Egg maturation strategy and survival trade-offs in holometabolous insects: a comparative approach

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One of the key predictions of general life-history theory is that reproduction incurs a survival cost. Although there is a convincing body of evidence to support this prediction at the intraspecific level in insects, evidence at the interspecific level is relatively scarce, as is the case for other animals. By employing two methods of phylogenetically controlled analysis, we demonstrate the existence of a negative correlation between life-span and early life investment in reproduction, across a wide diversity of Lepidoptera. The measure of initial reproductive effort used was the 'ovigeny index', defined as the proportion of the lifetime potential egg complement that is mature (ready to lay) upon female emergence. We present a graphical model for holometabolous insects, illustrating the trade-offs that are hypothesized to occur among capital resources (soma vs non-soma and initial eggs vs storage) in relation to variation in ovigeny index. These trade-offs, for which there is some empirical support, are postulated to underlie the life-span/ ovigeny index relationship observed in the Lepidoptera and also in other insect orders.   © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **90**, 293–302.

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INTRODUCTION

Egg maturation strategy and its associated trade-offs in insects

A key prediction of general life-history theory is that reproduction incurs a survival cost (Roff, 2002). In particular, various allocation models predict a trade-off between life-span and early life investment in reproduction (Gadgil & Bossert, 1970; Van Noordwijk & de Jong, 1986; Zera & Harshman, 2001; Novoseltsev *et al.*, 2002; Roff, 2002). For insects, there is a significant body of empirical evidence to support this prediction at the intraspecific level (Partridge & Farquhar, 1981; Luckinbill *et al.*, 1984; Rose, 1984; Ernsting & Isaaks, 1991; Kaitala, 1991; Kopelman & Chabora, 1992; Tatar, Carey & Vaupel, 1993; Valicente & O'Neill, 1995; Ellers & van Alphen, 1997; Partridge, Prowse & Pignatelli, 1999; Dixon, 2000; and see ref-

erences above), but data relating to the interspecific level are relatively scarce (Kaitala, 1991; Dixon, 2000; Jervis *et al.*, 2001; Pexton & Mayhew, 2002; Jervis, Ferns & Heimpel, 2003). Indeed, for animals as a whole, there are relatively few documented examples of any kind of cross-species reproduction/survival trade-off (Read & Harvey, 1989; Stearns, 1992; Roff, 2002; Jervis *et al.*, 2003). This most likely reflects differences in the intensity of research effort at the two taxonomic levels, rather than the existence of any constraint upon the presence of such a trade-off at the interspecific level.

The question thus remains as to whether a reproduction/survival trade-off occurs more generally. Focusing on holometabolous insects, we ask whether, given the known interspecific early life reproduction/life-span trade-off in the order Hymenoptera (Jervis *et al.*, 2001; Pexton & Mayhew, 2002), such a relationship also exists in another major order, the Lepidoptera. The scattered literature on egg maturation in Lepidoptera (Eidmann, 1931; Labine, 1968; Janzen,

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1984; Boggs, 1986, 1997a; Barbosa, Krischik & Lance, 1989; Sattler, 1991; Miller, 1996) tentatively suggests that it does (Jervis, Boggs & Ferns, 2005a). For example, the winter moth *Operophtera brumata* (L.) emerges with all of its eggs mature, and lives for several days at the most, whereas the zebra longwing butterfly *Heliconius charitonius* (L.) emerges with no mature eggs and can live for several months. However, a rigorous comparative analysis has yet to be undertaken to test whether investment in early life reproduction is negatively correlated with life-span within this order.

THE OVIGENY INDEX

We use the ovigeny index (OI) of Jervis *et al.* (2001) as the measure of early life reproduction in Lepidoptera. OI refers to the proportion of a female's eggs that are ready to lay at adult emergence, and is defined as the initial egg load (fully mature eggs) divided by the lifetime potential fecundity (i.e. OI = 1 denotes that all the oöcytes are mature upon emergence, whereas OI = 0 denotes emergence with no oöcytes ready to lay). OI varies interspecifically not only in Lepidoptera (Eidmann, 1931; Boggs, 1986, 1997a; Jervis *et al.*, 2005a) but also in Trichoptera (Stevens *et al.*, 1999; Stevens, Hansell & Monaghan, 2000), in Hymenoptera (Jervis *et al.*, 2001, 2003), and in Diptera (Oldroyd, 1964; J. C. Deeming, pers. comm.). A continuum of OI occurs among Hymenoptera (Jervis *et al.*, 2001) and apparently also among Lepidoptera (Jervis *et al.*, 2005a).

