Does development mode organize life-history traits in the parasitoid Hymenoptera?

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Summary

1. Several authors have proposed that inter-specific variation in parasitoid life histories can be classified according to a dichotomy of development modes: ectoparasitoids and idiobionts with one suite of traits, and endoparasitoids and koinobionts with an opposing set of traits.

2. The factual evidence for such a dichotomy is presently scant. Here, 10 predictions of the dichotomous hypothesis are assessed using life history data from 474 species of parasitoid Hymenoptera.

3. A degree of support for the dichotomy is found. As predicted, koinobiosis is associated with endoparasitism, and idiobiosis with ectoparasitism. Endoparasitism and/or koinobiosis are also associated with a shorter adult lifespan, a shorter window for parasitism, smaller eggs, a longer pre-adult lifespan and, in larval parasitoids, a greater oviposition rate and fecundity than ectoparasitism/idiobiosis.

4. However, several predictions are not upheld by the data. No significant relationship is found between development mode and either body size, the degree of host concealment or the stage of host attacked. Some trends are only found amongst larval parasitoids, and others do not hold for both endoparasitism and koinobiosis.

5. We conclude that there is at least some merit to the dichotomous hypothesis, though the most extensive depictions go beyond the present data. As a step towards formulating the dichotomy in a more rigid theoretical base, we discuss the selective pressures and constraints that are likely to account for the observed trends.

Key-words: comparative method, ectoparasitism, endoparasitism, idiobiont, koinobiont.

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Introduction

The parasitoid Hymenoptera is a species-rich group of insects that share a basic life history characteristic: offspring develop by feeding upon a single live host arthropod, eventually killing it (Quicke 1997). However, within this basic framework parasitoid wasps have evolved an enormous diversity of other life history traits. Consider first *Sericopimpla seri-*

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cata Kriechbaumer (Ichneumonidae: Pimplini), which is 12 mm long, lives up to 140 days as an adult, is ectoparasitic as a larva, permanently paralyses its host and lays 30 eggs in its life, each 2 mm long (Smithers 1956). In contrast, *Trioxys complanatus* Quilis Pérez (Braconidae: Aphidiinae) is only 1·3 mm long, only lives 28 days as an adult, is endoparasitic as a larva, does not permanently paralyse its host and lays 180 eggs in its life, each less than 0·1 mm long (Schlinger & Hall 1961; le Pelley 1968). Such inter-specific variation in life histories begs explanation.

Early hypotheses to explain inter-specific variation in parasitoid life histories centred around the

ecology of the host. Price (1972, 1973a, 1974) studied the parasitoids of the sawfly *Neodiprion swainei* Middleton (Hymenoptera: Diprionidae). He suggested that the parasitoid complex could be divided into two fractions: first, 'early succession' colonizers using larval hosts, which possessed high fecundity, large body size and low inter-specific competitive ability. Secondly, smaller 'late succession' colonizers using pupal hosts, and with low fecundity and high inter-specific competitive ability. Price suggested that the degree of mortality experienced by the host was the major selective force operating on this suite of traits. In a later comparative study of ichneumonid parasitoids (Price 1973b, 1975), he suggested that fecundity was best predicted by the degree of host concealment and the stage of host attacked, again advocating mortality as the major selective force involved. These studies led him to suggest a 'balanced mortality' hypothesis to explain fecundity and fecundity-related traits. In a similar study, Force (1974, 1975) investigated variation in the parasitoids of the gall midge, *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae). He suggested that the parasitoids of the midge had reproductive capacities inversely related to their inter-specific competitive abilities, and thus lay along an 'r/K continuum'. Finally, Askew (1975), studied parasitoids of the British oak-gall and oak leaf-miner communities, and came to similar conclusions: parasitoids directly attacking young galls or mines tend to be specialized and carry many eggs (r-strategists). Parasitoids attacking more mature galls or mines are polyphagous and carry fewer eggs (K-strategists). In the leaf-miner community, the early colonizers tend to be endoparasitoids with low inter-specific competitive ability and the late colonizers ectoparasitoids with high inter-specific competitive ability. This division according to development mode was furthered (Askew & Shaw 1986) by a new division (following Haeselbarth 1979), according to whether the host continued to develop after parasitism (koinobiosis) or ceased development after parasitization (idiobiosis). Askew & Shaw (1986) suggested that, in the oak leaf-miner community, this division was a better predictor of some life history traits, notably host range, than endo- or ectoparasitism, although endoparasitism tended to be associated with koinobiosis and ectoparasitism with idiobiosis.

