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Comparing parasitoid life histories

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Abstract

Species and clades are characterized by their unique combinations, or suites, of different life history traits. In parasitoids, traits include a core group common to other organisms, and a parasitoid-specific group. These organize into several sets of mutually covarying traits which overlap a little, but not wholly, with other sets. Across parasitoid species, host size, clutch size and body size tend to covary. Roughly independent of these is a dichotomy between idiobionts (host does not develop after parasitization), which tend to have fast development but slow adult life histories, and koinobionts (hosts develop after parasitization) with the opposite set of traits. Consistent links between the dichotomy and host characteristics remain elusive. A low ovigeny index (low allocation to early reproduction) is found in idiobionts, and is a predictor of some of the dichotomous set, but also more host feeding, egg resorption, solitary development, and larger bodies. Variation in fecundity, in taxonomically-restricted studies, is predicted by the host stage attacked, but this is not reflected in taxonomically-broad studies. The reasons behind trait co-variation are only partly understood. Analyses of evolutionary lability suggest that variation in development mode and body size tends to be clustered within higher taxonomic levels, with variation in other traits such as lifespan, fecundity and egg size more evenly distributed across taxonomic levels. Thus, taxonomically constrained radiations of parasitoids tend to retain a particular suite of traits that revolve around fundamental shifts in hosts and their use that occur relatively rarely. Parasitoids illustrate how the fast-slow continuum can be much less extensive than in mammals, how the ecology of the host affects the life histories of parasitic organisms, how different taxa require different life history theories, and how understanding resource allocation in early adult life can help explain life history variation.

Introduction

“Suite: a group of things forming a unit or constituting a collection.” (Webster’s New Collegiate Dictionary)

The life history of an organism describes the way it develops, reproduces, and when it can expect to die. Variation in life histories represents some of the most striking phenotypic differences across species, and a considerable challenge to explain in Darwinian terms (Stearns, 1992; Charnov, 1993; Roff, 2002). This is the realm of life history theory. The variation in life histories across species is exemplified by insect parasitoids, which develop to maturity by feeding on, eventually killing, the body of another host arthropod (Godfray, 1994). They are amongst the most species rich taxa (Santos & Quicke, 2011) and include the smallest living insects (species of Mymaridae, some <0.2mm long) as well as the impressive ichneumonids of the genus *Megarhyssa*, which may be 150mm long including a 100mm ovipositor (Quicke, 2015). They exploit one of the most varied biological resources on Earth (other insects and some other arthropods), and do so in an impressive variety of ways (Gauld & Bolton, 1988; Godfray, 1994; Quicke, 1997; Jervis & Ferns 2011).

In this paper I review how we have described and explained cross-species variation in insect parasitoid life histories, focussing on the parasitic wasps (Hymenoptera: Apocrita). I restrict myself to comparative studies which use species, or occasionally higher taxa, as datapoints. Most of the time the species are parasitoids, although some of the time they are hosts (whose parasitoid communities are compared e.g Hawkins 1994). Most of these studies have attempted to control for phylogenetic relationships (Harvey & Pagel 1991), although some of the older ones did not.

Although cross species variation in life histories is large (Table 1), often so too is intraspecific variation (e.g. Harvey et al., 1994; Guinnee et al., 2005; Pexton & Mayhew, 2005; Thorne et al., 2006; Wajnberg et al,.2012). Since the focus of comparative studies is understanding cross-species variation, intraspecific variation tends to be ignored, and will contribute to the error term of analyses where species averages are less accurately estimated as a result. Intraspecific variation however can be used to test hypotheses experimentally and thus contributes powerfully to the general theory which comparative studies also attempt to build.

Below I first introduce the life history traits in which parasitoid biologists are interested, and some life history paradigms that describe trait variation across species. I summarize what we know about the associations between traits, which I term "the suite". Finally I summarize challenges to understanding the evolution of life history suites in parasitoids.

Traits

Life history theory tends to focus on obvious measurable traits found widely across taxa. Several of these are found in parasitoids, meaning that general theory can potentially contribute towards an understanding of parasitoids, and that parasitoids can influence general theory. The general traits include offspring size (egg size), development time (pre-adult lifespan), adult body size, offspring number in a reproductive event (clutch size), the interval between reproductive events (oviposition rate), lifetime fecundity and adult lifespan (both normally female) (Table 1).

The sex ratio might be considered a core life history trait (Charnov, 1993), and in parasitoids can sometimes be linked quite well to some other general life history traits (Griffiths & Godfay, 1988; Hardy & Mayhew, 1998, West & Sheldon, 2002; but see Lewis et al., 2010). However, it is generally not included in comparative studies involving several of the above traits. This may be because of the relatively low population sex ratio variation shown by birds and mammals, which tend to dominate comparative life history studies. Furthermore, many of the important factors affecting cross-species variation in sex ratio (such as mating structure) are unlikely to appear in broad parasitoid datasets, or are expected to exert very taxon-specific effects (Smart & Mayhew, 2009). For the above reasons, I do not consider the sex ratio further below. Likewise, dispersal ability and dormancy are important life history traits with their own theory (Mayhew, 2006). Because of theoretical links with both the sex ratio and lifespan-fecundity, dispersal propensity probably deserves a wider consideration than it has currently received (see Asplen et al., 2009), but in practice is rarely estimated for large numbers of species (see Hardy & Mayhew, 1998 for an exception) and I shall not consider it more below.

Some life history traits are known to be dependent on temperature (e.g. development time) or to vary with latitude (e.g. Hawkins, 1994; Traynor & Mayhew, 2005a), and to account for this effect, Blackburn (1990) noted if the species in his dataset were tropical or temperate. Geographic variation in life histories is prominent in some other groups (e.g. Smith & Lyons, 2011).

Traits in comparative parasitoid life history studies also include some more particular to parasitoids (Table 1). These include ecto/endoparasitoidism (whether the juvenile parasitoid develops outside or inside the host) and idio/koinobiosis (whether the host does not continue to develop after parasitization, or does so). As a short-hand way of referring to these two traits together (they are often closely correlated), I refer to them below under the umbrella of “development mode” (following Mayhew & Blackburn, 1999).

A related trait is the type of egg: hydropic (with insufficient resources for embryogenesis, the rest taken from the host) and anhydropic (sufficient resources for embryogenesis), which can be taken as a rough indication of the investment per egg, and is often known or inferred when precise measurements of egg size are not reported (Jervis et al., 2001). Hence it is sometimes used as a proxy for offspring size.