OI not only measures the degree of early life concentration of lifetime egg production, but also reflects the presumed relative allocation of resources to reproduction by the juvenile and the adult stages (Jervis *et al.*, 2001; Jervis & Ferns, 2004). An OI of 1, or near to 1, indicates that the materials used for egg maturation derive mostly or entirely from stored larval resources. By contrast, an OI of $<< 1$ indicates that the materials for egg maturation derive, at most, only partly from such resources (e.g. in the fat body), with adult feeding being the most likely other source. Nonetheless, in some species with an OI $<< 1$, nutrients absent from the adult diet must still come from larval feeding (Boggs, 1981, 1986, 1994, 1997b; Rivero, Giron & Casas, 2001; O'Brien, Fogel & Boggs, 2002; Casas *et al.*, 2005; O'Brien, Boggs & Fogel, 2005).

Note that, a priori, OI does not perfectly correlate with the absolute amount of resources invested in reproduction at adult emergence, for two reasons: (1) if OI is not 1, immature oöcytes may be partially yolked prior to adult emergence (O'Brien, Boggs & Fogel, 2004) and (2) nontrivial amounts of resources may be contained in the nurse cells (trophocytes) that are associated with the immature oöcytes (Jervis & Ferns,

2004). Despite this, within or among species having equivalent ovarian developmental systems, OI can be taken to correlate with pre-emergence reproductive effort, at least when the latter is measured as the proportion of the adult's biomass that is invested in offspring (for a review of the evidence, see Jervis & Ferns, 2004;).

Variation in OI also has adaptive significance, affecting female age-specific realized fecundity and lifetime reproductive success (Flanders, 1950; Boggs, 1986; Heimpel & Rosenheim, 1998; Papaj, 2000; Roitberg, 2000; Rosenheim, Heimpel & Mangel, 2000; Jervis *et al.*, 2001; Ellers & Jervis, 2003, 2004; Thorne *et al.*, 2006). Furthermore, variation in OI can inform understanding of the evolution and diversity of life-histories (Boggs, 1986, 1990, 1997a; Gilbert & Jervis, 1998; Jervis & Vilhelmsen, 2000; Jervis *et al.*, 2001, 2005a; O'Brien *et al.*, 2004; Thorne *et al.*, 2006). Table 1 summarizes empirical and theoretical studies providing support for the view that there are adaptive suites of correlated traits involving initial reproductive investment, together with associated resource trade-offs, both within and between species.

MATERIAL AND METHODS

OIs were assessed for Lepidoptera using the methods of Jervis *et al.* (2001) applied to data reported in the literature. Where several OI values were available for a species (intraspecific variability in OI of insects is discussed by Ellers & Jervis, 2003, 2004; Jervis & Ferns, 2004; Thorne *et al.*, 2006), we used mean values. For adult life-span, we used mean values recorded under laboratory conditions. Combined OI and life-span data were extracted for 27 species distributed among 24 genera, nine families and, six superfamilies.

The taxonomic distributions of OI and life-span among the Lepidoptera in our database (for the full version, see Jervis *et al.*, 2005a) suggest that we are dealing with phylogenetically constrained traits. For example, extremely long-lived species are found only within the superfamily Papilionoidea, and an OI = 1 is confined to moths (six out of the 13 families for which we have OI data) (Jervis *et al.*, 2005a). Phylogeny therefore needs to be taken into account in our analyses. A composite cladogram (Fig. 1) was compiled from Minet (1991), Kristensen & Skalski (1996), G. S. Robinson (pers. comm.) (basal relationships within the order), Fang *et al.* (2000) (Noctuoidea), de Jong, Vane-Wright & Ackery (1996), Wahlberg, Weingartner & Nylin (2003), Wahlberg *et al.* (2005) (Papilionidae), Caterino *et al.* (2001) (Papilionidae) and Brower (2000) (Nymphalidae).