These early ideas about major divisions in life history strategies were supported by informal comparisons amongst relatively few communities or taxa. A step forward came through Blackburn's (1991a,b) formal life history comparisons across many families using modern statistical methods to control for phylogenetic relatedness (Harvey & Pagel 1991). Blackburn was partly motivated by the earlier studies on parasitoids and partly by other phylogenetically based comparisons then being made across

vertebrate taxa by Harvey and coworkers (e.g. Bennett & Harvey 1987, 1988; Elgar & Harvey 1987; Promislow & Harvey 1989; Read & Harvey 1989; Trevelyan, Harvey & Pagel 1990), where body size had been found to be a major correlate of other life history traits. In parasitoids, however, Blackburn found that very few life history traits correlated with body size. Pre-adult development time and egg size were correlated with body size, but adult lifespan was not, and neither was fecundity. However, he found some correlations between traits which were in line with the earlier parasitoid studies, notably that there was a 'fast-slow continuum' with more fecund taxa laying smaller eggs, and reproducing faster than less fecund taxa. Nonetheless, the degree of association between life history traits found by Blackburn was relatively small and the majority of variance in the data remains unexplained. One contributory factor is certainly that the data derive from multiple studies conducted under different circumstances by different authors, leading to a large error variance in the data through which biological correlations are difficult to detect. In addition, phylogenetic knowledge of parasitoid wasps is poor, and it is possible that the hypothesis of phylogenetic relatedness on which Blackburn's study was based is simply incorrect in many areas. However, an alternative possibility is that the appropriate questions were not asked of the data; in particular, there was no specific attempt to test the dichotomy in life history traits organized by development mode as suggested by Askew (1975) and Askew & Shaw (1986). The absence of a good description of the relationships between traits is frustrating because it is an essential first step towards an adequate theory of life history evolution for the group.

Two recent reviews (Godfray 1994; Quicke 1997) have attempted to summarize the inter-specific life history variation amongst parasitoids, and both have emphasized development mode as a major potential organizer of parasitoid life histories. Yet, there is little hard evidence in favour of such a dichotomy (reviewed in Quicke 1997) and there has been no formal comparative test using phylogenetic methods. Here, we re-examine Blackburn's life history data for the parasitoid Hymenoptera in the light of the dichotomous hypothesis using phylogenetic methods. A degree of support for the hypothesis is found, which enlarges the degree of inter-specific variation we can now explain in terms of inter-correlations between traits. This constitutes the first extensive and formal test of the dichotomous hypothesis. As a step towards a theoretical basis for inter-specific parasitoid life history variation, we discuss what the demonstrated relationships between traits might mean in terms of the selective forces and constraints underlying parasitoid life history evolution.

Methods

DATA

The same data were used as by Blackburn (1991a,b). These data are available in full in Blackburn (1990) or on request from the second author, and constitute life history information on 474 species of parasitoid Hymenoptera in 27 families covering all the most species rich taxa. These data were extracted from published life history studies, with the exception of some information on body lengths, which were measured from museum specimens. The following variables were used in our analyses:

1. *Ecto- or endoparasitism*: ectoparasitoids have larvae which feed externally on the host, whilst endoparasitoids feed inside the host's body.

2. *Idio- or koinobiosis*: idiobionts are parasitoids whose hosts do not continue to develop after parasitism, often because they are permanently paralysed by the wasp sting. Koinobionts are not paralysed or only temporarily paralysed, and the host continues to develop, only dying when the wasp completes development.

3. *Egg volume (mm³)*: calculated from the formula $V = 4/3\pi \times a \times b^2$ where a = half the egg length including the pedicel where present and b = half the maximum egg width. This assumes an ovoid egg shape, which has been shown statistically to be the best single measure of egg size (Blackburn 1991b), which can be calculated from literature records.

4. *Fecundity*: the maximum number of eggs reported laid by an individual of the species.

5. *Oviposition rate (eggs per day)*: the maximum reported rate at which eggs are laid on hosts. Since oviposition rate changes throughout the lifetime of a parasitoid, this is not simply fecundity divided by adult lifespan and not necessarily dependent on either of them.

6. *Adult lifespan (h)*: the mean time between adult eclosion and death (physiological death rate rather than a mortality rate).

7. *Pre-adult lifespan (h)*: the mean time between oviposition and eclosion of the adult. Over-wintering and diapause periods were excluded to attempt to control for strong climatic influences, which prevent development from proceeding. Species for which this was unclear were excluded.