Similarly, in order to improve data completeness, a proxy measure of clutch size is sometimes taken; that of solitary or gregarious development (e.g. Mayhew, 1998a; Traynor & Mayhew, 2005a; Jervis & Ferns, 2011). In solitary species, only one offspring successfully develops per host, whilst in gregarious species several may develop. This is often taken as indicating a small clutch size in solitary species but a larger one in gregarious species. It is often assumed that solitary species eliminate rivals by contest competition (Mayhew, 1998a), but many species of parasitoids with more scramble-style larval competition are also facultatively solitary (Mayhew, 1998b,c; Mayhew & Hardy, 1998), hence solitary development does not perfectly indicate the form of larval competition.

An index of allocation to early life reproduction in insects, the ovigeny index, (Jervis & Ferns, 2004) has proven useful in explaining life history variation in parasitoid wasps (Jervis et al., 2001; Jervis et al., 2003; Jervis & Ferns, 2011) and other insects (Jervis & Ferns, 2004; Jervis et al., 2005; Jervis et al., 2007a,b), and has formed the basis of some comparative life history datasets. The ovigeny index is estimated from data on the number of eggs ready to be laid on adult emergence, divided by the maximum potential fecundity. It emerged as a continuous trait to replace the previously used dichotomy of pro/synovigeny (eggs all matured by the start of adult life, versus some matured during adult life), when it was realized that the degree of synovigeny (measured via the ovigeny index) was highly variable across species whilst pro-ovigeny was very rare (Jervis et al., 2001).

Other more-parasitoid-specific traits include whether the adult female parasitoids feed on hosts, as well as characteristics of the hosts attacked. Hosts may be attacked in their different developmental stages (e.g. egg, larva, pupa or adult – adult parasitoids are unusual), the host niche may be concealed or exposed to various degrees (e.g. Blackburn, 1991a,b), and the host species may be of widely different body sizes (data absent in Blackburn (1990) and Jervis & Ferns (2011), but present in Traynor (2004), Le Masurier (1987) and Mayhew & Hardy (1998)). Time spent as a pupa is also of interest in some analyses and has received special focus (Blackburn 1991a, Jervis et al., 2011).

Although host range is a major life history feature of parasitoids that is predicted to be correlated with other life history traits (e.g. Askew & Shaw, 1986) as it is in Lepidoptera (Jervis et al., 2007b), there are considerable problems assembling parasitoid host range in large comparative datasets. Problems include errors of host recording in the original data, and variation in the study effort of different parasitoid species. So far, only one large multi-trait dataset (Traynor, 2004) has attempted to include it, though some more restricted studies have addressed it (e.g. Sheehan & Hawkins, 1991). Sometimes studies use idio/koinobiosis as a proxy for host range under the assumption that this is consistently associated with host range (e.g. Hawkins, 1994). Mortality rates in adults and juveniles are notable by their absence in broad comparative datasets, as are measures of host densities. These traits are likely to exert important selective effects on parasitoid life histories (e.g. Price, 1973, 74; Ellers et al., 2000; Ellers & Jervis, 2003, 2004), but are sparsely measured. Measures of host concealment and host-stage attacked are sometimes used as proxies for both, though possibly not effectively (e.g. Jervis et al., 2012).

As can be seen from a comparison of existing datasets (Table 1), the existing data are extremely gappy. Better known traits include easily-scored variables such as body length, temperate or tropical distribution, endo/ectoparasitism, idio-/koino-biosis, solitary/gregarious development, egg type, host adult body size, host stage attacked and host concealment. Other traits which require more detailed measurements, such as oviposition rate, egg size, and lifetime fecundity, are sometimes less well known.

Having introduced many of the traits of interest in parasitoids, I now briefly describe some explanatory frameworks which may make sense of some of them.

Potential explanatory frameworks

The *r*/*K* selection paradigm (MacArthur & Wilson, 1967; Pianka, 1970) assumes that life histories are selected according to the population dynamic type (*r* populations being rapidly increasing, *K* those at equilibrium), predicting that the former selects for "fast" life history traits such as high fecundity, with consequent small offspring size, rapid development with consequent small adult size, and frequent reproduction with consequent low adult lifespan. The *r*/*K* paradigm was popular for a decade, but has since waned because of doubts over its underlying assumptions (see Stearns 1977, 1992). However, the "suite" of associated life history traits embodied by the paradigm is still commonly proposed to exist, though the "*r*/*K* " label has been largely dropped in favour of the term "fast-slow continuum" (see Jeschke & Kokko, 2009).

Modern theoretical explanations for the fast-slow continuum often make use of metabolic scaling theory (see Brown et al., 2004). This allows us to predict how a multitude of traits will co-vary when optimizing a smaller number of traits like age and size at maturity under a given environmental constraint, such as a particular rate of adult mortality (e.g.Charnov, 1991; Kozlowski & Weiner, 1997; see Harvey & Purvis, 1999). This predictive power comes from the fact that metabolism is affected by body mass in well-defined ways. Changes in body mass therefore have predictable consequences on other traits that depend on metabolism, such as development time and potential fecundity (Brown et al., 2004). Given this, it is legitimate to ask if such traits are associated in the predicted way in parasitoids (for example a positive association between body mass and development time) (Blackburn, 1991a).

Balanced-mortality expresses the principle that in any population at equilibrium, mortality and fecundity should be balanced. Hypothetically, either of these two traits could act as a constraint to which the other responds. For example, in Charnov's (1991) model of female mammal life histories, fecundity is determined by adult body size, and juvenile mortality rates are presumed to simply equalize fecundity, an assumption that does a good job of predicting cross-species variation in these traits (Harvey & Purvis, 1999). However, many life history models make the opposite assumption; that mortality schedules select for a particular fecundity (Stearns,1992). In general, life history models emphasize the importance of considering both adult and juvenile mortality, because the difference between the two exerts a strong selective force (Stearns, 1992): for example increasing adult mortality relative to juvenile mortality can select for delayed maturation and hence higher fecundity in fish (Law & Grey, 1989) and semelparity in plants (Young, 1990). It is a pity that no life history models in parasitoids have explicitly considered the effects of independently varying externally imposed juvenile and adult mortality rates, hence the precise selective effects of mortality risks are not well-bedded in parasitoid-specific theory, even though predictions have been made about empirical patterns (Jervis et al., 2012).

