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Nonsiblicidal Behavior and the Evolution of Clutch Size in Bethylid Wasps

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abstract: Parent-offspring conflict over clutch size may lead to siblicidal behavior between juveniles. In parasitoid wasps, selection for siblicide in small broods is predicted to produce a dearth of gregarious broods with few eggs. Here we document the clutch size distribution in the Bethylidae, a large family of aculeate parasitoids. Small gregarious clutches are the most common. Further data suggest that the most common gregarious clutches in the parasitoid Hymenoptera as a whole contain only a few eggs. Across bethylid species, both clutch size and wasp size increase with host size. Within genera clutch size is more closely related to host size, but between genera or larger clades wasp size is more closely related to host size. The volume of the emerging wasp brood does not depend on whether a species lays single- or multiple-egg clutches once host size is taken into account. These data suggest that clutch size in bethylid wasps is best described by traditional optimality models and that siblicide plays little role in this and possibly other families. We propose several ecological reasons for the rarity of siblicide in bethylids: ectoparasitism, idiobiosis, and a suite of characteristics associated with high within-brood relatedness.

Keywords: parasitoid, Bethylidae, clutch size, body size, parent-offspring conflict, siblicide.

The evolution of clutch size has been one of the most enduring topics in both behavioral ecology and life-history theory (Lack 1947; Godfray et al. 1991; Lessells 1991; Roff 1992; Stearns 1992). Much interest has centered around the parent-offspring conflict that is associated with clutch size optimization (Macnair and Parker 1979; Parker and Macnair 1979; Parker and Mock 1987; Godfray and Parker 1991, 1992). The fitness of individual offspring within a brood generally (but not always) declines with increasing brood size, but, to maximize their own fitness, parents will often be selected to lay large broods. Thus, the optimal brood size for parents is often greater than for individual offspring.

If a juvenile finds itself competing with siblings, it may act to reduce the effective competition. One way of doing so is for juveniles to disperse after hatching, thereby reducing the proximity to competitors (Mangel and Roitberg 1993; Roitberg and Mangel 1993). Dominance over other siblings reduces the effectiveness of competing brood mates (Hahn 1981; Godfray and Parker 1991). Alternatively, competition may be reduced more directly by siblicide (O'Connor 1978; Stinson 1979; Godfray 1987*b;* Parker et al. 1989; Godfray and Harper 1990). Siblicide results in a genetic (inclusive fitness) cost that may be measured by the number and relatedness of siblings that are killed but accrues benefits in terms of increased individual fitness, such as greater adult size or a reduced risk of developmental mortality. As these costs and benefits are likely to depend on the size of the brood in which a juvenile develops, the incidence of siblicide should also depend on the initial brood size.

Parasitoid wasps have proved key model organisms in the development of theory surrounding this problem (Godfray 1994). Parasitoids are insects that lay their eggs on, by, or in a host organism (normally another insect), which provides the resources for offspring development. In some species of parasitoid, more than one offspring, sometimes several hundred, can develop together on a host. In such species, clutch size is often adjusted to the size of the host by the parent, and if the host is small single eggs may sometimes be laid. The larvae exhibit scramble as opposed to contest competition (Salt 1961; Visser 1996). However, in other parasitoid species, only one offspring develops successfully on each host because the larvae exhibit contest, not scramble, competition (Salt 1961), often manifested as fighting behavior (Clausen 1940; Marris and Casperd 1996) or physiologi-

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cal suppression (Fisher 1971; Vinson and Iwantsch 1980). Such species normally lay only one egg per host, but under some circumstances can be selected to lay more (reviewed in Rosenheim 1993; Godfray 1994). Species showing contest larval competition, where only one offspring develops successfully, are often referred to as ''solitary.'' Species showing scramble larval competition, where more than one larva develops successfully, are known as ''gregarious.'' However, because the clutch size and number of offspring that successfully complete development are rarely both known, most authors refer to species as solitary or gregarious on the basis of only clutch or final brood size (1 for solitary species, >1 for gregarious species). In this article, we use ''solitary'' or ''gregarious'' to refer only to clutch size. Species that are normally gregarious but sometimes lay single-egg clutches on small hosts are referred to as semigregarious (Werren 1984).

The evolution of clutch size in parasitoids is classically considered from the perspective of an ovipositing mother trying to maximize her own individual fitness (Godfray 1987*a*). Conventional clutch size models predict that clutch size should increase with host size (Charnov and Skinner 1984; Iwasa et al. 1984; Parker and Courtney 1984; Skinner 1985). This trend is seen both within and between gregarious species (Godfray 1994). Some clutch size models explore a range of types of larval competition, and in such models, solitary species are predicted as a special case in which competition for resources is contested and clutch size does not vary with host size: it is always one. Instead, wasp size varies with host size (e.g., Skinner 1985; Waage and Godfray 1985). Another suite of models that are rarely applied to parasitoids, known as size-number models (see Smith and Fretwell 1974; Clutton-Brock 1991; Clutton-Brock and Godfray 1991; Godfray et al. 1991), make this point more explicitly. Under simple sets of assumptions, parents are selected only to vary offspring number according to developmental resources (e.g., Parker and Begon 1986; Ebert 1994; Charnov and Downhower 1995). However, under certain conditions, such as when larval survival or fitness depends more strongly on brood size or host size, parents can be selected to vary offspring number less and vary offspring size more (Parker and Begon 1986; Ebert 1994). In some gregarious species both clutch size and the body size of resulting offspring increase on larger hosts (Hardy et al. 1992; Mayhew, in press). In the extreme, clutch size is always the same and wasp size is highly dependent on host size, as seen in solitary species. Thus in general we should expect the clutch size distribution of a taxon to reflect interactions between the size of the host, the size of the wasps, and the form of larval competition. The form of larval competition is normally considered as a constraint.

