Behav Ecol Sociobiol (2008) 62:843–852
DOI 10.1007/s00265-007-0510-3

ORIGINAL PAPER

Parental care and sexual size dimorphism in wasps and bees

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Received: 5 June 2007 / Revised: 5 October 2007 / Accepted: 13 October 2007 / Published online: 8 November 2007

Abstract Sexual size dimorphism, in which one sex is larger than the other, occurs when body size has differential effects on the fitness of males and females. Mammals and birds usually have male-biased size dimorphism, probably because of strong sexual competition among males. Invertebrates usually have female-biased size dimorphism, perhaps because their inflexible exoskeletons limit ovary size, leading to a strong correlation between female body size and fecundity. In this paper, we test whether an additional factor, the type of parental care provided, affects the degree of sexual size dimorphism. Among wasps and bees, there is a contrast between provisioning taxa, in which females must gather and transport heavy loads of provisions to nests they have constructed, and non-provisioning taxa, in which females lay eggs but do not construct nests or transport provisions. Males have no role in parental care in either case. An analysis of British wasps and bees shows that provisioning taxa have significantly more female-biased size dimorphism than non-provisioning taxa. This is true for simple cross species comparisons and after controlling for phylogeny. Our data imply that the demands of carrying provision loads are at least part of the explanation for this pattern. Thus, sexual size dimorphism is greatest in pompilid wasps, which carry the heaviest prey items. Bees, which transport minute pollen grains, exhibit the least dimorphism. We also find that cavity nesting species, in which nest construction costs may be minimized, exhibit reduced dimorphism, but this was not significant after controlling for phylogeny.

Keywords Sexual dimorphism · Parental care · Hymenoptera · Wasps · Bees

Introduction

The two sexes differ in size in most animals, with male-biased size dimorphism being the commonest pattern in birds and mammals, but a female bias being more usual in invertebrates and other ectotherms (e.g., Clutton-Brock et al. 1977; Berry and Shine 1980; Gilbert 1983; O'Neill 1985; Hurlbutt 1987; Nylin and Wedell 1994; Head 1995; Fairbairn 1997; Lindenfors et al. 2002; Blanckenhorn et al. 2007). Many hypotheses, both adaptive and nonadaptive, have been proposed to explain patterns of sexual size dimorphism, with a general adaptive explanation being that it occurs when body size has differential effects on the fitness of the two sexes. However, convincing tests have often proved elusive (e.g., Nylin and Wedell 1994; Cox 2006). In this paper, we test whether sexual size dimorphism is correlated with parental care strategies in wasps and bees.

Stinging wasps and bees (Hymenoptera: Aculeata *sensu* Ronquist 1999) are known for their varied and often elaborate parental care behavior. Immature larvae are provided with food by the mother in one of three different ways, referred to here as 'parasitoid', 'provisioner', or

Communicated by R.F.A. Moritz

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‘cuckoo parasite’ (Bohart and Menke 1976; Michener 2000). Although differing in parental care behavior, these three kinds of taxa differ little in morphology or in other aspects of their biology (but see below). In parasitoids, the mother lays eggs on or near an arthropod prey, which is usually first paralyzed by stinging. The parasitoid larva feeds on the host, which is killed, then pupates (Eggleton and Belshaw 1992). In provisioning taxa (the majority of aculeates), the mother constructs a nest, often divided into multiple cells. A single egg is laid into each cell, which is provisioned with one or more paralyzed arthropods in wasps or with nectar and pollen in bees. Each larva eats the provisions then pupates in the cell. Provisioners therefore resemble parasitoids, except that the mother places the prey in a protective nest for her larva. Cuckoo parasites oviposit in the nests of provisioners. Typically, the cuckoo parasite larva first destroys the host provisioner’s egg, then itself feeds on the provisions—cuckoo parasite larvae therefore do not have to compete with host larvae for food. Males provide no parental care in any taxa.

The ancestors of aculeates were probably parasitoids (see Ronquist 1999). Thus, today’s parasitoid and cuckoo parasitic aculeates effectively represent secondary reversions to the ancestral lifestyle. Recent phylogenetic work places bees and ‘digger wasps’ (formerly placed in the family Sphecidae) in a single superfamily (Apoidea), with the bees comprising a monophyletic group (Melo 1999; Danforth et al. 2006). The Pompilidae (spider-hunting wasps) represent a separate lineage. Bees include the largest number of independent origins of cuckoo-parasitic behavior: at least 17, and perhaps as many as 29 origins among nonsocial bees alone (Michener 2000). Approximately 20% of bee species are cuckoo parasites (Bohart and Menke 1976; Day 1988; Roubik 1989). The British nonsocial aculeate fauna is well studied and probably includes at least nine independent origins of cuckoo-parasitic and parasitoid life histories.

