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Sex ratio, sexual dimorphism and mating structure in bethylid wasps

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Abstract Sexual dimorphism has been linked to parasitoid mating structure by several authors. In turn mating structure has an important influence on predicted sex ratio optima. Here we test the relationship between sexual dimorphism and sex ratio using data from 19 species of bethylid wasps. Using phylogenetically based comparative methods we confirm the findings of a previous cross-species analysis that sex ratio (proportion of males) is strongly and negatively correlated with clutch size. Using cross-species comparisons we show an additional positive correlation of sex ratio and relative male size, as predicted. The relationship however is not significant when using phylogenetically based methods. The cross-species result is largely due to differences between two bethylid sub-families: the Epyrinae have relatively large males and relatively high sex ratios, whereas the Bethylinae have relatively small males and lower sex ratios. Our study illustrates the benefits and drawbacks of using cross-species versus phylogenetically based comparisons.

Key words Bethylid wasps · Sex ratio · Sexual dimorphism · Clutch size · Phylogeny

Introduction

Assumptions about mating structure have been central to the development of sex ratio theory. Fisher's explanation (Fisher 1930) for sex ratio equality assumes that the mating opportunities of individuals extend throughout the whole population (panmixis) while the theory of local mate competition (LMC) (Hamilton 1967, 1979) assumes that mating takes place only among members of ephemeral sub-groups, and predicts that the optimal sex ratio depends on the number of mothers (foundresses) contributing offspring to the group. Many subsequent theoretical developments have assumed either panmixis or strictly local (within group) mating (reviewed by Godfray 1994). Other models have considered the possibility of mating structures intermediate between these extremes (Taylor and Bulmer 1980; Frank 1986; Nunney and Luck 1988; Werren and Simbolotti 1989; Ikawa et al. 1993; Taylor 1993; Greeff 1995, 1996; reviewed by Antolin 1993; Hardy 1994). In general, these models predict that as the prevalence of local mating decreases, optimal sex ratio becomes progressively less female-biased than under strict local mating. For instance, the model of Nunney and Luck (1988) assumes that males disperse from the natal group once females in the group have mated, and search for further groups containing virgin females. The model predicts that sex ratio optima will be sensitive to post-dispersal male mating success. This influence is particularly apparent when offspring groups are produced by a single foundress.

The development of much sex ratio theory has been closely linked to empirical studies of parasitoid Hymenoptera. In many species, offspring develop gregariously in discrete groups and have female biased sex ratios (Godfray 1994). Although sex ratio bias is usually attributed to local mating, the mating structures of relatively few parasitoid species have been critically assessed (e.g. Suzuki and Hiehata 1985; Kazmer and Luck 1991; Nadel and Luck 1992; Molbo and Parker 1996; reviewed by Hardy 1994). Current evidence suggests that strict local mating is the exception rather than the rule (Hardy 1994) and detailed studies of the mating system of *Bracon hebetor*, a gregarious parasitoid with a female biased sex ratio, have even shown that individuals *avoid* mating locally (Antolin and Strand 1992; Ode et al.

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1995). Hence, models which explore intermediate mating structures are very pertinent to the understanding of parasitoid sex ratios but, largely due to practical difficulties associated with obtaining reliable estimates of parasitoid mating structures, tests of these are almost entirely lacking (a recent exception is Molbo and Parker 1996).

Sexual dimorphism is widespread but not ubiquitous in the Hymenoptera. Different morphologies probably result from the different selection pressures operating on males and on females (e.g. Hamilton 1979; Hurlbutt 1987; Gauld and Bolton 1988; Godfray 1994; Stubblefield and Seger 1994). In some species, such as fig-associated wasps, comparison of male and female morphologies provides a convincing indicator of male dispersal ability and hence mating structure; males which are similar to females disperse and mate non-locally, while those with very different morphologies do not disperse and mate at the natal site (Hamilton 1979; Godfray 1994; Greeff 1995; Herre et al. 1997; Cook et al. 1997; see also Danforth 1991 for male dimorphic bees). In most Hymenoptera sexual dimorphism is less pronounced than in these fig wasps, but inter-sexual variation in body size may still correlate with sexual differences in dispersal ability and mating structure (Hamilton 1979; Hurlbutt 1987; Stubblefield and Seger 1994). Within species, field studies show that larger females have greater dispersal (foraging) abilities than smaller females (Visser 1994; Kazmer and Luck 1995; West et al. 1996; Ellers et al. 1998). Females must disperse from the natal site to find new hosts but male dispersal, to find mating opportunities, is often not mandatory and is therefore likely to be under variable selection. In the absence of direct evidence, female morphology can be regarded as a "dispersing morphology" to which males can be compared in order to estimate relative dispersal ability. Relative dispersal is predicted to influence both mating structure and sex ratio (e.g. Hamilton 1967; Bulmer and Taylor 1980; Bulmer 1986; Hardy 1994).

Two studies have used morphology as an estimator of mating structure to test sex ratio trends across pairs of congeneric species. King and Skinner (1991) compared sex ratios in *Nasonia vitripennis* with those in *N. giraulti* (parasitoids of Diptera). Male *N. giraulti* are fully winged whereas male *N. vitripennis* have reduced wings and are thought incapable of dispersal. Due to the putative difference in male dispersal, sex ratios were expected to be higher in *N. giraulti* than in *N. vitripennis*, but the opposite result was found (further discussed by King and Skinner 1991; Hardy 1994). B. Stille and E.D. Parker (unpublished work) compared sex ratios and relative thoracic volumes of males in *Periclistus brandtii* and *P. caninae* (phytophagous gall wasps). In qualitative agreement with an expected positive correlation between dispersal ability and thoracic volume, *P. brandtii* had a female biased sex ratio while *P. caninae* had an unbiased sex ratio and a relatively larger thorax. Although genetic analysis also suggested that outbreeding is less common in *P. brandtii* than in *P. caninae* (B. Stille and E.D. Parker, unpublished work; summarised by Hardy 1994), the interpretation of both this and the study of King and Skinner (1991) is hampered by the likelihood of inter specific correlations of sex ratio and mating structure occurring by chance when comparison is restricted to a pair of species.

