundity increases strongly with female body size, usually in a span between 50 and 250 eggs for individuals raised under laboratory conditions (Karlsson & Wickman 1990), but the strength and shape of the relationship is temperature-dependent because oviposition is inhibited in cold temperatures (<18 °C) (Gotthard, Berger & Walters 2007); large females with large egg loads need more time for oviposition behaviour and are therefore more likely than small females to have their fecundity output set by the thermal environment. Oviposition is performed on a variety of grass species in shaded forest areas, and females usually lay one egg per host plant visit. Although grasses are abundant, female egg-laying behaviour is complex, and females reject the majority of hosts they visit (Wickman & Wiklund 1983). This pattern may be explained by females needing to find not only plants of good quality, but also a suitable microhabitat as other factors such as predation risk or risk of host plant desiccation are highly important in governing insect host choice (Awmack & Leather 2002; Wiklund & Friberg 2008). Thus, because the availability of suitable host plants is limited and cold and varying temperatures are common under field conditions, it seems likely that the selection should favour allocation strategies that correspond to the risk of time and egg limitation (Rosenheim 1999, Rosenheim 2011) and therefore give rise to size-dependent differences in patterns of allocation to reproduction and life span (Ellers & Jervis 2003).

To simulate optimal reproductive rate in *P. aegeria*, we required two kinds of data. First, we performed a reanalysis of a large data set compiled from previous laboratory experiments to estimate the relationships between early reproductive investment (as a measure of reproductive rate), life span, body size, lifetime fecundity and oviposition temperature. We used path analysis to explore and visualize these relationships, and we complemented the analysis with a survival analysis allowing estimation of age-dependent mortality rate. These relationships were then used to base well-informed assumptions in our model simulations. All assumptions and equations describing estimated relationships between model variables can be found in Table 1. Secondly, to test predictions from our simulations, we collected data on reproductive rates in the wild. These were calculated by dividing the number of dissected eggs from wild-caught females of known body size with their estimated potential fecundity. Statistics and estimated relationships between early reproductive investment (reproductive rate), life span, body size, lifetime fecundity and oviposition temperature can be found in Fig. 3. The estimated relationship between body size and egg load in the wild is depicted in Fig. 5. For more detailed description of

Table 1. List of assumptions and equations used in the simulations on *Pararge aegeria*. For detailed explanations, see main text, and for detailed statistics, see Appendix S1