As in most invertebrates, the vast majority of bees and wasps exhibit female-biased sexual size dimorphism: females are larger than males (e.g., Hurlbutt 1987; O’Neill 1985, 2001). Bees and wasps share common features with other invertebrates which may help to explain this pattern. In particular, the inflexibility of the invertebrate exoskeleton limits ovary size and egg number (Stearns 1977), so that dimorphism may usually be caused by stronger effects of body size on female fecundity than on the mating success of males (Ralls 1976; Fairbairn and Preziozi 1994; Head 1995). The degree of dimorphism, however, might depend on the type of parental care provided. In particular, nest construction and prey transport are activities carried out only by females. If their performance leads to stronger selection for larger female body size, we predict that sexual size dimorphism should be more female-biased in provisioners than in cuckoo parasites or parasitoids, which do not construct nests or transport prey. Thus, our main comparison will be between provisioning taxa and non-provisioning taxa, the latter being parasitoids and cuckoo parasites combined.

One reason why provisioning might favor larger female size is the physical demands of transporting provisions to the nest. In wasps that provision each offspring with a single paralyzed arthropod, each prey item must provide enough food to produce a new adult. As there is considerable inefficiency in the conversion of prey weight to adult wasp weight, such prey items can be ten times the weight of the transporting female parent (e.g., Field, 1992a, b). Even when each offspring is provisioned with several smaller food loads, the individual loads can still be heavy. For example, the ‘beewolf’ *Philanthus triangulum* provisions each offspring with one to five paralyzed honeybees (*Apis mellifera*), which she carries to the nest in flight. Each honeybee weighs 80–160 mg, compared with the average weight of 110 mg for the beewolf female herself (Strohm and Marliani 2002). Nevertheless, if transporting provisions selects for larger female size, taxa that provision each offspring with only a single prey item, such as pompilid wasps, should exhibit the most female-biased sexual size dimorphism. Conversely, because the individual food items (pollen grains) carried by bees are smaller than the individual items (prey) carried by wasps, bees might be expected to exhibit the least female-biased dimorphism. The greater divisibility of bee provisions may allow them to optimize load size so that body size is less constrained by having to carry provisions. Thus, we predict that the magnitude of female/male size dimorphism should be pompilids > apoid wasps > bees.

A second potential reason why provisioners might exhibit more female-biased sexual size dimorphism than non-provisioners is the effort required by female provisioners to construct nests. The majority of provisioning taxa construct nests de novo. Most of these dig burrows in the soil, although other substrates such as rotting wood are also used. Other species construct aerial nests using materials such as mud or vegetable matter gathered from the external environment. While provisioning itself has traditionally been thought of as the costliest aspect of parental care, nest-building appears to be energetically demanding, and recent experiments on the ground-burrowing digger wasp *Ammophila pubescens* suggested that nest construction and provisioning might have comparable costs (Field et al. 2007; see also Rosenheim et al. 1996). The effort involved in nest construction may not always be great, however, because some provisioners nest in preexisting cavities or crevices, thus presumably minimizing nest construction costs. A comparison between provisioners that use preexisting cavities and those that construct nests de novo provides a possible test of the hypothesis that nest construction drives the evolution of more female-biased size dimorphism.

The prediction that provisioning wasps and bees will exhibit more female-biased size dimorphism than non-provisioners assumes that there are no other systematic differences between the two groups that select for the opposite pattern. One difference, however, is that cuckoo parasites are known to produce more eggs than provisioners (Alexander and Rozen 1987; Iwata 1955; O'Neill 1985, 2001; Ohl and Linde 2003). This could require female cuckoo parasites to be larger, masking any opposite effect that the absence of provisioning might have. However, eggs of cuckoo parasites are individually smaller than those of provisioners (after controlling for body size: O'Neill 2001; Rosenheim et al. 1996; Ohl and Linde 2003), and a comparison in terms of the total volume of eggs carried has yet to be carried out. A second difference between cuckoo parasites and provisioners is that parasitic females usually invade the nests of their hosts, where they may be attacked by host females. If this leads to selection for increased female size, any effect that the absence of provisioning has on size dimorphism could again be masked. Almost all of the cuckoo parasites in our study attack nonsocial hosts, which leave their nests unoccupied for most of the day, while they are away foraging for provisions (e.g. Field and Foster 1995). This reduces the likelihood of agonistic encounters. Nevertheless, some of these parasites have noticeably harder exoskeletons than their hosts, presumably as an adaptation to avoid injury, suggesting that agonistic encounters do occur.

Materials and methods

Measuring body size

For most taxa, we used pinned specimens in the collections of the University Museum of Zoology, University of Cambridge, UK. We selected 122 species from 27 genera (Table 1 of Appendix) on the basis of whether enough specimens were present to provide a reasonable sample size for each sex. We avoided species where identification is difficult, in case some specimens were wrongly identified. Where possible, we selected ten specimens of each sex randomly for each species. When fewer than ten specimens were available, we measured all available specimens. Sample sizes for each sex were 9.8+0.22 for provisioners, and 9.4+0.32 for non-provisioners. Size data for 13 species of Pompilidae (seven genera) were taken from pinned specimens originally collected in malaise and water traps during 1983 at Santon Downham, Norfolk, U.K (Field 1992c). Sample sizes for these were larger: 67+16 for provisioners and 51+14 for non-provisioners. In addition, we obtained specimens of the non-provisioning pompilid *Ceropales maculata* (F.) from the University Museum of Zoology, as above. The total number of species in the analysis was therefore 136.