Godfray (1987*b*) first suggested that the form of larval competition might evolve flexibly according to brood size because the optimal clutch size for offspring is often smaller than it is for parents. Specifically, he showed that siblicidal or brood-reduction behavior among larvae can be selectively advantageous when clutches are gregarious but consist of few eggs, for instance, two, three, or four eggs. In such broods, the genetic cost of siblicide is small because not many relatives are killed, while the benefits are great. For example, in a brood size of two, killing a sibling doubles the developmental resources for the survivor. In contrast, it is very difficult for nonsiblicidal behavior to evolve when siblicide is prevalent because nonsiblicidal individuals will quickly be killed by their aggressive relatives. Such pressures are increased when several individuals or species oviposit on the same host because the genetic cost of brood reduction is reduced. Potentially, this could affect the distribution of clutch sizes in parasitoids because species with small gregarious broods would tend to evolve solitary life histories, whereas there would be no strong counter trend from the solitary state to gregariousness. Thus, the solitary state is an evolutionary trap, or ''black hole,'' from which nonsiblicide and gregariousness cannot easily evolve. As a consequence, clutch size distributions in parasitoids are expected to show a deficit of small gregarious broods. If substantial numbers of gregarious species exist, the consequent distribution will be bimodal (Godfray 1987*b*), otherwise we should expect a largely solitary clutch size distribution. In addition, solitary species should sometimes be found where the hosts are large enough to support several offspring, but siblicide constrains clutch size to a single egg.

Both these predictions received empirical support from a comparative study (le Masurier 1987*b*) of *Apanteles* (sensu lato, Nixon 1965), a genus of microgasterine braconid wasps with more than 1,300 described species. The distribution of clutch sizes is bimodal: 42% of species are solitary and the size of gregarious clutches ranges from two to >1,000, with a mode of 17–21. Only two species are recorded with a clutch size of two to six. Also, many solitary species parasitize hosts that could support larger broods: the relationship between brood volume and host size is less steep for solitary than gregarious species.

Although le Masurier's study showed a bimodal clutch size distribution, the underlying reasons for this distribution are still equivocal. Taxonomic revisions of *Apanteles* (see Shaw and Huddleston 1991) have now split it into several distinct genera, so it is no longer certain whether the bimodal clutch size distribution reflects that of a single taxon or of two or more taxa with quite distinct distributions. This of course does not alter the conclusion that many solitary species could lay larger broods. Also, there are statistical problems with the study, since it used species values as independent and therefore probably inflates the significance of the tests used. This last problem was unavoidable given that there are no estimates of phylogenetic relatedness for these species, but it does hamper interpretation of the study.

The taxonomic extent of bimodal clutch size distributions, like that proposed for *Apanteles*, has implications not just for parent-offspring conflict but also for a whole suite of life-history traits that are correlated with clutch size (e.g., Askew and Shaw 1986; Griffiths and Godfray 1988; Blackburn 1991*a*, 1991*b*). If bimodal distributions are widespread, one might be biologically justified in treating clutch size as a dichotomous rather than as a continuous variable (e.g., Ridley 1993). Some observations suggest that such distributions are not ubiquitous and hence that pressures for the evolution of siblicide may vary among taxa. For instance, semigregarious species often lay gregarious clutches of few eggs (see, e.g., Mayhew and Godfray 1997), while others consistently lay small gregarious broods (see, e.g., Rosenheim 1993). Many such species show no intrabrood aggression.

In this article we conduct the second comparative study of parasitoid clutch size distribution. We primarily use data on bethylid wasps (Hymenoptera: Bethylidae), a family with about 1,800 described extant species in 91 genera and five subfamilies (Gordh and Móczár 1990). Because phylogenetic hypotheses have been published for bethylid taxa, we are able to control for effects of relatedness using formal comparative methods (Harvey and Pagel 1991). We show that gregarious broods containing few eggs are the most common in bethylids, and they are the most common type of multiple-egg clutch across the parasitoid Hymenoptera in general. We also show that in bethylids both wasp size and clutch size are correlated with the size of the host. We discuss the implications of these data for clutch size theory and the evolution of siblicide in this group of organisms.

Biology of Bethylid Wasps

Bethylids are a species-rich and globally distributed family of aculeate wasps (Gauld and Bolton 1988). Adults range in size from about 1 to 10 mm. They parasitize the larvae, and sometimes the pupae, of Lepidoptera (usually Tortricidae, Pyralidae, and Gelechiidae) or Coleoptera (from a number of families associated with dead wood or stored products; Evans 1978). Uniquely among the parasitic aculeate families, a high proportion of bethylids are gregarious; all other families are largely solitary (Gauld and Bolton 1988). Eggs are laid on the exterior of the paralyzed host, often in very exact locations (e.g., Gordh and Hawkins 1981; Peter and David 1991). In many species, clutch size is known to be larger on larger hosts (Bridwell 1919; Kishitani 1961; Kühne and Becker 1974; Gordh 1976; Gordh and Evans 1976; Gordh et al. 1983; Klein et al. 1991; Hardy et al. 1992; Luft 1993). Usually the host does not recover from paralysis. Some species have been observed transporting hosts from one location to another (e.g., Maneval 1930), possibly in an attempt to conceal them in a protective position. In a number of species, mothers defend the host and brood from conspecifics (Doutt 1973; Kühne and Becker 1974; Baker 1976; Hardy and Blackburn 1991; Petersen and Hardy 1996). Females may also destroy the eggs or larvae of any previous clutches they find (Goertzen and Doutt 1975; Legaspi et al. 1987; Hardy and Blackburn 1991; Mayhew 1996, 1997). Such observations suggest that, in many cases, the offspring of only a single female complete development on a host. The larvae are immotile and hymenopteriform, develop in only a few days, and pupate near the host. The sex ratio of emerging offspring is usually female biased, more so for larger clutches, and the variance in sex ratio is often less than binomial (precise sex ratios; Green et al. 1982; Griffiths and Godfray 1988; Hardy 1992; Morgan and Cook 1994; Hardy and Cook 1995).

Developmental mortality is known in detail for eight bethylid species (I. C. W. Hardy, L. J. Dijkstra, J. E. M. Gillis, and P. A. Luft, unpublished manuscript), with mean clutch sizes ranging from two to 15.6. In all eight species, more than one offspring normally survives in gregarious broods; in seven of the eight species, mortality is below 0.3. In addition, how mortality varies with clutch size is known for four species (I. C. W. Hardy, L. J. Dijkstra, J. E. M. Gillis, and P. A. Luft, unpublished manuscript). In three species, mortality does not vary with clutch size, whereas in one species it decreases with clutch size. Furthermore, in one solitary species, a few instances of superparasitism are known, and more than one offspring is then able to complete development (Abraham et al. 1990). These data indicate that competition among bethylid larvae is generally scramble rather than contest. Direct observations of larval behavior and development tend to support this view. We know of only a single report of possible siblicide in bethylid larvae (Doutt 1973), despite numerous studies of juvenile behavior, development, and morphology (Voukassovich 1924; Maneval 1930; van Emden 1931; Vance and Parker 1932; Powell 1938; Jayaratnam 1941; Nickels et al. 1950; Ayyappa and Cheema 1952; Yamada 1955; Bognár 1957; Antony and Kurian 1960; Yoshida and Machida 1960; Venkatraman and Chacko 1961; Kühne and Becker 1974; Baker 1976; Cushman and Gordh 1976; Gordh 1976; Mertins 1980; Ndoye 1980; Gordh and Hawkins