In this paper we investigate the relationship between mean sexual dimorphism and sex ratio across 19 species of bethylid wasps. We are interested in sexual dimorphism as a possible correlate of male dispersal ability, and hence the probability of non-local mating (which is difficult to measure directly). Our investigation builds on a comparative study of bethylid sex ratio in relation to clutch size (Griffiths and Godfray 1988) and we consider sexual dimorphism as an additional influence on sex ratio. We begin by summarising the sex ratio biology of bethylids and the study of Griffiths and Godfray (1988).

Evidence for sex ratio, mating and dispersal in bethylids

Bethylids are gregarious or solitary ecto-parasitoids, almost exclusively parasitizing coleopteran or lepidopteran larvae. The host ceases development once parasitized. The hosts of solitary species are often clumped and may be parasitized by a single female (quasi-gregarious development). The sex ratios of most species are female biased with low variances (Green et al. 1982; Griffiths and Godfray 1988; Hardy et al. in press). In many species, adult females exclude competing conspecifics from the vicinity of paralysed hosts and females finding previously parasitized hosts may destroy the initial brood before ovipositing or reject the host if the initial brood is well developed (Venkatraman and Chacko 1961; Doutt 1973; Goertzen and Doutt 1975; Gordh and Evans 1976; Griffiths 1990; Hardy and Blackburn 1991; Mayhew 1996, 1997; Petersen and Hardy 1996). Consequently offspring groups are normally produced by a single foundress.

Bethylids pupate around the remains of the host. Males typically eclose before females and may mate with their sisters either before these have left their cocoons or immediately afterwards (Jayaratnam 1941; Gordh 1976; Gordh and Evans 1976; Mertins 1980; Gordh and Hawkins 1981; Gordh et al. 1983; Kapadia and Mittal 1986; Griffiths and Godfray 1988; Abraham et al. 1990). Male dispersal ability may be poor in some species as males are reported to be short-lived (Bridwell 1920; Wheeler 1928; Koch 1973; Kapadia and Mittal 1986; Gordh et al. 1993; Witethom and Gordh 1994) and "sluggish" (Antony and Kurian 1960) compared to females, and in some species males do not possess wings (Krombein 1979). Furthermore, genetic disadvantages associated with inbreeding are likely to be absent (Abraham et al. 1990; Cook 1993). Although such observations strongly suggest that local mating is predominant in bethylids (Griffiths and Godfray 1988), several lines of evidence indicate some non-local mating.

In many species males possess wings, and are capable of flight in at least some of these (Jayaratnam 1941; Bognár 1957; Antony and Kurian 1960; Koch 1973; Murphy and Moore 1990). Both field and laboratory observations indicate high proportions of males dispersing from the natal site (Koch 1973; Barrera et al. 1993; I.C.W. Hardy, J.B. Pedersen, M.K. Sejer, U.M. Linderoth, S. Stokkebo, unpublished work on *Goniozus nephantidis*, *G. legneri*). Presumably, dispersing males forage for mating opportunities with non-sibling females as these eclose or search for hosts. Although the host-searching (dispersal) tendency of females may increase after mating (Smith et al. 1994), dispersal of virgin females is also reported (Koch 1973; Hardy et al. unpublished). Virgin females of some species may be reluctant to mate post-dispersal (Gordh et al. 1983) but this is probably not the case in others (van Emden 1931; Cook 1993). Further, in some bethylids females are reported to be polyandrous (Ridley 1993) and may re-mate to replenish depleted sperm supplies (Gordh 1976).

Non-local mating may be promoted by lack of sib-mating opportunities. Evidence suggests that although males cannot always inseminate all of their sisters at eclosion, the majority of females developing in mixed sex broods disperse inseminated (Hardy et al. in press, unpublished). However, broods containing only females at eclosion occur commonly (7–50% of broods), chiefly due to developmental mortality of sibling males but also due to single egg clutches (van Emden 1931; Finlayson 1950; Yamada 1955; Hamilton 1967; Gordh and Evans 1976; Hardy and Cook 1995; Mayhew 1996; Mayhew and Godfray 1997; Hardy et al. in press). Unmated females can produce broods of male offspring (e.g. Koch 1973; Hardy and Cook 1995) but these males will have zero fitness unless they disperse to mate non-locally, or mate with their mothers (van Emden 1931; Hamilton 1967; Hardy and Cook 1995). Laboratory observations suggest that mother-son mating is unlikely in *G. nephantidis* because mothers usually do not survive long enough to mate with their sons and produce additional broods (Hardy et al. unpublished).

The relationship between clutch size and sex ratio

Griffiths and Godfray (1988) investigated the inter specific relationship between clutch size and sex ratio in bethylids. Noting that local mating is predominant, offspring groups are produced by a single foundress, and assuming that one male is sufficient to inseminate all females in a clutch, they predicted that sex ratio (proportion of males) would equal the reciprocal of offspring group size (optimal sex ratio = 1/clutch size). The mean sex ratio and clutch sizes of 20 species were broadly in agreement with their prediction: sex ratios were female biased and negatively correlated with clutch size. However, the sex ratios of many species were higher than predicted and other species had lower sex ratios. A methodological explanation is that data gathered from the literature are subject to rounding error (Griffiths and Godfray 1988). Biological explanations include the possibilities that single males may be insufficient to inseminate all sibling females, selecting for higher sex ratios (Griffiths and Godfray 1988). Developmental mortality may also cause deviation from a reciprocal sex ratio by altering the sexual composition of the brood between oviposition and eclosion and influencing sex allocation strategies (Green et al. 1982; Nagelkerke and Hardy 1994). Also possible is that bethylid sex ratios are influenced by non-local mating.