We used intertegular width as our measure of body size. Following Cane (1987), we measured the minimum distance across the thoracic dorsum between the tegulae to the nearest 0.02 mm, using a binocular microscope with an eyepiece graticule (excepting the largest species of *Anthophora* and *Megachile*, which were measured to the nearest 0.04 mm). Intertegular width provides a convenient measure of body size because museum specimens can be measured without removing them from their pins. It has been shown to correlate strongly with dry weight in bees (Cane 1987) and with wet weight in pompilid wasps (Field 1992c).

Statistical analysis

Comparison between provisioners and non-provisioners

We classified species into two parental care groups: " non-provisioners", comprising cuckoo-parasites and parasitoids; and "provisioners", which construct and provision nests. To test whether sexual size dimorphism is correlated with parental care strategy, we performed an analysis of covariance in which we regressed the $\log_{10}$ of mean female size on the $\log_{10}$ of mean male size, with parental care group and 'lifestyle' included as possible explanatory factors. This ANCOVA controlled for possible confounding effects of average body size differences between provisioners and non-provisioners. Lifestyle was divided into three categories: apoid wasps, apoid bees, and pompilid wasps (Fig. 1). The analysis produced a series of standard allometric regressions in which $\log\,(\text{female size}) = \log A + b \log\,(\text{male size})$, or $(\text{female size}) = \text{A}\,(\text{male size})^b$ (Fairbairn and Preziozi 1994; Harvey and Pagel 1991). If the slope, b, is significantly different from 1.0, the degree of size dimorphism is also correlated with mean body size (Fairbairn and Preziozi 1994; Fairbairn 1997).

Related species living in similar environments may be similar because of common ancestry rather than independent adaptation (e.g., Harvey and Pagel 1991). Controlling for phylogeny is thus desirable, although not under all models of evolution (Price 1997; Harvey and Rambaut 2000). As well as examining cross-species correlations, we analyzed independent contrasts using the computer program CAIC (version 2.6.9) developed by Purvis and Rambaut (1995a; see also Grafen 1989; Harvey and Pagel 1991). For apoids, we used Melo (1999), Michener (2000), Danforth et al. (2006), and Brady et al. (2006) to derive the genus-level phylogeny shown in Fig. 1. The higher-level phylogeny of pompilid wasps is uncertain, except for the division into