8. *Host stage attacked (at parasitoid oviposition)*: classified as eggs, larvae, nymphs, prepupae, pupae, adults or any combination of these.

9. *Host concealment*: classified following Hawkins & Lawton (1987) as exposed species (external feeders such as aphids and some lepidopteran larvae); semi-concealed species (leaf-miners, leaf rollers and web spinners); and concealed species (gallers, stem-borers and soil insects).

10. *Parasite window (h)*: the length of time for which an individual host is available for successful parasitism by a parasitoid species.

11. *Adult body length (mm)*: from the tip of the head excluding antennae to the rear tip of the abdomen excluding ovipositor.

ANALYSIS

Analysis was performed using phylogenetic regression (Grafen 1989) to control for the effects of relatedness between species. Controlling for these effects is important (see Harvey & Pagel 1991), because closely-related species may share adaptations through common ancestry; treating species as independent data points in comparative studies may thus over-estimate the actual number of times a trait or a relationship among traits has evolved. Phylogenetic regression solves this problem by partitioning the variance in traits between taxa either side of an ancestral node into standardized linear contrasts. These contrasts are phylogenetically independent because differences between pairs of sister taxa must have arisen since they last shared a common ancestor and so are not dependent on other lineages on other parts of the tree in the absence of confounding third variables (see Price 1997). These contrasts can then be analysed using standard linear modelling techniques, although regressions must be forced through the origin because the average change in the dependent variable in response to zero change in the independent variable must also equal zero (Garland, Harvey & Ives 1992). Continuous data were log-transformed prior to the calculation of contrasts (Garland *et al.* 1992).

Phylogenetic regression deals with categorical independent data in the same basic way as multiple regression, by assigning 'present or absent' dummy variables (coded as 1 or 0) for each factor level across taxa. These dummy variables are then treated in the same way as continuous data (Grafen 1989). Because phylogenetic regression, like multiple regression, can only be applied to continuous dependent variables, we analysed categorical dependent variables with two factor levels by assuming they were continuous (without transformation). Unordered categorical data with more than two factor levels could not be analysed as dependent variables, and in such cases the dependent and independent variables in the analyses were switched. Tests of the validity of phylogenetic regression under such circumstances are given by Grafen (1989), Grafen & Ridley (1996) and Ridley & Grafen (1996) and a test of the validity of Grafen's branch length assumptions in a slightly different context is given by Purvis, Gittleman & Luh (1994). Although some comparative methods obtain greater validity than phylogenetic regression under some circumstances (see above references), phylogenetic

regression allows multiple regression techniques, involving both categorical and continuous explanatory variables simultaneously, which gives it a huge practical advantage over other similar methods and was for us decisive.

The analyses performed here differ slightly from those performed previously by Blackburn (1991a,b). Blackburn used Pagel & Harvey's evolutionary covariance method (see Pagel & Harvey 1989; Harvey & Pagel 1991), and did not force regression equations on contrasts through the origin, which is now recognized to be necessary. The calculation of contrasts differs slightly between the evolutionary covariance method and phylogenetic regression, as the former assumes all branches in the phylogeny to be equal in length, whereas the latter first assumes that the ages of taxa are in direct proportion to the number of species they contain, and then corrects this to remove any correlation between the magnitude of a standardized contrast and its estimated variance. Phylogenetic regression uses a 'short regression' to calculate valid significance levels and a 'long regression' to calculate valid slopes (Grafen 1989). Output values of r^2 from both analyses cannot be trusted (Grafen 1989) and we do not report them.

Phylogenetic regression requires that the relatedness of species is known or can be estimated. Phylogenetic information is only recently becoming available for the major superfamilies, families and subfamilies of parasitoid Hymenoptera, but no effort has yet been made to contruct a super-tree from available cladistic analyses, and very few such analyses have addressed relationships between tribes, genera or species, which form the vast majority of contrasts in our analyses. Thus, even a super-tree combining available phylogenetic knowledge would still have to rely on taxonomy for the majority of nodes. Instead, we simply assumed that the phylogenetic relatedness of the parasitoid species in our data is approximated by taxonomy, which we derived through consultation with parasitoid taxonomists at The Natural History Museum, London, UK. Our taxonomic scheme classifies species into a series of hierarchical soft polytomous clusters defined as divisions, superfamilies, families, subfamilies, tribes, genera and species. The classification is available in Blackburn (1990) or on request from the second author.