Another interesting (physiological) paradigm that has come to be applied to life histories is that of capital- versus income breeding (Drent & Daan, 1980; Bonnet et al., 1998; Stephens et al, 2009). The paradigm developed from studies of endothermic vertebrates, and refers to whether a species uses primarily stored energy ("capital") to power reproductive effort, or whether organisms power reproduction by foraging at the same time ("income"). In endothermic vertebrates, where reproduction is expensive but forage not always available (e.g. in incubating birds or lactating mammals), this dichotomy has proved useful in explaining certain differences in behaviour across species, such as seasonality of breeding in primates (Brockman & van Schaik, 2005). Bonnet et al. (1998) have argued however that the concept also has relevance in ectotherms. Some insects do not feed as adults, and so are obvious capital breeders. The distinction between non-feeding and feeding adults, and other morphological proxies, have thus been used as predictors of other traits, for example in Lepidoptera (Tammaru & Haukioja, 1996; Jervis et al., 2005; Javois et al., 2011; Molleman et al., 2011).

In parasitoid wasps, the ovigeny index is likely to partially indicate capital or income breeding; pro-ovigenic species seem naively to be capital breeders as the eggs are fully developed before adulthood, though females may still feed to power host- and mate-finding (Jervis et al., 2008). Synovigenic species however can power egg maturation by either stored fat or other larval reserves, or from sources harvested during adulthood, for example by host feeding (see Casas et al., 2005; Jervis et al. 2008), so whilst they may tend more towards income breeding, the link between ovigeny and capital/income breeding is likely to be imperfect. Host feeding is thus another proxy that may relate to income breeding, since many parasitoids are apparently incapable of lipogenesis (Visser et al., 2010), and fats and proteins are a necessary component of eggs, whilst the most readily available foods available to adult parasitoids are sugars in nectar and honeydew (Jervis et al., 2008). One might therefore expect the ovigeny index and host feeding to be useful predictors of other life history traits, based on the utility of the capital/income distinction in other groups.

Studies on non-parasitoid taxa have shown that group-specific dichotomous traits can account for much of the variation in other traits across species. In birds, for example, whether a species is ground-nesting or not appears to account for much of the variation in other traits (Bennett & Owens, 2002). Furthermore, these traits are not phylogenetically labile, so that birds consist of a relatively small number of clades with quite divergent combinations of traits: one might argue that there is no simple life history suite but essentially two distinct sets of suites. In parasitoids, there are several potential categorical traits that may act in such a way, including solitary/gregarious development (Mayhew, 1998a), idio/koinobiosis and ecto/endoparasitoidism (Godfray, 1994), and host stage attacked (Price, 1974).

Most prominent has been the development of the “dichotomous hypothesis”, which originated from the comparison of life history traits in ecto/endoparasitoids (e.g. Askew, 1975), then extended to include host range as a response variable and idio-/koinobiosis as a predictor variable (Askew & Shaw, 1986, see above), and then extended further to include an array of other response variables (Gauld & Bolton, 1988; Blackburn, 1991b; Godfray, 1994; Quicke, 1997; Mayhew & Blackburn, 1999; Jervis & Ferns, 2011). In its broadest form, this proposes that idiobionts will tend to: take less time to develop, lay larger eggs, be ectoparasitoids, live longer as adults, be smaller, be less fecund, lay eggs less rapidly, have a lower ovigeny index, be more likely to host feed, lay eggs on more concealed hosts, attack later host stages and attack a broader host range than koinobionts. Some behavioural traits have also been suggested including nocturnal/diurnal flight, and the degree of sex allocation in response to host size and consequent sexual size dimorphism (Quicke, 1997). The supposed driving forces behind these differences are many, including avoidance of juvenile predation and host degradation on immobile hosts, reduced co-evolution of physiological interactions with hosts, selection for smaller egg size in endoparasitoids, hence selection for pro-ovigeny and less host feeding, and reduced longevity afforded by diversion of larval resources away from fat reserves into eggs (see Blackburn, 1991b; Godfray, 1994; Jervis & Ferns, 2011).

In all life history problems, trade-offs and constraints underpin the optimal outcome. The parasitoid is unlike a typical harvesting organism, such as a photosynthesizing plant, or an animal that develops to maturity by consuming a, potentially infinite, number of meals. Such organisms have the essentially open decision of defining their body size at reproductive maturity by simply deciding at what age and size to divert resources into reproduction instead of growth, with no prescribed resource-based maximum size. In parasitoids and other similar organisms, the single host, constrains the resources for development (even in koinobionts), and hence the maximum adult body size. In gregarious parasitoids, there is the additional constraint of dividing the host resources across the rest of the developing brood (see Mayhew & Glaizot, 2001; Crowley & Saeki, 2009). Hence a trade-off between offspring size and number is expected after accounting for the size of the host (e.g. Hardy et al., 1992), whilst a positive correlation between parasitoid body size and host body size is expected, especially in solitary species. Development time should be longer for those attacking larger hosts and longer for koinobionts, which may have delayed development (Blackburn, 1991a). Following the principle of minimizing time spend in vulnerable life history stages (Stearns, 1992), we might expect development time to be correspondingly shorter in those exposed to greater mortality risks (Blackburn, 1991a).

For the adult parasitoid, given that maturity is already reached, the major life history decision is one of allocation of stored resources to immediate current reproduction (eggs), or future survival and reproduction (e.g. fat) (Ellers, 1996;, Jervis et al. 2005; Jervis et al., 2008), which will result in a trade-off between survival and early reproduction. Theoretically, the trade-off is resolved in favour of reproduction, other factors being equal, if habitats contain many hosts and if host encounters are more unpredictable (Rosenheim, 1996; Sevenster et al., 1998; Ellers et al., 2000; Ellers & Jervis, 2003), and also if body size is small (Ellers & Jervis, 2003, 2004).

Trait associations in taxonomically-broad studies

Blackburn (1991a,b) showed that body size predicted life history traits across species much less in parasitoid Hymenoptera than in vertebrates. He did find that larger body size predicted longer development as expected, as well as larger eggs. Development is faster in idiobionts (particularly in the pupal stage), eggs hatch quicker in parasitoids of poorly concealed hosts, temperate clades take longer to develop than tropical ones, and parasitoids attacking eggs take longer to develop than those attacking pupae. These findings vindicate some of the predictions about development time made above.

He also found limited support for a fast-slow continuum, in that more fecund species had smaller eggs, and laid them quicker than less fecund species. Unlike in vertebrates however (Jeschke & Kokko, 2009), fecundity does not evolve predictably in response to body size change, neither is adult lifespan consistently related to body size. These modest findings may have reduced interest in broad comparative studies on parasitoid life histories. One contributing notion may have been that datasets were too noisy to detect much of value.

