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Comparing parasitoid life histories

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Review

Comparing parasitoid life histories

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Short Title: Comparing parasitoid life histories.

Key Words: balanced mortality, capital breeding, dichotomous hypothesis, evolutionary lability, fast-slow continuum, Hymenoptera, income breeding, insect fecundity, lifespan, parasitic wasps, ovigeny

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2
3 1 **Abstract**
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7 3 Species and clades are characterized by their unique combinations, or suites, of
8 4 different life history traits. In parasitoids, traits include a core group common to other
9 5 organisms, and a parasitoid-specific group. These organize into several sets of
10 6 mutually covarying traits which overlap a little, but not wholly, with other sets.

11 7 Across parasitoid species, host size, clutch size and body size tend to covary. Roughly
12 8 independent of these is a dichotomy between idiobionts (host does not develop after
13 9 parasitization), which tend to have fast development but slow adult life histories, and
14 10 koinobionts (hosts develop after parasitization) with the opposite set of traits.

15 11 Consistent links between the dichotomy and host characteristics remain elusive. A
16 12 low ovigeny index (low allocation to early reproduction) is found in idiobionts, and is
17 13 a predictor of some of the dichotomous set, but also more host feeding, egg
18 14 resorption, solitary development, and larger bodies. Variation in fecundity, in
19 15 taxonomically-restricted studies, is predicted by the host stage attacked, but this is not
20 16 reflected in taxonomically-broad studies. The reasons behind trait co-variation are
21 17 only partly understood. Analyses of evolutionary lability suggest that variation in
22 18 development mode and body size tends to be clustered within higher taxonomic
23 19 levels, with variation in other traits such as lifespan, fecundity and egg size more
24 20 evenly distributed across taxonomic levels. Thus, taxonomically constrained
25 21 radiations of parasitoids tend to retain a particular suite of traits that revolve around
26 22 fundamental shifts in hosts and their use that occur relatively rarely. Parasitoids
27 23 illustrate how the fast-slow continuum can be much less extensive than in mammals,
28 24 how the ecology of the host affects the life histories of parasitic organisms, how
29 25 different taxa require different life history theories, and how understanding resource
30 26 allocation in early adult life can help explain life history variation.

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29 Introduction

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

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34 The life history of an organism describes the way it develops, reproduces, and when it
35 can expect to die. Variation in life histories represents some of the most striking
36 phenotypic differences across species, and a considerable challenge to explain in
37 Darwinian terms (Stearns, 1992; Charnov, 1993; Roff, 2002). This is the realm of life
38 history theory. The variation in life histories across species is exemplified by insect
39 parasitoids, which develop to maturity by feeding on, eventually killing, the body of
40 another host arthropod (Godfray, 1994). They are amongst the most species rich taxa
41 (Santos & Quicke, 2011) and include the smallest living insects (species of
42 Mymaridae, some <0.2mm long) as well as the impressive ichneumonids of the genus
43 *Megarhyssa*, which may be 150mm long including a 100mm ovipositor (Quicke,
44 2015). They exploit one of the most varied biological resources on Earth (other
45 insects and some other arthropods), and do so in an impressive variety of ways (Gauld
46 & Bolton, 1988; Godfray, 1994; Quicke, 1997; Jervis & Ferns 2011).

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

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

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2
3 62 Below I first introduce the life history traits in which parasitoid biologists are
4 63 interested, and some life history paradigms that describe trait variation across species.
5
6 64 I summarize what we know about the associations between traits, which I term “the
7
8 65 suite”. Finally I summarize challenges to understanding the evolution of life history
9
10 66 suites in parasitoids.

11 12 13 68 **Traits**

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15 69 Life history theory tends to focus on obvious measurable traits found widely across
16
17 70 taxa. Several of these are found in parasitoids, meaning that general theory can
18
19 71 potentially contribute towards an understanding of parasitoids, and that parasitoids
20
21 72 can influence general theory. The general traits include offspring size (egg size),
22
23 73 development time (pre-adult lifespan), adult body size, offspring number in a
24
25 74 reproductive event (clutch size), the interval between reproductive events (oviposition
26
27 75 rate), lifetime fecundity and adult lifespan (both normally female) (Table 1).

28
29 76 The sex ratio might be considered a core life history trait (Charnov, 1993), and
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31 77 in parasitoids can sometimes be linked quite well to some other general life history
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33 78 traits (Griffiths & Godfay, 1988; Hardy & Mayhew, 1998, West & Sheldon, 2002; but
34
35 79 see Lewis et al., 2010). However, it is generally not included in comparative studies
36
37 80 involving several of the above traits. This may be because of the relatively low
38
39 81 population sex ratio variation shown by birds and mammals, which tend to dominate
40
41 82 comparative life history studies. Furthermore, many of the important factors affecting
42
43 83 cross-species variation in sex ratio (such as mating structure) are unlikely to appear in
44
45 84 broad parasitoid datasets, or are expected to exert very taxon-specific effects (Smart &
46
47 85 Mayhew, 2009). For the above reasons, I do not consider the sex ratio further below.
48
49 86 Likewise, dispersal ability and dormancy are important life history traits with their
50
51 87 own theory (Mayhew, 2006). Because of theoretical links with both the sex ratio and
52
53 88 lifespan-fecundity, dispersal propensity probably deserves a wider consideration than
54
55 89 it has currently received (see Asplen et al., 2009), but in practice is rarely estimated
56
57 90 for large numbers of species (see Hardy & Mayhew, 1998 for an exception) and I
58
59 91 shall not consider it more below.

53 92 Some life history traits are known to be dependent on temperature (e.g.
54
55 93 development time) or to vary with latitude (e.g. Hawkins, 1994; Traynor & Mayhew,
56
57 94 2005a), and to account for this effect, Blackburn (1990) noted if the species in his

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3 95 dataset were tropical or temperate. **Geographic variation in life histories is prominent**
4 96 in some other groups (e.g. Smith & Lyons, 2011).

5
6 97 **Traits in comparative parasitoid life history studies also include some** more
7
8 98 particular to parasitoids (Table 1). These include ecto/endoparasitoidism (whether the
9
10 99 juvenile parasitoid develops outside or inside the host) and idio/koinobiosis (whether
11
12 100 the host does not continue to develop after parasitization, or does so). As a short-hand
13
14 101 way of referring to these two traits together (they are often closely correlated), I refer
15
16 102 to them below under the umbrella of “development mode” (following Mayhew &
17
18 103 Blackburn, 1999).

19
20 104 **A related trait is the type** of egg: hydropic (with insufficient resources for
21
22 105 embryogenesis, the rest taken from the host) and anhydropic (sufficient resources for
23
24 106 embryogenesis), which can be taken as a rough indication of the investment per egg,
25
26 107 and is often known or inferred when precise measurements of egg size are not
27
28 108 reported (Jervis et al., 2001). Hence it is **sometimes** used as a proxy for offspring size.