The previous paragraphs demonstrate several problems with the data we have used and the analyses we have performed, most of which will only be improved upon in the course of time. We have persisted despite these problems in order to push forward ecological knowledge, as far as presently possible. We hope that future researchers will re-examine our conclusions in the light of more extensive data, new comparative methods and better knowledge of phylogeny.

PREDICTIONS

The life history data, the estimated phylogeny and phylogenetic regression were used to test the following predictions suggested by the early parasitoid studies mentioned in the introduction and which now collectively form the dichotomous hypothesis (see Godfray 1994; Quicke 1997): (1) The evolution of endoparasitism should be associated with koinobiosis and vice-versa. Endoparasitism/koinobiosis should then be associated with (2) higher fecundity, (3) larger adult body length, (4) longer pre-adult lifespan, (5) smaller eggs, (6) higher oviposition rates, (7) smaller parasite windows, (8) less concealed hosts, (9) shorter adult lifespan and (10) a greater prevalence of younger host stages attacked than ectoparasitism/idiobiosis. These predictions should hold more strongly for larval parasitoids, because the relationship between endoparasitism and koinobiosis is expected to be strongest in parasitoids of growing compared to non-growing host stages (Godfray 1994). Analyses were also performed in which the effect of idio- or koinobiosis was investigated whilst controlling for endo-ectoparasitism, and vice-versa, to attempt to separate their effects. Body size was controlled for in tests of log egg volume and log pre-adult lifespan, since previous studies have shown that both these are dependent on body size (Blackburn 1991a,b). Because 64 independent tests were made of the hypothesis that development mode influences other life history parameters, more than three tests would be expected to be significant at $P < 0.05$ by chance alone. Sequential Bonferroni correction (Rice 1989) was therefore performed on the significance levels for the general hypothesis that development mode influences life histories. More specific hypotheses are only tested once and do not require correction, so tests that were significant before, but not after Bonferroni correction are also reported.

Results

The null hypothesis that development mode is not correlated with other life history parameters is overwhelmingly rejected: after Bonferroni correction, eight tests were still significant, three of them highly so (Table 1). A further 16 tests gave significant results before Bonferroni correction, and stand in favour of one or more specific hypotheses. All of the regression coefficients are in the predicted direction, with the exception of those for log adult body length, some of those for degree of host concealment and host stage attacked (discussed below).

The evolution of endoparasitism and koinobiosis are significantly correlated (Table 1). Both endoparasitoids and koinobionts have smaller eggs than ectoparasitoids and idiobionts, and these relationships are much stronger when controlling for body

Table 1. Effect of development mode on other continuous or dichotomous life history traits. Numbers denote regression coefficients of endoparasitism or koinobiosis relative to ectoparasitism or idiobiosis. Numbers in parentheses denote denominator degrees of freedom in the phylogenetic regression

Dependent variable	Endoparasitism full data set	Koinobiosis full data set	Endoparasitism, full data set, controlling for koinobiosis	Koinobiosis, full data set, controlling for endoparasitism	Endoparasitism, only pure larval parasitoids	Koinobiosis, only pure larval parasitoids
Endoparasitism	—	0·19*(**) (42)	—	—	—	0·39** (18)
Koinobiosis	0·31*(**) (62)	—	—	—	0·57*(**) (26)	—
Log egg volume	−0·21(*) (85)	−0·23(*) (46)	−0·29(**) (60)	−0·16 (60)	−0·14 (46)	−0·32(*) (29)
Log egg volume	*−0·33*(**) (66)*	*−0·55*(**) (46)*	*−0·32*(**) (45)*	*−0·41*(**) (45)*	*−0·39(*) (34)*	*−0·67** (24)*
Log oviposition rate	0·09 (26)	0·16 (17)	0·09 (16)	0·11 (16)	0·30(*) (15)	0·41*(*) (9)
Log fecundity	0·14 (74)	0·10 (54)	0·11 (53)	0·05 (53)	0·40(**) (31)	0·10 (22)
Log parasite window	−0·22(**) (71)	−0·12 (56)	−0·28(**) (51)	0·00 (50)	−0·07 (29)	−0·12 (20)
Log pre-adult lifetime	0·04 (123)	0·07(*) (92)	0·01 (89)	0·07 (89)	0·08 (57)	0·06 (35)
Log pre-adult lifetime	*0·03 (94)*	*0·05 (65)*	*−0·01 (63)*	*−0·06 (63)*	*0·06 (44)*	*0·00 (29)*
Log adult lifetime	−0·17(**) (109)	−0·15(*) (79)	−0·06 (78)	−0·13 (78)	−0·23(**) (46)	−0·23(*) (30)
Log adult body length	−0·00 (122)	−0·02 (93)	−0·03 (89)	−0·00 (89)	0·03 (58)	0·00 (43)