Methods

Sex ratio and clutch size data

We gathered data on average clutch size and sex ratio of bethylid wasps. These data derived mostly from the list of 20 species provided by Griffiths and Godfray (1988) (data from 3 unidentified *Goniozus* species were excluded) and were supplemented with data from further studies, resulting in the addition of 9 species (Table 1). Where multiple estimates of clutch size and/or sex ratio were available for a species the overall mean was used (*cf.* Griffiths and Godfray 1988). Sex ratio data are secondary sex ratios (at adult eclosion) rather than primary sex ratios (at oviposition) and many of the available clutch size estimates actually refer to brood size (the number of adults developing from an offspring group). Because developmental mortality may be high (Hardy et al. in press), we used brood size as the estimator of offspring group size when both clutch and brood data were available but for consistency with Griffiths and Godfray (1988) we refer to offspring group size as "clutch size" throughout.

Morphometric measurements

To estimate sexual dimorphism, we measured specimens of both sexes of as many of the 29 species as possible. The major source of specimens was entomological museums but some originated directly from cultures or field collections (Table 1). Measurements were made using a dissecting microscope fitted with an ocular micrometer and were accurate to the nearest 1/130 mm. We measured the maximum length, width and height of the head (excluding eyes), mesosoma (= thorax plus propodeum, henceforward referred to as "thorax") and "abdomen" (= abdomen excluding propodeum). We also measured the length of the hind tibia and the maximum length of the forewing (excluding tegula). We were unable to obtain any specimens of five species and only obtained females of three species. With these and two solitary species excluded (the prediction "sex ratio = 1/clutch size" is inappropriate for single egg clutches) there were 19 gregarious species for which male and female morphologies, sex ratio and clutch size were all estimated (Table 1).

Taxon sampling

There are about 2000 described species in the family Bethylidae, belonging to more than 100 genera (Gordh and Móczár 1990). There are five extant sub-families but one (Glaxodoxinae) has only a single species and another (Mesitiinae) is small with very poorly known biology. These sub-families are not represented in our study. While all three major sub-families, Bethylinae, Epyrinae and Pristocerinae, are represented by species in our study, we were unable to obtain morphometric measurements of males in the Pristocerinae. Analyses involving sexual dimorphism are thus restricted to the Bethylinae and Epyrinae. The representation of taxa is detailed in

Table 1 Bethylid sex ratio, clutch size and sexual dimorphism

Species[1]	Sex ratio[2]	Clutch size[2]	Morphology	
			Sexual dimorphism[14] M male size F female size R residual	Number measured M males F females S source[15]
Sub-family Pristocerinae				
Pristocera rufa	0.17	15.9	M –	M 0
			F 0.376	F 1
			R –	S a
Sub-family Epyrinae				
Allepyris microneurus[3]	0.32	2.3	–	–
Laelius pedatus[4]	0.30	3.1	M 0.168	M 19
			F 0.241	F 17
			R −0.074	S b, c, d, e
Laelius utilis	0.29	3.4	M 0.186	M 10
			F 0.217	F 13
			R −0.053	S c, d
Laelius voracis	0.33	4.0	M 0.125	M 2
			F 0.135	F 7
			R 0.365	S b, c
Sclerodermus domesticus[5]	0.2	43.3	–	–
Sclerodermus immigrans	0.17	25.0	M –	M 0
			F 0.918	F 2
			R –	S c
Sclerodermus turkmenicum	0.04	105	–	–
Cephalonomia quadridentata[6] (=*gallicola*)	0.22	3.9	–	–
Cephalonomia stephanoderis[7]	0.19	1.0	M 0.057	M 1
			F 0.060	F 12
				S f
Cephalonomia tarsalis	0.5	2.0	M 0.059	M 7
			F 0.056	F 8
			R 0.036	S b, c
Cephalonomia waterstoni	0.33	2.0	M 0.028	M 5
			F 0.033	F 11
			R 0.163	S b, c
Prorops nasuta	0.25	1.0	M 0.042	M 8
			F 0.050	F 9
				S b, c
Sub-family Bethylinae				
Prosierola bicarinata	0.17	4.0	M 0.518	M 2
			F 1.173	F 3
			R 0.175	S b, g
Goniozus (*sensu stricto*) *jacintae*	0.25	1.8	M –	M 0
			F 0.381	F 2
			R –	S h
Goniozus (*sensu stricto*) *claripennis*	0.17	3.0	M 0.077	M 1
			F 0.325	F 3
			R −0.416	S i
Goniozus (*sensu stricto*) *procerae*	0.20	10.0	M 0.327	M 6
			F 0.320	F 3
			R 0.347	S j
Goniozus (*sensu stricto*) *triangulifer*[8]	0.34	1.59	M 0.286	M 3
			F 0.670	F 8
			R −0.230	S b, c
Goniozus (*sensu stricto*) *aethiops*	0.14	7.0	M 0.253	M 5
			F 0.480	F 7
			R 0.045	S b, g
Goniozus (*sensu stricto*) *natalensis*[9]	0.14	7.8	M 0.400	M 16
			F 0.600	F 11
			R −0.113	S k
Goniozus (*sensu stricto*) *indicus*	0.09	18.5	M 0.380	M 4
			F 0.410	F 4
			R 0.195	S b
Goniozus (*sensu stricto*) *platynotae* (=*floridanus*)	0.25	3.4	M 0.212	M 11
			F 0.347	F 19
			R −0.024	S b, c, l

Table 1 (Continued)

Species[1]	Sex ratio[2]	Clutch size[2]	Morphology	
			Sexual dimorphism[14] M male size F female size R residual	Number measured M males F females S source[15]
Goniozus (*Parasierola*) *legneri*[10]	0.12	10.3	M 0.200 F 0.374 R 0.435	M 7 F 11 S l, m
Goniozus (*Parasierola*) *cellularis*	0.20	5.0	M 0.223 F 0.397 R −0.103	M 7 F 15 S b, g
Goniozus (*Parasierola*) *emigratus*	0.136	13.6	M 0.120 F 0.220 R −0.116	M 12 F 16 S b, c, l
Goniozus (*Parasierola*) *nephantidis*[11]	0.22	10.2	M 0.230 F 0.456 R −0.114	M 24 F 14 S n
Goniozus (*Parasierola*) *gordhi* (=*gallicola*)	0.17	6.5	M 0.068 F 0.220 R −0.626	M 5 F 14 S g, l, o
Goniozus (*Parasierola*) *nigrifemur*[12]	0.17	7.7	M 0.256 F 0.296 R 0.434	M 3 F 10 S p
Goniozus thailandensis[13]	0.18	10.4	–	–