29
30 109 Similarly, in order to improve data completeness, a proxy measure of clutch
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32 110 size is sometimes taken; that of solitary or gregarious development (e.g. Mayhew,
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34 111 1998a; Traynor & Mayhew, 2005a; Jervis & Ferns, 2011). In solitary species, only
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36 112 one offspring successfully develops per host, whilst in gregarious species several may
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38 113 develop. This **is often taken as** indicating a small clutch size in solitary species but a
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40 114 larger one in gregarious species. It is often assumed that solitary species eliminate
41
42 115 rivals by contest competition (Mayhew, 1998a), but many species of parasitoids with
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44 116 more scramble-style larval competition are also facultatively solitary (Mayhew,
45
46 117 1998b,c; Mayhew & Hardy, 1998), hence solitary development does not perfectly
47
48 118 indicate the form of larval competition.

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50 119 An index of allocation to early life reproduction in insects, the ovigeny index,
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52 120 (Jervis & Ferns, 2004) has proven useful in explaining life history variation in
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54 121 parasitoid wasps (Jervis et al., 2001; Jervis et al., 2003; Jervis & Ferns, 2011) and
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56 122 other insects (Jervis & Ferns, 2004; Jervis et al., 2005; Jervis et al., 2007a,b), and has
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58 123 formed the basis of some comparative life history datasets. The ovigeny index is
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60 124 estimated from data on the number of eggs ready to be laid on adult emergence,
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126 125 divided by the maximum potential fecundity. It emerged as a continuous trait to
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128 126 replace the previously used dichotomy of pro/synovigeny (eggs all matured by the
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130 127 start of adult life, versus some matured during adult life), when it was realized that the

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3 128 degree of synovigeny (measured via the ovigeny index) was highly variable across
4 129 species whilst pro-ovigeny was very rare (Jervis et al., 2001).

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6 130 Other more-parasitoid-specific traits include whether the adult female
7
8 131 parasitoids feed on hosts, as well as characteristics of the hosts attacked. Hosts may be
9
10 132 attacked in their different developmental stages (e.g. egg, larva, pupa or adult – adult
11 133 parasitoids are unusual), the host niche may be concealed or exposed to various
12
13 134 degrees (e.g. Blackburn, 1991a,b), and the host species may be of widely different
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15 135 body sizes (data absent in Blackburn (1990) and Jervis & Ferns (2011), but present in
16 136 Traynor (2004), Le Masurier (1987) and Mayhew & Hardy (1998)). Time spent as a
17 137 pupa is also of interest in some analyses and has received special focus (Blackburn
18 138 1991a, Jervis et al., 2011).

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21 139 Although host range is a major life history feature of parasitoids that is
22 140 predicted to be correlated with other life history traits (e.g. Askew & Shaw, 1986) as
23 141 it is in Lepidoptera (Jervis et al., 2007b), there are considerable problems assembling
24 142 parasitoid host range in large comparative datasets. Problems include errors of host
25 143 recording in the original data, and variation in the study effort of different parasitoid
26 144 species. So far, only one large multi-trait dataset (Traynor, 2004) has attempted to
27 145 include it, though some more restricted studies have addressed it (e.g. Sheehan &
28 146 Hawkins, 1991). Sometimes studies use idio/koinobiosis as a proxy for host range
29 147 under the assumption that this is consistently associated with host range (e.g.
30 148 Hawkins, 1994). Mortality rates in adults and juveniles are notable by their absence in
31 149 broad comparative datasets, as are measures of host densities. These traits are likely to
32 150 exert important selective effects on parasitoid life histories (e.g. Price, 1973, 74;
33 151 Ellers et al., 2000; Ellers & Jervis, 2003, 2004), but are sparsely measured. Measures
34 152 of host concealment and host-stage attacked are sometimes used as proxies for both,
35 153 though possibly not effectively (e.g. Jervis et al., 2012).

36 154 As can be seen from a comparison of existing datasets (Table 1), the existing
37 155 data are extremely gappy. Better known traits include easily-scored variables such as
38 156 body length, temperate or tropical distribution, endo/ectoparasitism, idio-/koino-
39 157 biosis, solitary/gregarious development, egg type, host adult body size, host stage
40 158 attacked and host concealment. Other traits which require more detailed
41 159 measurements, such as oviposition rate, egg size, and lifetime fecundity, are
42 160 sometimes less well known.

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3 161 Having **introduced** many of the traits of interest in parasitoids, I now briefly
4 162 **describe some explanatory** frameworks which may make sense of some of them.
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8 164 **Potential explanatory frameworks**

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10 165 The r/K selection **paradigm (MacArthur & Wilson, 1967; Pianka, 1970)** assumes that
11 166 life histories are selected according **to the population** dynamic type (r populations
12 167 being rapidly increasing, K those at equilibrium), predicting that the former selects for
13 168 “fast” life history traits such as high fecundity, with consequent small offspring size,
14 169 rapid development with consequent small adult size, and frequent reproduction with
15 170 consequent low adult lifespan. The r/K paradigm was popular for a decade, but has
16 171 since waned because of doubts over its underlying assumptions (see Stearns 1977,
17 172 1992). However, the “suite” of associated life history traits embodied by the paradigm
18 173 is still commonly proposed to exist, though the “ r/K ” label has been largely dropped
19 174 in favour of the term “fast-slow continuum” (see Jeschke & Kokko, 2009).
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26 175 Modern theoretical explanations for the fast-slow continuum often make use
27 176 **of** metabolic scaling theory (see Brown et al., 2004). This allows us to predict how a
28 177 multitude of traits will co-vary when optimizing a smaller number of traits like age
29 178 and size at maturity under a given environmental constraint, such as a particular rate
30 179 of adult mortality (e.g. Charnov, 1991; Kozłowski & Weiner, 1997; see Harvey &
31 180 Purvis, 1999). This predictive power comes from the fact that metabolism is affected
32 181 by body mass in well-defined ways. Changes in body mass therefore have predictable
33 182 consequences on other traits that depend on metabolism, such as development time
34 183 and potential fecundity (Brown et al., 2004). Given this, it is legitimate to ask if such
35 184 traits are associated in the predicted way in parasitoids (for example a positive
36 185 association between body mass and development time) (Blackburn, 1991a).
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45 186 Balanced-mortality expresses the principle that in any population at
46 187 equilibrium, mortality and fecundity should be balanced. Hypothetically, either of
47 188 these two traits could act as a constraint to which the other responds. For example, in
48 189 Charnov’s (1991) model of female mammal life histories, fecundity is determined by
49 190 adult body size, and juvenile mortality rates are presumed to simply equalize
50 191 fecundity, an assumption that does a good job of predicting cross-species variation in
51 192 these traits (Harvey & Purvis, 1999). However, many life history models make the
52 193 opposite assumption; that mortality schedules select for a particular fecundity
53 194 (Stearns, 1992). In general, life history models emphasize the importance of
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3 195 considering both adult and juvenile mortality, because the difference between the two
4 196 exerts a strong selective force (Stearns, 1992): for example increasing adult mortality
5 197 relative to juvenile mortality can select for delayed maturation and hence higher
6 198 fecundity in fish (Law & Grey, 1989) and semelparity in plants (Young, 1990). It is a
7 199 pity that no life history models in parasitoids have explicitly considered the effects of
8 200 independently varying externally imposed juvenile and adult mortality rates, hence the
9 201 precise selective effects of mortality risks are not well-bedded in parasitoid-specific
10 202 theory, even though predictions have been made about empirical patterns (Jervis et al.,
11 203 2012).