Among animals generally, life-span is expected to correlate with body size (Calder, 1984; see also Read & Harvey, 1989) and, in one group of nonlepidopteran

Table 1. Empirical and theoretical studies showing correlations between the degree of egg maturation achieved by newly-emerged females, and other adult life-history traits, related to resource allocation and acquisition, in holometabolous insects

Correlated trait	Study
Resource allocation	
(a) Life-span/longevity	Eidmann (1931); Flanders (1950); Labine (1968); Janzen (1984); Boggs (1986, 1997a); Barbosa *et al.* (1989); Sattler (1991); Miller (1996); Jervis *et al.* (2001, 2003); [Ellers & van Alphen, 1997; Pexton & Mayhew, 2002]
(b) Egg type	Jervis *et al.* (2001)
(c) Allocation of abdominal resources to storage (fat body) vs eggs	[Ellers & van Alphen (1997); Pexton & Mayhew, 2002; Ellers & Jervis, 2003*, 2004*]
(d) Egg resorption capability	Jervis *et al.* (2001)
(e) Importance of nuptial gifts to female reproduction	Boggs (1990)
(f) Body size	Jervis *et al.* (2003) [Ellers & Jervis, 2003*, 2004*, Thorne *et al.*, 2006]
Resource acquisition	
(a) Mouthpart structure	Eidmann (1931); Gilbert & Jervis (1998)
(b) Adult feeding habit	Eidmann (1931); Flanders (1950); Boggs (1986); Jervis & Kidd (1986); Jervis *et al.* (1993); Jervis, Kidd & Heimpel (1996); Miller (1996); Gilbert & Jervis (1998); O'Brien *et al.* (2004)
(c) Host fidelity in parasitoids	Roitberg (2000)*
(d) Proportion of attacked hosts fed on by the parasitoid female (degree of 'host-feeding').	[Jervis & Kidd, 1986*]

Theoretical studies (modelling) are denoted by an asterisk. 'Egg type' is the degree of yolk-poorness**,** linked to the need, by the eggs of some parasitoids, to absorb host fluids. Studies in parentheses report correlations at the intraspecific level.

insects, OI has been shown to decline interspecifically with increasing body size (parasitoid wasps: Jervis *et al.*, 2003; Jervis & Ferns, 2004). Therefore, there was an a priori assumption that body size (a major determinant of the total amount of capital resources derived from larval feeding and that are allocatable to either reproduction or survival) has the potential to contribute to an OI/life-span relationship among Lepidoptera. To test for an effect of female body size on OI and/or life-span, we used data on body mass at emergence, gathered from the literature (Jervis *et al.*, 2005a) and from unpublished laboratory records (C. L. Boggs and D. A. Andow, unpubl. data). Data were obtained for the majority of lepidopteran taxa within our database: 16 species, 15 genera, six families, and five superfamilies.

We used two methods of analysis in testing our hypotheses: (1) the method of independent comparisons (Harvey & Pagel, 1991), on the grounds that it made the most efficient use of our database and (2) the test of correlated evolution between a continuous and a dichotomous variable (Purvis & Rambaut, 1995), because most ($N = 18$) of the species in our database have an OI = 0, and this might bias any regression obtained by method (1). In applying the latter method to the relationship involving OI and body mass, and

also that involving OI and life-span, the comparison was made between extreme synovigeny *sensu* Jervis *et al.* (2001) (OI = 0) and other values of OI (i.e. OI > 0). This yielded more comparisons than when comparing OI = 0 with OI = 1.

All variables were transformed to logarithms to achieve normality. The test using Purvis & Rambaut's method (1995) was one-tailed in the case of the life-span/OI relationship, our expectation being that low-OI species are longer-lived than high-OI species. All branch lengths were set to one in the analysis because they are known for only a small fraction of the clades in Figure 1.