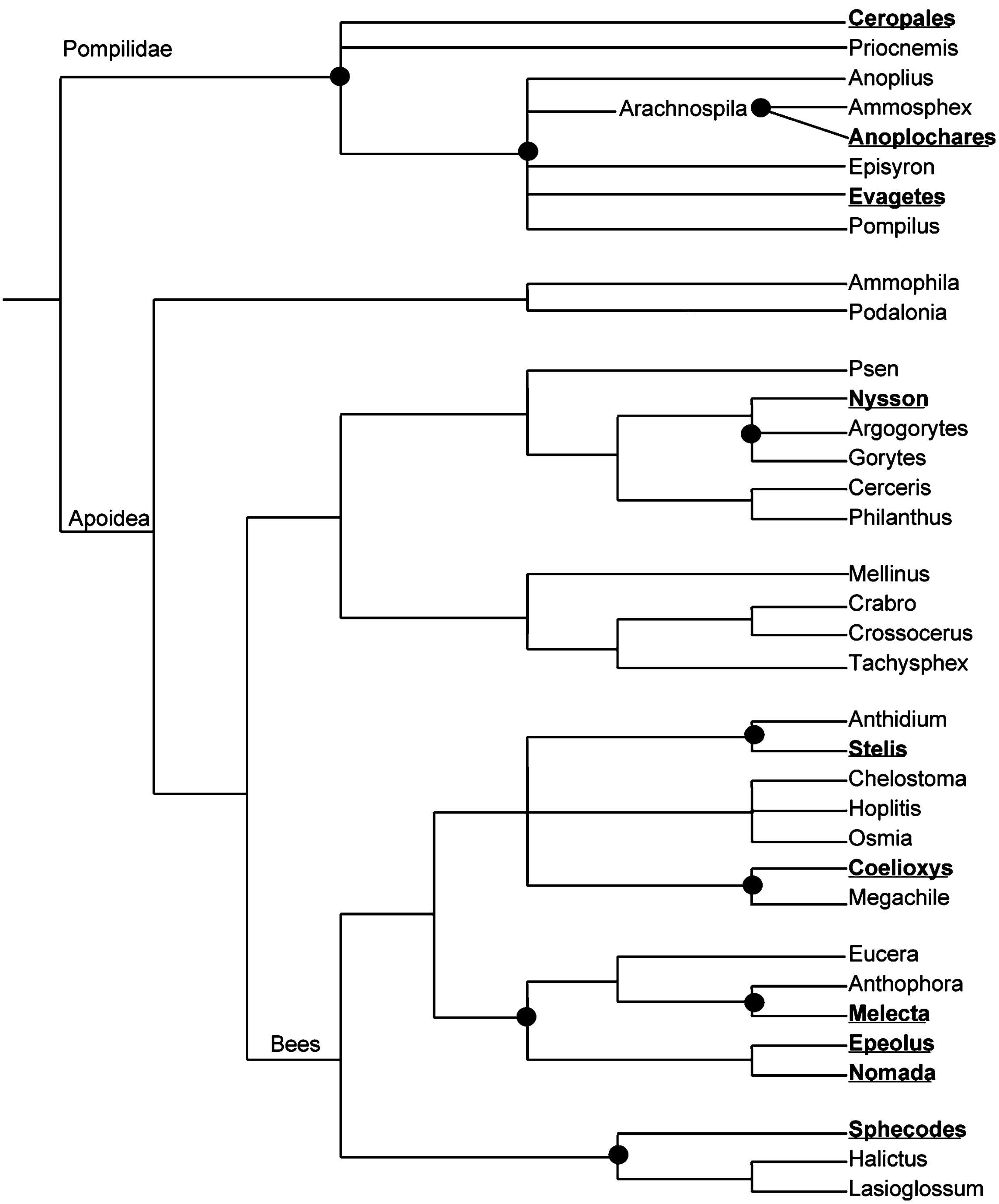

Fig. 1 Genus-level phylogeny used in our analyses. Monophyletic clades containing bees and pompilid wasps are indicated. We refer to taxa not in either of these clades as 'apoid wasps'. The names of non-provisioning taxa are *underlined*: all are cuckoo parasites except for the subgenus *Anoplochares*, which are parasitoids. The nine nodes at which independent contrasts were calculated in the BRUNCH analysis are indicated by *filled circles*. Branch lengths are arbitrary, chosen to maximize clarity

subfamilies, three of which are represented in our phylogeny (Fig. 1; Day 1988). Within each genus, species were coded as a single unresolved polytomy, except for the pompilid genus *Arachnospila*, which was split into its two subgenera. The two species in the subgenus *Anoplochares* are parasitoids, whereas the species in the subgenus *Ammosphex* are provisioners. The two *Anoplochares* are the only parasitoids included in our analysis: all other non-provisioners were cuckoo parasites. For this reason, we did not attempt to analyse cuckoo parasites and parasitoids separately. Equal branch lengths were assumed in all analyses.

As suggested by Purvis and Rambaut (1995b), we first used the CRUNCH procedure in CAIC to obtain a regression through the origin of contrasts in log(female size) on log(male size). We thus obtained a slope that was unbiased by the more species-rich taxa in the dataset. We then used this slope to calculate residuals from the line: the extent and direction in which each species differs from the average relationship. We next analyzed the residuals using the BRUNCH procedure in CAIC, to locate independent contrasts between pairs of non-provisioning and provisioning lineages. The null hypothesis is that provisioning and non-provisioning lineages do not differ in terms of sexual size dimorphism. In that case, the contrasts should have a mean of zero. We tested this using a one-sample *t* test. The output from CAIC includes tests of assumptions underlying analysis of independent contrasts (see Purvis and Rambaut 1995b): none of these assumptions was violated by any of our analyses.

Comparison between cavity nesters and species that construct nests de novo

Sexual size dimorphism in cavity nesters and non-cavity nesters was compared using methods similar to those above. Non-provisioners and pompilid wasps were omitted from this analysis—pompilids because published natural history data are insufficient to reliably determine whether they are cavity nesters. Cross-species comparisons involved regressing log(female size) on log(male size) with lifestyle, and whether each taxon nests in cavities, as possible explanatory factors. Independent contrasts between cavity-nesting and non-cavity-nesting taxa were calculated using residuals from a regression of contrasts in log(female size) on log(male size) for provisioning taxa only (excluding pompilids). Underlying assumptions were again not violated.

Sixteen of the 73 species included in this analysis were categorized as cavity nesters using information in Danks (1970), Richards (1980), Lomholdt (1984), Betts (1986), Edwards (1997–1998) and Edwards and Broad (2005–2006). These included species in the genera *Psen*, *Crossocerus*, *Anthidium*, *Chelostoma*, *Hoplitis*, *Megachile*, and *Osmia*. A further seven species were identified as only sometimes using cavities (genera *Crossocerus*, *Anthophora*, *Hoplitis*, *Megachile*). Analyses were carried out twice, with or without classing these seven species as cavity nesters.