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18 204 Another interesting (physiological) paradigm that has come to be applied to
19 205 life histories is that of capital- versus income breeding (Drent & Daan, 1980; Bonnet
20 206 *et al.*, 1998; Stephens *et al.*, 2009). **The paradigm developed from studies of**
21 207 endothermic vertebrates, and refers to whether a species uses primarily stored energy
22 208 (“capital”) to power reproductive effort, or whether organisms power reproduction by
23 209 foraging at the same time (“income”). In endothermic vertebrates, where reproduction
24 210 is expensive but forage not always available (e.g. in incubating birds or lactating
25 211 mammals), this dichotomy has proved useful in explaining certain differences in
26 212 behaviour across species, such as seasonality of breeding in primates (Brockman &
27 213 van Schaik, 2005). Bonnet *et al.* (1998) **have** argued however that the concept also has
28 214 relevance in ectotherms. Some insects do not feed as adults, and so are obvious capital
29 215 breeders. The distinction between non-feeding and feeding adults, and other
30 216 morphological proxies, have thus been used as predictors of other traits, for example
31 217 in Lepidoptera (Tammaru & Haukioja, 1996; Jervis *et al.*, 2005; Javois *et al.*, 2011;
32 218 Molleman *et al.*, 2011).

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43 219 In parasitoid wasps, the ovigeny index is likely to partially indicate capital or
44 220 income breeding; pro-ovigenic species seem naively **to be capital** breeders as the eggs
45 221 are fully developed before adulthood, though females may still feed to power host-
46 222 and mate-finding (Jervis *et al.*, 2008). Synovigenic species however can power egg
47 223 maturation by either stored fat or other larval reserves, or from sources harvested
48 224 during adulthood, for example by host feeding (see Casas *et al.*, 2005; Jervis *et al.*
49 225 2008), so whilst they may tend more towards income breeding, the link between
50 226 ovigeny and capital/income breeding is likely to be imperfect. Host feeding is thus
51 227 another proxy that may relate to income breeding, since **many** parasitoids are
52 228 apparently incapable of lipogenesis (Visser *et al.*, 2010), and fats and proteins are a

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3 229 necessary component of eggs, whilst the most readily available foods available to
4 230 adult parasitoids are sugars in nectar and honeydew (Jervis et al., 2008). One might
5 231 therefore expect the ovigeny index and host feeding to be useful predictors of other
6 232 life history traits, based on the utility of the capital/income distinction in other groups.

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9 233 Studies on non-parasitoid taxa have shown that **group-specific dichotomous**
10 234 **traits can account** for much of the variation in other traits across species. In birds, for
11 235 example, whether a species is ground-nesting or not appears to account for much of
12 236 the variation in other traits (Bennett & Owens, 2002). Furthermore, these traits are not
13 237 phylogenetically labile, so that birds consist of a relatively small number of clades
14 238 with quite divergent combinations of traits: one might argue that there is no simple
15 239 life history suite but essentially two distinct sets of suites. In parasitoids, there are
16 240 several potential categorical traits that may act in such a way, including
17 241 solitary/gregarious development (Mayhew, 1998a), idio/koinobiosis and
18 242 ecto/endoparasitoidism (Godfray, 1994), and host stage attacked (Price, 1974).

19 243 **Most prominent** has been the development of the “dichotomous hypothesis”,
20 244 which originated from the comparison of life history traits in ecto/endoparasitoids
21 245 (e.g. Askew, 1975), then extended to include host range as a response variable and
22 246 idio-/koinobiosis as a predictor variable (Askew & Shaw, 1986, see above), and then
23 247 extended further to include an array of other response variables (Gauld & Bolton,
24 248 1988; Blackburn, 1991b; Godfray, 1994; Quicke, 1997; Mayhew & Blackburn, 1999;
25 249 Jervis & Ferns, 2011). In its broadest form, this proposes that idiobionts will tend to:
26 250 take less time to develop, lay larger eggs, be ectoparasitoids, live longer as adults, be
27 251 smaller, be less fecund, lay eggs less rapidly, have a lower ovigeny index, be more
28 252 likely to host feed, lay eggs on more concealed hosts, attack later host stages and
29 253 attack a broader host range than koinobionts. Some behavioural traits have also been
30 254 suggested including nocturnal/diurnal flight, and the degree of sex allocation in
31 255 response to host size and consequent sexual size dimorphism (Quicke, 1997). The
32 256 supposed driving forces behind these differences are **many**, including avoidance of
33 257 juvenile predation and host degradation on immobile hosts, reduced co-evolution of
34 258 physiological interactions with hosts, selection for smaller egg size in endoparasitoids,
35 259 hence selection for pro-ovigeny and less host feeding, and reduced longevity afforded
36 260 by diversion of larval resources away from fat reserves into eggs (see Blackburn,
37 261 1991b; Godfray, 1994; Jervis & Ferns, 2011).

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3 262 In all life history problems, trade-offs and constraints underpin the optimal
4 263 **outcome.** The parasitoid is unlike a typical harvesting organism, such as a
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6 264 photosynthesizing plant, or an animal that develops to maturity by consuming a,
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8 265 potentially infinite, number of meals. Such organisms have the essentially open
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10 266 decision of defining their body size at reproductive maturity by simply deciding at
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12 267 what age and size to divert resources into reproduction instead of growth, with no
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14 268 prescribed resource-based maximum size. In parasitoids and other similar organisms,
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16 269 **the single host, constrains the resources for development (even in koinobionts),** and
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18 270 hence the maximum adult body size. In gregarious parasitoids, there is the additional
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20 271 constraint of dividing the host resources across the rest of the developing brood (see
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22 272 Mayhew & Glaizot, 2001; Crowley & Saeki, 2009). Hence a trade-off between
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24 273 offspring size and number is expected after accounting for the size of the host (e.g.
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26 274 Hardy et al., 1992), whilst a positive correlation between parasitoid body size and host
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28 275 body size is expected, especially in solitary species. Development time should be
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30 276 longer for those attacking larger hosts and longer for koinobionts, which may have
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32 277 delayed development (Blackburn, 1991a). Following the principle of minimizing time
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34 278 spend in vulnerable life history stages (Stearns, 1992), we might expect development
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36 279 time to be correspondingly shorter in those exposed to greater mortality risks
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38 280 (Blackburn, 1991a).

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40 281 For the adult parasitoid, given that maturity is already reached, the major life
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42 282 history decision is one of allocation of stored resources to immediate current
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44 283 reproduction (eggs), or future survival and reproduction (e.g. fat) (Ellers, 1996; Jervis
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46 284 et al. 2005; Jervis et al., 2008), which will result **in** a trade-off between survival and
47
48 285 early reproduction. Theoretically, the trade-off is resolved in favour of reproduction,
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50 286 other factors being equal, if habitats contain many hosts and if host encounters are
51
52 287 more unpredictable (Rosenheim, 1996; Sevenster et al., 1998; Ellers et al., 2000;
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54 288 Ellers & Jervis, 2003), and also if body size is small (Ellers & Jervis, 2003, 2004).