1981; Gordh et al. 1983; Gordh and Medved 1986; Abraham et al. 1990). Bethylid larvae do not change their position on the host after hatching and do not have fighting mandibles (see references just listed above). Larval *Prosierola bicarinata* Brues however develop anterior protrusions that are inserted into the host and used to feed from parts of the host that are distant from the site of larval attachment (Doutt 1973). During this stage in their development, some larvae appear to die as a result of being pierced and fed on by their siblings. It may be significant that *P. bicarinata* lays from three to five eggs per host, but even in this species several offspring often develop successfully on the same host. No other bethylid species have been described with larval morphology such as this. In addition, indirect forms of siblicide, known as physiological suppression, are probably not applicable to bethylids because they are ectoparasitic. Thus the available evidence indicates that larval competition in bethylids is better reflective of scramble than contest competition and that siblicide is rare. This being the case, we would expect that bethylids do not commonly lay small broods in which selection for siblicide is predicted to be strong.

Methods

Data Collection

We collected data on clutch size for 52 bethylid species in 14 genera and three subfamilies from the published literature. Because the bethylid literature has been extensively and recently cataloged (Gordh and Móczár 1990), we are confident that we have a large proportion, and possibly all, of the published clutch size records for this family in which the wasp was identified down to species. Of the two subfamilies not represented, one (the Galodoxinae) has only a single described species, and the other (the Mesitiinae) is also small (about 180 described species), with a very poorly known biology.

For each species, an average clutch size was recorded. Where a mean clutch size was recorded or could be calculated from raw data, we used this value. Sometimes just a range was given, in which case a ‘‘median’’ was calculated, defined as the mean of the two extremes of the range. However, if a modal clutch size was also given, this was used in preference to the median. To compare with our bethylid data we extracted data for *Apanteles* from le Masurier (1987*a*, 1987*b*) and from a large-scale comparative study across the whole of the parasitoid Hymenoptera (Blackburn 1990, 1991*a*, 1991*b*).

To test whether bethylid clutch size and wasp size evolve in response to host size, we complemented the clutch size data with records of the size of adult wasps and of host size. We took body length (excluding antennae) as a measure of wasp size because this was most frequently recorded in the literature and supplemented these records with our own measurements of preserved specimens (see ‘‘Acknowledgments’’ for sources). Where we had measurements of both sexes, we took the mean of average male length and average female length as our species measure. Again, where possible we took mean lengths for our average measures for each sex, but where only ranges were given, medians were used.

Host size data proved the most problematic to collect (in common with le Masurier 1987*b*). Ideally, we would have used the fresh weights of the same hosts from which clutch size was recorded. Although we were always able to collect data from the same host species, very few studies mention the size of the actual host individuals used. When host size is given, the most common measure is the length of the larva, which may scale differently with host weight in different taxa. Because it was the only variable that could be collected sufficiently frequently from the literature, we were forced to use the body length of the adult host (excluding antennae) as a measure of host size. However, because adult host length varies by more than an order of magnitude, wasp length by nearly an order of magnitude, and clutch size by nearly two orders of magnitude, robust trends in the data should survive quite large measurement errors (as indeed they did in le Masurier's 1987*b* study). Also, we can gain some estimate of the accuracy of host size measurements by comparing the adult host size with those size measurements given in the clutch size literature. Adult host length is positively correlated with the length of the actual hosts on which clutches were recorded ($\log_{10}$ adult length $= 0.146 + 0.6867 \times \log_{10}$ larval length, $n = 14$, $r^2 = 0.635$, $F = 20.91$, df $= 1, 12$, $P < .001$). Usually, adult length is smaller than larval length, but in four out of 14 cases it is larger. Thus, adult host length is an imperfect but nonetheless quite accurate estimate of the lengths of the actual host that individuals used. The raw data and list of source references are available from us on request.

Data Analysis

For our initial data inspection we carried out least-squares regression on the species values, $\log_{10}$ transforming all variables to stabilize the variance. This analysis shows the distribution of character states and allows direct comparison with le Masurier (1987*b*). However, because species are related through phylogeny, statistics treating species values as independent data points should be interpreted with extreme caution, especially when they

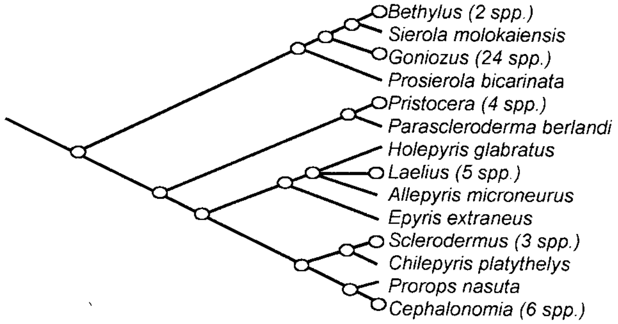

Figure 1: Estimate of phylogeny used in the comparative analyses. Species in the same genus are clustered in soft polytomies. Each node (*circle*) represents an independent contrast. In computing contrasts, all branches are assumed to be equal in length.

are used to test a priori ecological or evolutionary hypotheses (Felsenstein 1985; Rees 1995; Harvey 1996). Therefore, we also used Comparative Analysis by Independent Contrasts (CAIC; Purvis and Rambaut 1995), which partitions the variance in species characters into phylogenetically independent linear contrasts. For our estimate of phylogeny we clustered subfamilies according to Evans (1964) and Sorg (1988). Genera in the Bethylinae were clustered according to Polaszek and Krombein (1994) and in the Epyrinae and Pristocerinae according to Sorg (1988). The latter studies are cladistically based and are therefore used in preference to taxonomy. The position of the genus *Allepyris* does not appear in any published cladograms; Kieffer (1914) places it next to *Laelius* taxonomically, but A. Polaszek (personal communication) has suggested *Holepyris* as a more closely related genus. To reflect this uncertainty, we placed it in trichotomy (thus, a soft polytomy) with both *Holepyris* and *Laelius.* Since we have no information on within-genera relatedness, we cluster all species in the same genus within soft polytomies. Genera and species are defined according to Gordh and Móczár (1990). The resulting estimate therefore includes the best current information while remaining conservative where information is lacking (fig. 1). In the absence of branch length information we assumed all branches to be equal in length (Purvis et al. 1994). Species data were $\log_{10}$ transformed prior to the calculation of contrasts. The appropriateness of the data transformation and of branch lengths to a "Brownian motion" model of evolution (assumed in calculating the contrasts; Felsenstein 1985) was confirmed by examining the absolute values of contrasts against their estimated nodal values. Contrasts were then analyzed by linear regression through the origin (Garland et al. 1992). Normality of variance was tested by examining the absolute values of contrasts against the square root of the variance of the raw contrasts (Garland et al. 1992). Where the assumption of normality of variance was clearly inappropriate, nonparametric statistics were used. All significance tests that we report are two-tailed.