| Parameter	Denotation	Value	Comment	Source
Ovigeny index		0		Berger, Walter & Gotthard (2008)
Oviposition time budget		09·00–17·00		Obs. at Stockholm and Skåne sites
Oviposition threshold		18°C		Gotthard, Berger & Walters (2007)
Host encounter rate		6·7 eggs h^{-1}	Modelled for 4–14 eggs h^{-1}	Wickman & Wiklund (1983)
Variance in encounter rate		6·7	Poisson distribution	Wickman & Wiklund (1983)
Extrinsic mortality	P	0·05–0·20	Covers reasonable range	
Variance in host quality	q_σ^2	0·01, 0·16	Normally distributed, mean = 1	
Body mass	B	40–100 mg	Natural range in population	Multiple (see Table A1)
Potential fecundity	F	0·14*$B^{1.6}$	Simulated for B = 40–100 mg	See Fig A1
Age-dependent mortality rate		1·15	Mortality increases with age	Multiple (see Table A1)
Daily intrinsic mortality rate	μ	0·15*R−0·017*F	Optimized in simulations	Multiple (see Table A1)
Reproductive rate	R	0·01–1	Optimized in simulations	
Daily egg load		$R*F$	Optimized in simulations	
Female host selectivity	s	0·1–0·9	Optimized in simulations	
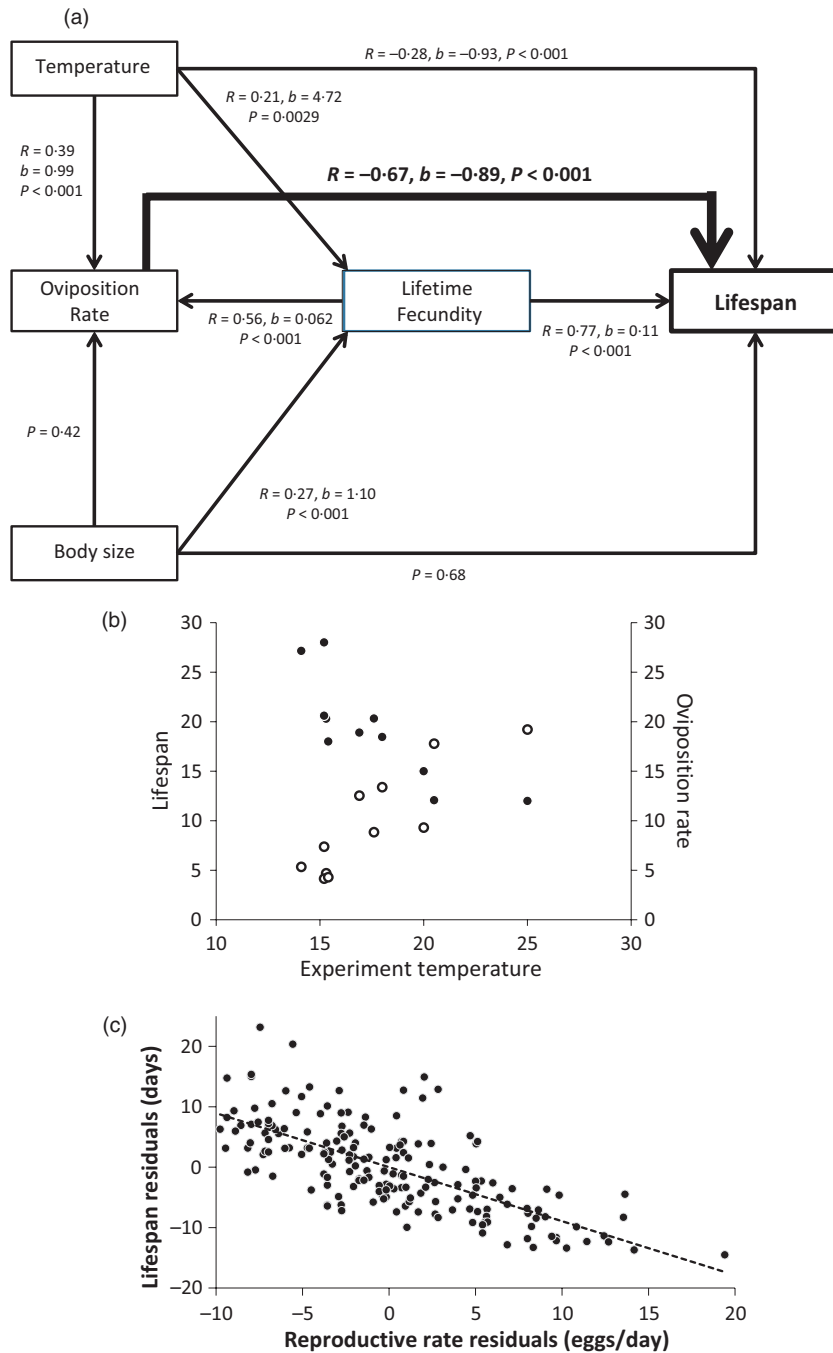
Fig. 3. (a) Path diagram of daily oviposition rate early in life (as a measure of reproductive rate) and lifespan in *Pararge aegeria*. Each path's standardized partial correlation coefficient (*R*) and slope coefficient (*b*) are given together with statistical significance. (b) Average lifespan in days (filled circles, left-hand axis) and average daily oviposition rate early in life (open circles, right-hand axis) regressed against the average experimental temperature. (c) Extracted residuals of lifespan regressed on oviposition rate.

the data collecting, statistical methodology and results, see the Appendix S1.

ASSUMPTIONS

In order to predict the body size allometry of reproductive rate (estimated by daily egg load) in *P. aegeria* in the wild, a simulation model was constructed combining the results from the survival analysis with field observa-

tions and climate data from the Riala field site (Table 1). Temperature and sun radiation data recorded hourly for the time period 1996–2008 (excluding 2003 owing to missing data) were obtained from the nearest located weather station Svanberga, 30 km north of Riala, and calibrated using temperature loggers set out at the field site in 2007 and 2008. Butterflies were assumed to need at least 18 °C to perform oviposition behaviour as this is the temperature threshold for oviposition in *P. aegeria* (Gotthard,