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56 289

57 290 **Trait associations in taxonomically-broad studies**

58 291 Blackburn (1991a,b) showed that body size predicted life history traits across species
59
60 292 much less in parasitoid Hymenoptera than in vertebrates. He **did find that** larger body
293 size predicted longer development as expected, as well as larger eggs. Development is
294 faster in idiobionts (particularly in the pupal stage), eggs hatch quicker in parasitoids
295 of poorly concealed hosts, temperate clades take longer to develop than tropical ones,

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3 296 and parasitoids attacking eggs take longer to develop than those attacking pupae.

4 297 These findings vindicate some of the predictions about development time made

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6 298 above.

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8 299 He also found limited support for a fast-slow continuum, in that more fecund
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10 300 species had smaller eggs, and laid them quicker than less fecund species. Unlike in
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12 301 vertebrates however (Jeschke & Kokko, 2009), fecundity does not evolve predictably
13
14 302 in response to body size change, neither is adult lifespan consistently related to body
15
16 303 size. These modest findings may have reduced interest in broad comparative studies
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18 304 on parasitoid life histories. One contributing notion may have been that datasets were
19
20 305 too noisy to detect much of value.

21
22 306 However, an alternative reason for the modest results is that parasitoids have
23
24 307 different life history suites from other organisms. This alternative found some support
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26 308 when Mayhew & Blackburn (1999) used the same data to test the dichotomous
27
28 309 hypothesis and found reasonable support for it. Idio/koinobiosis evolves in concert
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30 310 with ecto/endoparasitoidism. Koinobionts are almost always endoparasitoids,
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32 311 although idiobionts are commonly either endo or ectoparasitoids.
33
34 312 Koinobionts/endoparasitoids also have smaller eggs, short adult lifespans, (but longer
35
36 313 development as found by Blackburn, 1991a), attack hosts available over a shorter time
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38 314 window, and, in larval parasitoids, have greater fecundity and oviposition rates than
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40 315 idiobionts/ectoparasitoids. These findings were largely replicated in another dataset
41
42 316 with only a few species in-common (Jervis & Ferns, 2011).

43
44 317 The findings were significant in that they suggested: a) that taxonomically
45
46 318 broad parasitoid datasets could contain significant signals about associations between
47
48 319 traits; b) that parasitoid-specific concepts or predictions might lend more
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50 320 understanding than borrowing predictions from studies on other taxa; c) that the
51
52 321 fullest depictions of the dichotomous hypothesis went too far (e.g. there was no
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54 322 association with adult body size, degree of host concealment or stage of host
55
56 323 attacked); d) reasons why the expected fast-slow continuum was not so strong in
57
58 324 parasitoids. For example, a strong link between body size and adult lifespan or
59
60 325 fecundity is not expected because development mode has a strong effect on lifespan
326 and fecundity thus is a confounding variable. In addition, development mode has
327 opposite effects on pre-adult lifespan and adult lifespan, confounding the usual
328 positive association between these variables: koinobionts have fast adults (short

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3 329 lifespan, high fecundity, small eggs, more rapid oviposition), but slowly developing
4 330 juveniles.

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6 331 A qualifier on the extent of the dichotomy concerns the studies of Hawkins
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8 332 (1994), which looked at the parasitoid communities of different host species. Hawkins
9
10 333 found that communities of parasitoids attacking exposed hosts tend to consist of more
11 334 koinobionts. However, despite being in the direction predicted by the dichotomous
12 335 hypothesis, the frequency of traits in communities of species probably depends not
13 336 just on evolutionary changes in the parasitoid life-history (supposed to underlie the
14 337 dichotomy), but also how parasitoid clade richness is affected by life history, as well
15 338 as the assembly of ecological communities of different parasitoids on a host. Thus,
16 339 whether this finding supports the dichotomy is presently ambiguous because we do
17 340 not know which of these forces most underlies it.

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21 341 Traynor & Mayhew (2005a) used Blackburn's (1990) dataset to investigate an
22 342 outstanding question; what explains variation in clutch size and adult body size
23 343 (which were not associated with most other variables in the above studies). They
24 344 found that body size is predicted by the stage of host attacked; for example, egg
25 345 parasitoids tend to be smaller than those attacking larvae and pupae. There was also
26 346 evidence for a trade-off between body size and clutch size after controlling for the
27 347 stage of host attacked, mirroring an evolutionary correlation between body size and
28 348 solitary/gregarious development found across families by Mayhew (1998a). Thus, it
29 349 seems likely that body size, host size and clutch size form a set of mutually co-
30 350 evolving traits roughly independent of the other life history traits belonging to the
31 351 dichotomy. Traynor & Mayhew (2005a) also found that clutch size in gregarious
32 352 species was negatively correlated with latitude.

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36 353 In the late 1990s, renewed interest in the trade-offs governing adult parasitoid
37 354 life histories prompted Jarvis and co-workers to develop a second dataset of parasitoid
38 355 life histories, based around species for which the ovigeny index had been estimated.
39 356 Analysis of this dataset showed that a high ovigeny index was negatively correlated
40 357 with adult lifespan, and associated with anhydropic eggs, koinobiosis, longer pre-adult
41 358 lifespan, gregarious development, maximum egg load, an inability to resorb eggs and
42 359 tendency not to host feed (Jarvis et al., 2001; Jarvis & Ferns, 2011). Adult body size
43 360 was associated with a lower ovigeny index in an early study (Jarvis et al., 2003). This
44 361 association disappeared in a larger dataset (Jarvis & Ferns, 2011), but the authors
45 362 cautioned against ejecting body size prematurely from the "ovigeny" suite of traits as

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3 363 the body size data were very incomplete and probably imperfectly representative of
4 364 body mass. Oviposition seems likely to be a trait that partly mediates the interaction
5 365 between development mode and other life history traits, whilst extending a network of
6 366 associations to other traits not likely to be driven by development mode *per se*, such
7 367 as gregarious development, possibly host feeding (Heimpel & Collier, 1996), egg
8 368 resorption (Flanders, 1950; Quicke, 1997), and possibly body size.

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10 369 The latter dataset has also been used to test the relationship between fecundity
11 370 and host stage attacked (Jervis et al. 2012). This relationship has been claimed for
12 371 more taxonomically-restricted studies but is not significant at this broad taxonomic
13 372 scale (see below). It was predicted on the basis of the balanced-mortality principle
14 373 (that early host stages experience more mortality, hence parasitoid fecundity is
15 374 selected to rise), and the effects of host abundance (that earlier host stages are more
16 375 abundant, selecting for higher fecundity (Godfray 1994)).

17
18 376 Overall then, far from being too noisy to infer much about the life histories of
19 377 a diverse group, taxonomically-broad datasets have laid much of the framework for
20 378 the next generation of parasitoid life history studies.

21 379

22 380 **Trait associations in taxonomically-restricted studies.**

23 381 Several important studies contributing an understanding of the above traits across
24 382 species have been conducted on taxonomically more-restricted datasets, hence may or
25 383 may not be reflective of patterns more generally.