Results

Clutch Size Distribution

The distribution of average species clutch sizes in bethylids ranges from one to 94 and is skewed toward larger clutches, with a mean of 8.05 and median 4.00. Of the 52 species, eight are only known to be solitary, 27 are known to be semigregarious, and 17 are only known to be gregarious. Of the semigregarious and gregarious species, the median clutch size was 4.75 (fig. 2*a*). Twelve species lay average brood sizes of two or three eggs, where siblicide is strongly expected to evolve and reduce

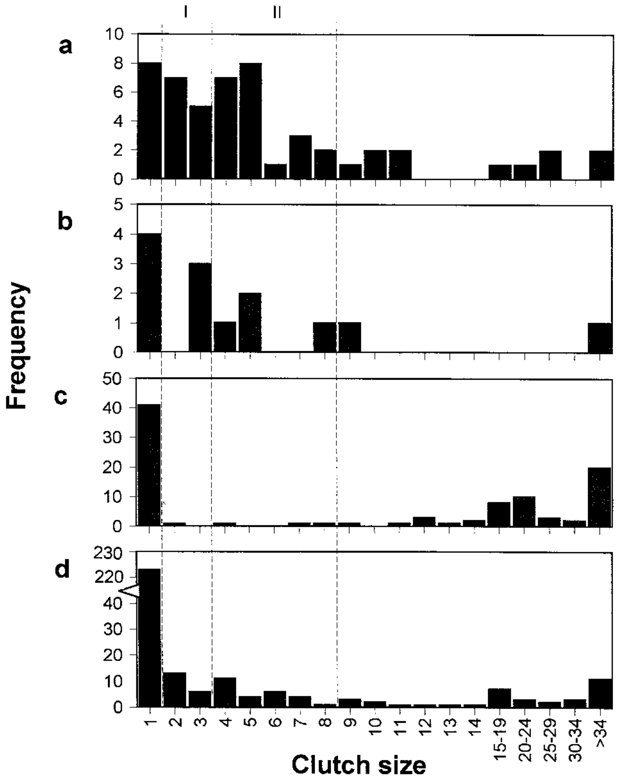

Figure 2: Clutch size frequency distributions in Bethylidae by species (*a*) and by genus (*b*) compared with *Apanteles* (*c*) and a sample across the whole of the parasitoid Hymenoptera (*d*). Frequency denotes number of species (*a* and *d*), number of genera (*b*), and percentage of species (*c*). Dotted lines give a general indication of gregarious clutch sizes where selection for siblicide is most strongly predicted (*I*) and only sometimes predicted (*II*).

brood size to one. A total of 37 species are known to sometimes lay clutches of two or three eggs. A further seven species lay broods averaging four eggs, and 14 more lay clutches of five to eight eggs, where siblicide may be expected on occasion.

Because the species data set is biased toward some genera (especially *Goniozus*) the distribution of mean clutch sizes for each genus was also examined. The distribution of generic clutch sizes ranges from one to 47.1, with mean 7.49 and median 4.00. Excluding solitary genera, the median clutch size was 3.36 (fig. 2*b*). No genera average two eggs per clutch, but three average three eggs, and a further four genera average between four and eight eggs.

Both these distributions contrast strongly with *Apanteles*, where only one out of 57 gregarious species lay clutches of two or three eggs and only three between four and eight (le Masurier 1987*b*) (fig. 2*c*). A sample across the whole of the parasitoid Hymenoptera (Blackburn 1990, 1991*a*, 1991*b*), including eight bethylid and 12 *Apanteles* species, shows that 73.6% of species are solitary (223 out of 303). Of the 80 gregarious species sampled, the modal clutch size is 2, and the median is 6.45 (fig. 2*d*). Thus, as in bethylids, but unlike *Apanteles*, small gregarious clutches are very common.

Clutch Size and Wasp Size versus Host Size in Bethylids

No bethylid species laid large clutches on small hosts, but on large hosts both small and large clutches were found (fig. 3*a*). Because the variance in clutch size increases with host size even after $\log_{10}$ transformation, we use nonparametric methods to analyze these data. Species with larger hosts also tended to lay larger clutches ($r_s = 0.578$, $n = 51$, $P < .0005$). However, under formal comparative methods, when both extant and assumed ancestral states are compared, the same relationship does not hold; differences in host size are not significantly associated with differences in clutch size ($r_s = 0.323$, $n = 18$, $P > .05$; fig. 3*b*). Of the 18 contrasts, seven are negative (sign test $P = .481$). However, the relationship is dependent on the taxonomic level at which contrasts are made: within genera, $\log_{10}$ clutch size is very strongly positively related to $\log_{10}$ host length ($Y = 1.73X$, $n = 6$, $r^2 = 0.929$, $t = 8.104$, df = 5, $P = .0005$), but at deeper nodes in the phylogeny, $\log_{10}$ clutch size is not significantly correlated with $\log_{10}$ host length ($Y = 0.322X$, $n = 12$, $r^2 = 0.050$, $t = 0.76$, df = 11, $P = .463$; fig. 3*b*).

Species with larger hosts also tended to have longer bodies ($\log_{10}$ wasp length = $0.218 + 0.304 \times \log_{10}$ adult host length, $r^2 = 0.275$, $F = 18.18$, df = 1, 48, $P < .001$; fig. 4*a*). However, under formal comparative methods, comparing both extant and assumed ancestral states, this relationship was also not significant ($Y = 0.206X$, $n = 18$, $r^2 = 0.177$, $t = 1.915$, df = 17, $P > .05$; fig. 4*b*). Five of the 18 contrasts were negative (sign test $P = .096$). Again, the relationship differed with the taxonomic level at which contrasts were made: within genera, $\log_{10}$ wasp length is not significantly correlated with log host length ($Y = -0.0295X$, $n = 6$, $r^2 = 0.014$, $t = -0.27$, df = 5, $P = .798$), but at deeper nodes in the phylogeny $\log_{10}$ wasp size is positively correlated with $\log_{10}$ host length ($Y = 0.437X$, $n = 12$, $r^2 = 0.462$, $t = 3.08$, df = 11, $P = .011$; fig. 4*b*).