[1] Taxonomy is according to Evans (1964), Sorg (1988), Gordh and Móczár (1990) and Polaszek and Krombein (1994), but note that *G. indicus*, *G. natalensis* and *G. procerae* may be synonymous (Polaszek et al. 1994). [2] Sex ratios are given as proportion males. Average clutch size and sex ratio data were taken from Griffiths and Godfray (1988) with the following exceptions: [3] Yamada (1955); [4] Mertins (1980), Morgan and Cook (1994); [5] von Kühne and Becker (1974); [6] van Emden (1931); [7] Koch (1973), Abraham et al. (1990), Infante et al. (1994), Barrera et al. (1993); [8] Legaspi et al. (1987); [9] Conlong et al. (1988); [10] Gordh et al. (1983), Hardy et al. (in press); [11] Ramachandra Rao and Cherian (1928), Jayaratnam (1941), Antony and Kurian (1960), Nandihalli and Prasad (1985), Hardy and Cook (1995); [12] Hardy et al. (in press); [13] Witethom and Gordh (1994), Hardy et al. (in press) [14] Body size is illustrated by mean thoracic volumes (mm^3). Sexual dimorphism is shown as residuals from cross-species regression of male on female log10 mean thorax volume (solitary species excluded) [15] Sources of specimens: (a) Museum National d'Histoire Naturelle, Paris; (b) Smithsonian Institution, Washington DC; (c) British Museum of Natural History, London; (d) Dept Entomol Univ Wisconsin, Madison; (e) D.J.W. Morgan, culture; (f) M. Kern, field collection, Togo; (g) Dept Entomol, Univ California, Riverside; (h) Australian National Insect Collection, CSIRO, Canberra; (i) J. de Rond, The Netherlands; (j) Dept Entomol Univ Wageningen; (k) D. Gillespie, culture; (l) Dept Entomol Univ California, Berkley; (m) I.C.W. Hardy, field collection, California; (n) I.C.W. Hardy, culture; (o) Museum of Comparative Zoology, Harvard Univ; (p) Dept Entomol, Coll Agric and Home Economics, Las Cruces, New Mexico

Table 2 Representation of bethylid sub-families. The table is pessimistic because the totals column includes many solitary species which cannot be included in the samples

Sub-family	Total[a] genera (species)	Sampled[b] genera (species)	
		Sex ratio and clutch size data only	With sexual dimorphism
Galodoxinae	1 (1)	0	0
Mesitiinae	13 (179)	0	0
Pristocerinae	21 (517)	1 (1)	0
Epyrinae	50 (733)	4 (9)	2 (6)
Bethylinae	10 (409)	3 (16)	3 (14)

[a] Totals according to Gordh and Móczár (1990), but with *Odontepyris* placed in the Bethylinae (Polaszek and Krombein 1994), *G. thailandensis* added (Gordh and Witethom 1994) and with distinction between *Goniozus sensu stricto* and *Goniozus Parasierola* (see text)
[b] Genera represented only by solitary species are excluded. *S. turkmenicum* is excluded (see text)

Table 2. Although sampling of the Bethylinae is disproportionately high, the majority of the data, and the calculated contrasts, derived from other sub-families. Bethylids have a worldwide distribution and most geographic areas are represented by species included in our analyses: Africa, Europe, India, South East Asia, Australia, Hawaii and North and Central America. More data are always desirable, but we consider that the present evidence constitutes a reasonably representative sample of bethylid diversity.

Analysis

In their analysis, Griffiths and Godfray (1988) treated species data as statistically independent with the justification that sex ratio is likely to be an evolutionarily labile character (there is ample evidence for within-species adaptive variation in bethylids, e.g. Green et al. 1982). Although this counters the possibility of a phylogenetic constraint, it does not fully dispense with the possibility that a confounding correlation with an unknown third variable may generate spurious significance (Ridley 1989). Nevertheless, comparison among closely related species minimizes this problem (Harvey 1991; Harvey and Pagel 1991) and the study of Griffiths and Godfray (1988) can be viewed as a useful guide indicating a general relationship between sex ratio and clutch size (Griffiths 1990; Godfray 1994).

In the present study, we build initially on the methodology of Griffiths and Godfray (1988) and then repeat the analysis employing phylogenetically independent contrasts (Felsenstein 1985; Harvey and Pagel 1991; Purvis and Rambaut 1995; Harvey 1996). Using species as data points allows direct comparison with Griffiths and Godfray (1988), illustrates the distribution of species characters and gives greater statistical power if the phylogeny is unresolved, but also leads to a greater chance of rejecting a valid null-hypothesis. Phylogenetically based comparative methods lead to a great reduction in statistical power in this case, due to the poorly resolved phylogeny and taxonomy of the Bethylidae (Evans 1978; Purvis and Garland 1993; Polaszek and Krombein 1994), but may have greater validity due to the elimination of taxonomic bias (Purvis et al. 1994; Price 1997).

Species data as independent

We repeated the regression of Griffiths and Godfray (1988) of arcsin square-root transformed sex ratio on $\log_{10}$ clutch size across 26 gregarious species [we excluded *Sclerodermus immigrans* as in the original paper (Bridwell 1920) it is unclear whether data refer to this or a congeneric species]. We also performed the regression across the subset of 19 gregarious species for which we had complete morphometric data.