26 384 Traynor (2004) developed a dataset of 382 species, similar to that of
27 385 Blackburn (1990) but covering just Ichneumonoidea (ichneumonids and braconids).
28 386 In addition to including most of Blackburn's variables, it included more host-related
29 387 information including host adult body length (Table 1), and detailed host range and
30 388 geographic information. The documented host and geographic range of a parasitoid
31 389 depends greatly on how well studied it is, and this therefore has to be accounted for
32 390 when studying these traits. Traynor (2004) did this by quantifying how well studied
33 391 species were (pages of publications from which the species data was collected), which
34 392 could then be used as a control variable.

35 393 Despite the fact that in this taxon there are many fewer transitions between
36 394 development mode than across the Apocrita as a whole, these data showed some
37 395 further support for the dichotomous hypothesis. There was an association between
38 396 ectoparasitoidism and idiobiosis, which were also associated with longer adult

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3 397 lifespans, and, notably, lower fecundity (cf Jervis & Ferns, 2011). There was **no**
4 398 **relationship** between egg volume and development mode, although fecundity was
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6 399 negatively correlated with egg size. Surprisingly, development time did not correlate
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8 400 with development mode, although it was positively correlated with body size. Body
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10 401 size also predicted egg size, and surprisingly, adult lifespan. It seems therefore that in
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12 402 ichneumonoids, the importance of allometric effects and those of development mode
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14 403 are slightly different than in parasitoid wasps as a whole. **As a result, perhaps taxon-**
15 404 **specific allometries should now be investigated.**

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17 405 Although Traynor (2004) found an association between development mode
18 406 and host niche and host exposure across species, as found in some **host-based** studies
19 407 (Hawkins, 1994), with koinobionts more associated with exposed hosts, importantly
20 408 this relationship was not significant after controlling for phylogeny, which may help
21 409 explain why community studies find such a relationship but not phylogenetic
22 410 comparative studies. The data also provide support for the association between host
23 411 size, clutch size and parasitoid adult body size: parasitoid body size correlated with
24 412 host body size (Figure 1), and clutch size also correlated with host size after
25 413 controlling for parasitoid body size.

26 414 **The dichotomous hypothesis claims** that koinobionts have more restricted host
27 415 ranges than idiobionts. This claim is **supported by** studies of the parasitoid
28 416 communities of particular groups of hosts, such as the oak leaf miner community in
29 417 England (Askew & Shaw, 1986) and Japan (Sato, 1990), and of the aphid parasitoid
30 418 community of an English field (**where, note that the idiobionts are all**
31 419 **hyperparasitoids**, Müller et al., 1999). The single comparison of metopiine and
32 420 pimpline ichneumonids is also consistent with this claim (Sheehan & Hawkins, 1991)
33 421 (for some other comparisons see Shaw (1994)). However, Traynor (2004) found no
34 422 association between these traits either before or after accounting for the degree to
35 423 which the parasitoid had been studied. The accuracy of literature-derived host range
36 424 data might be questioned. However, Traynor did find that, after controlling for the
37 425 intensity with which each species had been studied, there was a correlation between
38 426 temperate (as opposed to tropical) distribution and host range. Other geographic
39 427 correlations included more rapid development in tropical groups, and larger
40 428 geographic ranges in larger bodied and temperate groups, and those attacking hosts
41 429 with a large geographic range.

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3 430 Another proposed predictor of host range has been solitary/gregarious
4 431 development (Wharton, 1984; Shaw & Huddleston, 1991, Sheehan, 1991; Smith,
5 432 1991; Traynor & Mayhew, 2005b; Hoffmeister et al.,2005), though the **evidence is**
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7 433 based on relatively few informal comparisons. An association might be mediated by
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9 434 selection for investment in reproduction over survival in gregarious species (see
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11 435 Pexton & Mayhew, 2002), which may decrease oviposition specificity (see
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13 436 Hoffmeister et al., 2005). An interesting prediction of the latter hypothesis is that the
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15 437 ovigeny index should be correlated with gregarious development, which it is (see
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17 438 above, Jervis & Ferns, 2011).

18 439 The explanation of lifetime fecundity is one of the most outstanding issues in
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20 440 parasitoid life histories. The datasets of Price on parasitoids of a sawfly (Price, 1972,
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22 441 1974) and ichneumonid ovarioles (Price, 1973) , and tachinid and conopid flies (Price,
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24 442 1975), have been important **contributions about this. The original studies suggested**
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26 443 that parasitoids attacking later life history stages of their hosts tended to be less
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28 444 fecund than those attacking earlier stages. The ichneumonid and tachinid/conopid
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30 445 findings have proved robust when accounting for phylogeny (Jervis et al., 2012) but
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32 446 the associations are lost in taxonomically-broad studies (see above). **A** likely reason is
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34 447 that broader studies introduce more confounding variables; for example, the density of
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36 448 hosts, and mortality risks, likely vary enormously across host species, whilst fecundity
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38 449 is affected by other forces such as egg size (Blackburn, 1991b), itself affected by
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40 450 development mode (Mayhew & Blackburn, 1999). In addition, ichneumonids tend to
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42 451 all finish development in later host life-history stages, meaning that there is probably
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44 452 a stronger correlation between host stage attacked and mortality than is typical for
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46 453 other parasitoids. Force (1974) claimed similar findings to Price in studies of a gall
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48 454 midge, but attributed the differences in fecundity to differences in interspecific
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50 455 competitive ability.

51 456 Mayhew & Hardy (1998) looked at the evolution of clutch size and body size
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53 457 in bethylid wasps (Bethylidae), and found that wasp body size and clutch size were
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55 458 both positively correlated with host size across species: at deep taxonomic levels
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57 459 (above genus), body size responded to host size changes, but amongst more recent
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59 460 contrasts (among genera), clutch size responded instead. This taxon **lacks** obligate
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61 461 solitary development, meaning that clutch size is not restricted by parent-offspring
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63 462 conflict (see below). This reinforces the association between these three traits
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65 463 provided by broader studies. Similarly, **Le** Masurier (1987) found a positive

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3 464 correlation between brood size and host size in gregarious species, although in solitary
4 465 species body size responded instead, though to a relatively low extent. Such species
5 466 are constrained by parent-offspring conflict to develop alone despite the fact that
6 467 larger hosts would allow more offspring to develop (see Godfray, 1987). These last
7 468 studies raise the important issue of the phylogenetic lability of different traits to which
8 469 I now turn.

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12 471 **Evolutionary lability of life histories.**

13 472 The phylogenetic lability of different life history traits may help establish **which traits**
14 473 **drive variation in other traits**. Some authors (e.g. Shaw, 1983; Gauld, 1988) **suggested**
15 474 **that development mode** was likely to **be phylogenetically** constrained, and developed
16 475 hypotheses **about what drove changes in it** (see also Jervis & Ferns, 2011; Whitfield,
17 476 2003). Downton & Austin (2001) used a **coarse** phylogeny to suggest that
18 477 ectoparasitism was ancestral and at least 3 independent evolutions of endoparasitism
19 478 have occurred, with some transitions back to ectoparasitism again, findings largely
20 479 consistent with an earlier analysis of Whitfield (1998). Both braconids and
21 480 ichneumonids show several transitions from an idiobiont ectoparasitoid ancestor to
22 481 koinobiosis and endoparasitism (Belshaw et al., 1998; Quicke & Belshaw, 1999;
23 482 Quicke et al., 2009). Whitfield (1992, see also Quicke, 1993) suggested at least two
24 483 independent transistons to endoparasitism in the cyclostome braconids. Host
25 484 concealment may have evolved in parallel with development mode, but there have
26 485 clearly also been some transitions within each mode (Belshaw & Quicke, 2002).