Berger & Walters 2007; supported for wild-caught females in this study, see Appendix S1). As our analysis of field-caught females found no effect of temperatures outside the flight period on egg loads (Appendix S1), we did not assume any temperature limitations on egg maturation rates. We assumed that females can retain eggs matured on previous days, which has been confirmed by repeated laboratory observations (Berger, Walter & Gotthard 2008; M. Olofsson & D. Berger, unpublished). Host encounter rate during benign weather conditions was assumed to follow a poisson distribution and the mean and variance were estimated from the data of Wickman & Wiklund (1983) on female oviposition during 8 h of optimal weather with an average oviposition rate of 6·7 eggs per hour. This is an approximation as it is an estimate based on observations during a single year and within a limited area. This approximation does, however, not confound the effect of host plant limitation with regulation of search behaviour owing to egg limitation (only females that indeed were trying to find host plants for oviposition were followed). The incidence of female host plant selectivity is predicted to underestimate the number of encountered hosts that actually could have been accepted for oviposition. As we had no knowledge about female selectivity *a priori* and preferred to let it co-evolve with reproductive rate in our simulations, we also ran scenarios with higher host plant encounter rates. *P. aegeria* females were observed to lay eggs between 09·00 and 17·00 at Riala, which is in accordance with yearly observations at another field site in Skåne, southern Sweden (C. Wiklund, pers. obs.), and was assumed to be the daily oviposition time budget. Variation in fitness associated with oviposition choice is likely pronounced in *P. aegeria* as in most butterflies owing to variation in host nutritional status, exposure to natural enemies and microclimatic conditions (Damman & Feeney 1988; Minkenberg, Tatar & Rosenheim 1992; Papaj 2000; Doak, Kareiva & Kingsolver 2006; Wiklund & Friberg 2008). However, estimating such variation is not an easy task. Thus, here we instead simulate optimal selectivity (s) and reproductive rates (R) under different scenarios of variation in host quality (q_σ^2) sampled from a normal distribution. Likewise, natural levels of predation at the field site are unknown. Therefore, the optimal rate of reproduction (optimal daily egg load) was simulated for several reasonable (0·05–0·20) levels of daily extrinsic mortality rate (P).

The incorporated relationships between daily intrinsic mortality risk (μ) and potential lifetime fecundity (F), age (a) and reproductive rate (R) were estimated from the survival analysis. We estimated the allometric relationship between potential lifetime fecundity and body mass using the relationships from the studies of Karlsson & Wickman (1990) and Gotthard, Berger & Walters (2007) in which a total of 76 females were followed in laboratory settings optimal for egg laying, thus making sure that body mass and not any other variable such as nectar resources, host plant availability or temperature affected total reproduc-

tive output. We first performed robust regression to detect potential outliers with large impact on our estimate. One observation was detected as an outlier. Although this observation did not have much impact on the estimate of the exponent, we nevertheless removed it before performing the final analysis. Female body mass explained lifetime fecundity according to the relationship: 0·14*Body mass$^{1·6(\pm0·48)}$, $R^2 = 0·38$, $n = 75$, $P < 0·001$ (Fig. A1 in Appendix S1). This exponent was significantly different from one, indicating weak positive allometry of reproductive potential. Reproductive rate (R) and female host selectivity (s) were optimized for female potential fecundities (F) between 50 and 225 eggs (corresponding to a body mass interval of 40–100 mg which covers the natural range) in each scenario of extrinsic mortality (P) and variation in host quality (q_σ^2). We ran 100 000 simulations for each combination of reproductive rates, potential fecundities and selectivities in all scenarios. Female daily egg loads and the optimal rate of reproduction (R) (expressed as daily egg loads divided by each female's lifetime potential fecundity (F)) can then be calculated by maximizing reproductive success over the life span (L) of females:

$$\mathrm{LRS} = \sum_{i=1}^{L} f(R, s, F, P, q_\sigma^2) \qquad \text{eqn 5}$$

PREDICTIONS

The simulations show that egg loads increase asymptotically with female body mass because selection will favour longer life span and a reduced proportion of investment in reproduction as the likelihood of time limitation on female oviposition increases with the greater potential fecundity of larger body size. Although high extrinsic mortality selects for increased egg loads, the qualitative prediction that female egg loads should scale hypoallometrically with female body size is relatively insensitive to changes in mortality ($P = 0·05$–$0·20$) (Fig. 4a). This is also true for higher and lower levels of average host abundance (mean = 4–14 hosts per hour). Similar to predictions from the general model, small females are predicted to be more selective in their host plant choice and gain relatively more from this behaviour (Fig. 4b). Again, more variation in host quality naturally gives more incentive for females to be selective (compare thick lines in Fig. 4b). The main explanation for the insensitivity of the predicted optimal allometry in our model on *P. aegeria* in comparison with the general model is the empirically derived linear trade-off between reproductive rate and life span. At already high values of reproductive rate, increasing reproductive rate further results in large disproportionate reductions in life span, and conversely, at already low rates of reproduction, decreasing reproductive rate further results in large disproportionate reductions in reproduction while giving only modest proportional
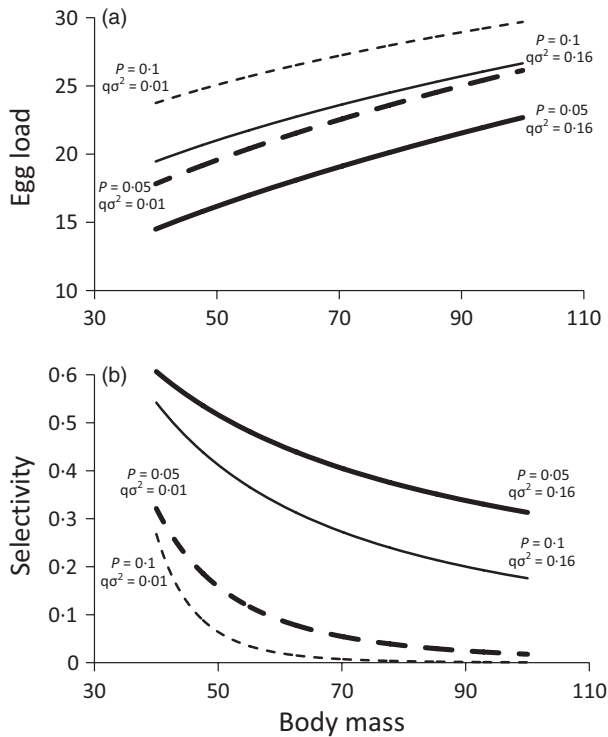
Fig. 4. In (a), size-dependent optimal egg loads in the four different scenarios from top to bottom: P (extrinsic mortality) = 0·1, q_σ^2 (variance in host quality) = 0·01, and P = 0·1, q_σ^2 = 0·16, and P = 0·05, q_σ^2 = 0·01, and P = 0·05, q_σ^2 = 0·16. In b), optimal host plant selectivity for the same four scenarios now in reversed order from bottom to top: P = 0·1, q_σ^2 = 0·01, and P = 0·1, q_σ^2 = 0·16, and P = 0·05, q_σ^2 = 0·01, and P = 0·05, q_σ^2 = 0·16.