* $P < 0.05$ ** $P < 0.01$ after Bonferroni correction for multiple comparisons. (*) $P < 0.05$ (**) $P < 0.01$ before Bonferroni correction. Numbers in italic denote regressions controlling for log adult body length.

size. In addition, both endoparasitoids and koinobionts live significantly shorter adult lives than ectoparasitoids and idiobionts. Endoparasitoids attack hosts that are available for a significantly shorter length of time than ectoparasitoids, and koinobionts take longer to develop to adulthood than idiobionts. These trends provide support for the dichotomous hypothesis. Several other trends are in the predicted direction, but are not significant (Table 1). These would merit future testing in the light of more extensive data, improved comparative methods and better knowledge of parasitoid phylogeny: both endoparasites and koinobionts in general tend to display higher oviposition rates and higher lifetime fecundities than ectoparasites and idiobionts. Our results give no indication that adult body size nor the degree of host concealment (Table 2) or host stage attacked (Table 3) are linked with development mode.

Degree of host concealment was expected to be strongly correlated with development mode based on previous informal comparisons made across the Ichneumonoidea superfamily (Gauld 1988; Belshaw *et al.* 1998). To examine the source of this discrepancy, we performed 'naive' comparative tests on our raw data (in our case species level) for the Ichneumonoidea to compare with the raw data in Belshaw *et al.* (1998, in their case generic level). This showed that the discrepancy originates partly at the level of the raw data: in our data set koinobiont ichneumonoid species do not have significantly more exposed hosts than idiobiont ichneumonoid species ($G_2 = 3·18$ on 85 species, $P > 0·05$), whereas the data in Belshaw *et al.* (1998) show that koinobiont ichneumonoid genera have significantly more exposed hosts than idiobiont ichneumonoid genera ($G_2 = 82·64$ on 102 genera, $P < 0·001$). However, both the ectoparasitic ichneumonoid species in our data and genera in Belshaw *et al.* (1998) have significantly more concealed hosts than endoparasitic species/genera (our data: $G_2 = 22·85$ on 118 species, $P < 0·005$; Belshaw *et al.* 1998: $G_2 = 22·85$ on 102 genera, $P < 0·005$). The relationship in our data was not significant using phylogenetic regression (Table 2), although significance was higher than in the full data set and power was very low due to poorly resolved taxonomy. Thus, although the raw data are at least suggestive of a relationship between ectoparasitism and use of concealed hosts within one major superfamily, there is currently no phylogenetically-based evidence to support this.

Mean adult body size hardly differs at all between different development modes. Endoparasitism tends to be more associated with exposed hosts as predicted, but not significantly so, and the trend is in the opposite direction to that of koinobiosis. The regression coefficients on host stage attacked suggest that koinobiosis is more associated with attacking

Table 2. Effect of degree of host concealment on development mode. Positive regression coefficients denote a greater frequency of endoparasitism or koinobiosis than ectoparasitism or idiobiosis, and negative numbers denote a greater frequency of ectoparasitism or idiobiosis than endoparasitism or koinobiosis. Coefficients are all relative to exposed hosts, which thus receive coefficients of zero. None of the regressions are significant

Degree of host concealment	Endoparasitism[a]	Koinobiosis[b]	Endoparasitism, controlling for koinobiosis[c]	Koinobiosis, controlling for endoparasitism[d]	Endoparasitism, only pure larval parasitoids[e]	Koinobiosis, only pure larval parasitoids[f]	Endoparasitism, only Ichneumonoidea[g]
Exposed	0·00	0·00	0·00	0·00	0·00	0·00	0·00
Semi-concealed	-0·01	0·04	0·00	0·03	0·04	0·07	0·09
Concealed	-0·10	0·05	-0·09	0·03	-0·11	0·07	-0·09

[a]$F_{2, 31} = 1.91$, [b]$F_{2, 35} = 0.18$, [c]$F_{2, 39} = 0.79$, [d]$F_{2, 39} = 0.11$, [e]$F_{2, 17} = 1.74$, [f]$F_{2, 16} = 0.21$, [g]$F_{2, 12} = 2.82$.

eggs, nymphs and larval hosts than prepupae, pupae and adult hosts. However, the relationship is not significant. Endoparasitoids are least associated with attacking larvae, prepupae and pupae, and most associated with eggs, nymphs and adults, but again the relationship is not significant.