As our measures of dimorphism we calculated residuals from regressions of male on female characters (previously $\log_{10}$-transformed to stabilize the variance) across 19 species. We employed this method because it is not always valid to use male/female proportions as measures of sexual dimorphism due to allometric scaling (Ranta et al. 1994). We however performed additional analyses with $\log_{10}$(male character/female character) as the dimorphism measures (Boomsma 1989). The hypothesis that sex ratio and sexual dimorphism will be correlated does not specify which of the many possible measures of dimorphism should be considered. However, measurements of dimorphism are likely to be highly correlated and we restricted analysis to straightforward measures. The characters used are summarized in Table 3 and an example (thorax volume) of sexual dimorphism is given in Fig. 1. The resulting residuals represent the difference between observed and expected male size, given female size. The influences of sexual dimorphism and $\log_{10}$ clutch size on transformed sex ratio were explored by multiple regression with stepwise omission of non-significant explanatory variables. When explanatory variables, such as measures of dimorphism, are correlated this leads to the acceptance of the variable that explains the most variance when removed from the statistical model.

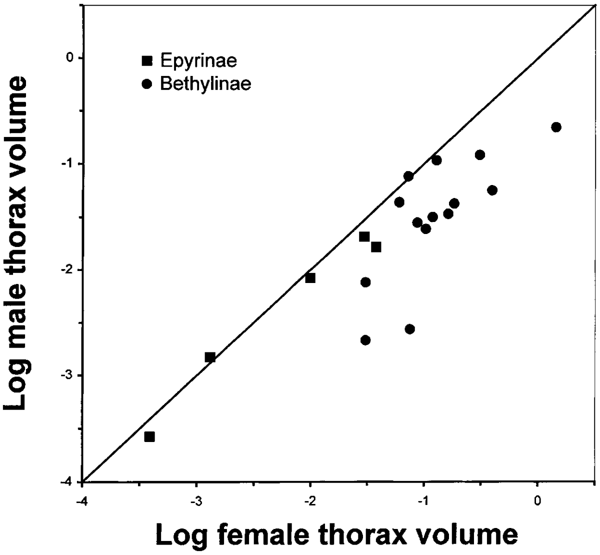

Fig. 1 Sexual dimorphism in the bethylids sampled. Males are generally smaller than females

Phylogenetically based comparisons

Standardized linear contrasts were calculated in the comparative analysis by independent contrasts (CAIC) package (Purvis and Rambaut 1995) which partitions the variance in species characters into phylogenetically independent linear contrasts.

For our estimate of phylogeny we clustered sub-families 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): these two studies are cladistically based and therefore used in preference to taxonomy. The position of the genus *Allepyris* does not appear in any published cladograms but Kieffer (1914) places it next to *Laelius* taxonomically. Genera and species were defined according to Gordh and Móczár (1990); however, due to non-uniformity of current taxonomic opinion, we retained the original distinction between the genera *Goniozus sensu stricto* and *Parasierola* (which may be synonymised as *Goniozus*, Gordh and Evans 1976). Data from *G. thailandensis* were excluded from phylogenetically based comparative analysis as we were unable to place this recently described species (Gordh and Witethom 1994) into one of these two genera. Since we have no information on bethylid within-genera relatedness, we clustered all species in the same genus within soft polytomies. The resulting estimate of phylogeny is given in Fig. 2. In the absence of branch length information we assume all branches of the phylogeny to have equal length (Purvis et al. 1994).

Table 3 Definitions of the 7 measures of sexual dimorphism, and the influence of clutch size and sexual dimorphism on sex ratio. Clutch size was $\log_{10}$ transformed and measures of dimorphism were residuals from regressions of $\log_{10}$ transformed male on $\log_{10}$ transformed female morphometric characters. Wing and tibia measures are lengths. Head, thorax and abdomen measures are volumes, calculated as equal to length × height × width. Head + thorax + abdomen was included as an estimator of dimorphism of total body volume. However, as abdomen is a unreliable measure (the abdomens of preserved specimens were often shrivelled) we also included head + thorax as an explanatory variable. Statistics are from stepwise multiple regression

Explanatory variables	Coefficient (SE)	r^2	Significance
Clutch size	−0.35 (0.05)	0.735	$F_{(1,16)} = 45.6, P < 0.0001$
Wing	−0.14 (0.08)	0.04	$F_{(1,15)} = 2.75, P = 0.118$
Tibia	0.20 (0.22)	0.012	$F_{(1,12)} = 0.85, P = 0.374$
Head	0.92 (0.77)	0.019	$F_{(1,11)} = 1.39, P = 0.262$
Thorax	0.10 (0.04)	0.092	$F_{(1,16)} = 5.69, P = 0.029$
Abdomen	−0.11 (0.07)	0.036	$F_{(1,14)} = 2.77, P = 0.118$
Head + Thorax	−0.12 (0.22)	0.004	$F_{(1,13)} = 0.29, P = 0.599$
Head + Thorax + Abdomen	0.27 (1.15)	0.001	$F_{(1,10)} = 0.06, P = 0.811$

We regressed arcsin square-root transformed sex ratio contrasts on $\log_{10}$ clutch size contrasts, with the regression forced through the origin (Garland et al. 1992) for 12 contrasts (from 25 species). To explore the influence of sexual dimorphism on sex ratio we calculated the slopes of the regression (through the origin) of contrasts on male on female $\log_{10}$ transformed body size measures. Residuals for each species were calculated as equal to the species value for males minus the product of the contrasts regression slope and the species value for females. Contrasts on each of these sets of residuals (the measures of dimorphism) were then calculated in CAIC. The influences of sexual dimorphism contrasts and $\log_{10}$ contrasts clutch size on arcsin square-root transformed sex ratio contrasts were explored by stepwise multiple regression through the origin ($n = 8$ sets of contrasts, from 19 species).

Results

Species data as independent

Sex ratio (proportion males) was significantly negatively correlated with clutch size across 26 gregarious species ($F_{(1,24)} = 34.83$, $r^2 = 0.59$, $P < 0.001$, Fig. 3) and also across the subset of 19 species with measured dimorphism ($F_{(1,17)} = 31.62$, $r^2 = 0.65$, $P < 0.001$). Multiple regression of clutch size and the seven measures of sexual dimorphism further showed that sexual dimorphism in thorax volume is significantly correlated with sex ratio: when males have relatively larger size, sex ratio is higher (Table 3, Fig. 4). Repeating the analysis using $\log_{10}$(male character/female character) as measures of sexual dimorphism lead to an identical interpretation.

