

Body size, host choice and sex allocation in a spider-hunting pompilid wasp

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Two important relationships in parasitoid evolutionary ecology are those between adult size and fitness and between host quality and sex ratio. Sexually differential size–fitness relationships underlie predicted sex-ratio relationships. Despite each relationship receiving considerable attention, they have seldom been studied simultaneously or using field data. Here we report the biology of *Anoplius viaticus paganus* Dahlbom, a little known parasitoid of spiders, using field and laboratory data. We found that larger foraging females were able to select larger host spiders from the field, thus identifying a relatively novel component of the size–fitness relationship. Larger offspring developed from larger hosts and, in agreement with the prediction of the host quality model of sex allocation, were generally female. Data on the size–fitness relationship for males are lacking and, in common with many prior studies, we could not evaluate sexually differential size–fitness relationships as an explanation for the observed sex-ratio patterns. Nonetheless, *A. v. paganus* exhibited one of the strongest relationships between host size and offspring sex ratio yet reported. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, 87, 285–296.

ADDITIONAL KEYWORDS: *Anoplius* – field data – host size – sex ratio – size–fitness relationship.

INTRODUCTION

The relationship between adult body size and evolutionary fitness is one of the most fundamental for the understanding of the evolution of behavioural and life-history traits of a wide range of organisms. Parasitoid wasps are no exception, with this relationship predicted to underlie important reproductive decisions such as host selection, sex allocation and clutch size (e.g. van den Assem, van Iersel & Los-den Hartogh, 1989; Heinz, 1991; King, 1993; Godfray, 1994; Visser, 1994; Mesterton-Gibbons & Hardy, 2004). There are several pervading problems with assessing this relationship, however. One is that body size may influence many components of fitness, such as potential or realized fecundity, longevity, dispersal ability, host-finding

and host-handling ability, mate-finding and mating ability and contest ability (e.g. Lawrence, 1981; Godfray, 1994; King & King, 1994; King & Lee, 1994; Visser, 1994; Antolin, Ode & Strand, 1995; Kazmer & Luck, 1995; Petersen & Hardy, 1996; Ellers, van Alphen & Sevenster, 1998; Zaviezo & Mills, 2000). For a given study species, it is usually difficult to evaluate all of these components and thus to attain a full understanding of what makes up the size–fitness relationship. The majority of studies have been limited to studying how fecundity and/or longevity are related to body size (reviewed by King, 1987; Godfray, 1994; Visser, 1994). The consideration of initially unevaluated fitness components has the potential not only to change the estimated form, strength or direction of the relationship but also to alter greatly the way that reproductive decisions are understood. For instance, the demonstration of a size-related advantage in dyadic contests between female parasitoids changed the view of maternal clutch size decisions from one of

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static optimization (Hardy, Griffiths & Godfray, 1992) to a more complex game-theoretic problem (Petersen & Hardy, 1996; Mesterton-Gibbons & Hardy, 2004).

Another pervading problem with assessing the size–fitness relationship is that evaluation of components in the laboratory is unlikely to reflect accurately their importance in nature. This is because the relationship can depend strongly on the environment in which it is measured, yet the majority of studies have been laboratory-based (Godfray, 1994; Visser, 1994; Rivero & West, 2002). Field assessments of size–fitness relationships have found that they are variable in direction and/or strength and can differ from laboratory estimates (and from the assumptions of theory) in terms of direction, strength and form (Visser, 1994; Kazmer & Luck, 1995; West, Flanagan & Godfray, 1996; Ellers *et al.*, 1998; Ellers, Bax & van Alphen, 2001). Also, few studies have provided information on the size distribution of hosts in the field and thus the resources naturally available to parasitoids.

Here we contribute towards addressing some of the above problems. We evaluated the relationship between body size and a little-studied component of foraging ability, the size of the host caught by females, and also the available host distribution. Our data derived from the study of naturally foraging females. We further employed field and laboratory studies to evaluate the importance of host size for fitness-related aspects of behaviour and life history: host-handling time, sex allocation, development time and the size of offspring that developed from a given host. Our most important results were that wasps actively select large hosts from populations in the field, and that larger wasps caught larger hosts. Larger hosts required longer handling times but tended to give rise to larger wasp progeny. Female wasps tended to develop on larger hosts and to be larger than were male wasps.