RESULTS

Data on female body mass were available for 15 independent contrasts between female body mass and either life-span or OI. There was no significant relationship between body mass and life-span ($F_{1,14} = 0.30$, $P = 0.591$) or between body mass and OI, in the latter case using both the independent comparisons method ($F_{1,14} = 0.12$, $P = 0.738$) and Purvis & Rambaut's method (paired *t*-test, $t_4 = 2.46$, two-tailed $P = 0.133$). Variation in body mass therefore does not underly the life-span/OI relationship recorded here (see below).
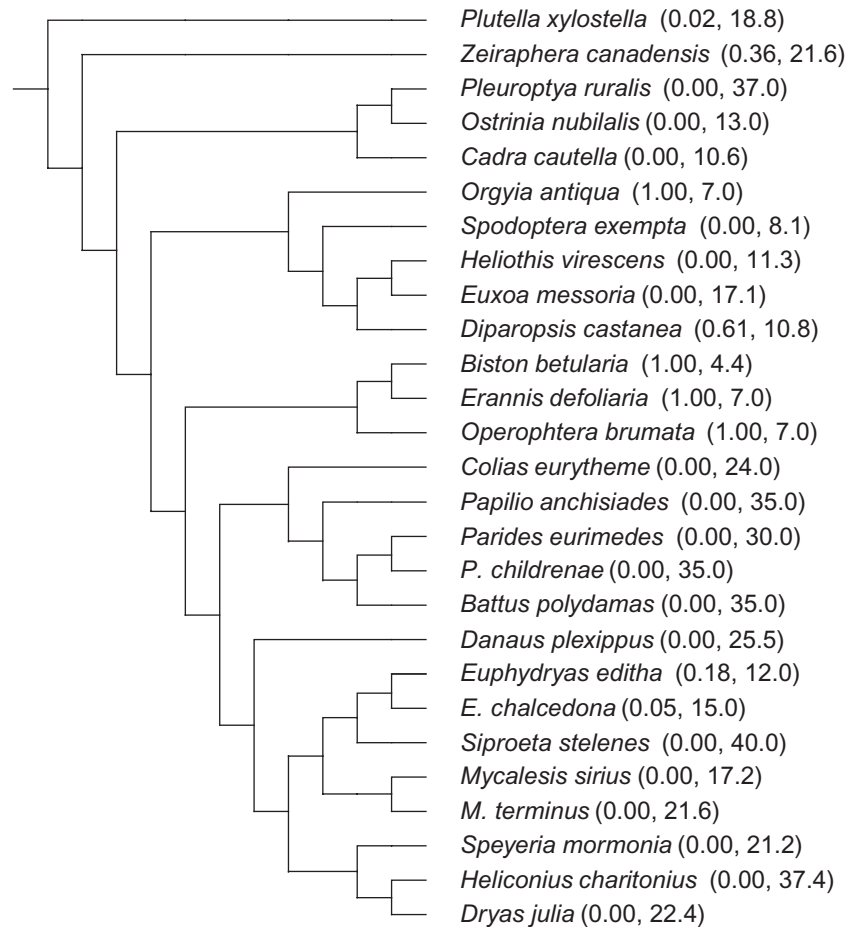
Figure 1. Composite phylogeny of the Lepidoptera used in the statistical analyses (see text for details). Mapped onto the cladogram, in parentheses, are mean ovigeny index and mean life-span in days (in that order) for each species.

Twenty-six independent contrasts between life-span and OI were available for testing our main hypothesis by means of the method of Harvey & Pagel (1991). Using these, life-span and OI were significantly negatively correlated (line forced through the origin, slope = −0.266, $F_{1,25} = 6.72$, $P = 0.016$) (Fig. 2). OI accounted for 21.2% of the variation in life-span. Using the method of Purvis & Rambaut (1995), life-span was significantly longer in extremely synovigenic (OI = 0) evolutionary lines (paired *t*-test, $t_{10} = 2.67$, one-tailed $P = 0.022$; geometric means: 21.7 days and 11.0 days for OI = 0 and OI > 0, respectively).

Thus, the empirical data support our hypothesis of a trade-off between survival and initial (capital) investment in reproduction among Lepidoptera.

Hierarchical analysis of variance showed that the largest percentage of the variation in both OI and life-span occurred at the level of the superfamily within the order (69.6% and 68.7%, respectively). The smallest percentage of the variation in OI was at the level of the family within the superfamily (3.3%), and of life-span at the level of the genus within the family (6.6%).

DISCUSSION

Using rigorous methodologies applied to a phylogenetically diverse array of species, we have shown that life-span and the degree of egg maturation at adult emergence, as measured by OI, are inversely related among Lepidoptera. It was by no means a foregone conclusion that a negative correlation between survival and reproduction would emerge from a comparative analysis of the type conducted here because it is possible for positive empirical correlations to be recorded between traits that are expected to trade-off in a functional sense (Van Noordwijk & de Jong, 1986; Zera & Harshman, 2001).