Clutch size across species was not significantly related to wasp size ($r^2 = 0.0022$, $F = 0.110$, df = 1, 49, $P > .75$; fig. 5*a*). The contrasts on $\log_{10}$ clutch size were not correlated with the contrasts on $\log_{10}$ wasp length ($Y = -0.00613X$, $n = 18$, $r^2 = 4.46 \times 10^{-6}$, $t = 0.00870$, df = 17, $P = .993$; fig. 5*b*). Ten of the 18 contrasts were negative (sign test $P = .815$). Thus, clutch size is not a simple allometric consequence of body size.

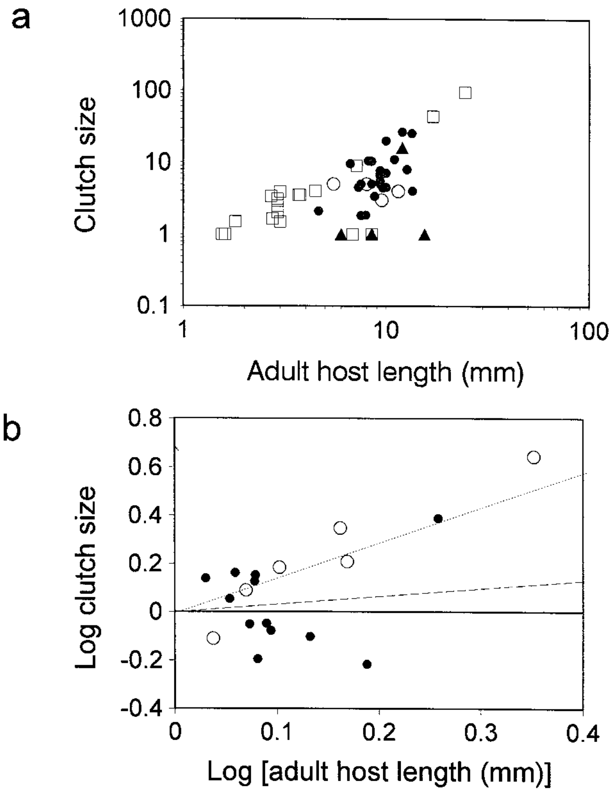

Figure 3: Clutch size against the adult length of the host in Bethylidae. For the raw species data (*a*), closed circles represent *Goniozus* spp., open circles other Bethylinae, open squares Epyrinae, and triangles Pristocerinae. For the contrasts (*b*), open circles are within genera (*dotted regression line*), and closed circles are deeper nodes in the phylogeny (*dashed regression line*).

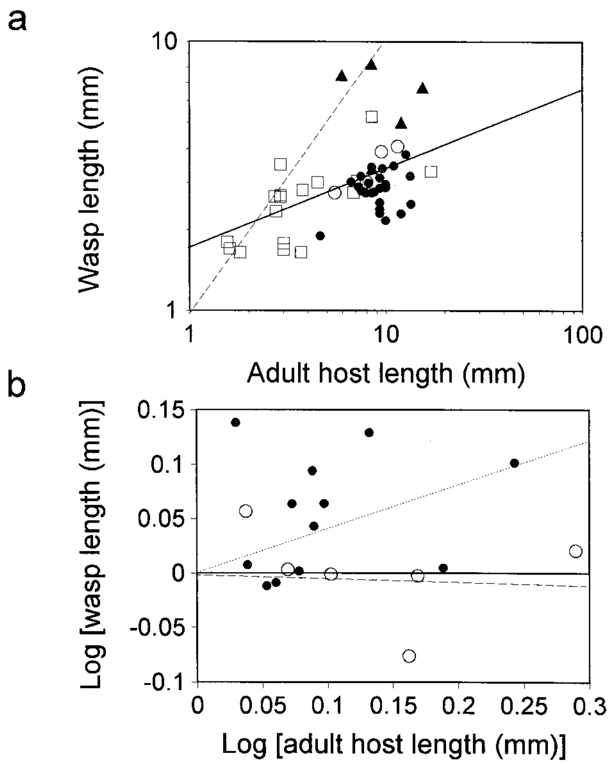

Figure 4: Wasp length against the adult length of the host in Bethylidae. For the raw species data (*a*), closed circles represent *Goniozus* spp., open circles other Bethylinae, open squares Epyrinae, and triangles Pristocerinae. The solid line is the regression line and the dashed line is where wasps and hosts are the same size ($Y = X$). For the contrasts (*b*), open circles are within genera (*dashed regression line*), and closed circles are deeper nodes in the phylogeny (*dotted regression line*).

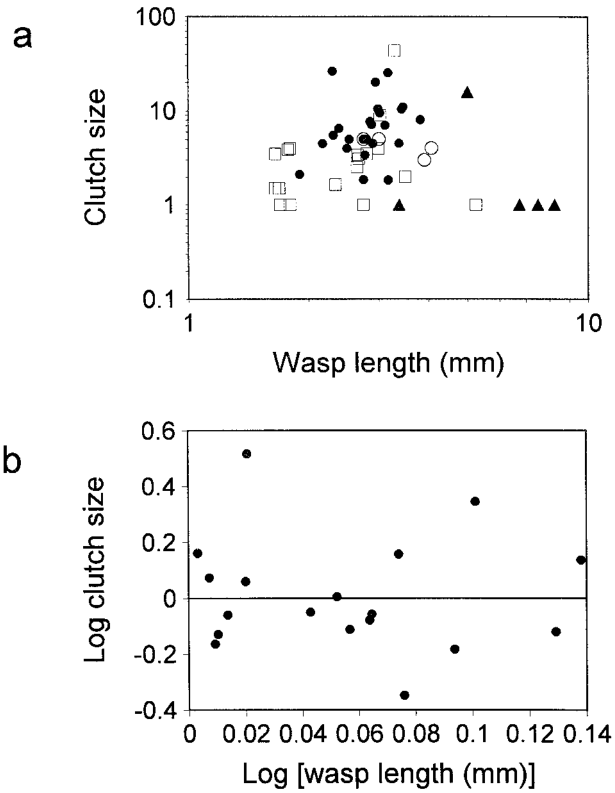

Figure 5: Clutch size against the length of the wasp in Bethylidae, plotted by species (*a*) and as contrasts (*b*). For the raw species data (*a*), closed circles represent *Goniozus* spp., open circles other Bethylinae, open squares Epyrinae, and open triangles Pristocerinae.