increase in life span. Rather than being a mathematical by-product, this result may reflect the real situation for most organisms for which reproductive physiology is shaped by prior selection. Thus, while our general model serves to illustrate well the evolution of reproductive rate free of physiological constraints, our simulation on *P. aegeria* serves well to predict optimal intraspecific allometry given a (linear) species-specific trade-off function set within the realm of developmental and biophysical constraints.

DATA

Egg loads were predicted to be slightly larger in our simulations than that observed in the field. Such a discrepancy may be explained by our calculation of empirical egg loads not accounting for females being able to mature eggs during the period of egg laying itself. Nevertheless, this effect is likely small as females caught late in the day usually had depleted their egg stores and it is also not predicted to change the allometric relationship itself given that egg maturation rates show the same size dependence across all hours of the day. To compare predicted allometry of egg loads with empirical data, we therefore scaled average egg loads and reproductive rates by adjusting their means by a constant. However, the simulated
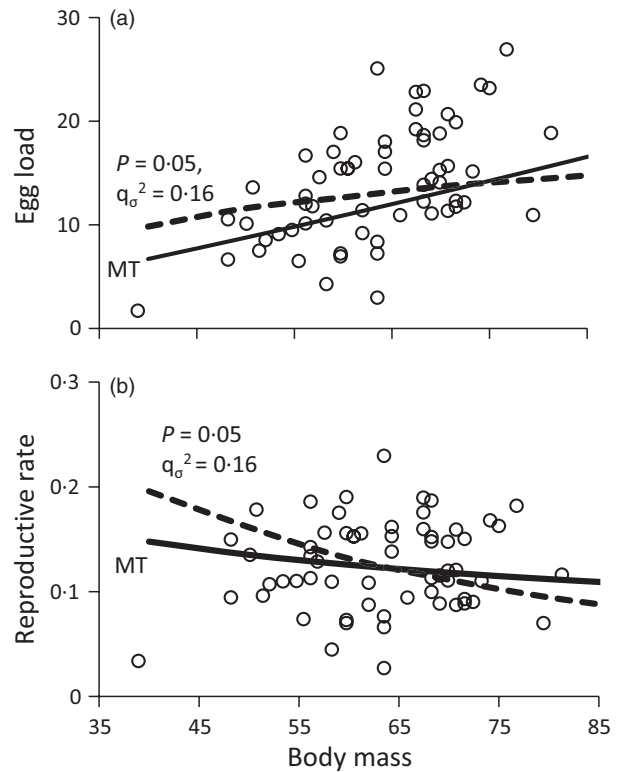

Fig. 5. (a) Estimated egg loads of wild-caught females at the Riala field site in 2008 at 09·00 are depicted as a function of female body size. For comparison to model predictions, the simulated optimum of daily egg loads is depicted by the hatched line. The thin full line depicts the neutral expectation from metabolic scaling (MT). (b) The same predictions and data expressed as reproductive rate calculated as the daily egg load divided by the predicted potential fecundity. Basing model predictions for optimal egg loads and reproductive rates for temperature data from only 2008 when the butterflies were caught gave identical predictions and are not shown.