There is no evidence that interspecific variation in body size underlies the observed relationship because female body mass did not correlate with either life-span or OI.
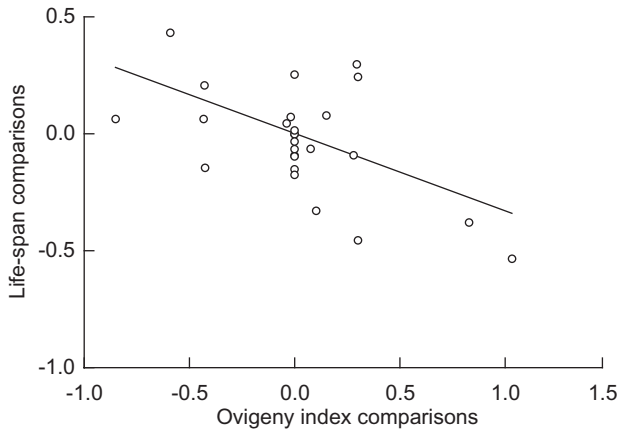
Figure 2. The relationship between log life-span and log ovigeny index, revealed by the method of independent comparisons (Harvey & Pagel, 1991). With this method, an independent comparison or 'contrast' is obtained from each node in the phylogeny for each measured variable. These independent contrasts (not the individual taxa) are used in statistical comparisons, thereby avoiding the pseudoreplication that would otherwise occur as the result of trait variation (in both life-span and ovigeny index) being phylogenetically constrained (see text).

Figure 3. Graphical model of allocation of initial (capital) resources, pre-emergence, in relation to ovigeny index. The model integrates the hypothesis of Boggs (1981) with the ovigeny 'concept' of Jervis *et al*. (2001). The resources are: soma ('sturdy body'; Boggs, 1981) (dotted line) and 'non-soma' (continuous line). Soma comprises body structures other than internal reproductive tissues, oöcytes and nutrient stores. 'Initial eggs' refers to the amount of energy or biomass contained in the fully chorionated oöcytes present in both ovaries.

Blackburn (1991) and Jervis *et al*. (2003) similarly found no relationship between body size and life-span among parasitoid Hymenoptera. Although Jervis *et al*. (2003) showed body size and OI to be negatively correlated among such insects, this trade-off is probably largely attributable to factors that relate specifically to the interaction between parasitoid size and the availability (abundance and spatial distribution) of insect hosts (Jervis & Ferns, 2004), and which might not play an equivalent role in shaping the life-histories of herbivores such as Lepidoptera.

The OI/life-span relationship may be a characteristic of holometabolous insects generally. As noted in the Introduction, OI and life-span are negatively correlated among members of another major insect order, the Hymenoptera. The available data suggest a similar trade-off occurs among caddis flies (order Trichoptera) (Novak & Sehnal, 1963; D. J. Stevens and J. Jannot, unpubl. data).

Based on the hypothesis of Boggs (1981), differential allocation of capital obtained from larval feeding can be taken to underlie the interspecific OI/life-span trade-off occurring within insect groups. In accordance with this hypothesis, species whose females are shorter-lived should, all else being equal, invest more resources during metamorphosis in reproduction (non-soma) at the expense of building a 'sturdy body' (i.e. soma, defined as body structures other than internal reproductive tissues, oöcytes, and nutrient stores) (Boggs, 1981). Among Lepidoptera, the restriction to
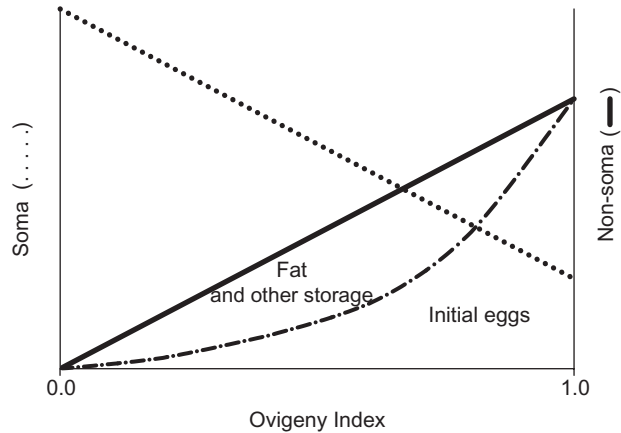
very high-OI species of female winglessness and the associated reduction in thoracic musculature (Sattler, 1991) can be regarded as further evidence of a link between egg maturation strategy and the trade-off between soma vs non-soma. Currently, the allocation pattern among species of Hymenoptera is not known. However, in the two species of Trichoptera studied by Stevens *et al*. (1999, 2000), relative allocation between soma and non-soma is correlated with the interspecific OI/life-span trade-off that is apparent among these insects.

