

Sex-biased parental care and sexual size dimorphism in a provisioning arthropod

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Abstract

The diverse selection pressures driving the evolution of sexual size dimorphism (SSD) have long been debated. While the balance between fecundity- and sexual selection has received much attention, explanations based on sex-specific ecology have proven harder to test. In ectotherms, females are typically larger than males, and this is frequently thought to be because size constrains female fecundity more than it constrains male mating success. However, SSD could additionally reflect maternal care strategies. Under this hypothesis, females are relatively larger where reproduction requires greater maximum maternal effort – for example where mothers transport heavy provisions to nests.

To test this hypothesis we focussed on digger wasps (Hymenoptera: Ammophilini), a relatively homogeneous group in which only females provision offspring. In some species, a single large prey item, up to 10 times the mother's weight, must be carried to each burrow on foot; other species provide many small prey, each flown individually to the nest.

We found more pronounced female-biased SSD in species where females carry single, heavy prey. More generally, SSD was negatively correlated with numbers of prey provided per offspring. Females provisioning multiple small items had longer wings and thoraxes, probably because smaller prey are carried in flight.

Despite much theorising, few empirical studies have tested how sex-biased parental care can affect SSD. Our study reveals that such costs can be associated with the evolution of dimorphism, and this should be investigated in other clades where parental care costs differ between sexes and species.

Keywords: Sexual dimorphism, Parental care, Hymenoptera, Wasps

Introduction

Sexual dimorphism is ubiquitous. Males and females normally use different strategies to optimize their fitnesses, and therefore differ in their optimum trait values. Dimorphism is therefore expected to evolve, although it may be constrained by genetic correlations between the sexes (Lande 1980; Chippendale et al. 2001). One of the most obvious examples of dimorphism is sexual size dimorphism (SSD). In birds and mammals, SSD is commonly male-biased, whereas in invertebrates and other ectotherms, it is females that are typically larger than males (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). Whether SSD is male- or female-biased is thought to result from (1) differences in sex-specific patterns of sexual selection, typically on males, versus fecundity selection, typically on females (Fairbairn et al 2007); and (2) sex-specific ecological selection pressures, such as intersexual competition for resources (e.g. Ralls 1976; Herrel et al 1999) or differences in the reproductive roles of the two sexes (e.g. Myers 1978). The latter hypothesis, concerning sex-specific reproductive roles, is known as the dimorphic niche hypothesis (Ralls 1976; Shine 1989; reviewed in Hedrick & Temeles 1989). The relative importance of the different explanations for variation in SSD remains unclear (e.g. Ralls 1976; Hedrick & Temeles 1989; Shine 1989; Nylin and Wedell 1994; Blanckenhorn 2005; Cox 2006; del Castillo & Fairbairn 2011). Unambiguous evidence for ecological factors affecting size dimorphism are mainly confined to within-species studies of feeding morphology (Temeles et al 2008, but see Reimchen & Nosil 2004), while broad comparative studies often make it difficult to disentangle the effects of

diverse reproductive traits (e.g. Han & Fu 2013, but see Stephens & Wiens 2009).

In arthropods, females are usually larger than males, although the extent of SSD varies, and a minority of taxa exhibit male biased SSD (Andersson 1994; Fairbairn et al 2007; Stillwell et al 2010). One possible explanation for the prevalence of female-biased SSD in arthropods is based on patterns of sexual- versus fecundity selection as outlined above. Specifically, the inflexibility of the arthropod exoskeleton will limit female ovary size and egg number (Stearns 1977), suggesting that dimorphism may result from stronger effects of body size on female fecundity than on the mating success of males (Ralls 1976; Head 1995). Others have instead argued that patterns of sexual selection on males alone may drive both male- and female-biased SSD (Fairbairn and Preziosi 1994; see also Preziosi & Fairbairn 2000). In this paper, however, we focus on an ecological explanation for variation in SSD in line with the dimorphic niche hypothesis: variation in the costs of maternal care. Parental care is well known to be extremely costly in arthropods (e.g. Hunt et al 2002), and is nearly always carried out by females only (Costa 2006; Trumbo 2012; Gilbert & Manica 2015). Care involves diverse behaviours such as constructing nests; gathering and defending resources; and transporting, provisioning and defending offspring (Hinton 1981; Choe & Crespi 1997; Costa 2006). Larger individuals are likely to have an advantage in carrying out many of these behaviours. Our hypothesis is that females should be relatively larger where reproduction requires periods of greater maximum size-dependent effort. Size-dependent effort might select for larger females where larger females experience reduced costs when building nests (e.g. gathering and packing breeding resources such as dung masses; Hunt et al 2002) or when defending offspring or nesting resources against larger or