A secondary aim of our study was to report the general behaviour and ecology of our study species, *Anoplius viaticus paganus*, which has been little described. *A. v. paganus* is a nest-digging wasp, and in this respect differs from many parasitoid species used to study the above relationships; we begin with a brief description of its biology.

BIOLOGY OF *ANOPLIUS VIATICUS PAGANUS*

Anoplius viaticus paganus Dahlbom is a parasitoid of spiders. It is a pompilid wasp (Hymenoptera: Pompilidae), distinguished from other *A. viaticus* by its red hind legs. In this paper we refer to the red-legged (eastern European) subspecies on which we worked as *A. v. paganus* and use '*A. viaticus*' to denote other species members. Pompilids have very similar nesting (offspring provisioning) behaviours and near homoge-

nous morphologies (Evans & Yoshimoto, 1962; Day, 1988; Field, 1992a). They are generally active, searching for their spider prey under warm and sunny conditions and are usually found in open habitats. Spiders are paralyzed upon capture and further development ceases (idiobiontism). Females commonly dig nests into the ground, generally only after capturing a spider. The spider is then placed into the nest, an egg is laid onto it and it is fed upon by the developing wasp larva (Field, 1992a).

A. v. paganus is found in eastern Europe and has some uncharacteristic properties (which it shares with the *A. viaticus* that are found in western Europe, Field, 1992a,b). Adult females become active in March, which is much earlier than for other pompilids (e.g. Field, 1992a), and seem very tolerant of cold weather. The females dig a simple nest that typically consists of a burrow and a single cell. Each nest is provisioned with a single paralyzed spider bearing a single wasp egg. The larva consumes the spider within 2 weeks and then pupates. In mid-summer adults emerge and mate. Only the females overwinter. Newly mated females do not nest before overwintering (as for *A. viaticus*, Field, 1992a). Nesting females sometimes commit intraspecific parasitism. Paralyzed spiders may be stolen from other females while they are being carried to a nest site or while left unattended during nest digging. Completed nests are also sometimes reopened by 'intruder' females which generally destroy the original egg and either lay their own egg onto the spider and reseal the nest or remove the spider, eventually placing it in their own nest (as described for *A. viaticus*, Field, 1992b).

MATERIAL AND METHODS

We studied *A. v. paganus* in Kiskunság National Park, Hungary, and in the laboratory, between 1985 and 1995.

FIELD SITE AND COLLECTIONS

The study area consisted of 1–3-m high sand dunes covered by grass (*Festuca*) and low vegetation with small bare patches between the plants. The dunes were criss-crossed by small unpaved roads, with no or sparse vegetation and very little car traffic, along which the wasps moved and nested.

Wasps were captured using nets and stored individually in vials until killed and measured or until marked on the surface of the thorax using modelling enamel paint for subsequent field observations. Paralyzed spiders (hosts) were collected from inside or near the entrance to wasps' nests, or while being carried by a wasp. Since *A. v. paganus* has been observed to steal hosts from conspecifics' nests, it is not possible to be

certain that a wasp caught carrying a host would have eventually parasitized it, or that the wasp was the host's original captor. Due to the low density of wasps, we are, however, confident that such paired data reflect the characteristics of successful parasitoids in nearly all cases. Spiders were killed and measured in the field, and were identified to family, or, where possible, to species level (Loksa, 1969, 1972), then they were dried in the laboratory until their weight stabilized to obtain the dry weight.

Several nests were excavated after the wasp had oviposited. If both egg and spider were undamaged by the excavation process, the size of the spider was measured and it was placed in a small glass vial containing a plug of moist cotton wool at the base and closed with a plug of dry cotton wool. These tubes were buried in sand until the wasp offspring pupated. Pupae were transferred to the laboratory and checked daily for the emergence of adult wasps. Emergent wasps were killed and their size was measured. All wasp and spider dimensions were measured by vernier callipers to an accuracy of 0.1 mm. Weights were measured using an analytical balance with an accuracy of 0.001 g.

We also assessed seasonal change in host-spider assemblage using pitfall traps (8 cm in diameter) containing ethylene glycol. This was because *A. v. paganus* hunts spiders that move or hunt on the surface (rather than 'sit-and-wait' web-spinners). Six times during the study (for dates see Fig. 3), 50 traps were placed for 3 weeks in two 5 × 5-m grids, one on each side of a road where the wasps were relatively common.