However, an alternative reason for the modest results is that parasitoids have different life history suites from other organisms. This alternative found some support when Mayhew & Blackburn (1999) used the same data to test the dichotomous hypothesis and found reasonable support for it. Idio/koinobiosis evolves in concert with ecto/endoparasitoidism. Koinobionts are almost always endoparasitoids, although idiobionts are commonly either endo or ectoparasitoids. Koinobionts/endoparasitoids also have smaller eggs, short adult lifespans, (but longer development as found by Blackburn, 1991a), attack hosts available over a shorter time window, and, in larval parasitoids, have greater fecundity and oviposition rates than idiobionts/ectoparasitoids. These findings were largely replicated in another dataset with only a few species in-common (Jervis & Ferns, 2011).

The findings were significant in that they suggested: a) that taxonomically broad parasitoid datasets could contain significant signals about associations between traits; b) that parasitoid-specific concepts or predictions might lend more understanding than borrowing predictions from studies on other taxa; c) that the fullest depictions of the dichotomous hypothesis went too far (e.g. there was no association with adult body size, degree of host concealment or stage of host attacked); d) reasons why the expected fast-slow continuum was not so strong in parasitoids. For example, a strong link between body size and adult lifespan or fecundity is not expected because development mode has a strong effect on lifespan and fecundity thus is a confounding variable. In addition, development mode has opposite effects on pre-adult lifespan and adult lifespan, confounding the usual positive association between these variables: koinobionts have fast adults (short lifespan, high fecundity, small eggs, more rapid oviposition), but slowly developing juveniles.

A qualifier on the extent of the dichotomy concerns the studies of Hawkins (1994), which looked at the parasitoid communities of different host species. Hawkins found that communities of parasitoids attacking exposed hosts tend to consist of more koinobionts. However, despite being in the direction predicted by the dichotomous hypothesis, the frequency of traits in communities of species probably depends not just on evolutionary changes in the parasitoid life-history (supposed to underlie the dichotomy), but also how parasitoid clade richness is affected by life history, as well as the assembly of ecological communities of different parasitoids on a host. Thus, whether this finding supports the dichotomy is presently ambiguous because we do not know which of these forces most underlies it.

Traynor & Mayhew (2005a) used Blackburn's (1990) dataset to investigate an outstanding question; what explains variation in clutch size and adult body size (which were not associated with most other variables in the above studies). They found that body size is predicted by the stage of host attacked; for example, egg parasitoids tend to be smaller than those attacking larvae and pupae. There was also evidence for a trade-off between body size and clutch size after controlling for the stage of host attacked, mirroring an evolutionary correlation between body size and solitary/gregarious development found across families by Mayhew (1998a). Thus, it seems likely that body size, host size and clutch size form a set of mutually co-evolving traits roughly independent of the other life history traits belonging to the dichotomy. Traynor & Mayhew (2005a) also found that clutch size in gregarious species was negatively correlated with latitude.

In the late 1990s, renewed interest in the trade-offs governing adult parasitoid life histories prompted Jervis and co-workers to develop a second dataset of parasitoid life histories, based around species for which the ovigeny index had been estimated. Analysis of this dataset showed that a high ovigeny index was negatively correlated with adult lifespan, and associated with anhydropic eggs, koinobiosis, longer pre-adult lifespan, gregarious development, maximum egg load, an inability to resorb eggs and tendency not to host feed (Jervis et al., 2001; Jervis & Ferns, 2011). Adult body size was associated with a lower ovigeny index in an early study (Jervis et al., 2003). This association disappeared in a larger dataset (Jervis & Ferns, 2011), but the authors cautioned against ejecting body size prematurely from the "ovigeny" suite of traits as the body size data were very incomplete and probably imperfectly representative of body mass. Ovigeny seems likely to be a trait that partly mediates the interaction between development mode and other life history traits, whilst extending a network of associations to other traits not likely to be driven by development mode *per se*, such as gregarious development, possibly host feeding (Heimpel & Collier, 1996), egg resorption (Flanders, 1950; Quicke, 1997), and possibly body size.

The latter dataset has also been used to test the relationship between fecundity and host stage attacked (Jervis et al. 2012). This relationship has been claimed for more taxonomically-restricted studies but is not significant at this broad taxonomic scale (see below). It was predicted on the basis of the balanced-mortality principle (that early host stages experience more mortality, hence parasitoid fecundity is selected to rise), and the effects of host abundance (that earlier host stages are more abundant, selecting for higher fecundity (Godfray 1994)).

Overall then, far from being too noisy to infer much about the life histories of a diverse group, taxonomically-broad datasets have laid much of the framework for the next generation of parasitoid life history studies.

Trait associations in taxonomically-restricted studies.

Several important studies contributing an understanding of the above traits across species have been conducted on taxonomically more-restricted datasets, hence may or may not be reflective of patterns more generally.

Traynor (2004) developed a dataset of 382 species, similar to that of Blackburn (1990) but covering just Ichneumonoidea (ichneumonids and braconids). In addition to including most of Blackburn's variables, it included more host-related information including host adult body length (Table 1), and detailed host range and geographic information. The documented host and geographic range of a parasitoid depends greatly on how well studied it is, and this therefore has to be accounted for when studying these traits. Traynor (2004) did this by quantifying how well studied species were (pages of publications from which the species data was collected), which could then be used as a control variable.

Despite the fact that in this taxon there are many fewer transitions between development mode than across the Apocrita as a whole, these data showed some further support for the dichotomous hypothesis. There was an association between ectoparasitoidism and idiobiosis, which were also associated with longer adult lifespans, and, notably, lower fecundity (cf Jervis & Ferns, 2011). There was no relationship between egg volume and development mode, although fecundity was negatively correlated with egg size. Surprisingly, development time did not correlate with development mode, although it was positively correlated with body size. Body size also predicted egg size, and surprisingly, adult lifespan. It seems therefore that in ichneumonoids, the importance of allometric effects and those of development mode are slightly different than in parasitoid wasps as a whole. As a result, perhaps taxon-specific allometries should now be investigated.

Although Traynor (2004) found an association between development mode and host niche and host exposure across species, as found in some host-based studies (Hawkins, 1994), with koinobionts more associated with exposed hosts, importantly this relationship was not significant after controlling for phylogeny, which may help explain why community studies find such a relationship but not phylogenetic comparative studies. The data also provide support for the association between host size, clutch size and parasitoid adult body size: parasitoid body size correlated with host body size (Figure 1), and clutch size also correlated with host size after controlling for parasitoid body size.