Brood Volume versus Host Size

Following le Masurier (1987*b*), a proportional estimate of brood volume was calculated as the product of the clutch size and the cube of wasp length. Species with larger hosts also tended to have larger brood volumes ($\log_{10}$ brood volume $= 0.575 + 1.741 \times \log_{10}$ adult host length, $r^2 = 0.579$, $F = 67.38$, df $= 1, 49$, $P < .001$). Analysis of covariance was used to test whether the relationship differed for solitary, semigregarious, and gregarious species. Neither the intercepts nor the slopes were significantly different (intercepts: $F = 0.691$, df $= 2, 48$, $P > .5$, slopes: $F = 0.170$, df $= 2, 46$, $P > .75$; fig. 6*a*).

The contrasts on $\log_{10}$ brood volume increased significantly with the contrasts on $\log_{10}$ host length ($Y = 1.551X$, $n = 18$, $r^2 = 0.539$, $F = 19.90$, df $= 1, 17$, $P = .0003$; fig. 6*b*). Only one contrast was negative (sign test $P = .0001$). The negative contrast was between the genera *Allepyris*, *Laelius*, and *Holepyris*. *Holepyris* has a host about two times longer than *Laelius* and *Allepyris* but actually has a smaller brood volume. Another contrast, between *Parascleroderma* and *Pristocera*, positively outlies the regression. *Pristocera* spp. have only slightly larger hosts but have much larger estimated brood volumes. Both these outliers can be explained by the inadequacy of adult body length as an estimate of host size; *Holepyris* has long thin (adult) hosts compared with those of *Allepyris* and *Laelius* (pyralid moth larvae as opposed to dermestid beetle larvae), while the adult hosts of *Parascleroderma* (clerid beetles) are much longer than their larvae.

To test whether taxa that laid solitary clutches had smaller brood volumes than expected from the size of the host, we followed the procedure for categorical covariant analysis in CAIC (Purvis and Rambaut 1995). First, to calculate valid residual brood volumes, the slope of the contrasts on $\log_{10}$ brood volume against $\log_{10}$ adult host length was fitted to the species data, and residuals from the slope were calculated. Species were then categorized in an ordered way according to whether they were solitary (1), semigregarious (2), or gregarious (3). Finally, contrasts on residual brood volume were calculated

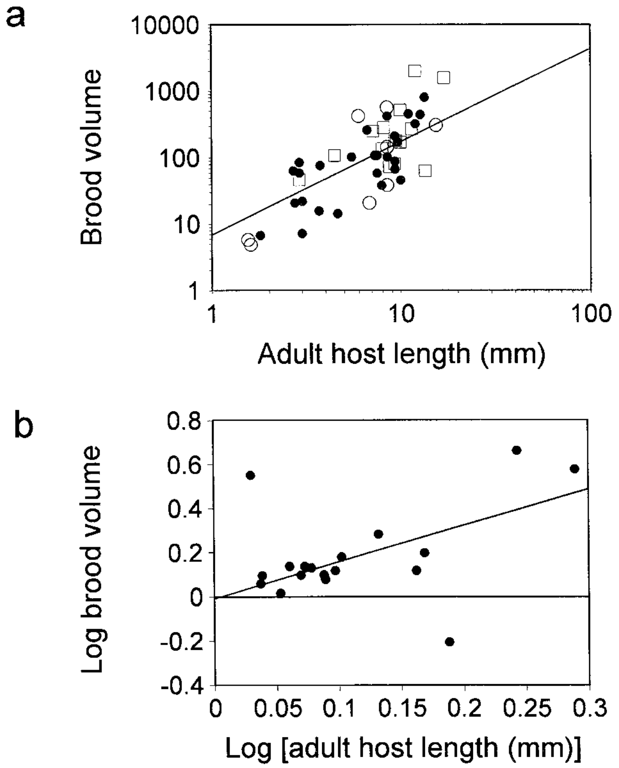

Figure 6: Estimated brood volume against the adult length of the host in Bethylidae, plotted for each species (*a*) and as contrasts (*b*). The regression lines are shown, which for the contrasts are forced through the origin. For the raw species data (*a*), open squares represent gregarious species, open circles solitary species, and closed circles semigregarious species.

against the contrasts on clutch size categories. If solitary clutches are associated with smaller brood volumes for a given host size, the contrasts on residual brood volume should be significantly greater than zero. This was, however, not the case (mean = 0.118, SE = 0.061, $n = 7$, $t = 1.938$, df = 5, $P > .1$), and three of the seven contrasts were negative (sign test $P = 1.00$). Thus, the clutch size category does not significantly influence brood volume relative to host size.

Discussion

Oh, false dichotomy! (Ridley 1996, p. 163)

This article contains two important results concerning the evolution of clutch size in parasitoid wasps. First, clutch size distributions like that proposed for *Apanteles* are not ubiquitous among the parasitoid Hymenoptera, small gregarious broods can be very common, at least in some taxa, and are the most common gregarious brood size in the Hymenoptera as a whole. Such data call into question the extent to which siblicide modulates clutch size, and vice versa, in parasitoid wasps.

Second, changes in host size may be accompanied by both changes in clutch size and changes in wasp size; among closely related bethylid species clutch size is larger on larger hosts with relatively little change in body size. However, when more distantly related taxa are compared, wasp size is larger on larger hosts, and clutch size is relatively invariant.

Together these data argue that clutch size in bethylids is best described by traditional optimality models rather than models of parent-offspring conflict. Below, we discuss the trends in clutch and wasp size with host size before going on to discuss why siblicide is rare in bethylid wasps.