Results

Comparison between provisioners and non-provisioners

Sexual size dimorphism (mean female size/mean male size) ranged from 0.93 to 1.46 (for *Anthidium manicatum* and *Priocnemis pusilla*, respectively) and was slightly left-skewed, with an overall geometric mean of 1.14 considering species as independent data points (Fig. 2). Female size was strongly correlated with male size across taxa (Fig 3). Considering species as independent data points, a simple allometric regression of log(female size) on log(male size) accounted for 95.9% of the total variance in log(female size). Sexual size dimorphism (female/male) was greater for provisioning species than for non-provisioners, regardless of overall body size: females of 29.3% of the 82 provisioning species had sizes below a common regression line of female on male size fitted to all species, compared with 87% of the 54 non-provisioners (Fig. 3). Using genus means in the regression instead of individual species, all ten non-provisioning genera fell below the regression line.

The full quantitative analysis included both lifestyle and parental care group as explanatory variables, as well as log (male size). The minimally adequate model, accounting for 98.5% of the variance in log(female size), had a common slope of 0.95 (F=0.79 with 5,124 *df* for removing all terms involving differences in slope; p=0.56) but a significant interaction between parental care group and lifestyle (F= 8.30; 2,129 *df*; $p<0.0001$ for the interaction between parental care group and lifestyle). The intercept was larger for provisioning than non-provisioning species in all three lifestyle groups, confirming that females are relatively larger in species that construct and provision nests (Figs. 3 and 4). The three lifestyle groupings differed in their extent

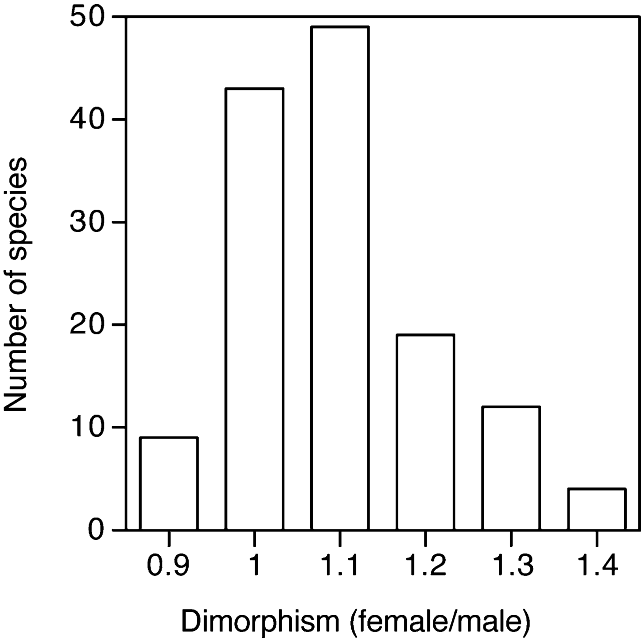

Fig. 2 Frequency distribution of untransformed sexual size dimorphism (mean female size/mean male size) for the 136 taxa included in the study

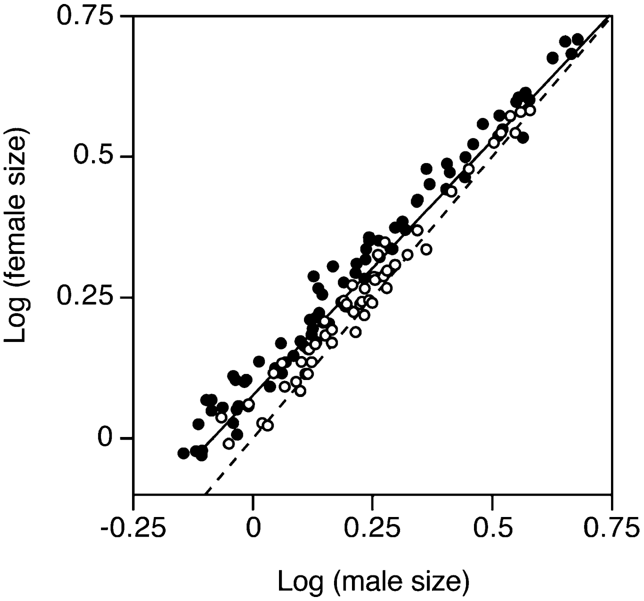

Fig. 3 The relationship between $\log_{10}$(male size) and $\log_{10}$(female size) for non-provisioning (*open circles*) and provisioning (*closed circles*) wasps and bees. The *solid line* is from a simple least-squares regression, and the *dashed line* represents the case where female size = male size

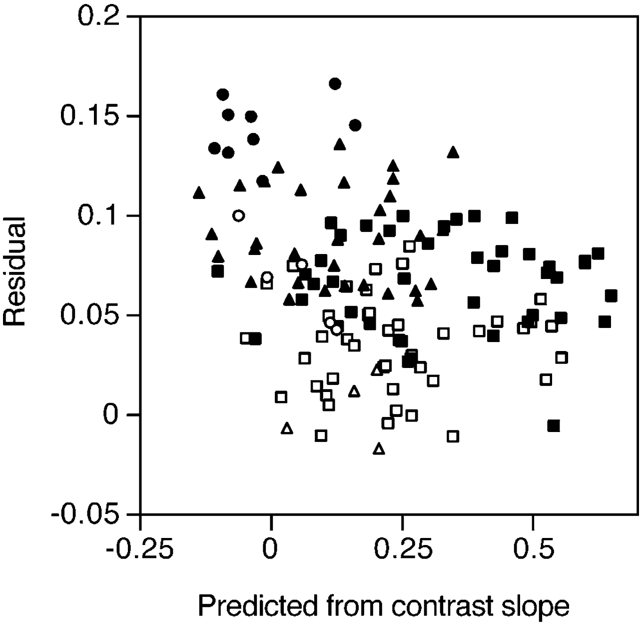

Fig. 5 Residuals for each species predicted from regression through the origin of contrasts in $\log_{10}$(female size) on $\log_{10}$(male size). *Open symbols* are non-provisioning taxa, *solid symbols* are provisioners. *Circles* are pompilids, *triangles* are apoid wasps, and *squares* are bees