The dichotomous hypothesis claims that koinobionts have more restricted host ranges than idiobionts. This claim is supported by studies of the parasitoid communities of particular groups of hosts, such as the oak leaf miner community in England (Askew & Shaw, 1986) and Japan (Sato, 1990), and of the aphid parasitoid community of an English field (where, note that the idiobionts are all hyperparasitoids, Műller et al., 1999). The single comparison of metopiine and pimpline ichneumonids is also consistent with this claim (Sheehan & Hawkins, 1991) (for some other comparisons see Shaw (1994)). However, Traynor (2004) found no association between these traits either before or after accounting for the degree to which the parasitoid had been studied. The accuracy of literature-derived host range data might be questioned. However, Traynor did find that, after controlling for the intensity with which each species had been studied, there was a correlation between temperate (as opposed to tropical) distribution and host range. Other geographic correlations included more rapid development in tropical groups, and larger geographic ranges in larger bodied and temperate groups, and those attacking hosts with a large geographic range.

Another proposed predictor of host range has been solitary/gregarious development (Wharton, 1984; Shaw & Huddleston, 1991, Sheehan, 1991; Smith, 1991; Traynor & Mayhew, 2005b; Hoffmeister et al.,2005), though the evidence is based on relatively few informal comparisons. An association might be mediated by selection for investment in reproduction over survival in gregarious species (see Pexton & Mayhew, 2002), which may decrease oviposition specificity (see Hoffmeister et al., 2005). An interesting prediction of the latter hypothesis is that the ovigeny index should be correlated with gregarious development, which it is (see above, Jervis & Ferns, 2011).

The explanation of lifetime fecundity is one of the most outstanding issues in parasitoid life histories. The datasets of Price on parasitoids of a sawfly (Price, 1972, 1974) and ichnemonid ovarioles (Price, 1973) , and tachinid and conopid flies (Price, 1975), have been important contributions about this. The original studies suggested that parasitoids attacking later life history stages of their hosts tended to be less fecund than those attacking earlier stages. The ichneumonid and tachinid/conopid findings have proved robust when accounting for phylogeny (Jervis et al., 2012) but the associations are lost in taxonomically-broad studies (see above). A likely reason is that broader studies introduce more confounding variables; for example, the density of hosts, and mortality risks, likely vary enormously across host species, whilst fecundity is affected by other forces such as egg size (Blackburn, 1991b), itself affected by development mode (Mayhew & Blackburn, 1999). In addition, ichneumonids tend to all finish development in later host life-history stages, meaning that there is probably a stronger correlation between host stage attacked and mortality than is typical for other parasitoids. Force (1974) claimed similar findings to Price in studies of a gall midge, but attributed the differences in fecundity to differences in interspecific competitive ability.

Mayhew & Hardy (1998) looked at the evolution of clutch size and body size in bethylid wasps (Bethylidae), and found that wasp body size and clutch size were both positively correlated with host size across species: at deep taxonomic levels (above genus), body size responded to host size changes, but amongst more recent contrasts (among genera), clutch size responded instead. This taxon lacks obligate solitary development, meaning that clutch size is not restricted by parent-offspring conflict (see below). This reinforces the association between these three traits provided by broader studies. Similarly, Le Masurier (1987) found a positive correlation between brood size and host size in gregarious species, although in solitary species body size responded instead, though to a relatively low extent. Such species are constrained by parent-offspring conflict to develop alone despite the fact that larger hosts would allow more offspring to develop (see Godfray, 1987). These last studies raise the important issue of the phylogenetic lability of different traits to which I now turn.

Evolutionary lability of life histories.

The phylogenetic lability of different life history traits may help establish which traits drive variation in other traits. Some authors (e.g. Shaw, 1983; Gauld, 1988) suggested that development mode was likely to be phylogenetically constrained, and developed hypotheses about what drove changes in it (see also Jervis & Ferns, 2011; Whitfield, 2003). Dowton & Austin (2001) used a coarse phylogeny to suggest that ectoparasitism was ancestral and at least 3 independent evolutions of endoparasitism have occurred, with some transitions back to ectoparasitism again, findings largely consistent with an earlier analysis of Whitfield (1998). Both braconids and ichneumonids show several transitions from an idiobiont ectoparasitoid ancestor to koinobiosis and endoparasitism (Belshaw et al., 1998; Quicke & Belshaw, 1999; Quicke et al., 2009). Whitfield (1992, see also Quicke, 1993) suggested at least two independent transitons to endoparasitism in the cyclostome braconids. Host concealment may have evolved in parallel with development mode, but there have clearly also been some transitions within each mode (Belshaw & Quicke, 2002).

Mayhew (1998a) performed a reconstruction of the evolutionary history of solitary and gregarious development across the parasitoid Hymenoptera, showing that solitary development is likely ancestral, with at least 43 transitions to gregarious development, mostly at deep phylogenetic levels, though some are known to have occurred within genera (e.g. Mayhew & van Alphen, 1999; Pexton & Mayhew, 2004). Values of the parameter *Rho* (a branch length scaling parameter) in Phylogenetic Regressions of body size and clutch size across parasitoid Hymenoptera have suggested that body size is more constrained than clutch size (Traynor & Mayhew, 2005a).

Besides suggesting a degree of inflexibility in these traits, hence that they are sometimes likely to act as constraints and drivers of other variables, these results need to be put into a broader context. So far there have been no studies considering the lability of a large number of traits across taxonomically-broad datasets, but Traynor (2004) performed one for her Ichneumonoidea data (Table 2). For some traits, variation was almost entirely restricted to differences between the two families, indicating considerable constraint. The most constrained were parasitoid adult body length and the corresponding lengths of their host adults, both of which contrasted strongly between ichneumonids and braconids; ichenumonids are a radiation of large wasps attacking large hosts, and braconids are a radiation of smaller wasps attacking smaller hosts; variation at other taxonomic levels is relatively trivial (Table 2).

Significant variation at the subfamily level was found for development mode, solitary/gregarious development, pre-adult lifespan, and several other traits. At genus level, significant variation is found for egg size and fecundity. The latter two traits, and longevity show variation spread quite evenly across taxonomic levels. Further analysis, for example using the retention index of each trait plotted onto cladograms, suggested that host order is highly conserved, host concealment is only moderately conserved, whilst host stage attacked and host ecological niche are less conserved (Traynor, 2004).