27 486 Mayhew (1998a) performed a reconstruction of the **evolutionary history of**
28 487 solitary and gregarious development across the parasitoid Hymenoptera, showing that
29 488 solitary development is likely ancestral, with at least 43 transitions to gregarious
30 489 development, mostly at deep phylogenetic levels, though some are known to have
31 490 occurred within genera (e.g. Mayhew & van Alphen, 1999; Pexton & Mayhew, 2004).
32 491 Values of the parameter *Rho* (a branch length scaling parameter) in Phylogenetic
33 492 Regressions of body size and clutch size across parasitoid Hymenoptera have
34 493 suggested that body size is more constrained than clutch size (Traynor & Mayhew,
35 494 2005a).

36 495 Besides suggesting a degree of inflexibility in these traits, hence that they are
37 496 sometimes likely to act as constraints and drivers of other variables, **these results need**
38 497 **to be put into a broader context**. So far there have been no studies **considering the**

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3 498 **lability of a large number of traits** across taxonomically-broad datasets, but Traynor
4 499 (2004) performed one for her Ichneumonoidea data (Table 2). For some traits,
5 500 variation was almost entirely restricted to differences between the two families,
6 501 indicating considerable constraint. The most constrained were parasitoid adult body
7 502 length and the corresponding lengths of their host adults, both of which contrasted
8 503 strongly between ichneumonids and braconids; ichneumonids are a radiation of large
9 504 wasps attacking large hosts, and braconids are a radiation of smaller wasps attacking
10 505 smaller hosts; variation at other taxonomic levels is relatively trivial (Table 2).

16 506 **Significant variation at the subfamily level was found for development mode,**
17 507 **solitary/gregarious development, pre-adult lifespan, and several other traits. At genus**
18 508 **level, significant variation is found for egg size and fecundity. The latter two traits,**
19 509 **and longevity show variation spread quite evenly across taxonomic levels.** Further
20 510 analysis, for example using the retention index of each trait plotted onto cladograms,
21 511 suggested that host order is highly conserved, host concealment is only moderately
22 512 conserved, whilst host stage attacked and host ecological niche are less conserved
23 513 (Traynor, 2004).

29 514 Though this is a taxonomically restricted analysis, it does tend to support the
30 515 underlying assumption of the dichotomous hypothesis that development mode is
31 516 constrained and drives other traits, whilst some continuous components of the
32 517 dichotomous suite evolve more flexibly. This is also consistent with the conclusions
33 518 of Jervis & Ferns (2011) that ovigeny reflects some but not all of the dichotomy suite
34 519 and is not the sole organizer. Perhaps the most surprising result is how constrained
35 520 body size (of host and parasitoid) is, given that it is a continuously varying trait with
36 521 much intra-specific variation (e.g. Thorne et al., 2006).

522 523 **Summarizing and explaining the suite**

524 The available data tentatively suggest that two sets of, largely **independent**, traits seem
525 to summarize parasitoid life history variation at deep taxonomic levels; changes in
526 parasitoid body size (likely responding largely to host size (hence taxon and stage
527 attacked) and clutch size), and changes in development mode (ecto/endoparasitoidism,
528 idio/koinobiosis) (Figure 2). These changes together represent particular host
529 exploitation ecologies. Within the constraints of these relatively fixed traits, other
530 traits respond probably more flexibly. In the dichotomous set, these probably include
531 continuous traits like ovigeny index, pre-adult lifespan, adult longevity, egg size, and

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3 532 maximum egg load. The combinations of these traits selected by development mode
4 533 give rise to a limited fast-slow continuum in adult traits, excluding body size (Figure
5 534 2). The ovigeny index, or its correlates, have further knock-on consequences for other
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7 535 traits such as host feeding and egg resorption (not shown), possibly body size, and
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9 536 brood size. Finally, more tentatively, fecundity related traits are possibly affected by
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11 537 host density and juvenile mortality rates.

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13 538 Most of the proposed sets of parasitoid life history variation show some degree
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15 539 of overlap and interaction, meaning they can be considered as part of a single larger
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17 540 framework (Figure 2). The framework contains some relatively tight elements (e.g.
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19 541 egg size and development mode) but also looser ones (e.g. ovigeny and body size),
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21 542 and associations between distant traits in the framework are likely looser (e.g. ovigeny
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23 543 is associated with solitary/gregarious development but development mode is not). In
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25 544 addition some are relatively well supported (e.g. associations between host size and
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27 545 parasitoid size are found in taxonomically broad data as well as taxonomically
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29 546 restricted data) whilst support for others is weaker (e.g. associations between host
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31 547 range and development mode, and host stage attacked and fecundity, are only found in
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33 548 taxonomically restricted data).

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35 549 The reasons behind some of the associations seem well understood, whilst
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37 550 reasons for others remain largely unresolved. The development of dynamic
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39 551 programming models targeted at adult parasitoid life history decisions, together with
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41 552 studies of the physiological underpinnings of adult behaviour from intraspecific
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43 553 studies (Jervis et al. 2008), has lent some confidence in the likely reasons for the
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45 554 ovigeny “suite”. For example, a negative association between ovigeny and lifespan is
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47 555 likely due to a trade-off in early-life resource allocation between fat and eggs (e.g.
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49 556 Ellers, 1996; Ellers & van Alphen, 1997; Pexton & Mayhew, 2002), whilst the
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51 557 association between small body size and high ovigeny index is understood to be a
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53 558 response to stochasticity in reproductive opportunities combined with minimal total
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55 559 resources to allocate to survival and reproduction. Theoretical modelling and
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57 560 intraspecific studies of the clutch size/host size/body size suite have also led to
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59 561 plausible explanations of their association (Mayhew, 1998b,c; Mayhew & Glaizot,
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61 562 2001; Crowley & Saeki, 2009).

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63 563 Where there is more than one potential driver of a trait, analyses that control
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65 564 for one of them can potentially distinguish between those potential drivers.
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67 565 Unfortunately, in practice, interpreting the results of such analyses is more complex

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3 566 than one might anticipate, and does not lead to clear conclusions. For example, Jervis
4 567 & Ferns (2011) found that development time was significantly correlated with
5 568 idio/koinobiosis when controlling for ecto/endoparasitoidism, but not vice-versa.
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8 569 Unfortunately, the reverse was the case when also controlling for body size. When
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10 570 controlling for ovigeny index, idio/koinobiosis was significantly associated with
11 571 development time, but not vice-versa. However, ovigeny index was associated with
12 572 development time after controlling for ecto/endoparasitoidism, but only before
13 573 correcting for multiple comparisons. Controlling for body size also removed that
14 574 relationship. The results are partly confusing due to the gappy nature of the data
15 575 which makes sample size, hence power, vary from analysis to analysis, and partly
16 576 because several of the relationships are only marginally significant, hence findings are
17 577 very sensitive. At present therefore it seems that likely causation will have to be
18 578 assessed by other means.