of dimorphism, with pompilid wasps showing the most and bees the least (Figs. 4 and 5). The difference in dimorphism between provisioning and non-provisioning taxa was greater in pompilids and apoid wasps than in bees (Fig. 4).

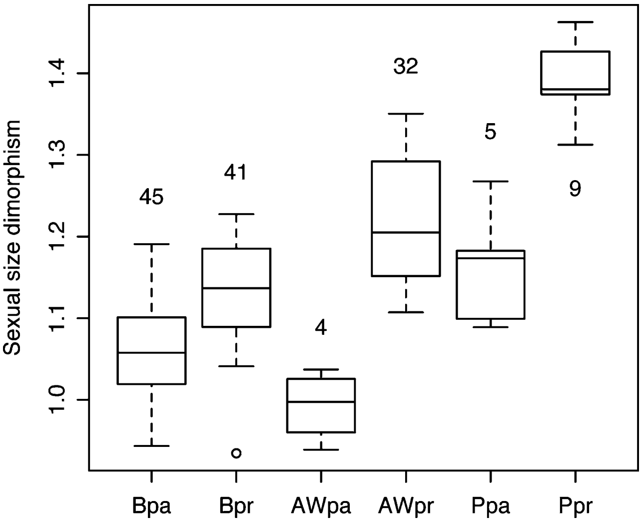

Fig. 4 *Box and whisker plots* illustrating untransformed sexual size dimorphism for non-provisioning and provisioning wasps and bees that have the three lifestyles included in our analysis. On the *x*-axis, *upper case letters* indicate lifestyles (*B* Bees, *AW* apoid wasps, *P* pompilid wasps) and *lower case letters* indicate parental care group (*pa* Non-provisioning taxa, *pr* provisioning taxa). Numbers are sample sizes (number of species)

Independent contrasts

In Fig. 5, the residuals for each species are plotted against the values predicted using the slope from the CRUNCH analysis of independent contrasts in log(female size) on log (male size). The data again show that non-provisioning taxa tend to have relatively smaller females than provisioners. Residuals are larger on the left of the graph because the apoid wasps and especially the pompilids in our analysis, which have the most female-biased sexual size dimorphisms, tend to be clustered there. The BRUNCH procedure identified nine independent contrasts in the residuals (see Fig. 1), which have an expected mean of zero under the null hypothesis. However, eight out of nine contrasts were negative, and a one-sample *t* test showed that the mean contrast was significantly less than zero ($t=-3.09$; $p=0.018$ with 7 *df*; 1 *df* used in estimating the regression line). Of the eight negative contrasts, all four involving wasps were more negative than all four involving bees. Nearly all of the non-provisioners in our analysis were cuckoo parasites, but results for the two included parasitoids fitted the same pattern: both exhibited less female-biased size dimorphism than either of the two provisioners in the same genus (*Arachnospila*). The single positive contrast, in which a provisioning lineage had less female-biased size dimorphism than a non-provisioning lineage, was the contrast between the provisioning bee *Anthidium* and the cuckoo-parasitic bee genus *Stelis* (Fig. 1).

The slope for the regression of log(female size) on log (male size) from the 55 contrasts produced by the CRUNCH procedure was 0.956, SE 0.027, very similar to that found when treating species as independent data points. The 95% confidence limits for the slope thus included 1.0 (0.90–1.01).

Comparison between cavity nesters and species that construct nests de novo

Using species as independent data points, there was a tendency for cavity-nesting taxa to have less female-biased sexual size dimorphism than non-cavity nesters. Females of 56% of the 23 species that always or sometimes use cavities had sizes below a common regression line of log(female size) on log(male size) fitted to all provisioning taxa (excluding pompilids), compared with 46% of the 50 non-cavity-nesting species. However, the significance of this difference depended on how the seven species that only sometimes use cavities were categorized. When they were categorized as cavity-nesting, the effect of cavity nesting was significant ($p=0.04$; lifestyle: $p=0.005$; log(male size): $p<0.0001$). When they were categorized as non-cavity-nesting, there was no effect of cavity nesting on dimorphism ($p=0.16$). Whichever way these seven species were categorized, the BRUNCH procedure identified six independent contrasts. Of these, four were negative, indicating that a cavity-nesting lineage had less female-biased dimorphism than a non-cavity-nesting lineage. In all analyses, however, the mean contrast did not differ significantly from zero ($p=0.99$ with 4 *df*).