Though this is a taxonomically restricted analysis, it does tend to support the underlying assumption of the dichotomous hypothesis that development mode is constrained and drives other traits, whilst some continuous components of the dichotomous suite evolve more flexibly. This is also consistent with the conclusions of Jervis & Ferns (2011) that ovigeny reflects some but not all of the dichotomy suite and is not the sole organizer. Perhaps the most surprising result is how constrained body size (of host and parasitoid) is, given that it is a continuously varying trait with much intra-specific variation (e.g. Thorne et al., 2006).

Summarizing and explaining the suite

The available data tentatively suggest that two sets of, largely independent, traits seem to summarize parasitoid life history variation at deep taxonomic levels; changes in parasitoid body size (likely responding largely to host size (hence taxon and stage attacked) and clutch size), and changes in development mode (ecto/endoparasitoidism, idio/koinobiosis) (Figure 2). These changes together represent particular host exploitation ecologies. Within the constraints of these relatively fixed traits, other traits respond probably more flexibly. In the dichotomous set, these probably include continuous traits like ovigeny index, pre-adult lifespan, adult longevity, egg size, and maximum egg load. The combinations of these traits selected by development mode give rise to a limited fast-slow continuum in adult traits, excluding body size (Figure 2). The ovigeny index, or its correlates, have further knock-on consequences for other traits such as host feeding and egg resorption (not shown), possibly body size, and brood size. Finally, more tentatively, fecundity related traits are possibly affected by host density and juvenile mortality rates.

Most of the proposed sets of parasitoid life history variation show some degree of overlap and interaction, meaning they can be considered as part of a single larger framework (Figure 2). The framework contains some relatively tight elements (e.g. egg size and development mode) but also looser ones (e.g. ovigeny and body size), and associations between distant traits in the framework are likely looser (e.g. ovigeny is associated with solitary/gregarious development but development mode is not). In addition some are relatively well supported (e.g. associations between host size and parasitoid size are found in taxonomically broad data as well as taxonomically restricted data) whilst support for others is weaker (e.g. associations between host range and development mode, and host stage attacked and fecundity, are only found in taxonomically restricted data).

The reasons behind some of the associations seem well understood, whilst reasons for others remain largely unresolved. The development of dynamic programming models targeted at adult parasitoid life history decisions, together with studies of the physiological underpinnings of adult behaviour from intraspecific studies (Jervis et al. 2008), has lent some confidence in the likely reasons for the ovigeny "suite". For example, a negative association between ovigeny and lifespan is likely due to a trade-off in early-life resource allocation between fat and eggs (e.g. Ellers, 1996; Ellers & van Alphen, 1997; Pexton & Mayhew, 2002), whilst the association between small body size and high ovigeny index is understood to be a response to stochasticity in reproductive opportunities combined with minimal total resources to allocate to survival and reproduction. Theoretical modelling and intraspecific studies of the clutch size/host size/body size suite have also led to plausible explanations of their association (Mayhew, 1998b,c; Mayhew & Glaizot, 2001; Crowley & Saeki, 2009).

Where there is more than one potential driver of a trait, analyses that control for one of them can potentially distinguish between those potential drivers. Unfortunately, in practice, interpreting the results of such analyses is more complex than one might anticipate, and does not lead to clear conclusions. For example, Jervis & Ferns (2011) found that development time was significantly correlated with idio/koinobiosis when controlling for ecto/endoparasitoidism, but not vice-versa. Unfortunately, the reverse was the case when also controlling for body size. When controlling for ovigeny index, idio/koinobiosis was significantly associated with development time, but not vice-versa. However, ovigeny index was associated with development time after controlling for ecto/endoparasitoidism, but only before correcting for multiple comparisons. Controlling for body size also removed that relationship. The results are partly confusing due to the gappy nature of the data which makes sample size, hence power, vary from analysis to analysis, and partly because several of the relationships are only marginally significant, hence findings are very sensitive. At present therefore it seems that likely causation will have to be assessed by other means.

Why ovigeny and development mode are associated remains unresolved. Jervis et al. (2001) suggested several reasons which all involved development mode affecting an intermediate variable that is also known to be linked to ovigeny (egg size, adult lifespan, oviposition rate, and pupal development time). There are difficulties explaining why some of these variables should be affected by development mode independent of ovigeny index, and why simultaneously the ovigeny index should be associated with them independently of development mode. Jervis & Ferns (2011) also suggested that pupal development time might mediate the association between ovigeny index and development mode, because both would seem to select for longer pupal development and both are associated with it (Blackburn, 1991a; Jervis & Ferns 2011). However, there is no evidence that these associations occur independently of each other, nor if they are tight enough to cause the overlap between the dichotomous and ovigeny suites that is observed.

One solution to this problem, shown in Figure 2, is if both ovigeny and development mode are selected for by some common ecological variable or set of variables. Possibly host density is one such variable (Blackburn, 1991b; Godfray, 1994). High host density might plausibly select for a high ovigeny index (Ellers & Jervis, 2003), whilst the developmental flexibility offered by endoparasitoidism/koinobiosis (see Harvey et al., 1994), along with the selection for other fast life history traits, may favour the exploitation of hosts found in greater densities (Blackburn, 1991b; Godfray, 1994). These ideas require more-explicit comparative testing at broad taxonomic scales, since using host-stage-attacked as a density proxy currently does not provide any supporting evidence.

General conclusions and remaining challenges

What does the study of comparative parasitoid life history suites contribute to life history theory in general? First it shows that the fast-slow continuum can be much more limited in some organisms than in mammals. The continuum is also reduced in fish and birds and plants compared to mammals (Franco & Silvertown, 1996; Jeschke & Kokko, 2009), which in fish and birds is due to a positive, rather than negative relationship between body size and fecundity, a likely result of viviparity in mammals and subsequent extensive parental care. In parasitoids, the continuum is reduced further, being confined to adult traits and omits body size.

Second, parasitoids show how the ecology and nature of the host and the way it is exploited (e.g. host density, host size, host mortality rates, parasitoid development mode) can affect life history evolution in parasitic organisms. Third, parasitoids show how a consideration of allocation to survival and reproduction in early adult life can help explain many other life history traits. This work is already beginning to pay dividend in other insects, and the principle is much more general. Fourth, parasitoids expand the list of cases where biology-specific categorical traits, not part of the core life history traits, have a major effect on a large number of traits. Such traits are a thorn in the side of those who hope for a single all-encompassing life history theory or paradigm.