Information on the pattern of allocation within non-soma in relation to OI is currently available only at the intraspecific level, in the parasitoid wasp *Asobara tabida* (Nees). In this species, a trade-off occurred between initial egg load and the quantity of fat reserves, both within and among populations (Ellers & van Alphen, 1997). Furthermore, within a north–south cline in western Europe, as OI increased, allocation to eggs increased at the expense of allocation to storage, and vice versa, with the result that low-OI females were longer-lived, in accordance with the interspecific OI/life-span relationships recorded for parasitoid wasps (Jervis *et al*., 2001).

The clinal population differences in *A. tabida* suggest that a similar OI-linked trade-off within non-soma is likely to occur at the interspecific level in insects. This has yet to be determined, but it is noteworthy that the parasitoid wasp *Aphaereta pallipes* (Say), when compared size-for-size with its congener

Aphaereta genevensis (Fischer), has a higher initial egg load, smaller fat reserves, and a lower longevity when deprived of adult food (Pexton & Mayhew, 2002).

Figure 3 integrates the model of Boggs (1981) with the empirical evidence on OI-related allocation, and illustrates the trade-offs that occur among capital resources at two levels among holometabolous insect species: soma vs non-soma and initial eggs vs. storage. The trade-off between soma and non-soma is straightforward, being directly based on the hypothesis of Boggs (1981); for empirical evidence, see above. Regarding the second trade-off, the proportionate allocation to reserves is predicted to be generally lowest for insect species with an OI at either of the two extremes, and highest for species with an intermediate OI (Fig. 3). The prediction for species with OI = 0 might appear counter-intuitive because the longer life expectancy of females can be seen as imposing a greater nutrient demand upon reserves (Jervis *et al*., 2001). However, a longer life provides greater opportunities for exogenous nutrient acquisition, which would reduce the requirement for storage (Boggs, 1981). In support of this, newly-emerged migratory monarch butterflies, *Danaus plexippus* (L.), have small fat reserves that more than double in quantity later on in female life (Brower, 1985). The predicted allocation at OI = 1 is, by contrast, more easily understandable: minimal, if any, reserves are needed because egg maturation is total and expected life-span is short, with the former reducing the requirement for reserves, and the latter reducing the time available to utilize them.

Our model should be considered as highly provisional. The assumption of rectilinearity in the allocations to soma and non-soma is likely to be incorrect. Also, we know of some exceptions regarding the hypothesized allocation to fat body. Nontrivial allocation occurs in cyclorraphan flies having an OI = 0 (Spradbery & Sands, 1981) and in diprionid sawflies and lasiocampid moths having an OI = 1 (Leverton, 2001; Herz & Heitland, 2002). For low-OI species, possible causal factors include: (1) marked stochasticity in the availability of foods (e.g. nectar sources) to adults; (2) insufficient carry-over of key egg production nutrients that are absent from the adult diet; and (3) the occurrence of reproductive diapause. For high-OI species, possible causal factors include a risk-aversive strategy in relation to time-limitation that results from stochasticity in oviposition opportunities (this does not apply to parasitoid Hymenoptera) (Jervis *et al*., 2005a). Also, a strategy of allocating little or none of the carried-over resources to fat (the main carried-over reserve; Chapman, 1998) may not be possible for Hymenoptera 'Parasitica' generally because it appears that such insects are incapable of lipogenesis (Giron & Casas, 2003). Furthermore, relative allocation between initial eggs and reserves is likely to vary with body mass among parasitoid wasp species (note that both initial egg load and ovigeny index are negatively correlated with body size in such insects, Jervis *et al*., 2003). The generality of our model thus needs to be rigorously tested by comparative analyses of OI and life-span, coupled with biochemical measurements, performed on an extensive and diverse set of species, including some chosen from within each of the remaining holometabolous orders, particularly the biologically very diverse orders, Diptera and Coleoptera.