Both endoparasitism and koinobiosis are independently correlated with egg size, and the relationship of endoparasitism to parasite window is independent of koinobiosis. However, no new relationships become significant when either endoparasitism or koinobiosis is controlled for.

Godfray (1994) suggested that the dichotomy should be stronger between pure larval parasitoids, because the links between koinobiosis and endoparasitism, and idiobiosis and ectoparasitism should be strongest then. This study suggests some support for that prediction: of the significant results already mentioned, all remain significant if only pure larval parasitoids are considered, with the exception of pre-adult lifespan and parasite window, where the power of the test becomes considerably smaller. However, the relationship between koinobiosis and endoparasitism becomes much stronger, as predicted, and three new significant results emerge: the relationship between endoparasitism and oviposition rate, and koinobiosis and oviposition rate become significant, as does the relationship between endoparasitism and fecundity (Table 1).

Discussion

This study provides the first formal comparative evidence that the dichotomies in development mode in the parasitoid Hymenoptera are associated with a suite of other life history characteristics after controlling for estimated phylogeny. These associations themselves do not constitute a theory of life history evolution, because they say nothing explicit about the selection pressures or constraints involved. Ultimately, however, some such hypothesis is desirable. Thus, we first consider below why development mode might show the particular associations revealed by this study. We then consider how variation in development mode itself may arise.

CONSEQUENCES OF DEVELOPMENT MODE

Associations between development modes

Parasitoids that develop inside their host are much more likely to allow their host to continue to develop to some extent (koinobiosis), whilst parasitoids that feed on their hosts externally are much more likely to permanently paralyse their host or attack only non-growing host stages (idiobiosis). These relationships form the basis of the dichotomous hypothesis and they are the strongest associations found in this study.

Table 3. Effect of host stage attacked on development mode. Parasitoids that can oviposit in several host stages were classified according to the youngest host stage attacked because predictions relate to the ability to attack young host stages. Positive regression coefficients denote a greater frequency of endoparasitism or koinobiosis than ectoparasitism or idiobiosis, and negative coefficients denote a greater frequency of ectoparasitism or idiobiosis than endoparasitism or koinobiosis. Coefficients are all relative to eggs and thus are predicted to be increasingly negative as the age of host stage increases. None of the regressions are significant

Host stage attacked	Endoparasitism[a]	Koinobiosis[b]	Endoparasitism, controlling for koinobiosis[c]	Koinobiosis, controlling for endoparasitism[d]
Egg	0·00	0·00	0·00	0·00
Nymph	−0·04	0·03	−0·16	0·11
Larva	−0·20	−0·03	−0·23	0·10
Prepupa	−0·26	−0·35	−0·22	−0·20
Pupa	−0·12	−0·17	−0·11	−0·05
Adult	−0·04	−0·18	0·06	−0·16

[a] $F_{5,38} = 2·30$, [b] $F_{5,52} = 2·37$, [c] $F_{5,61} = 1·45$, [d] $F_{5,61} = 2·17$.

Possible reasons for this association have been discussed by Gauld (1988) with reference to the Ichneumonoidea. He hypothesized that the primitive state for this superfamily was ectoparasitic idiobiosis on concealed hosts in plant tissue. Koinobiosis allowed exposed hosts to be used for oviposition whilst allowing the parasitoid to develop after the host had concealed itself. Ectoparasitic koinobiosis, however, entails a high risk of egg mortality; from dessication, from host ecdysis and from host movement. These problems may require elaborate counter-adaptations or moist habitats, which means they will always be rare. Endoparasitism counters all these problems at one stroke and would quickly accompany the evolution of koinobiosis. In some lineages, endoparasitism may have arisen prior to koinobiosis as a response to increasing exposure of host pupae. This may not select for accompanying koinobiosis, but the very special trends in host utilization required means that endoparasitic idiobiosis is rare. In summary, Gauld's (1988) hypothesis encompasses phylogenetic constraints, short-term selection pressures and macro-evolutionary arguments. We do not know to what extent such arguments might apply to other superfamilies, but we consider that the ancestral combination of ectoparasitism and idiobiosis, and the pressures to reduce egg mortality in koinobionts by developing endoparasitism are likely to to be quite important. Hypotheses such as Gauld's might be tested by mapping extant host utilization and development modes onto a phylogenetic tree, and using parsimony algorithms to reconstruct the evolutionary transitions, which have taken place.