physically stronger enemies (e.g., Goubault et al. 2007). The specific hypothesis we focus on, however, is that females should be relatively larger when they have to transport all of the food that an offspring will require in a single load, such that the maximum effort required is relatively high. Females should be progressively smaller as they are able to divide food into multiple, smaller loads that each require less effort.

Shreeves and Field (2008) used a comparative analysis to show that, in wasps and bees, where only females provide parental care, the degree of dimorphism is correlated with parental care strategies. Provisioning taxa, in which females must construct and provision nests, showed consistently more female-biased size dimorphism than cuckoo-parasitic taxa, in which females do not provision, but instead oviposit in the nests of provisioning taxa. Shreeves and Field (2008) suggested two possible explanations for this pattern. The first was that if nest construction is physically demanding (e.g. digging a burrow in hard soil), there might be selection for increased female size in provisioning taxa compared with cuckoo parasites, which do not construct nests. In support of this explanation, those provisioning taxa in which construction costs may be minimized, because females nest in pre-existing cavities, tended to have less female-biased SSD than taxa where females construct their own nests. This pattern was not significant, however, after controlling for phylogeny, although the sample size available was small.

The second explanation, which could operate simultaneously with the first, was that the demands of transporting provisions to the nest select for larger size (see also Coelho 1997). This would again result in more female-biased dimorphism in provisioners than cuckoo parasites, since only females transport provisions. In support of this idea, Shreeves and Field (2008) found that pompilid wasps, which provision each offspring with a single relatively large prey item, exhibited more female-biased size

dimorphism than apoid wasps, in which each offspring is usually provided with several smaller items that are carried individually to the nest so that the maximum level of effort required is presumably smaller. Bees, in which provisions are tiny pollen grains, showed the least dimorphism. There are, however, other explanations for these results (Shreeves and Field 2008). For example, pompilids were also the only taxa in the analysis that prey exclusively on spiders. Spiders are normally larger than the female wasp, and may be particularly dangerous and difficult to hunt, potentially providing an alternative explanation for larger female size in pompilids. In this paper, we carry out a better controlled test of the hypothesis that SSD is correlated with the costs of transporting provisions, by examining a single, monophyletic lineage of provisioners in which provision weight varies interspecifically. We thus provide a rare comparative test of the dimorphic niche hypothesis.

Ammophiline digger wasps (Apoidea: Sphecidae, Ammophilini) are particularly well suited to a test of the dimorphic niche hypothesis. There is a recently derived molecular phylogeny for ammophilines (Field *et al.* 2011), and in one species that provides multiple prey items per offspring, experimental fieldwork has shown that provisioning is costly in terms of lifetime reproductive success (Field *et al.* 2007). Furthermore, whilst most of the species' ecology is largely similar across the tribe, there is considerable interspecific variation in the likely maximum costs involved in transporting offspring food. Some ammophilines provision each offspring with only a single, large prey item, which can be 10 times the weight of the transporting female parent (e.g. Weaving 1989a; Field, 1992a, 1993). In contrast, other species provide each offspring with up to ten or more individually smaller prey, which are carried to the nest one at a time (e.g. Kazenas 1971; Weaving 1989a; Field *et al.* 2007). Detailed studies of individual species suggest that providing offspring with

multiple prey (1) gives mothers finer control over offspring size but (2) may lead to more prey theft from nests by conspecifics (Field 1992a) and (3) may or may not influence the frequency of natural enemy parasitism (Rosenheim 1989; Field 1992a). Here, we carry out a phylogenetically-controlled test of the hypothesis that provisioning with individually larger prey requires greater maximum size-dependent effort and therefore selects for more female-biased SSD.