Discussion

The main finding from our comparative analysis was that sexual size dimorphism is more female-biased in wasps and bees that construct and provision nests than in non-provisioning wasps and bees. This was the result from both simple cross-species comparisons, and after taking phylogeny into account. In addition, wasps are more size-dimorphic than bees, with pompilid wasps showing the greatest dimorphism and bees the least. The slope of the relationship between male and female size did not differ significantly from 1.0, suggesting that increases in mean body size are not being driven by selection for greater female size in particular.

A priori, we identified two reasons why provisioning taxa might have more female-biased size dimorphism than non-provisioning taxa. Our first hypothesis was that the physical requirements of transporting larval provisions could select for increased body size in females. Pompilid wasps provide a possible test of this hypothesis, as they differ from nearly all of the other taxa we analyzed in providing only a single prey item for each offspring. Their individual prey must therefore be extremely large relative to the size of the transporting mother (Day 1988; Field 1992c). We indeed found that pompilids have more female-biased size dimorphism than apoid wasps and bees and that the difference in dimorphism between provisioning and non-provisioning taxa is greatest in pompilids. However, it is possible that pompilids also differ from apoid wasps and bees in some other way that affects dimorphism. For example, they are the only taxa in our analysis that prey on spiders, which may be particularly difficult or even dangerous to subdue, perhaps leading to selection for larger size in females. In this context, it is noteworthy that females of the pompilid *Episyron rufipes* (L.) often fly with their prey rather than dragging it along the ground as most pompilids do (Day 1988; Field 1992c). Females of a second pompilid, *Pompilus cinereus* (F.), carry prey lifted partly off the ground (Bristowe 1948; J.F. personal observations). Flying with prey or lifting is likely to be more physiologically challenging than dragging it along the ground, and several taxa are known to drag large prey but fly with smaller ones (e.g., Kurczewski and Elliott 1978; Field 1992a). If the demands of prey transportation drive patterns of sexual size dimorphism, *E. rufipes* and *P. cinereus* might be expected to have particularly female-biased dimorphism. Indeed, they exhibit two of the three most female-biased size dimorphisms among the 14 pompilids in our analysis.

Sexual size dimorphism was least marked in the bees we analyzed, and bees also exhibited the smallest difference between provisioning and non-provisioning taxa. This may again be consistent with transport of provisions driving dimorphism: the individual items (pollen grains) carried by bees are very small, so that body size may be least constrained by transport costs in bees. The hypothesis that increased load size selects for sexual size dimorphism is supported by data from other taxa in which males carry females in nuptial flights (thynnine wasps and caddisflies: Evans 1969; Petersson 1995; O'Neill 2001). These species exhibit male-biased size dimorphism in comparison with related taxa. The female-biased size dimorphism in birds of prey, compared to the male bias more usually seen in birds, is more contentious. It was initially thought to result because larger females were better foragers (Wheeler and Greenwood 1983). More recently, however, improved foraging ability of smaller males has been implicated (Tornberg et al. 1999; Kruger 2005; Weimerskirch et al. 2006).

Our second hypothesis for why provisioning taxa have more female-biased size dimorphism than non-provisioners was the effort required for nest construction. Nest construction often involves physically demanding activities such as digging or transporting nesting materials, but it is only females of provisioning taxa that construct nests. Consistent with this hypothesis, we found that cavity-nesting taxa, in which nest construction costs may be minimized, tend to have less female-biased size dimorphism than non-cavity nesters. However, this effect was not significant after controlling for phylogeny and was significant in simple cross-species comparisons only if taxa that do not always use cavities were categorized as cavity-nesting. We would need a larger dataset, including more unequivocal cavity nesters, to definitively isolate the effect of nest construction on dimorphism. Published natural history data are often imprecise, so that it is unclear whether a species uses preexisting cavities in dead wood/plant stems, or constructs cavities itself. There may also be genuine intraspecific variation. Furthermore, even preexisting cavities may have to be cleaned out and prepared before nesting, so that the extent to which cavity nesting reduces the demands of nest construction is unclear.

Sexual size dimorphism depends on the balance between factors promoting increased male size as opposed to those promoting increased female size. Competition between males for females is known to result in male-biased size dimorphism in mammals (e.g., Clutton-Brock et al. 1977; Lindenfors et al. 2002). If the mating systems of cuckoo parasites differed systematically from those of their hosts, such that cuckoo parasites experienced greater male–male competition, this could account for the less female-biased size dimorphism in parasitic taxa. However, there is no evidence or logical reason why this should be the case (see reviews in Alcock et al. 1978; O'Neill 2001). Each parasitized host cell produces only a single parasite adult, and males of parasitic taxa must search for females which have emerged from the nests of their provisioning hosts, so that female dispersion should not differ greatly between the two parental care groups. Nevertheless, male–male competition probably explains the single contrast in our analysis in which a provisioning lineage (*Anthidium manicatum*) exhibited less female-biased size dimorphism than a parasitic lineage (*Stelis*). *A. manicatum* is unusual among wasps and bees in that males are strongly territorial, defending areas that contain female foodplants. This leads to frequent fights, with territory owners tending to be larger than nonowners, and larger males tending to win territorial contests (Severinghaus et al. 1981).