allometries still contrast the relationship between body mass and egg loads found for the wild-caught females (Fig. 5). Body masses and egg loads of wild-caught butterflies were both estimated with error. Therefore, to estimate allometric exponents and compare model predictions with the empirical data, we performed reduced major axis regression (RMA) on log-transformed data using the lmodel2-package in *R* (R Development Core Team 2011). The RMA estimate of the allometric exponent was equal to 1·07 (R = 0·68, P < 0·001, n = 62, CI = 0·88–1·29), indicating isometry or weak positive allometry of egg loads. Using the same approach for calculating allometric exponents predicted by our simulations assures unbiased comparisons with the empirical data. These exponents were estimated to 0·34–0·49 depending on variation in host plant quality, host density and extrinsic mortality level (Fig. 4a). No matter the exact scenario, model predictions of a negative egg load allometry owing to the size-dependent incidence of time limitation were always quite far away from the empirically derived isometric allometry. Arguably, the empirical egg load allometry can better be explained by a neutral sce-

nario, assuming that egg loads are a product of metabolic constraints on the conversion rate of reproductive reserves into eggs (body mass–scaling constant predicted equal to 0·75 according to MT), and the amount of reproductive reserves accumulated during juvenile development (potential fecundity, as a measure of total reproductive reserves, was found to scale with a positive allometry of 1·6 to adult mass (above and Fig. A1 in Appendix S1)). These two components would translate into an allometry of 1·2 for egg load on body mass. In Fig. 5a, untransformed egg loads are regressed on body mass together with simulated predictions and predictions from MT, where the daily egg load is equal to: $c*mass^{0.75*1.6}$, where the normalization coefficient c scales the data. In Fig. 5b, relationships are given for egg loads converted to reproductive rate (egg load/potential fecundity) and MT predictions: reproductive rate = $c*mass^{1.6*0.75-1.6}$.

Discussion

Recently, the 'rate of living hypothesis', first formulated by Pearl in 1928, has regained popularity as an explanation for variation in life span (Finkel & Holbrook 2000; Monaghan, Metcalfe & Torres 2009; Munch & Salinas 2009), fuelled by the recent uprise of the Metabolic Theory of Ecology (Gillooly *et al.* 2001; Brown *et al.* 2004; Dell, Pawar & Savage 2011) applying biophysical and thermodynamic first principles to explain biological rates. However, while biophysical constraints clearly set rules on organism production rates, we still know little about the absoluteness and nature of these constraints (Maynard Smith *et al.* 1985; Hochachka & Somero 2002; Kozlowski & Konarzewski 2004; Glazier 2005; Clarke 2006), and thus, how and to which extent they influence intraspecific allometries of reproductive rate and life span (Ricklefs & Wikelski 2002; Speakman 2005).

Previous investigations of reproductive rate at the species level in insects have shown evidence for adaptive variation in response to ecological variables (Jervis & Ferns 2004; Jervis, Boggs & Ferns 2007) and a negative correlation with body size in particular (Jervis, Ferns & Heimpel 2003; Jervis, Boggs & Ferns 2005). However, tests of adaptive hypotheses concerning intraspecific allometries are far scarcer, and the few studies we have found (Thorne *et al.* 2006; Pöykkö 2009) present mixed results without attempts to quantify covariation between reproductive rates and fitness. According to our optimality model, reproductive rate should decrease with female body size when ecological factors limit reproductive output. These results parallel the predictions of the theoretical examination of ovarian dynamics in synovigenic parasitoids by Ellers & Jervis (2003). However, under realistic ecological scenarios, optimal reproductive rates will follow closely predictions from metabolic theory. The simulations on *P. aegeria* further show that reproductive rate allometry was better predicted from biophysical rules than the optimality analysis. Clearly, some assumptions needed to be made in our simulations, so we do not consider our theoretical optimum of egg load allometry in *P. aegeria* to be an exact estimate. Nevertheless, the qualitative result, that reproductive rate is predicted to decrease strongly with body size, is insensitive to changes in model parameters and is a general pattern emerging from ecological limitation on reproductive opportunities. Thus, the rather large discrepancy between observed and theoretical egg loads needs additional explaining. Below, we discuss in sequence how behavioural allometry, developmental rules on resource allocation and metabolic impact on biological rates may shape reproductive rates in female insects.

BEHAVIOUR

Females may adjust their oviposition behaviour in accordance with their carried egg load (Rausher 1985; Jaenike 1990; Minkenberg, Tatar & Rosenheim 1992; Papaj 2000). Our model confirms that large females with more eggs to oviposit are less selective when placing their eggs while small females instead display highly selective oviposition behaviour. Parental investment in terms of female host selectivity buffers fitness costs associated with suboptimal reproductive rates by allowing females to trade off host quality and number (Fig. 6). Host choice is therefore predicted to correlate with female body size, especially in a scenario where metabolic constraints govern reproductive output. Thus, reproductive allometry should best be studied in combination with compensatory reproductive behaviours. In the real situation, there are likely costs of being selective as increased flying enabling more sampling of hosts may take time from female foraging, for example. As we did not incorporate such a cost into our model, we may have overestimated the benefits of increased selectivity slightly. Interesting to note, however, is that in many insects, egg-laying females feed on the very same host used for egg laying (Papaj 2000; Awmack & Leather 2002), thus in effect evading this trade-off.