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24 579 Why ovigeny and development mode are **associated remains unresolved**.
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26 580 Jervis et al. (2001) suggested several reasons which all involved development mode
27 581 affecting an intermediate variable that is also known to be linked to ovigeny (egg size,
28 582 adult lifespan, oviposition rate, and pupal development time). There are difficulties
29 583 explaining why some of these variables should be affected by development mode
30 584 independent of ovigeny index, and why simultaneously the ovigeny index should be
31 585 associated with them independently of development mode. Jervis & Ferns (2011) also
32 586 suggested that pupal development time might mediate the association between
33 587 ovigeny index and development mode, because both would seem to select for longer
34 588 pupal development and both are associated with it (Blackburn, 1991a; Jervis & Ferns
35 589 2011). However, there is no evidence that these associations occur independently of
36 590 each other, nor if they are tight enough to cause the overlap between the dichotomous
37 591 and ovigeny suites that is observed.

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46 592 One solution to this problem, shown in Figure 2, is if both ovigeny and
47 593 development mode are selected for by some common ecological variable or set of
48 594 variables. Possibly host density is one such variable (Blackburn, 1991b; Godfray,
49 595 1994). High host density might plausibly select for a high ovigeny index (Ellers &
50 596 Jervis, 2003), whilst the developmental flexibility offered by
51 597 endoparasitoidism/koinobiosis (see Harvey et al., 1994), along with the selection for
52 598 other fast life history traits, may favour the exploitation of hosts found in greater
53 599 densities (Blackburn, 1991b; Godfray, 1994). These ideas require more-explicit

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3 600 comparative testing at broad taxonomic scales, since using host-stage-attacked as a
4 601 density proxy currently does not provide any supporting evidence.
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8 603 **General conclusions and remaining challenges**

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10 604 What does the study of comparative parasitoid life history suites contribute to
11 605 life history theory in general? First it shows that the fast-slow continuum can be much
12 606 more limited in some organisms than in mammals. The continuum is also reduced in
13 607 fish and birds and plants compared to mammals (Franco & Silvertown, 1996; Jeschke
14 608 & Kokko, 2009), which in fish and birds is due to a positive, rather than negative
15 609 relationship between body size and fecundity, a likely result of viviparity in mammals
16 610 and subsequent extensive parental care. In parasitoids, the continuum is reduced
17 611 further, being confined to adult traits and omits body size.
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23 612 Second, parasitoids show how the ecology and nature of the host and the way
24 613 it is exploited (e.g. host density, host size, host mortality rates, parasitoid development
25 614 mode) can affect life history evolution in parasitic organisms. Third, parasitoids show
26 615 how a consideration of allocation to survival and reproduction in early adult life can
27 616 help explain many other life history traits. This work is already beginning to pay
28 617 dividend in other insects, and the principle is much more general. Fourth, parasitoids
29 618 expand the list of cases where biology-specific categorical traits, not part of the core
30 619 life history traits, have a major effect on a large number of traits. Such traits are a
31 620 thorn in the side of those who hope for a single all-encompassing life history theory or
32 621 paradigm.
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40 622 It is useful in empirical science to imagine the ideal dataset and ideal analysis
41 623 and to compare that with what does exist and has and can be done. For comparative
42 624 studies of parasitoid life histories we would wish for many more rows of data and for
43 625 less gappiness within rows. More rows (species) are necessary to help describe
44 626 accurately how some traits vary simultaneously with other traits across sister taxa.
45 627 The problem is especially acute in parasitoids which are an extremely rich radiation,
46 628 but poorly described and even more poorly studied (Santos & Quicke, 2011).
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48 629 Taxonomically-broad studies omit a more substantial fraction of the variation present.
49 630 We are fortunate in having a long and continuing tradition of description of basic life
50 631 history traits in parasitoids, largely thanks to interest in biological control of pests, and
51 632 can expect future datasets to be much more extensive than those covered here. A
52 633 qualification is the extensive time needed to gather literature-based data. The
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3 634 accumulation of data in a standardized format would be facilitated by a centrally
4 635 maintained online database, such as exists for mammals (PanTHERIA) and fish
5 636 (FishBase). **Such investments need** long-term funding to succeed.

6 637 The ovigeny index is an example of a relatively new trait that has added a
7 638 column of data that has been extremely valuable in resolving variation in other traits.
8 639 Host size data also needs to be much more extensively added to datasets, and field
9 640 studies of host density and parasitoid life tables, both as adults and juveniles, are
10 641 probably necessary to resolve issues of juvenile mortality and fecundity at broad
11 642 taxonomic scales. Probably some data already exist in a suitable format from
12 643 biological control work, but it would need to be compiled and standardized, and much
13 644 more needs to be gathered. Traits investigated also tend to be female-focussed (e.g.
14 645 the fecundity-related traits all refer to female rather than male fecundity). This befits
15 646 interest in the oviposition behaviour of parasitoids, in turn stemming from an interest
16 647 in biological control, population dynamics, community ecology, and the behavioural
17 648 ecology of female decision-making. There has been much less interest in male life
18 649 history traits, but there is likely to be much to be gained from studying male traits
19 650 more widely. An equivalent index of early reproductive investment for males, the
20 651 spermatogeny index, has been suggested for males (Boivin et al. 2005), and it
21 652 would be interesting to observe how this index correlates with traits such as lifespan,
22 653 body size, mating system, dispersal, sexual size dimorphism, and sex allocation (see
23 654 Boivin et al., 2005; Macedo et al., 2013; Boulton et al., 2014). Appropriate datasets
24 655 have however yet to be compiled as spermatogeny is rarely investigated.

25 656 The ideal way to investigate associations between multiple traits is through the
26 657 use of multi-variate analyses, such as Principle Component Analysis (PCA) (Jeschke
27 658 & Kokko, 2009). Gappiness has largely prevented this in taxonomically broad studies
28 659 (species with missing data are excluded). Nonetheless, perhaps scope already exists
29 660 for analysis of a more limited set of traits on a more limited set of species. As data-
30 661 sets become more species-rich and less gappy, the potential for such analyses will
31 662 increase, and will enable broad pictures such as Figure 2 to be inferred from single
32 663 analyses. Of course, all comparative analyses rely on a phylogenetic framework,
33 664 another area of uncertainty for parasitoid workers (see Davis et al., 2010). Despite
34 665 extensive phylogenetic work in the last two decades, **relationships in ancient rapid**
35 666 **radiations remains hard to resolve.**

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3 667 Whilst this review has focussed on broad patterns across taxa, important
4 668 residual variation remains. For example, important functional groups, such as egg or
5 669 pupal parasitoids, are exceptions to the dichotomy in that they are idiobionts but
6 670 endoparasitoids. Do their core life histories better reflect expectations from the
7 671 idiobiont or endoparasitoid part of their development? What role does host stage
8 672 attacked play in controlling this, and what causes the variation remaining within these
9 673 groups. These remain important questions to answer using both broad and
10 674 taxonomically focussed studies.