Clutch Size and Wasp Size versus Host Size

The results reported in this article suggest that both clutch size and wasp size may evolve in response to host size. Although much attention has been given to the way clutch size responds to host size in bethylids and other parasitoids, the evolution of body size or offspring size has received very little attention (Godfray et al. 1991; Godfray 1994). A possible reason is that clutch size theory was first applied to birds, in which growth is relatively determinate, and was only later applied to insects, where this assumption is often inappropriate (see Charnov and Skinner 1984; Godfray 1987*a;* Godfray et al. 1991). As a result, some insect clutch size models actually assume determinate growth (e.g., Parker and Courtney 1984), whereas others are not explicit about size but instead consider overall offspring fitness, which is often highly correlated with size (e.g., Skinner 1985; Waage and Godfray 1985). However, models that simultaneously consider size and number can be useful because they direct attention to the continuum of strategies facing an ovipositing mother or a species engaged in a host shift (Parker and Begon 1986; Ebert 1994). At one end of the continuum, clutch size can remain constant on all kinds of hosts and only offspring body size varies (solitary wasps). At the other end of the continuum, wasp size can remain constant and only clutch size varies. In between is a range of strategies where both size and number can vary on hosts of different size. There is evidence that this occurs in at least some parasitoids, although it is rarely investigated (le Masurier 1987*b;* Hardy et al. 1992; Mayhew 1998). This study suggests that both changes in wasp and clutch size occur across species in bethylids, but the extent of each depends on taxonomic level; within genera, clutch size mainly changes, whereas at deeper nodes in the phylogeny wasp size mainly changes. The range in clutch size (one to 94) is an order of magnitude larger than the range in wasp size (about 1.5–7 mm), but the range in wasp size is greater than in *Apanteles* spp. (2–4 mm).

Together, these data are best described by offspring size–number models, and the assumptions of these models may in turn point toward important features of the biology that modulate clutch size evolution. Theory suggests that changes in wasp size may be caused by density-dependent mortality among offspring (Parker and Begon 1986) or by changes in the offspring fitness curve with host size (Ebert 1994). Data across bethylid species are insufficient for us to assess whether density-dependent mortality is the cause across species. In the two species that also show this trend among individuals, density-dependent mortality is probably not the cause because developmental mortality does not increase with clutch size (see Hardy and Cook 1995; Mayhew, in press). In two other bethylid spp., mortality is not higher in larger broods (I. C. W. Hardy, L. J. Dijkstra, J. E. M. Gillis, and P. A. Luft, unpublished manuscript). However, it is possible that the fitness accrued from large size could depend on host size across species. For example, Mamaev and Yagdyev (1981) found that single *Sclerodermus turkmenicum* Mamaev and Kravchenko could not paralyze large coleopteran larvae but that several wasp individuals confined together artificially could overcome a single large host. This would provide strong selection pressure for an increase in body size on larger hosts. Hawkins and Smith (1986) outlined another selective pressure that could operate in gregarious species; larger broods are sometimes better able to utilize a host, resulting in increased per capita fitness for larger broods as long as brood size is not excessively large (Allee effect). Alternatively, body size could simply be changing in response to other life-history variables not measured here, which are themselves correlated with host size (e.g., Blackburn 1991*a*, 1991*b*). Finally, the trend may also be caused by a simple constraint on body size when larvae only feed from one host; wasp size cannot be larger than host size. Thus, when host size becomes smaller for a solitary species, wasp size must also decrease. It is possible that all four factors contribute to the observed trends.

That average body size changes with host size at deeper nodes in the phylogeny but not within genera indicates that it is a conserved trait that evolves only slowly. Since there is often great intraspecific size variation in parasitoids, this result may seem surprising, but it may be that selective pressures on average body size are only weak or that they require other changes in physiology or morphology that slow the response to selection. In contrast, a wasp can probably change its clutch size relatively easily by distributing its eggs differently across host individuals. In bethylids, average clutch size changes with host size within genera (and also within species), indicating that it is indeed evolutionarily labile. These data therefore additionally indicate that models appropriate to one taxonomic level may not be appropriate to other taxonomic levels. We believe these data call for more empirical investigations into the reasons for changes in body size with host size.

Prevalence of Small Gregarious Broods

Clutch size distributions are now known for two parasitoid taxa of approximately equal species richness: *Apanteles* and the Bethylidae. In the former taxon, clutch size is bimodal with few species laying small gregarious broods, while in the latter, small gregarious broods are common. Why should this be? Rarity of small gregarious broods is predicted in the presence of siblicidal behavior. Larval fighting behavior is common in solitary *Apanteles* spp. (le Masurier 1987*a*, 1987*b*). The larvae of solitary bethylid species do not appear to differ morphologically from gregarious forms and are nonmotile (e.g., Williams 1919; Maneval 1930; Bognár 1957; Abraham et al. 1990). In addition, in one solitary species, more than one larva may complete development on a host (Abraham et al 1990). The fact that solitary species tend to have brood volumes equivalent to gregarious forms for the size of their host also indicates that clutch size is limited either by host size or by variable wasp size but not by larval behavior. The different clutch size distributions of *Apanteles* and bethylids may thus be partly explained by the prevalence of siblicide in one group but not in the other. The theory of parent-offspring conflict over clutch size makes predictions about how different life histories or ecological circumstances might affect the evolution of siblicidal behavior (Rosenheim 1993; table 1). Several factors increase the genetic cost of siblicide: female-biased sex ratios, single sexed broods, inbreeding, monandry, thelytoky, and a low incidence of superparasitism all increase the relatedness between larvae at a host, making it difficult for siblicide to evolve (table 1). Siblicide could also entail survival risks, for instance, if larvae are injured in fights. Further, it is conceivable that offspring fitness may increase with density (an Allee effect) in some cases (Hawkins and Smith 1986; Godfray 1987*a*). For example, some endoparasitoids cannot eclose from the host unless it is completely consumed (Flanders 1935; Taylor 1937; Streams and Fuester 1967). Such species would suffer large fitness costs from siblicide. Locally mating or inbreeding species may also suffer an Allee effect because if they become solitary they cannot easily find a mate. Other species may require large brood sizes to overcome host defense reactions, such as encapsulation (Godfray 1987*a*). If the clutch size is initially high, the costs of

Table 1: Comparative biology of *Apanteles* and Bethylidase and features that could favor siblicide over nonsiblicide