Natural history of ammophiline wasps

Ammophilines exhibit little interspecific variation in terms of gross morphology: they are relatively large wasps with long thin abdomens. While prey size varies interspecifically, ammophilines are otherwise also relatively homogeneous ecologically. Nests of all species are short burrows dug in the ground, each containing a single offspring. The wasp larva feeds on the prey provided by its mother, then pupates in the nest. Detailed studies of individually marked *A. pubescens* (J. Field & W.A. Foster, in prep.) and *A. sabulosa* (Field 1992a) show that long-lived females may provision 10-20 different offspring in their lives. A few species are progressive provisioners, and maintain more than one nest simultaneously (including 4 species in this study: *E. dives* and *Ammophila azteca*, *pubescens* and *rubiginosa*). In nearly all taxa, prey are lepidopteran caterpillars which are paralysed by the mother's sting, an exception being *Eremochares dives* which preys on immature Orthoptera (Kazenas 1971). Most species appear to be generalists in terms of prey species (e.g. Evans 1959; Weaving 1988; Field 1992b). Although male mating tactics have been little studied, there is no evidence of major variation, such as male territoriality, that could affect optimal male size.

Aside from prey size, one source of variation that could conceivably influence optimum female size and hence sexual dimorphism in ammophilines is variation in the method of prey carriage and its effect upon transport costs (e.g. Marden 1987, Lighton et al. 1993). In ammophilines that provide each offspring with a single large prey item, mothers carry their prey to the nest on foot, held off the ground using their mandibles and fore-legs. In contrast, species that provide several smaller prey per offspring typically fly with their prey, and in species in which prey size varies, females often carry large prey on foot, intermediate prey in short hopping flights, and small prey in longer flights (e.g. Field 1992a; see also Table 1 in Powell 1964). The relative costs of carriage in flight versus carriage on foot are not known, but flight is likely to be costlier for a given prey size. If so, species that fly with prey would be expected to be more dimorphic, acting against our main hypothesis and making this study a conservative test of our main prediction.

Methods

Data collection

We obtained data for as many ammophilines as possible for which there are published prey size data, among the 40 species included in the molecular phylogeny of Field et al. (2011). Absolute prey size is rarely reported in the literature, but a sample of nests is typically opened and the number of prey provided per offspring recorded. Since most species provision the full complement of prey before their egg even hatches, all prey are available to be counted at the same time. The prey provided to a larva constitute the only food available to it before adulthood, so that there is likely to be a strong correlation between total provision weight

and resulting adult offspring weight (e.g. Field 1992a; J. Field, unpubl data). The number of prey per offspring (PPO) thus provides an estimate of prey size relative to female size which is ideal for our purposes: the more prey per offspring, the relatively smaller the prey must be. Indeed, this relationship is observed intraspecifically in *A. sabulosa*: total prey weight provided to offspring was constant across nests, because of a strongly inverse relationship between prey number and individual prey size (Field 1992a; studies of non-ammophiline wasps that report similar relationships are referenced therein). In the literature, only the observed PPO range across the nests in a population is reported for every species, and we therefore used the midpoint of this range ($(\text{maximum PO} + \text{minimum PPO})/2$: see Table 1).

Morphometric data came from specimens loaned from museums, the first author's own collections, and from samples kindly sent by private collectors and by the authors of published studies that report PPO. Three measurements were taken from each specimen. The first was thorax length, estimated as the length of the scutum excluding the extended posterior lip that occurs in some species. The second measurement was right forewing length, estimated as the distance between (1) the inner edge of the wing veins forming the proximal corner of submarginal cell 1 and (2) the inner edge of the wing veins forming the distal corner of the marginal cell. Thorax and wing terminology refer to Bohart and Menke (1976, Figures 2a and 5). These two metrics were chosen because they could be located in all species, and because they relate to a female's ability to fly with a load. Longer wings, and a larger thorax allowing a larger flight muscle mass, should both allow more lift to be generated (Marden 1987). Measurements were made to the nearest 0.05mm using a Leica MZ6 binocular microscope equipped with an eyepiece graticule.