11 675 Beyond description of the suite, there is the job of explaining it. Intraspecific
12 676 studies on continuous traits, and modelling studies, are vital avenues allowing us to
13 677 attribute causation. In particular, the generation of dynamic models, that have already
14 678 investigated ovigeny, might be extended to explore the comparative observations
15 679 more broadly across other traits. Selection experiments are one avenue of intraspecific
16 680 study that is underused, but which is held in high esteem in allowing causal inference
17 681 (see Stearns, 1977). Comparative studies can potentially add to arguments about
18 682 causation; for example, by testing to see if associations are retained whilst controlling
19 683 for another potentially causative trait, but really require larger and less gappy data.
20 684 More studies of phylogenetic lability can also add to this, and particularly in a broad-
21 685 taxonomic context. Path analysis (e.g. Shine, 1996), and methods based on
22 686 information transfer (Hannisdal & Peters, 2011) which both attempt to infer causative
23 687 relationships from observational data, might also bear fruit.

24 688 There continues to be a place for both taxonomically-broad and more
25 689 restricted studies. The number of traits with which parasitoid life history workers must
26 690 deal is extensive, whilst even single subfamilies can be very species rich indeed. The
27 691 added control given by taxonomically restricted datasets has been illuminating.

28 692 **Postscript**

29 693 When I was a PhD student, my supervisor published a landmark synthesis of life
30 694 history and behavioural work in parasitoids (Godfray, 1994). In the two decades since,
31 695 interest in adult allocation to survival and reproduction, the underpinning nutritional
32 696 basis, and the behavioural and ecological correlates and consequences, have been
33 697 perhaps the standout change. The work of Mark Jervis and coauthors has since
34 698 provided the comparative, and to a large extent theoretical, context for the ovigeny set
35 699 of traits, at the core of parasitoid life history variation. On re-reading Mark's papers
36 700 whilst preparing this article, I was struck by the dedication required to assemble his

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3 701 datasets, the care that went into the analyses and the writing of the papers, and the
4 702 underlying breadth of biological vision. I hope that readers will take a moment to
5 703 ponder these points. With Mark's untimely death we lose a loved and respected
6 704 colleague whose contributions have been rich, and which are likely also to be
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8 705 enduring.
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13 707 **Acknowledgments.**

14 708 I thank Ian Hardy and Eric Wajnberg for the opportunity to contribute this article,
15 709 Peter Ferns for providing me with a copy of the data from Jervis & Ferns (2011), two
16 710 anonymous referees and George Heimpel for comments.
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For Peer Review

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3 990 **Figure legends**

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6 992 **Figure 1** Adult body length of parasitoid against adult body length of host in

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8 993 Ichneumonoidea (data from Traynor, 2004, **Pearsons $r = 0.507$, $n = 209$, $P < 0.001$.**)

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10 994 **The relationship is also significant after controlling for phylogeny (see Traynor 2004).**

11 995 The line is $y = x$.

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14 997 **Figure 2** Sets of associated life history traits in parasitoid Hymenoptera as described

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16 998 in this review, showing the overlap between them. Solid boxes represent traits known

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18 999 to be in the set via taxonomically broad comparative studies. Dotted boxes represent

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20 1000 less-well-evidenced components. Causal arrows are speculative.

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1003 Table 1. Some life history traits included in large comparative datasets of parasitoid
 1004 wasps. **Data coverage is shown for (1) Blackburn (1990), (2) Jervis & Ferns (2011)**
 1005 **(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)
<i>Generic</i>							
<i>traits</i>							
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)
<i>Parasitoid</i>							
<i>traits</i>							
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)	

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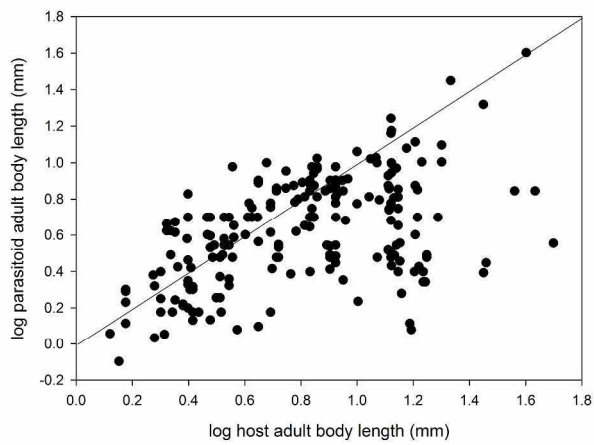
1
2
3 1007 Table 2: Nested ANOVA (see Harvey & Pagel, 1991) of life history traits of
4
5 1008 Ichneumonoidea from Traynor (2004). Numbers indicate the proportion of the total
6
7 1009 variance in each trait (rows) found at each taxonomic level (columns) (* $P < 0.05$ **
8
9 1010 $P < 0.001$). (Species level is never significant as species variance is obtained from the
10
11 1011 genus error). **Only binary and continuous traits were included, but not categorical**
12
13 1012 **traits with >2 factor levels.** “Residual” values are those taken by fitting the slope of a
14
15 1013 phylogenetic regression of the trait against the degree of study (pages of sources used
16
17 1014 to assemble the data for each species) through the raw species data for the trait and
18
19 1015 degree of study.
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21 1016

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

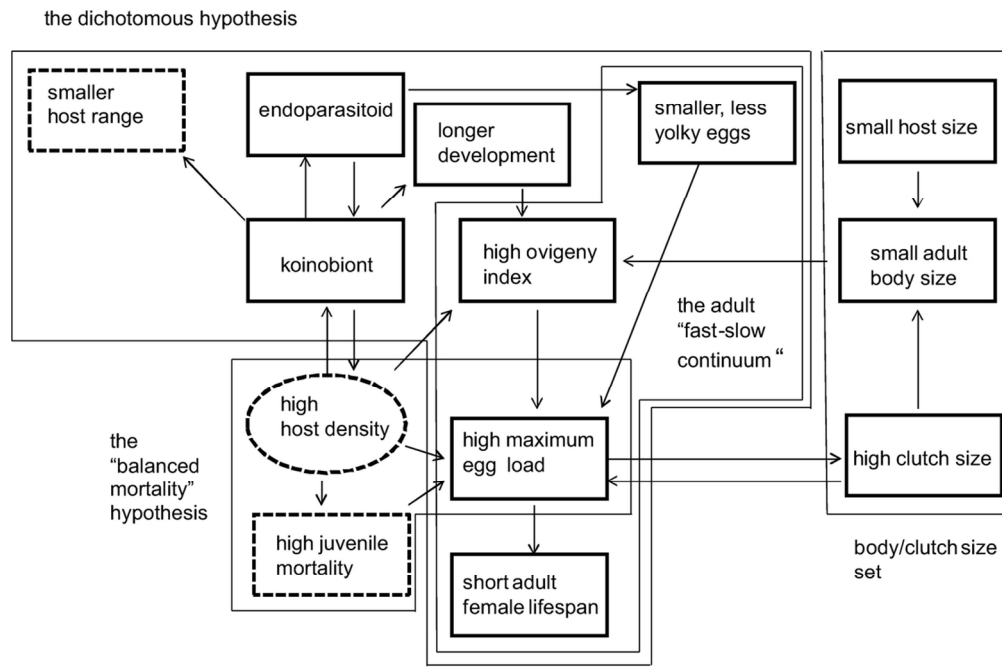
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296x419mm (300 x 300 DPI)



111x73mm (300 x 300 DPI)

Review

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