It is also important to note that although we did not model the case of a clutch-laying organism explicitly, the incorporation of female host selectivity effectively parallels the effect of clutch laying. For the case of adaptive plasticity in clutch size, this can be seen by considering that an increased number of eggs per plant reduces female host limitation but likely decreases the chances of survival of each individual offspring, just like decreased selectivity reduces host limitation at the cost of accepting poorer hosts reducing average offspring survival. For species that are obligate clutch layers, the results still hold generality as long as females become time-limited during egg laying. The incidence of time limitation, however, seems likely to be less pronounced as fewer hosts are needed to deplete female egg stores. Indeed, the evolution of clutch laying is predicted to at least partially be a result of ecological time limitation on female reproduction (Leather 1988; Papaj 2000; Gotthard, Berger & Walters 2007).
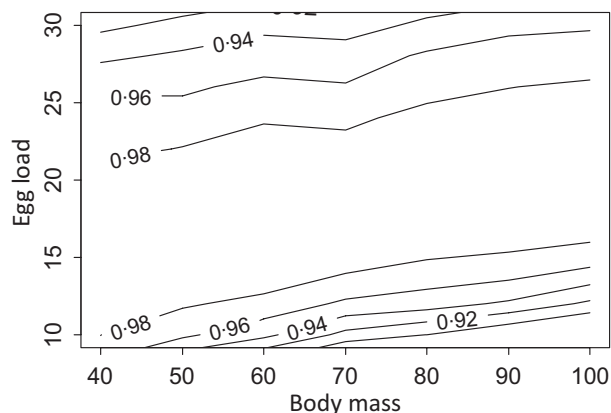
Fig. 6. Contour plot of predicted size-specific fitness sensitivities (fitness at optimal strategy = 1) associated with variation in egg loads under a scenario of extrinsic mortality (*P*) equal to 0·05 and variation in host plant quality (q_σ^2) equal to 0·16.

Other forms of behavioural compensation in response to biophysical constraints are often observed; perhaps, the most common one is that of thermoregulation to compensate the deterministic effects of temperature on metabolic rates seen in ectothermic organisms (Angilletta *et al.* 2003; Huey, Hertz & Sinervo 2003; Angilletta 2009). Compensatory behavioural allometry may thus be a common mechanism mitigating fitness consequences of biophysical constraints owing to previous selection and depleted genetic variance (Ricklefs & Wikelski 2002; Lind & Cresswell 2005; Dial, Greene & Irschick 2008). Below, we discuss two major types of potential constraints that can influence reproductive allometry: those associated with sequential allocation of resources to reproduction during juvenile development in holometabolous insects and those associated with body size–rate relationships of energy transport and conversion.

DEVELOPMENTAL RULES

One striking feature of our data on *P. aegeria* is the very modest egg loads of small females caught in the wild. A possible explanation is that body size variation is mostly attributed to variance in host quality or abundance and that many small individuals complete development but are in poor condition. However, in this case, one would also expect strong size-dependent differences in longevity, which typically is not observed for intrinsic life spans of laboratory-reared females that still differ markedly in reproductive potential (Karlsson & Wickman 1990; Gotthard, Berger & Walters 2007). These patterns also seem consistent in the distantly related tropical satyrine *Bicyclus anynana* (Saastamoinen *et al.* 2010). The proportion of carbon and nitrogen (prime building material for eggs) invested into the female abdomen increases with overall body size in *P. aegeria* (Karlsson & Wickman 1990), as well as in other butterflies (Wickman & Karlsson 1989; Boggs 2009). Theory would predict such

positive reproductive allometry to be a result of strong directional selection for increased reproductive success (Kozlowski 1992; Kozlowski & Weiner 1997; Kodric-Brown, Sibly & Brown 2006). However, the sequential manner resources are devoted to growth, and building of soma early on in development and to reproductive tissue at latter stages is a very consistent pattern among holometabolous insects (Honek 1993; Davidowitz, D'Amico and Nijhout 2003; Nijhout 2003; Shingleton *et al.* 2007). As an example, the ovaries in *Drosophila melanogaster* increase in size by 15 times only during the third and last larval instar (Hodin & Riddiford 2000). Thus, a shortening of the growth period may cause a proportionally larger reduction of reproductive tissue than in overall body size and life span as default, and constraint and adaptive explanations for positive intraspecific allometry of reproductive rate are therefore not easily disentangled, nor mutually exclusive.