	Prevalence in		
Biology	Apanteles *spp.*	*Bethylidae*	*Positive (+) or negative (−) effect on prevalence of siblicide*
Female-biased sex ratios	Common (le Masurier 1987*a*, 1987*b*), but male-biased and equal sex ratios also known in gregarious species (Tanaka et al. 1992; Caballero et al. 1993); sex-ratio variance unknown	Found in majority of species, no male-biased sex ratios known (Griffiths and Godfray 1988); sex ratios precise (Hardy 1992)	− (Godfray 1987*b*)
Single-sex broods	All male broods occur at low rate (Godfray and Hardy 1993)	May occur due to developmental mortality of males and subsequent virgin mothers (Hardy and Cook 1995)	− (Rosenheim 1993)
Thelytoky	Occurs rarely (Clausen 1940; le Masurier 1987*a*)	Rare/reported cases dubious (Gordh 1976)	− (Godfray 1987*b*)
Superparasitism	Frequent in solitary species, also occurs in gregarious species (le Masurier 1987*a*, 1987*b*)	Occurs (Goertzen and Doutt 1975), but frequency reduced due to brood guarding (Hardy and Blackburn 1991) and ovicide (Legaspi et al. 1987; Mayhew 1998)	+ (Godfray 1987*b*)
Inbreeding	Relatively low: mating only partially local in *A. glomeratus* (Kitano 1976; Tagawa and Kitano 1981); some gregarious species have unbiased or male-biased sex ratios (Tanaka et al. 1992; Caballero et al. 1993); superparasitism occurs in gregarious species (le Masurier 1987*a*)	Prevalent in most gregarious species (Griffiths and Godfray 1988; Cook 1993; Hardy 1994), but some evidence for nonsibling mating (Hardy and Mayhew, in press)	− (Godfray 1987*b*)
Multipaternity within broods	Both monandry and polyandry occur (Ridley 1993)	Both monandry and polyandry occur (Ridley 1993)	+ (Macnair and Parker 1979)
Ectoparasitism	All endoparasitic (Gauld and Bolton 1988)	All ectoparasitic (Gauld and Bolton 1988)	− (Godfray 1987*b*)
Idiobiosis	All koinobionts (Gauld and Bolton 1988)	All idiobionts (Gauld and Bolton 1988)	?
Direct benefits of siblicide (e.g., cannibalism)	Possible (fighting larvae) (le Masurier 1987*a*, 1987*b*)	Probable—cannibalism known (Doutt 1973)	+ (Parker and Mock 1987)
Direct costs of siblicide (e.g., risk of injury)	Unknown	Unknown	− (Godfray 1987*b*)
Allee effect	Unlikely: do not need to consume host completely; solitary species can develop successfully (le Masurier 1987*a;* 1987*b*); mating only partially local (see above)	Likely in gregarious species: reduced clutches do not suffer higher mortality in one species (Hardy et al. 1992), solitary species can develop successfully (Bognár 1957), but locally mating species may suffer reduced fitness (Godfray 1987*a*)	− (Godfray 1987*a*, 1987*b*)
Initially high clutch size	Ancestral state probably solitary (Shaw and Huddleston 1991); current clutch size range broad (le Masurier 1987*a*, 1987*b*)	Ancestral state probably solitary (Gauld and Bolton 1988); current clutch size range broad	− (Godfray 1987*b*)
Nonsiblicidal allele recessive, or penetrates incompletely	Genetics unknown	Genetics unknown	+ (Godfray 1987*b*)

siblicide are larger because more relatives must be killed. However, if direct benefits accrue from siblicide, such as cannibalism, such costs might be offset. Finally, the extent to which siblicide evolves depends on the details of inheritance of siblicidal and nonsiblicidal behavior (Godfray 1987*b*).

The biologies of *Apanteles* and Bethylidae show some differences that match the theoretical predictions (table 1): superparasitism is frequent in *Apanteles* but probably rare in bethylids because in the latter group parents often guard the host or brood from conspecific females, and ovicide or larvicide also occur when females encounter a previously parasitized host. Thus, offspring developing together on a host are likely to be siblings. The degree of local mating and inbreeding is known to be low in one gregarious species of *Apanteles* and is implied to be low in several other species from their relatively equal or even male-biased sex ratios. However, local mating and inbreeding are thought to be high in many bethylids, and sex ratios are commonly female biased and are never known to be male biased. Sex ratios in bethylids are often precise (Green et al. 1982; Hardy 1992; I. C. W. Hardy, L. J. Dijkstra, J. E. M. Gillis, and P. A. Luft, unpublished manuscript), which indicates that single-sexed broods should be rare and relatedness between siblings reduced relative to species with binomial or greater than binomial sex-ratio variance. However, single-sexed broods do occur when females are unmated or when males die early in development (Hardy and Cook 1995). We know of no estimates of sex-ratio variance in *Apanteles* species (Hardy 1992). Together, this indicates that the average relatedness of larvae at a host may generally be greater in bethylids than in *Apanteles.*

There are some other striking differences in biology that may be relevant to the evolution of siblicide. *Apanteles* are endoparasites and koinobionts (host continues to develop after parasitism), whereas bethylids are ectoparasites and idiobionts (host ceases development upon parasitism). Siblicidal ectoparasites may risk losing contact with the host, and this may be especially important in bethylids, in which eggs are positioned very precisely on the host exterior and in which developmental mortality is known to be affected by egg position (Gordh and Hawkins 1981). Ecto- or endoparasitism might also affect the strength of selective pressures from multiparasitism in different ways. For instance, an endoparasite can probably do little to combat the presence of ectoparasites, but ectoparasites can probably compete effectively against both ectoparasites and endoparasites. We do not know to what extent these forces act in nature. Idiobionts feed on hosts that are often permanently paralyzed and do not continue to develop. The host starts to deteriorate as a resource immediately after paralysis, so rapid parasitoid development may be at a premium. If siblicide prevents efficient feeding, idiobionts may then scramble to feed on the host, in contrast to koinobionts, which may contest control of the still-developing host. Furthermore, while fighting larval morphology is widespread among the braconids (Salt 1961), the possibility exists that it has yet to evolve in bethylids or that such morphology might conflict with other aspects of biology mentioned above. The possible effects of such characteristics on the evolution of siblicide and clutch size provide many opportunities for future research.

Our data have shown that clutch size distributions that lack small gregarious broods are not the rule in parasitoids and may actually be the exception. Many bethylids have brood sizes where theory predicts siblicide should evolve, yet siblicidal behavior appears to be rare in this group. In contrast, our data indicate that some, perhaps many, parasitoid taxa experience comparatively weak selection pressure for siblicide such that it does not evolve or is not maintained as easily as in other taxa. This diversity requires an evolutionary explanation. The present theoretical framework suggests several ecological factors that might explain this diversity, and applying such thinking to the biology of *Apanteles* and bethylids indicates avenues for further research. Other parasitoid taxa may be identified that can be treated in the same way. We see formal comparisons between the life histories of siblicidal and nonsiblicidal taxa as the next step in testing theory about the evolution of siblicide and clutch size in parasitoids.

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