Phylogenetically based comparisons

Confirming the results of cross-species analysis, contrasts on sex ratio were significantly negatively correlated with contrasts on clutch size (12 contrasts from 25 species: $F_{(1,11)} = 21.74$, $r^2 = 0.664$, $P < 0.001$, Fig. 5). Three of the contrasts were positive, meaning that the taxon or taxa with the greater clutch size also had the higher sex ratio. However, these always represented small differences. Whenever a taxon had a much higher clutch size in a contrast, it also has a much lower sex ratio (Fig. 5).

Regression of the eight sets of contrasts on clutch size and on measures of sexual dimorphism detected no significant influence of clutch size on sex ratio ($F_{(1,7)} = 3.65$, $r^2 = 0.34$, $P = 0.096$) or of any of the dimorphism measures. However, as found in the cross-species comparisons, the dimorphism measure which explained the most variance was (contrasts on) thorax volume, and this was positively (though not significantly) correlated with sex ratio ($F_{(1,6)} = 1.78$, $r^2 = 0.14$, $P = 0.228$). Repeating the analysis using $\log_{10}$(male character/female character) as measures of sexual dimorphism gave the same interpretation.

The results of the phylogenetically based analysis differed from those of the cross-species analysis. While the cross-species analysis suggests that changes in di-

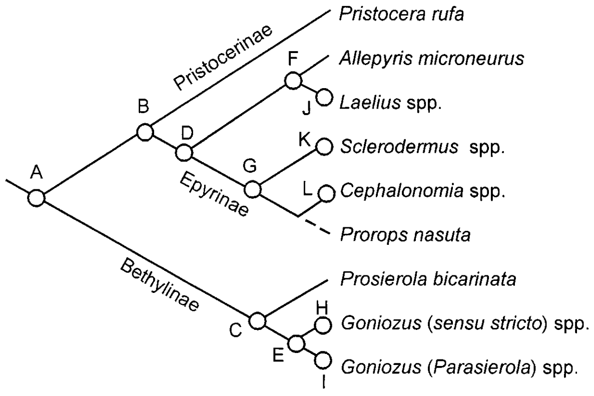

Fig. 2 Estimate of phylogenetic relationships of the 3 bethylid subfamilies and 7 genera used in the phylogenetically based comparative analyses. The phylogenetic position of *Prorops* is shown, but data were excluded from analysis as *P. nasuta* is solitary. Branch lengths were assumed equal when calculating independent contrasts. The *letters* at nodes refer to contrasts plotted in Figs. 5 and 6

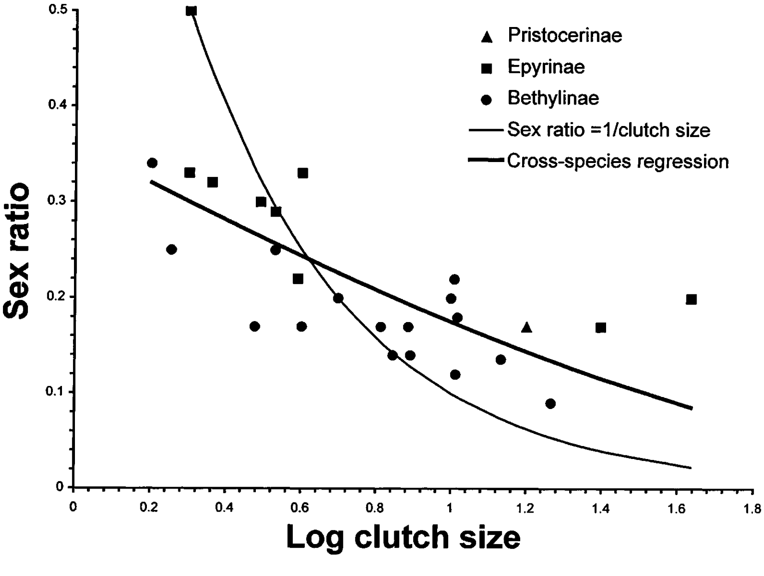

Fig 3. Cross-species regression of sex ratio (proportion males) on $\log_{10}$ clutch size for all gregarious species. The sex ratio predicted under single foundress, strict local mating, and unlimited insemination capacity is also shown

morphism are accompanied by changes in sex ratio, the lack of significance of the phylogenetically based analysis shows that this is not always the case. To examine where such changes are likely to have occurred, we calculated residuals of arcsin square-root transformed sex ratio from the regression of sex ratio contrasts on clutch size contrasts (Fig. 5) for each species. This controls for variation in clutch size. Contrasts on residual sex ratio were then calculated and regressed (though the origin) on contrasts on residual thorax volume. The relationship was positive but not significant ($F_{(1,7)} = 1.59$, $r^2 = 0.185$, $P = 0.248$, Fig. 6). The largest change in sex ratio in response to sexual dimorphism occurs at the split between the sub-families Bethylinae and Epyrinae (contrast A, Fig. 6), but a large change also occurs within the genus *Cephalonomia* (contrast L, Fig. 6). Within the genera *Goniozus* (*sensu stricto*) and *Goniozus* (*Parasierola*) sex ratio appears to have been little effected by large changes in dimorphism (contrasts H and I, Fig. 6).