Our third metric, intended to reflect overall body size, was dry weight. Pinned specimens were dried by placing them in an oven at 70°C for 48 hours, preliminary studies having shown that dry weight did not change detectably after 24 hours. After 48 hours, each specimen was removed from the oven and immediately weighed, including the pin, on a Sartorius balance to 0.0001g. The specimen was then relaxed so that it was no longer brittle, by keeping it in a humid atmosphere overnight. After relaxing, it was carefully removed from its pin, and the pin alone weighed after drying. Specimen dry weight was obtained by subtracting pin weight from the combined weight of pin+wasp. Specimens were then repinned intact. Preliminary work suggested that the relationship between dry weight and thorax or wing length might be altered in the minority of specimens that had been stored in alcohol, and we therefore did not weigh these. For this reason, and because we did not want to risk damaging old museum specimens by removing them from their pins (Gilbert 2011), the sample size for dry weight was often smaller than for thorax or wing length.

The same person carried out all measurements for a given metric, and measurement error, estimated by blind re-measurement of a sample of 25 specimens, was 1.3%, 0.7%, and 2.7% for thorax, wing and weight, respectively. Table 1 summarizes the data sources.

Statistical analysis

A species was included in the analysis only if at least five specimens of each sex were available for each of the three morphometrics. This allowed 21 species to be included, from five genera: *Ammophila* (16 species), *Podalonia* (2 species), *Eremnophila* (one species), *Eremochares*

(one species) and *Hoplammophila* (one species) (Table 1). All morphological variables were log₁₀-transformed before analysis. For a given total weight of prey provided to an offspring, the weight of individual prey should be proportional to 1/n, where n is the number of prey provided. If female weight is proportional to individual prey weight according to our hypothesis, the expected relationship between PPO and female weight or weight dimorphism would be exponential, but linearized by log transformation.

To analyse the data incorporating evolutionary relationships, we used Phylogenetic Generalised Least Squares (PGLS) models fitted using the R package caper (Orme et al 2012) and using the phylogeny given in Field et al (2011). For example, to test whether PPO was correlated with sexual dimorphism, the dependent variable was log(mean female weight), with log(mean male weight), PPO, and their interaction as potential explanatory variables (e.g. Ranta et al. 1994; Shreeves and Field 2008). We used a reverse stepwise procedure to test the significance of each model term, using likelihood ratio tests (distributed as chi-squared) as a criterion for model selection.

Results

Sexual size dimorphism and relative prey size

The phylogeny used in this study, along with extant character states used in our analyses and their reconstructed ancestral states, are given in Fig. 1. Across species, the weights of the two sexes were strongly correlated, with females always heavier than males. When we treated PPO as a binary variable (i.e. single vs. multiple prey items), species provisioning

single, relatively large prey items had significantly heavier females for a given male weight than did species provisioning multiple, relatively smaller prey items (PGLS, dropping “PPO”, LR=10.81, df=1, p=0.001; Fig. 2). Multiple prey items did not affect the slope of the relationship between female and male weight (dropping the “PPO x male weight” interaction, LR=2.18, df=1, p=0.139; Fig. 2).

Treated as a scalar count variable, PPO was also negatively associated with female weight even after accounting for male weight (PGLS, LR=6.77, df=1, p=0.009), but again was not associated with the slope of the relationship between male and female weight (PGLS, dropping the “PPO x male weight” interaction, LR=1.92, df=1, p=0.166).

Sexual size dimorphism (untransformed female weight/male weight) based on dry weight varied from 1.18 to 2.96 among the 21 species included in the analysis. Using this ratio as a response variable, “dimorphism”, there was a negative relationship between dimorphism and PPO: species that capture relatively fewer prey were more dimorphic (PGLS, LR=5.10, df=1, p=0.023; Fig. 3). Note that residuals for this model were slightly non-normal owing to two outliers (*A. wrightii*, *P. affinis*); removing these outliers to normalize residuals had no qualitative effect on the result (PGLS, outliers removed: n=19, LR=4.56, df=1, p=0.033).