It is useful in empirical science to imagine the ideal dataset and ideal analysis and to compare that with what does exist and has and can be done. For comparative studies of parasitoid life histories we would wish for many more rows of data and for less gappiness within rows. More rows (species) are necessary to help describe accurately how some traits vary simultaneously with other traits across sister taxa. The problem is especially acute in parasitoids which are an extremely rich radiation, but poorly described and even more poorly studied (Santos & Quicke, 2011). Taxonomically-broad studies omit a more substantial fraction of the variation present. We are fortunate in having a long and continuing tradition of description of basic life history traits in parasitoids, largely thanks to interest in biological control of pests, and can expect future datasets to be much more extensive than those covered here. A qualification is the extensive time needed to gather literature-based data. The accumulation of data in a standardized format would be facilitated by a centrally maintained online database, such as exists for mammals (PanTHERIA) and fish (FishBase). Such investments need long-term funding to succeed.

The ovigeny index is an example of a relatively new trait that has added a column of data that has been extremely valuable in resolving variation in other traits. Host size data also needs to be much more extensively added to datasets, and field studies of host density and parasitoid life tables, both as adults and juveniles, are probably necessary to resolve issues of juvenile mortality and fecundity at broad taxonomic scales. Probably some data already exist in a suitable format from biological control work, but it would need to be compiled and standardized, and much more needs to be gathered. Traits investigated also tend to be female-focussed (e.g. the fecundity-related traits all refer to female rather than male fecundity). This befits interest in the oviposition behaviour of parasitoids, in turn stemming from an interest in biological control, population dynamics, community ecology, and the behavioural ecology of female decision-making. There has been much less interest in male life history traits, but there is likely to be much to be gained from studying male traits more widely. An equivalent index of early reproductive investment for males, the spermatogeny index, has been been suggested for males (Boivin et al. 2005), and it would be interesting to observe how this index correlates with traits such as lifespan, body size, mating system, dispersal, sexual size dimorphism , and sex allocation (see Boivin et al., 2005; Macedo et al., 2013; Boulton et al., 2014). Appropriate datasets have however yet to be compiled as spermatogeny is rarely investigated.

The ideal way to investigate associations between multiple traits is through the use of multi-variate analyses, such as Principle Component Analysis (PCA) (Jeschke & Kokko, 2009). Gappiness has largely prevented this in taxonomically broad studies (species with missing data are excluded). Nonetheless, perhaps scope already exists for analysis of a more limited set of traits on a more limited set of species. As data-sets become more species-rich and less gappy, the potential for such analyses will increase, and will enable broad pictures such as Figure 2 to be inferred from single analyses. Of course, all comparative analyses rely on a phylogenetic framework, another area of uncertainty for parasitoid workers (see Davis et al., 2010). Despite extensive phylogenetic work in the last two decades, relationships in ancient rapid radiations remains hard to resolve.

Whilst this review has focussed on broad patterns across taxa, important residual variation remains. For example, important functional groups, such as egg or pupal parasitoids, are exceptions to the dichotomy in that they are idiobionts but endoparasitoids. Do their core life histories better reflect expectations from the idiobiont or endoparasitoid part of their development? What role does host stage attacked play in controlling this, and what causes the variation remaining within these groups. These remain important questions to answer using both broad and taxonomically focussed studies.

Beyond description of the suite, there is the job of explaining it. Intraspecific studies on continuous traits, and modelling studies, are vital avenues allowing us to attribute causation. In particular, the generation of dynamic models, that have already investigated ovigeny, might be extended to explore the comparative observations more broadly across other traits. Selection experiments are one avenue of intraspecific study that is underused, but which is held in high esteem in allowing causal inference (see Stearns, 1977). Comparative studies can potentially add to arguments about causation; for example, by testing to see if associations are retained whilst controlling for another potentially causative trait, but really require larger and less gappy data. More studies of phylogenetic lability can also add to this, and particularly in a broad-taxonomic context. Path analysis (e.g. Shine, 1996), and methods based on information transfer (Hannisdal & Peters, 2011) which both attempt to infer causative relationships from observational data, might also bear fruit.

There continues to be a place for both taxonomically-broad and more restricted studies. The number of traits with which parasitoid life history workers must deal is extensive, whilst even single subfamilies can be very species rich indeed. The added control given by taxonomically restricted datasets has been illuminating.

Postscript

When I was a PhD student, my supervisor published a landmark synthesis of life history and behavioural work in parasitoids (Godfray, 1994). In the two decades since, interest in adult allocation to survival and reproduction, the underpinning nutritional basis, and the behavioural and ecological correlates and consequences, have been perhaps the standout change. The work of Mark Jervis and coauthors has since provided the comparative, and to a large extent theoretical, context for the ovigeny set of traits, at the core of parasitoid life history variation. On re-reading Mark's papers whilst preparing this article, I was struck by the dedication required to assemble his datasets, the care that went into the analyses and the writing of the papers, and the underlying breadth of biological vision. I hope that readers will take a moment to ponder these points. With Mark's untimely death we lose a loved and respected colleague whose contributions have been rich, and which are likely also to be enduring.

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Figure legends

Figure 1 Adult body length of parasitoid against adult body length of host in Ichneumonoidea (data from Traynor, 2004, Pearsons $r = 0.507$, $n = 209$, $P < 0.001$.). The relationship is also significant after controlling for phylogeny (see Traynor 2004). The line is $y = x$.

Figure 2 Sets of associated life history traits in parasitoid Hymenoptera as described in this review, showing the overlap between them. Solid boxes represent traits known to be in the set via taxonomically broad comparative studies. Dotted boxes represent less-well-evidenced components. Causal arrows are speculative.

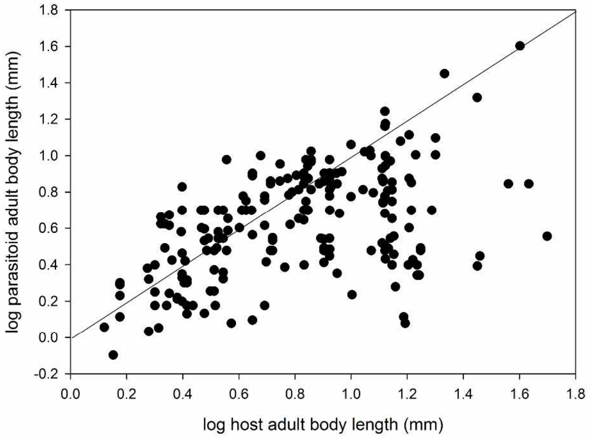
Table 1. Some life history traits included in large comparative datasets of parasitoid wasps. Data coverage is shown for (1) Blackburn (1990), (2) Jervis & Ferns (2011) (covering all parasitic wasps), and (3) Traynor (2004) covering Ichneumonoidea only.