Discussion

Cross-species comparisons

Cross-species comparison has found a positive relationship between sex ratio and relative male size. This accords with theoretical predictions of mating structure on sex ratio if non-local mating is more common in species with relatively larger males. Although there is much evidence to suggest that some non-local mating does occur in bethylids, we lack direct evidence for a correlation between the prevalence of non-local mating and sexual dimorphism. However, evidence from other hymenopterans suggests that this correlation is likely (see Introduction) and our confidence is increased by the fact that of the sexual dimorphism measures we investigated, thorax volume was the most influential. For example, abdomen or head size would not necessarily indicate dispersal ability whereas the functional relationship between dispersal and the volume of the thorax (which houses the wing muscles) is much more likely. We know of no more parsimonious explanation of our result that when males are relatively large, sex ratio is higher. An alternative possibility is that sexual size dimorphism arises due to competitive asymmetries between males and females during larval development. If males were relatively weak competitors, they would tend

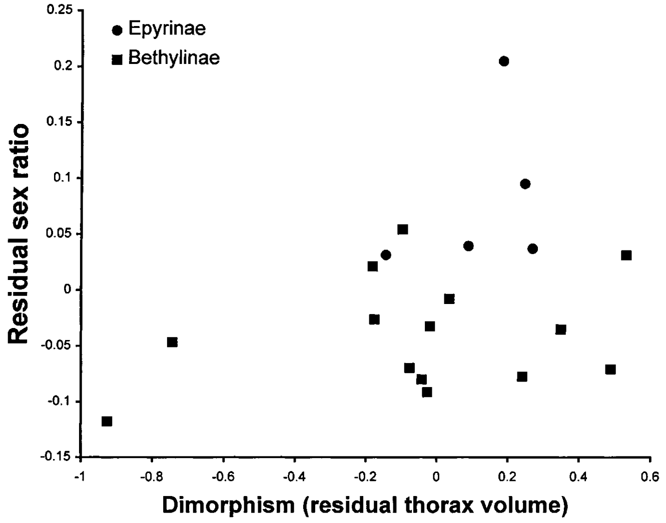

Fig. 4 The relationship between sex ratio and sexual dimorphism. Sex ratio is shown as residuals from the regression of clutch size on sex ratio across all gregarious species. Larger dimorphism residuals indicate relatively larger males

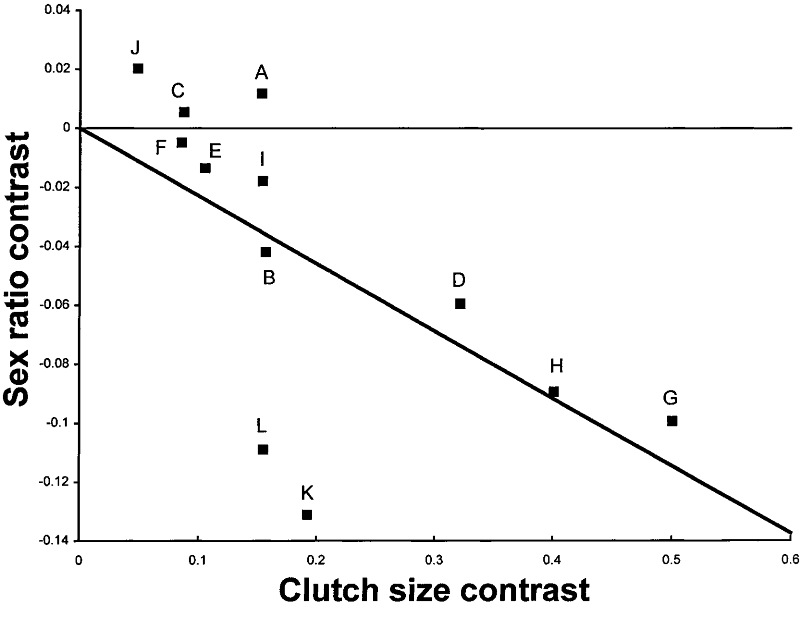

Fig. 5 Regression of contrasts on arcsin square-root transformed sex ratio against contrasts on $\log_{10}$ clutch size for all gregarious species. The regression equation is $y = -0.229x$, SE of slope = 0.049. *Letters* match contrasts to phylogeny, see Fig. 2

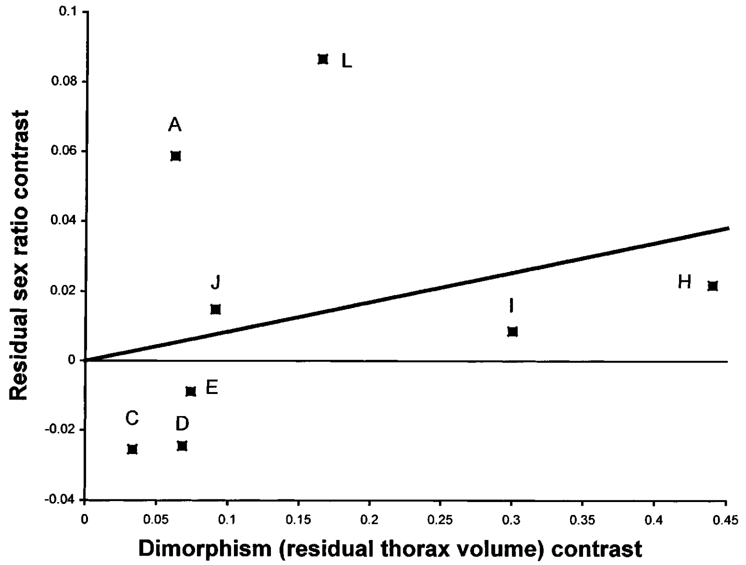

Fig. 6 The relationship between residual sex ratio contrasts and sexual dimorphism contrasts. The regression equation is $y = +0.0851x$, and is not significant. *Letters* match contrasts to phylogeny, see Fig. 2

to be larger on emergence when sex ratios were higher because they would have had fewer female competitors. Such results have been found in the gregarious braconid *Bracon hebetor*, but the asymmetry appears to be weak (Ode et al. 1996). The only investigation of sexual asymmetries in larval competition in a bethylid found that the sexual composition of *G. nephantidis* clutches influenced male but not female size (Varndell 1995). Males were smaller in clutches with low or high sex ratios and larger when sex ratios were approximately equal. Our sex ratio results would not be explained if the other bethylid species in our sample conformed to this pattern, but evidence is too scant for proper evaluation of the role of asymmetries.