Ideally, an organism should be able to reach the adult stage at any given body size with an optimal proportion of resources devoted to reproduction and life span, respectively. In agreement with this expectation, different body parts and organs show highly orchestrated development under variable resource qualities in insects (Stevens, Hansell & Monaghan 2000; Shingleton *et al.* 2007). However, if resource abundance varies unpredictably during ontogeny, it is less clear how such homoeostasis should be maintained for organs that grow during different phases of development (Boggs 2009). In such a scenario, resource allocation rules and organ growth may rather be canalized and correspond to the target (genetic) adult size than show developmental plasticity, given that there are maintenance costs associated with keeping a developmental machinery that enables plasticity (DeWitt, Sih & Wilson 1998).

In addition to the predictability of the environment, the relative prevalence of plasticity vs. canalization of development will also depend on how often the alternative phenotypes are expressed and exposed to selection, as well as the potential reproductive output of each phenotype (Van Tienderen 1991). Consider that a large female of *P. aegeria* weighing 100 mg has a potential fecundity of about 225 eggs compared to a small female weighing 40 mg producing just above 50 eggs over her life (Fig. A1 in Appendix S1). In our simulations, the larger female is predicted to have around three times as high fitness as compared to the smaller female. If then, for this species utilizing abundant grasses as host plants, the relative probability of developing into the large female is about 80% vs. 20% for developing into a small female, the relative contribution to the next generation of these alternative phenotypes equal: (0·8*3)/(0·2*1) = 12 : 1 in favour of the large phenotype. Thus, any plasticity inferring a global cost to the genotype must increase the relative fitness of the rare small phenotype by 12 times as much as the corresponding reduction in relative fitness of the larger common

phenotype. Following this line of reasoning, organisms experiencing more variation in juvenile growth conditions (e.g. temperature, food availability, season length), giving rise to large phenotypic variation in body size, are predicted more likely to display corresponding adaptive plasticity in their allocation to reproduction and soma because both large and small phenotypes are exposed readily to selection.

In contrast, our data on *P. aegeria* show that the egg load is in direct proportion to female body size, which may indicate constraints on female reproductive allocation at two separate levels. First, in the way energy is devoted to different parts of the organism during development, rendering high variability in reproductive potential but not life span with changes in size at metamorphosis owing to unpredictable variation in food resources. Secondly, reproductive effort seems constrained by inflexible rates of egg maturation during adulthood (Berger, Walter & Gotthard 2008), which may prevent adaptive disposal of the resources attained, implying that metabolic constraints on rate–body mass relationships may play an additional role in shaping reproductive rates.

METABOLIC RATES

The rates of different biological processes are bound by a shared physiology (Brown *et al.* 2004; Clarke 2006), and one can hypothesize that the possibilities for large and small females to fine-tune their rates of egg maturation may be limited because many other correlated temperature-dependent processes are under simultaneous selection (Angilletta 2009). For example, it seems improbable that thermal reaction norms for adult flight activity should be under size-dependent selection, and this reasoning should apply for many more basic metabolic processes. In the simplest of scenarios then, the rate of adult reproductive output could be the product of accumulated reserves (that may vary widely with juvenile growth conditions) and the overall rate of metabolism and energy turnover governing the full set of physiological processes of the animal.

Allometric mass exponents of metabolic rate in insects have been estimated to 0·83 on average (Glazier 2005) but average development time over seven insect orders including 326 species scales exactly according to predictions from metabolic theory (allometric exponent = 0.75, M. Dillon & M. Frazer, pers. comm.). Both these estimates entail large interspecific variation, underlining the crux of the matter; metabolic constraints are global, but not absolute (Maynard Smith *et al.* 1985; Brown *et al.* 2004; Glazier 2005). Nevertheless, given constraints on organismal production and death rates, a relatively weaker statistical relationship between life span and body size is expected in comparison with that between reproductive output and body size, because energy expenditure is predicted to scale with the familiar exponent of 0·75 and mortality rates are predicted to decrease with body size giving an allometric mass exponent of -0.25 (Kleiber 1947; Brown *et al.* 2004). This proportionality of reproductive and mortality rates is in fact exactly analogous to the assumption of a trade-off between reproduction and life span in our general model (eq. 1).

To date, it is not clear to what extent metabolic constraints on interspecific allometries can be directly applied to intraspecific variation. It is known that allometric relationships observed among species within lower taxonomic levels may differ quite markedly from the allometry studied at higher levels (Hines 1982; Glazier 2005; Dial, Greene & Irschick 2008), illustrating that natural selection is able to generate variation in metabolic scaling. Furthermore, adaptive plasticity in temperature- or body mass-dependent biological rates are common for many traits that undergo differential ecological selection pertaining to differences in optima of the sexes (Clutton-Brock & Parker 1992; Bonduriansky *et al.* 2008), life stages (Gotthard, Nylin & Wiklund 2000; Bowler & Terblanche 2008; Berger, Friberg & Gotthard 2011) or developmental morphs (West-Eberhard 2003; Cardoen *et al.* 2011; Aalberg-Haugen, Berger & Gotthard 2012). However, intraspecific variation typically entails differences in the overall rate, and not in allometric scaling. The fundamental biophysical laws that govern overall shifts in metabolic rate vs. shifts in the allometric slope should by first principles be the very same for interspecific and intraspecific variation. However, the mechanisms of compensation may well be different for intra- vs. interspecific variation owing to the very different evolutionary time-scales, as well as the much wider body size range studied in comparative analyses.