Wing and thorax length

After accounting for dry weight, females of species that capture relatively small prey (high PPO) had relatively long wings and thoraxes (PGLS; wing: LR=8.85, df=1, p=0.003; thorax: LR=14.22, df=1, p<0.001; Fig 4a,

362 b). There was no interaction between PPO and dry weight in either case
363 (PGLS, both NS). For males, PPO was associated with neither wing nor
364 thorax length (PGLS; wing: LR=0.60, df=1, p=0.438; thorax: LR=1.89,
365 df=1, p=0.168; Fig. 4c, d).

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Discussion

Our findings are consistent with the dimorphic niche hypothesis, which states that sex-specific ecological selection pressures drive patterns of SSD (Ralls 1976). Only female digger wasps provision offspring, and in species with relatively larger prey which presumably each require more effort to handle and transport, we found that females are relatively larger compared with conspecific males. These results are in turn consistent with Shreeves & Field's (2008) suggestion that the demands of female parental care might explain why provisioning taxa in general have more female-biased SSD than non-provisioning taxa such as cuckoo parasites. Shreeves & Field (2008) provided some evidence in support of their idea, but could not completely discount competing explanations based on other potential differences between provisioning and non-provisioning taxa. Most of these differences are avoided in the present analysis, where we have focused on a single, relatively homogeneous lineage. We now consider factors other than prey size that could potentially influence SSD in ammophilines, then discuss evidence that the demands of parental care influence dimorphism in other taxa.

The correlation we have found between relative prey size and SSD does not indicate direction of causation. It is possible that variation in factors other than prey size drives SSD, and that SSD in turn drives prey size selection. However, while differences in the physical demands of prey carriage are unlikely to be the sole ecological factor driving interspecific variation in ammophiline SSD, there is currently little evidence for significant variation in other factors. Such factors might include differences in fecundity, differences in the demands of nest construction and prey capture, and the possibility that females of some species are more likely to fight over burrows and prey, perhaps depending

on female density (e.g. Parker et al. 1980). Differences in the hardness of the nesting substrate could be important if they affect the demands of nest construction. However, most ammophilines nest in relatively soft, sandy soil, although at least one species not included in our analyses uses harder substrates (Weaving 1989b). Interestingly, SSD appeared to be more variable among species that provide only a single large prey item per offspring than among species that provide several small prey (Fig. 3). This might partly be because species that provide only a single large prey item have less fine control over offspring size, which will depend largely on the size of the single prey (Field 1992a). In addition, however, the species in our analysis that provide only a single prey item come from four different genera, whereas 9 of the 10 multiple-prey species are from the same genus (Table 1): differences in dimorphism may thus partly reflect common ancestry, although we have to an extent controlled for this by using phylogenetic analysis.

Our findings concerning wing and thorax morphology provide further evidence that relative prey size influences sexual dimorphism. We found that ammophiline species capturing relatively smaller prey that are more likely to be carried in flight had longer wings and thoraxes for their body weights than species that capture relatively large prey carried on foot. These relationships were significant only for females, the prey-carrying sex. Longer wings, and a larger thorax allowing larger flight muscles, are both potential correlates of a greater load-carrying ability while flying. Marden (1987) found that body mass, flight muscle mass and wing size were all strongly positively correlated with maximum experimentally liftable weight across a range of taxa, but that flight muscle mass explained the most variation after controlling for body mass. Our findings also suggest that the frequency of prey carriage in flight, rather than the relative size of the individual prey carried, drives these

aspects of body shape: species with relatively smaller prey more often carry prey in flight, but the individual prey themselves are smaller in comparison with body weight. The costs of carrying a given weight of prey in flight versus on foot remain unquantified, but our results suggest that thorax and wing length may not always be ideal surrogates for overall body weight in morphometric analyses.

Mating systems are not known to vary among ammophiline species, although male behaviour has been little studied. Mating involves the male sitting astride the female, grasping her around the neck with his mandibles while contacting the tip of her abdomen with the genitalia at the tip of his own abdomen (J. Field, pers. obs.). The range of female sizes that is available as potential mates may therefore depend on a male's own body length; a shorter male might be unable to simultaneously grasp and mate with a larger female. It is therefore not surprising that body sizes of the two sexes are strongly correlated (Fig. 2), and it would be interesting to know whether males are longer and thinner in taxa where females are relatively large compared with males.