In conclusion, our results imply that the demands of transporting provisions, and perhaps also the demands of nest construction, have led to selection for larger body size, so that provisioning wasps and bees have more female-biased size dimorphism than do non-provisioners. This apparently outweighs any selection that could operate in the opposite direction, for example, if non-provisioners must carry more eggs than provisioners, or if they are more often involved in agonistic interactions with their hosts. There may, however, be other factors contributing to the observed pattern. Thus, the difference between the sexes in the relationship between provision weight and resulting adult weight could differ between parasitic and provisioning taxa. For example, female cuckoo parasites might allocate more resources to cuticle thickness and fewer resources to body size than do female provisioners. There may also be differences between taxa in the precise allometric relationship between thorax width and body mass. This would imply caution in comparing groups with different body shapes, such as bees and pompilid wasps (Fig. 4), but should not invalidate comparisons of more closely related taxa, as in our analysis controlling for phylogeny. Nearly all of the non-provisioners in our study are cuckoo parasites of provisioners, so that the larvae of both groups feed on similar distributions of provision masses. At a mechanistic level, cuckoo parasites could achieve a less female-biased mean dimorphism than their hosts through having a lower threshold provision mass above which female eggs are laid: hymenopteran females have direct control over offspring sex.

Comparisons of sexual size dimorphism between appropriate groups of taxa could provide an indirect measure of the extent to which different forms of parental care select for increased body size. To the extent that increased body size reflects increasingly costly parental care, such exploratory analyses might also suggest taxa in which more time-consuming direct measurement of parental care costs, using experimental manipulations, would be particularly rewarding (e.g., Tallamy and Denno 1982; Agrawal et al. 2005; Field et al. 2007).

Acknowledgements This work complies with current UK laws. We thank Nick Isaac for advise on using CAIC.

Appendix

Table 1 Summary of dimorphism data for provisioning and non-provisioning taxa included in the study

Family/subfamily	Provisioners	F/M	SE (*n*)	Non-provisioners	F/M	SE (*n*)
Pompilid wasps	Total	1.40	0.018 (5)		1.11	0.016 (2)
Pepsinae	*Priocnemis*	1.38	0.031 (4)	–		–
Pompilinae	*Arachnospila*	1.39	0.009 (2)	*Arachnospila*	1.14	0.044 (2)
	Anoplius	1.38	– (1)	*Evagetes*	1.22	0.047 (2)
	Episyron	1.45	– (1)	–		
	Pompilus	1.43	– (1)	–		
Ceropalinae	–	–	–	*Ceropales*	1.10	– (1)
Apoid wasps	Total	1.23	0.019 (11)		0.99	– (1)
Sphecidae	*Ammophila*	1.17	0.028 (2)	–		
	Podalonia	1.28	0.022 (2)	–		
Crabronidae						
Crabroninae	*Tachysphex*	1.32	0.009 (2)	–		
	Crabro	1.20	0.048 (3)	–		
	Crossocerus	1.22	0.021 (7)	–		
	Mellinus	1.32	0.030 (2)	–		
Pemphredoninae	*Psen*	1.20	0.039 (4)	–		
Bembecinae	*Argogorytes*	1.20	0.002 (2)	*Nysson*	0.99	0.020 (4)
	Gorytes	1.15	0.031 (3)	–		
Philanthinae	*Cerceris*	1.20	0.038 (4)	–		
	Philanthus	1.31	– (1)	–		
Bees	Total	1.10	0.026 (9)	–	1.05	0.008 (6)
Halictidae	*Halictus*	1.17	0.028 (3)	*Sphecodes*	1.09	0.018 (13)
	Lasioglossum	1.18	0.013 (12)	–		
Megachilidae	*Anthidium*	0.93	– (1)	*Coelioxys*	1.03	0.017 (5)
	Chelostoma	1.09	0.003 (2)	*Stelis*	1.05	0.008 (3)
	Hoplitis	1.05	0.012 (2)	–		
	Megachile	1.11	0.012 (7)	–		
	Osmia	1.17	0.015 (8)	–		
Apidae	*Anthophora*	1.06	0.004 (5)	*Epeolus*	1.04	0.036 (2)
	Eucera	1.11	– (1)	*Melecta*	1.06	0.004 (2)
	–	–	–	*Nomada*	1.05	0.015 (20)

For each genus, the average sexual size dimorphism (F/M) is given together with the standard error (SE) and sample size (*n*: number of species). The total for each lifestyle (pompilid wasps, apoid wasps, bees) is the mean across the included genera. Family and subfamily names are taken from Day (1988), Melo (1999), and Danforth et al. (2006). All of the non-provisioners are cuckoo parasites except for the parasitoids in the genus *Arachnospila*.

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