Fecundity-related traits

Koinobionts and endoparasitoids of larval hosts oviposit faster than larval idiobionts and ectoparasitoids, and larval endoparasitoid have higher fecundity than larval ectoparasitoid. In addition, both koinobionts and endoparasitoids have larger eggs than idiobionts and ectoparasitoids. Development mode is mainly hypothesized to affect fecundity-related traits through the action of mortality schedules (Price 1974; Blackburn 1991b). Specifically, koinobionts/endoparasitoids might experience higher juvenile mortality than idiobionts/ectoparasitoids, either because they attack more exposed or younger hosts, which will themselves experience higher mortality, or because endoparasitoids suffer in competition from ectoparasitoids. As a result, koinobionts/endoparasitoids would be selected for higher fecundity and faster oviposition, thus trading-off egg size. Another pressure selective for larger egg size in ectoparasitoids and idiobionts may be that they must contain within the egg all the nutrients required prior to larval feeding, whilst endoparasitoids or koinobionts can absorb nurients from the host prior to hatching (Godfray 1994). There is some evidence for the latter, since in some endoparasitoids eggs swell greatly after oviposition and prior to eclosion (Shaw & Huddleston 1991).

It is unfortunate that at present we have no direct measures of field mortality in our data set and it is unlikely that they exist in the primary literature, since the vast majority of parasitoid mortality studies are laboratory based (see, for example, Hardy *et al.* 1998). We do, however, have measures of fecundity, which is likely to balance with mortality in the long term. Blackburn (1991a,b) carried out extensive investigations on fecundity. He found several correlations in line with our results. More fecund taxa laid smaller eggs and oviposit faster than less fecund taxa, and have shorter parasite windows than more fecund taxa. These are 'fast' life history traits of the sort that we also found associated with endoparasitism or koinobiosis. Our data

also include information on host concealment and host stage attacked, which form the basis of some of the mortality arguments (Gauld 1988). However, we found no association between development mode and either of these two variables. If we reject these two causes, competition remains as an untested cause of the proposed mortality variance. Although there is some experimental evidence that ectoparasitoids are competitively superior to endoparasitoids (see Salt 1961), without the appropriate field data we cannot test if mortality does, indeed, differ between development modes.

Lifespan and body size

Koinobionts and endoparasitoids have shorter adult lifespans than idiobionts and ectoparasitoids. In addition, koinobionts have longer pre-adult lifespans than idiobionts. One obvious reason for the latter result is that idiobionts have immediate development, as opposed to delayed development in koinobionts. Adult lifespan is likely to reflect both within-lifetime trade-offs in the partitioning of resources to growth and survival (see Ellers 1996; Ellers & van Alphen 1997), as well as external sources of mortality, such as predation (see Gauld 1987), or abiotic factors, such as weather (see Roitberg *et al*. 1993; Weisser *et al*. 1997). Thus, adult lifespan should correlate better with fecundity than development mode, as long as all forms of development mode start from the same level of reserves allocated to survival and reproduction, and as long as external sources of adult mortality, such as predation or abiotic factors, are similar across development modes. Since it does not, it seems likely that one of the above assumptions is broken, although we do not know which, and the issue may only be resolved once data on mortality schedules for both juvenile and adult stages of parasitoids become available.

We have not found the predicted correlation between development mode and adult body size, despite this including some of our most extensive and reliable data. Why then should this prediction fail? Adult body size is likely to reflect the interaction between host size and clutch size. Although we have no direct measures of host size, other interspecific comparative studies (le Masurier 1987; Mayhew & Hardy 1998; Mayhew 1998) have shown that these three traits are closely related because developmental resources must be shared amongst members of a clutch. Since we could not control for or investigate host size, we lack adequate means to test the independent effect of development mode, except to say that it does not appear to be the single major determinant of body size.

Ecological traits

We have found a relationship between length of the window for parasitism and ectoparasitism. Blackburn (1991a) found a negative relationship between the fecundity and parasite window, but could offer no explanation for the trend. One possibility, however, is that fast life history traits (such as found in endoparasitoids, but not ectoparasitoids) are associated with greater searching efficiency (see Godfray 1994) and thus allow parasitoids to use hosts that are available for shorter time periods. This prediction remains untested.