Although within-clade comparative tests are rare, evidence from a variety of taxa is consistent with the idea that the physical demands of carrying heavy loads can drive SSD. For example, male-biased size dimorphism is observed in several taxa where males carry females in nuptial flights (e.g. thynnine wasps, caddisflies: Evans 1969; Petersson 1995; O'Neill 2001). In terms of parental care, male belostomatine bugs exhibit sex role reversal, with the male providing parental care via back-brooding. Accordingly belostomatines also display male-biased size dimorphism, reflecting the demands of carrying and aerating the eggs (Iglesias et al 2012). In vespertilionid bats, females carry embryos weighing up to 30% of their own body weight, and also transport young after birth. As expected, Myers (1978) found that SSD was greater in

species where a greater total weight of young is carried. Less clear-cut is the female-biased size dimorphism in birds of prey, which contrasts with the male-biased dimorphism typical for birds in general. Selection on foraging ability was initially thought to favour larger female birds of prey (Wheeler and Greenwood 1983), but in fact may instead select for smaller males according to more recent studies (Tornberg et al. 1999; Krüger 2005; Weimerskirch et al. 2006). However, in hawk owls (*Ninox* spp.), some species show a reversed pattern in which males are larger. In these species, breeding males show “prey-holding behaviour” whereby males capture and hold a single large prey item for a whole day without consuming it, a behaviour that has been implicated in selection for large male size (Pavey 2008).

Although the demands of parental care have the potential to drive patterns of sexual dimorphism in provisioning taxa, this may depend on mothers being able to determine offspring sex directly, so that the sex that cares for offspring can be provided with more food during development. Hymenopteran females do indeed have direct control over the sex of individual offspring. Mechanistically, a more female-biased size dimorphism in taxa that capture larger prey is presumably achieved through mothers having a higher threshold total provision weight above which they lay female eggs. In both scarabaeid and silphid beetles, male involvement in nest-building and parental care varies among species (Halffter et al 1997, Costa 2006). As a hypothesis for future study, the relative disparity between male and female parental effort might also be predicted to affect size dimorphism in these taxa. Indeed, some scarabaeines provision their offspring in discrete chambers analogous to the cells of ammophilines (e.g. Monteith & Storey 1981; Edwards & Aschenborn 1989; Favila 1993; Halffter 1997). However, direct control

483 of offspring sex may be absent in scarabaeines, potentially constraining
484 the evolution of sexual size dimorphism.

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486 Compliance with ethical standards

487

488 The authors declare that they have no conflict of interest. This article
489 does not contain any studies with human participants or animals
490 performed by any of the authors.

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Figure captions

Fig. 1 Phylogeny of ammophiline digger wasps used in this study, showing both extant and reconstructed ancestral states for the continuous variables sexual size dimorphism (SSD; female weight/male weight) and number of prey per offspring (PPO; midpoint value). Both SSD and PPO values have been scaled from 0 to 1 to represent the minimum and maximum in the dataset, respectively. Maximum likelihood ancestral state reconstruction was carried out using the `ace()` function in the `ape` package in R (Paradis et al 2004)

Fig. 2 The relationship between \log_{10} (male weight) and \log_{10} (female weight) for 21 species of ammophiline wasps. Open circles and dashed line represent species that invariably provide one large prey item per offspring (PPO=1), while filled circles and solid line represent species that sometimes or always use more than one smaller prey item per offspring (PPO>1). Dotted line represents the case where female size = male size

Fig. 3 The relationship between the number of prey provided per offspring and untransformed sexual weight dimorphism, i.e. mean female weight/mean male weight, for 21 species of ammophiline wasps. Lines are from PGLS regression

Fig. 4 Relationship between the number of prey provided per offspring by 21 species of ammophilines and residuals from regression of either (a, c) \log_{10} (wing length) on \log_{10} (dry weight) or (b, d) \log_{10} (thorax length) on \log_{10} (dry weight). (a) and (b) are for females (F) only, while (c) and (d)

743 are for males (M) only. Best-fitting PGLS regression lines are shown
744 when the relationship was statistically significant

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