Trait	Measurement (Blackburn, 1990)	Species (/474spp) (Blackburn, 1990)	Measurement (Jervis & Ferns, 2011 data)	Species (/133spp) (Jervis & Ferns, 2011 data)	Measurement (Traynor, 2004)	Species (/382spp) (Traynor, 2004)	Example variation (data source , 1,2, or 3, above)
Generic traits							
Egg size	Length, width	219, 201	-	-	Length, width	60, 56	0.04-3.5mm length (1)
Predult lifespan	Mean (h)	317	Mean (d)	64	Mean (d)	109	10-57d (2)
Adult body size	Length	332	Forewing length	68	Length	316	0.34-28.15mm length (1)
Clutch size	Mean offspring per host	303	-	-	Mean brood size	135	1-347 (1)
Oviposition rate	Max eggs laid per day	51	Max eggs laid per day	45	-	-	1.1-58 (1)
Lifetime fecundity	Maximum eggs laid	169	Maximum potential	105	Maximum eggs laid	55	20-3000 (2)
Adult lifespan	Mean (h)	261	Mean (d) food and hosts provided	91	Mean (d)	87	3.6-96.5d (2)
Tropical or temperate	Binary	440	-	-	Binary, plus both	348	72% temperate (1)
Parasitoid traits							
Ecto/endo parasitoid	Binary	447	Binary	128	Binary	255	36% ectoparasitoids (1)
Idiobiont/ koiniobiont	Binary	326	Binary	126	Binary	174	62% idiobionts (1)
Hydropic/ anhydropic	-	-	Binary	125	-	-	34% hydropic (2)

eggs							
Solitary/ gregarious	Binary	303	Binary	130	Binary	191	74% solitary (1)
Ovigeny index	-	-	Range 0-1	133	-	-	0-1 (2)
Host feeding	-	-	Yes/No	115	-	-	43% yes (2)
Host stage attacked	12 categories	442	12 categories	124	15 categories	281	-
Host concealment	3 categories	262	3 categories	122	3 categories	355	47% exposed, 33% semi-concealed, 20% concealed (1)
Adult host size	-	-	-	-	Body length	255	1.32-50mm (3)
Pupal period	h	292	d	17	d	79	6.5-14.5d (2)

Table 2: Nested ANOVA (see Harvey & Pagel, 1991) of life history traits of Ichneumonoidea from Traynor (2004). Numbers indicate the proportion of the total variance in each trait (rows) found at each taxonomic level (columns) (* $P < 0.05$ ** $P < 0.001$). (Species level is never significant as species variance is obtained from the genus error). Only binary and continuous traits were included, but not categorical traits with >2 factor levels. “Residual” values are those taken by fitting the slope of a phylogenetic regression of the trait against the degree of study (pages of sources used to assemble the data for each species) through the raw species data for the trait and degree of study.

Variables	Proportion of total variance				
	Family	Subfamily	Tribe	Genus	Species
Ecto/endoparasitism	0.520	0.396**	0.034	0.036**	0.014
Idio/koinobiosis	0.388	0.376**	0.116	0.065	0.056
Solitary / gregarious	0.002	0.570**	0.126	0.144	0.159
Feeding site (haemolymph / tissue)	0.071	0.132	N/A	0.000	0.796
Pupation site (internal / external to host’s body)	0.393	0.345*	0.132	0.108*	0.033
Preadult lifespan	0.546	0.147*	0.022	0.178	0.107
Longevity	0.177	0.282	0.235	0.194	0.112
Brood size	0.517	0.152	0.139*	0.049	0.143
Fecundity	0.007	0.478	0.181	0.259*	0.075
‘Residual’ parasitoid geographic range	0.196	0.233	0.176	0.239	0.157
Parasitoid mean latitude	0.306	0.285**	0.163	0.134	0.112
Parasitoid body length	0.764*	0.114*	0.088	0.041**	0.018
Egg volume	0.032	0.404	0.157	0.310*	0.096
Host body length	0.970**	0.020**	0.004	0.005**	0.001
Parasite window	0.010	0.231	0.127	0.549*	0.085
‘Residual’ host geographic range	0.179	0.282*	0.143	0.236*	0.160
Host mean latitude	0.123	0.356*	0.173	0.219*	0.129
‘Residual’ number of host species attacked	0.309	0.204	0.179	0.180	0.129
Degree of study	0.200	0.344*	0.174	0.150	0.132



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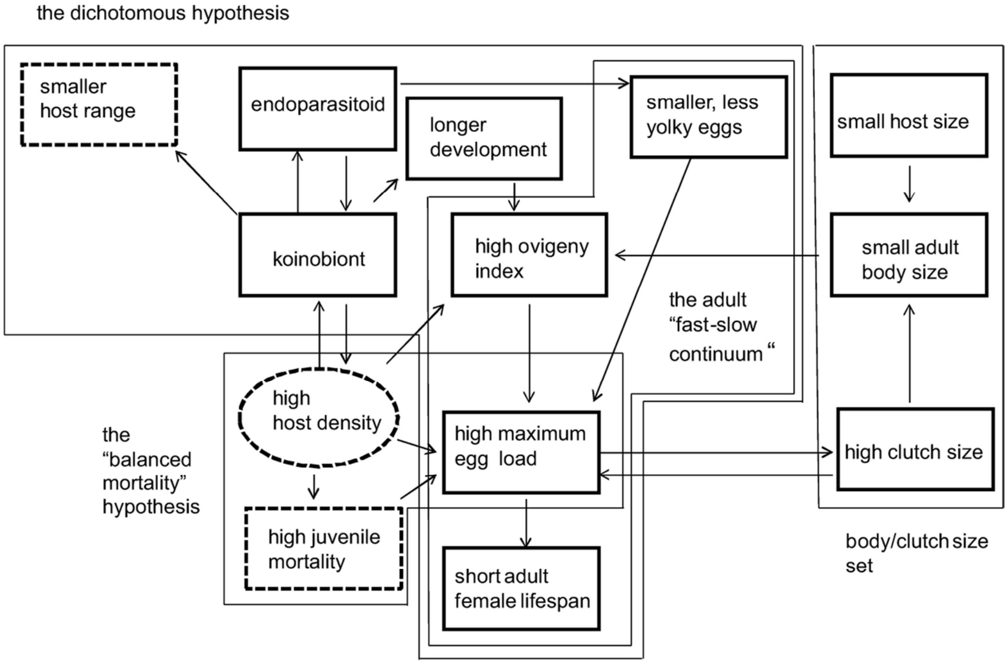

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