A more curious result is that development mode apparently has no influence on the stage of host attacked. Koinobionts are hypothesized to be able to attack younger host stages and in consequence experience higher juvenile mortality than idiobionts. However, our results provide no confirmation of this. On reflection, the prediction itself is perhaps naive. For example, Gauld (1988) hypothesizes koinobiosis as evolving to allow later host stages to be used for development, as opposed to earlier host stages to be used for oviposition. Alternatively, earlier host stages can be attacked by idiobionts if they accept a smaller body size, as found in many egg parasitoids. It may be that the relationship holds at more detailed level only, for instance, between different larval or nymphal instars, on which we have no data, or between very closely related species. Another possibility is that the relationship is quite weak and requires more extensive data; it is in the generally predicted direction, at least for idio/koinobiosis. Future studies mights make use of Mills' classification of parasitoid guilds for endopterygote insects (see Mills 1994a,b) as factors in the initial analysis.

Another unexpected result is that the degree of host concealment apparently does not influence development mode. Previous informal comparisons within the Ichneumonoidea (Gauld 1988; Belshaw *et al*. 1998) suggested that such an association might exist. Our raw data suggest that such a relationship might exist at least for ecto-/endoparasitism in the Ichneumonoidea, but due to low statistical power through poorly resolved phylogeny, phylogenetically-based evidence is still lacking. However, this is clearly one possible trend that deserves future investigation. Such an investigation would require more detailed phylogenetic information for the superfamily than was available for our study, preferably species-level data on life histories (not available in Belshaw *et al*. 1998), and more detailed categorization of host concealment. We see this latter step as necessary because 'exposed' hosts, as perceived by human observers, may not be 'exposed' to parasitoids. Indeed, the lower mobility of semi-concealed or concealed hosts may make them more susceptible to biotic forms of mortality, and there is some evi-

dence that they do support larger parasitoid assemblages (reviewed by Hawkins 1994). Additionally, semi-concealed hosts are more likely to be associated with endoparasitism and koinobiosis than exposed hosts in some of our analyses (Table 2). In future, we recommend classifying data as actually presented in the primary analyses (i.e. leaf-miner vs. stem-borer) to try and remove anthropomorphic bias at the analysis stage.

CAUSES OF VARIATION IN DEVELOPMENT MODE

Is development mode the ultimate cause of the relationships seen in this study or is it simply a proximate substitute for some other ultimate selection pressure, such as mortality schedules? We see two reasons why development mode might be retained as the central element of any comprehensive theory of parasitoid life histories. The first is that development mode might be phylogenetically constrained. The ancestral development mode of parasitoids was probably idiobiont ectoparasitism (Gauld & Bolton 1988) and some large taxa, such as the Aculeata, almost exclusively maintain that ancestral state (Whitfield 1992). Endoparasitism undoubtedly necessitates complex adaptations, and there may thus be considerable constraint on its evolution (see Shaw 1983; Askew & Shaw 1986; Gauld 1988). Nonetheless, endoparasitism (and koinobiosis) has probably evolved numerous times in the parasitoid Hymenoptera (Whitfield 1992), although possibly associated with very specific patterns in host utilization (Gauld 1988). Thus, although development mode may strongly reflect selective pressures, it probably also reflects the evolutionary history of each lineage.

The second reason why development mode might be retained as the major organizer would be if it several selective factors are required to take its place. Fecundity, which may be taken as a rough indicator of mortality, performs quite well at predicting many of the other life history traits (Blackburn 1991b), but does not predict as many traits as development mode. In addition, development mode may influence host availability and selection on egg size independent of mortality schedules.

Conclusions

This study has shown that development mode is a good predictor of several life history traits in the parasitoid Hymenoptera. Even so, data in this study were not extensive enough to test all of the predictions made under the dichotomous hypothesis and, when additional data become available, other predictions should be tested, for example, those relating to host range (see Sato 1990; Sheehan & Hawkins

1991; Shaw 1994), search mode and competitive ability (see Hawkins *et al.* 1990; Godfray 1994), host feeding (see Jervis & Kidd 1986), type of egg maturation and diurnal activity (see Quicke 1997). In addition, the causes underlying the associations shown are still a matter of speculation and there is a need for formal causative hypotheses, which might be tested. In particular, we think there is a need for comprehensive mathematical theories of parasitoid life history variation along the lines of those for mammals (e.g. Charnov 1993; Kozlowski & Weiner 1997). Ideally, such competing hypotheses could then be addressed by new empirical studies, employing more extensive data (more taxa and more variables), improved comparative methods and better resolved estimates of phylogeny.

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