The interpretation of three previous comparative studies of the influence of sexual dimorphism and/or non-local mating on parasitoid sex ratios is impaired by the low statistical power attained when comparing only two species (Suzuki and Hiehata 1985; King and Skinner 1991; B. Stille and E.D. Parker, unpublished work). By comparing across many more species our study circumvented this problem but in consequence was unable to employ additionally the more desirable behavioural (Suzuki and Hiehata 1985) or genetic (B. Stille and E.D. Parker, unpublished work) techniques for estimating the prevalence of non-local mating. Despite the inevitable errors associated with using sex ratio and clutch size averages derived from the literature and with indirect estimation of mating structure, we were able to detect, additional to the more important influence of clutch size, a correlation between sexual dimorphism and sex ratio. The situation in which the effect of non-local mating on sex ratios is predicted to be most marked (Nunney and Luck 1988) is when offspring groups are produced by a single foundress, as is the case in bethylids. Our results emphasise the need for further, direct, assessment of bethylid mating structures and of the relationship between dimorphism and mating structure. These will be able to employ methodologies developed using other parasitoids (e.g. Kazmer and Luck 1991; Nadel and Luck 1992; Molbo and Parker 1996; and see Hardy 1994).

Our investigation of the influence of sexual dimorphism (non-local mating) on sex ratios produced by single foundresses complements cross-species comparisons of fig-pollinator wasp (Agaonidae) sex ratios. Agaonid males do not disperse from the natal fig and thus there is no non-local mating but, in contrast to the Bethylidae, foundress number may vary considerably. Sex ratio responses to foundress number have been shown within many species (Herre et al. 1997). Cross-species comparisons further show that, at a given foundress number, the sex ratios of species which have larger average numbers of foundresses (less sibling mating) are higher than those of species with smaller foundress numbers (more sibling mating) (Herre et al. 1997). Together, the results of comparative studies on the Bethylidae and the Agaonidae support predictions (see Hardy 1994) that sex ratios will be higher when local mate competition is less prevalent due to either local mating between non-siblings or non-local (non-sibling) mating.

Phylogenetic considerations

Griffiths and Godfray (1988) predicted and found a negative relationship between average sex ratio and average clutch size across bethylid species (the relationship is also expected and found within species: Green et al. 1982; Hardy and Cook 1995; Hardy et al. in press). However, the treatment of data from related species as statistically independent by Griffiths and Godfray (1988) has been criticized (Ridley 1989). Using phylogenetically based comparative methods we have validated the relationship, despite the reduced power arising from the poorly resolved phylogeny. This increases, to some extent, our confidence in the interpretation of results from other cross-species (not phylogenetically corrected) comparisons of hymenopteran sex ratios (e.g. Waage 1992, Herre et al. 1997).

In discord with the results of our cross-species analyses, when we used phylogenetically based analyses we found no significant relationship between sex ratio and relative male size (even so, the same measure of dimorphism, thorax volume, was found to be the most important in both analyses). Two explanations for this difference are that the result from the cross-species comparisons is a taxonomic artifact, and that size differences genuinely correlate with sex ratio but the relationship was not detected in the phylogenetic analysis. We discuss these alternatives in turn.

Arguments against using species data in comparative studies include that the traits under consideration are not evolutionarily labile (Ridely 1989). We have used measures of sex ratio, clutch size and morphology. The evidence for within species lability of bethylid sex ratios and clutch sizes is overwhelming (e.g. Green et al. 1982; Hardy et al. 1992; Hardy and Cook 1995; Mayhew and Godfray 1997; Hardy et al. in press). However, Griffiths and Godfray (1988) suggested that clutch size may correlate with phylogeny due to evolutionary conservation of host range and hence host size (within species, gregarious bethylids tend to lay larger clutches on larger hosts, e.g. Hardy et al. 1992). Phylogenetically based comparisons of all available bethylid clutch size and host size data show that clutch size is correlated with host size within bethylid genera, but at deeper nodes in the phylogeny it is not (Mayhew and Hardy, 1998). Further, parasitoid size is not correlated with host size within genera, but at deeper nodes it is (Mayhew and Hardy, 1998). These results suggest that morphology is less evolutionarily labile than primarily behavioural characteristics such as clutch size and sex ratio. Figure 1 shows that, in our sample, species belonging to the Epyrinae are usually less dimorphic than those in the Bethylinae, and Figs. 3 and 4 show that the species in Epyrinae tend to lie above the cross-species regression and species in the Bethylinae below. Phylogenetically based analysis of sex ratio residuals (Fig. 6) confirmed that the split between the Bethylinae and Epyrinae is important in this relationship. Without better data we cannot determine whether the cross-species result is due to a relatively higher dispersal ability among Epyrinae males or to differences in sex ratio and dimorphism which are unrelated to dispersal. Although phylogenetically based comparisons suggest the latter, their interpretation is severely hindered by low power (see below).

Another objection to cross-species comparisons is that spurious significance may be generated by a confounding correlation with unknown variables (Ridley 1989; Price 1997). In the present study, we compared across closely related species which minimizes, but does not dispense with, this problem (Harvey 1991; Harvey and Pagel 1991). However, even phylogenetically based comparisons may not control for confounding variables and it is not automatically invalid to perform cross-species comparisons as well (Price 1997).

The lack of significance of body size as a correlate of sex ratio under phylogenetically based analysis could be explained by the reduced statistical power attained when using a poorly resolved phylogeny and fewer data (species without measured sexual dimorphism excluded). In this analysis, even the strong relationship between sex ratio and clutch size, found by both cross-species and phylogenetically based analyses of the larger data set, was not significant. We thus currently lack the statistical power to assess from phylogenetically based comparisons whether bethylid sex ratios are influenced by relative male size and non-local mating. Sex ratio, clutch size and morphometric data from yet more species (especially those in unexamined genera) would help to resolve this, but more important would be a phylogeny of the Bethylidae with intra-generic resolution (particularly within *Goniozus*).

Conclusions

Our study illustrates the conflicts associated with choosing comparative methodology: the potentially most valid method also has the lowest power. We agree that, where possible, phylogenetically-based studies are preferable and should be used in concert with cross-species analyses. However, our study shows that cross-species analyses can be useful indicators of real biological trends and thus point the way for further investigation. This investigation is heuristic since the basic data derive from potentially inaccurate sources and particularly because the relationship between sexual dimorphism and actual mating structure is expected but unproven. Nevertheless, our results suggest some support for the important prediction that sex ratios will be higher when local mating is less prevalent.

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