Note also that our model applies to insects experiencing optimal nutritional conditions as larvae, as do the data used in the empirical analyses, at least as far as we could ascertain. It is likely that, under natural conditions, many insect species will commonly experience some degree of larval nutritional stress due to factors such as reduced host quality (herbivores and parasitoids), prey scarcity (predators) (Strong, Lawton & Southwood, 1984; Jervis & Boggs, 2005; Jervis, Copland & Harvey, 2005b; Mevi-Schutz & Erhardt, 2005) and disturbances (Stevens *et al*., 1999, 2000). As well as reducing the amount of carried-over resources (via a reduction in body size, Pexton & Mayhew, 2002; Ellers & Jervis, 2003, 2004), such stress likely brings about an alteration, at the intraspecific level, in the shape of each of the two major trade-offs shown in Figure 3: that between soma and non-soma (e.g. on Trichoptera, Stevens *et al*., 1999, 2000; on Lepidoptera, Boggs & Dau, 2004), and that between initial eggs and storage (Pexton & Mayhew, 2002; Ellers & Jervis, 2003). A consequence of a change in the latter trade-off would be an alteration in OI, which is a prediction of dynamic programming models (Ellers & Jervis, 2003, 2004). Such phenotypic plasticity has been shown to be adaptive for caddis and parasitoid wasps (Stevens *et al*., 1999, 2000; Ellers & Jervis, 2003, 2004).

Despite the aforementioned caveats, the graphical model has heuristic value; first, by providing a preliminary framework for understanding allocation rules used by holometabolous insects in relation to reproductive strategy and, second, by pointing to the need for future investigators to address the integration of resource allocation, acquisition, and utilization over the life-cycle, rather than focus solely on the adult. The results of a recent study by Mevi-Schutz & Erhardt (2005) on the map butterfly (*Araschnia levana* L.), strengthen the case for such an approach; see also Stevens *et al*. (1999, 2000) and Jervis & Boggs (2005).

The most significant insights into the form and adaptive significance of the relationship between OI and pattern of resource allocation would be gained through the use of the mathematical technique of sto-

chastic dynamic programming, rather than through elaboration of our graphical model. The former approach would enable integration of intraspecific variability in carry-over of resources with state-dependence in individual female foraging behaviour and the stochasticity the females face with respect to both oviposition site and adult food availability. Ideally, such modelling should take account of: (i) females of synovigenic species (i.e. OI < 1) drawing upon a diverse set of biochemical resources in fueling somatic functions and egg manufacture (pro-ovigenic species, i.e. OI = 1, need to fuel only somatic functions); (ii) these resources being utilised to differing extens with respect to particular physiological functions; and (iii) individuals altering their pattern of utilisation when exogenous nutrients are limiting (Casas *et al.*, 2005; O'Brien *et al.*, 2002, 2004, 2005; Bernstein & Jervis, in press).

Our study is predicated on the assumption that OI, being a quantitative measure of investment of capital in early life reproduction, participates in functional (i.e. physiological) trade-offs between life-history traits that draw upon a common, limited pool (whole body at one level, non-soma at the other level) of resources (Van Noordwijk & de Jong, 1986; Zera & Harshman, 2001; Roff, 2002). However, we should stress that variation in initial allocation to reproduction, and thus variation in OI, might not necessarily be driving variation in other traits such as life-span. Additionally, a negative correlation between life-span and early life reproductive effort can theoretically be explained without invoking any resource trade-off (Stearns & Hoekstra, 2000; Weinert & Timiras, 2003). Furthermore, the resource limitation basis of negative correlations involving reproduction has recently been challenged by findings from both the nematode *Caenorhabditis elegans* (Maupas) and the fruit-fly *Drosophila melanogaster* Meigen, although the implication for resource allocation as an ultimate factor in the evolution of trade-offs is not yet clear (Barnes & Partridge, 2003; Barnes *et al.*, 2005). Our approach assumes trade-offs to have evolved in the context of a given range of resource availability, imposing at least some degree of resource limitation, which in our view is valid whether or not resource limitation is in fact the ultimate cause of the observed intertrait relationship.

Beyond the obvious need for more thorough statistical tests (e.g. incorporation of data, which are mostly lacking, on branch lengths in the phylogeny we used) and also further empirical information on the relative allocation of resources at each of the two levels in the trade-off hierarchy, the OI/life-span negative correlation obtained here is, by itself, insufficient for a full understanding of any underlying functional trade-off. The latter must be validated by physiological studies involving: (1) hormonal manipulation (Zera & Harshman, 2001; Zhao & Zera, 2002; Zera, 2003) and (2) nutrient tracking techniques (Casas *et al.*, 2005; O'Brien *et al.*, 2002, 2005; O'Brien, Boggs & Fogel, 2003), or preferably both of these approaches, applied to individual species. The underlying genetic control is also of interest. Nonetheless, the results of our analysis, when considered along with the empirical evidence assembled here, shed important light on the resource allocation rules used by holometabolous insects.

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