ADDITIONAL LIFE-HISTORY PARAMETERS AND REPRODUCTIVE RATE ALLOMETRY

Other behavioural and physiological processes not included in our model may significantly contribute to the variation in reproductive rates and life span. Reallocation of resources from flight muscle to egg production or from eggs to soma occurs in many insects and could reduce fitness consequences of putative developmental constraints on resource allocation during juvenile development (Zera & Denno 1997; Karlsson 1998; Stjernholm, Karlsson & Boggs 2005; Saastamoinen, Ikonen & Hanski 2009). However, reallocation is likely to come at a cost and may not be promoted by selection if future conditions for reproduction are unpredictable (Rosenheim, Heimpel & Mangel 2000). There is nevertheless comparative evidence for a negative correlation between the proportion of reserves invested in early reproduction and the level of reallocation of oocytes back to soma in insects (Jervis, Boggs & Ferns 2005), suggesting that further work on reproductive rates should include study of reallocation patterns.

Similarly, we did not assume any impact of adult income on reproductive rates. A positive influence of adult resource intake on reproduction and life span is

expected (Boggs 1992, 2009). It is also predicted that small females should compensate their smaller reproductive budgets attained during the juvenile period by feeding more as adults (at a cost of foraging). In most holometabolous insects, all protein and fat reserves incorporated into reproduction are attained during larval growth (Shingleton *et al.* 2007); adult foraging is therefore not predicted to have large effect on reproductive allometry in this group of insects. Nevertheless, in the continuum between income and capital breeding, adult foraging may play an important part in determining factual reproductive rates observed in the wild. Important to note for the effects of both adult income and resource reallocation is thus that their effects on reproduction can be important in overcoming developmental constraints on resource allocation during juvenile development but that these effects do not change predictions of the optimal reproductive allometry to large extent.

Parental investment through plasticity in egg size may evolve to compensate constraints on reproductive allometry; if fitness varies with egg size, large females are predicted to invest in larger eggs in response to time-limited oviposition (Rosenheim 1996;). Among satyrine butterflies, and *P. aegeria* in particular, non-adaptive explanations related to a mechanistic relationship between maternal size and egg size seem to adequately explain observed variation in egg size however (Wiklund & Karlsson 1984; Wiklund, Karlsson & Forsberg 1987; Bauerfeind & Fischer 2007; Gibbs, Van Dyck & Karlsson 2010), which also seems to be the case for egg size variation across insect taxa (Gilbert & Manica 2010). Nevertheless, adaptive covariation between egg and body size seems to be a likely outcome of selection in species that experience time constraints on female ovispostion. This is further predicted to be pronounced in species evolving under high extrinsic mortality rates (e.g. predation), because selection should favour genotypes that convert their energy reserves into production fast, even if offspring survival increases slowly with increase in egg size.

Conclusions

Developmental rules governing resource allocation to life span and reproduction during ontogeny are ubiquitous among insects, indeed in most organisms, and observed allometries may be a shared result of both adaptive plasticity and physiological predetermination. Similarly, metabolic constraints on biological rates are universal, but the degree to which these physiological properties are hampering any single trait response is difficult to predict. We have here outlined general predictions of adaptive variation in reproductive rate and showed that the resulting optimal allometry in the absence of biophysical constraints is always negative as a result of ecological limitation on reproductive opportunities. We then contrasted these predictions with allometries based on the assump-

tions of rules set by metabolic and developmental processes, both for the general scenario and for the specific case of *P. aegeria*. In both our general model and our simulations on *P. aegeria*, fitness consequences associated with modest variation in reproductive rate were small and further mitigated by adaptive responses in female reproductive behaviour, suggesting potential for behavioural compensation of putative biophysical constraints. Thus, while reproductive rates may commonly be suboptimal, selection on adjusting these rates further may be weak (Fig. 6). To better understand the relative prevalence of biophysical constraints vs. adaptive variation in reproductive rates, we encourage more studies putting quantitative estimates of the allometric scaling of metabolism, life span and reproduction into ecological context. These studies should focus on testing allometry (i) against proper null hypotheses in species where adaptive and neutral hypotheses generated from metabolic theory differ qualitatively, (ii) in species where ontogenetic growth and development of body parts can be measured precisely, (iii) in species where variance in the size of body parts can be partitioned into environmental and genetic components and (iv) in combination with co-evolving behavioural allometries.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Methods and Results for path analysis and survival analysis of laboratory reared females, and egg loads of wild caught females.

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