LABORATORY OBSERVATIONS

We carried out laboratory investigations to assess relationships between characteristics of wasp offspring and their hosts. Adult female wasps were kept individually in cages measuring 28 × 28 × 30 cm. Each cage was illuminated and heated by a 100 W light bulb. Honey and water were provided *ad libitum* as food for the wasps. The bottom of each cage consisted of eight glass boxes (5.7 × 13.7 × 9.4 cm) that could be removed individually and replaced from the outside without disturbing the wasps. These boxes were filled with a selection of dry, medium-wet and wet sand, in which the wasps could dig nests and bury hosts. Wasps were allowed to accommodate to a cage for at least 2–3 days before experimental observations began.

One spider of known size was placed into each cage on the morning on which observations began. Some spiders had been parasitized previously, and others were intact and vigorous. Wasps were observed directly and the duration of their various behaviours

was measured using a stopwatch. Sometimes the wasp destroyed the spider and ate it (7/65 cases), but commonly it paralyzed the spider, dug a nest, placed the spider inside and laid an egg on the spider's ventral surface. Boxes containing these nests were then removed, labelled and placed in the shade on a balcony. Any adult wasps that subsequently emerged were killed and measured.

STATISTICAL ANALYSIS

Due to practical constraints and because *A. v. paganus* is rare, for the laboratory work we used each mother wasp several times. However, host encounters were separate events with successive ovipositions generally separated by a period of days. We thus consider each host–parasite interaction as being independent. We confirmed that different mothers had not received significantly differently sized spiders (Kruskal–Wallis, $\chi^2 = 21.21$, d.f. = 14, $P > 0.05$, $N = 56$) or different ages/sexes of spiders (Kruskal–Wallis, $\chi^2_{14} = 22.30$, $P > 0.05$, $N = 60$). There was also no significant difference in the sex (Kruskal–Wallis, $\chi^2_{14} = 20.24$, $P > 0.1$, $N = 60$) or the dry weight of offspring (Kruskal–Wallis, $\chi^2_{14} = 15.43$, $P > 0.1$, $N = 58$) between the mothers.

Data on sex ratios (proportion of offspring that were male) were explored using logistic analyses available in the statistical package GLIM; these were semiparametric analyses suitable for data with non-normally distributed error variances and did not require prior transformation (Crawley, 1993; Wilson & Hardy, 2002). Significance was assessed by the change in deviance, G (which approximates χ^2) when explanatory variables were removed from a statistical model. The percentage change in scaled deviance (%Dev) provided an informal measure of explanatory power (akin to r^2 for normal errors).

We explored relationships between offspring body size, developmental time and host size using standard backwards stepwise analyses of covariance (assuming normally distributed error variances). Once a most parsimonious model was obtained, we checked the assumption of normality by plotting the standardized residuals against the standard normal cumulative distribution function (Crawley, 1993; Wilson & Hardy, 2002).

In several cases (e.g. examining relationships between pairs of variables) nonparametric tests were employed, using the SPSS statistical package.

RESULTS

HOST AVAILABILITY AND CHOICE IN THE FIELD

Members of 17 spider families were collected using pitfall traps, but only five families were represented commonly (Fig. 1). Despite variation in seasonal abun-

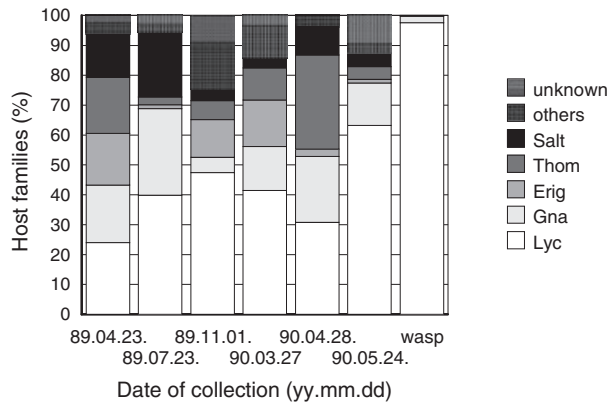


Figure 1. Relative abundance of spider families from pitfall traps and wasp captures. Spiders were trapped before (November, $N = 158$; March, $N = 251$), during (April, $N = 208$ and 150) and after (May, $N = 685$; July, $N = 231$) the wasp's period of hunting activity, which is generally from the very end of March to the beginning of May ($N = 459$). Salt, Salticidae; Thom, Thomisidae; Erig, Eridonidae; Gna, Gnaphosidae; Lyc, Lycosidae; others, 12 other spider families that were represented by less than 10 individuals; wasp, spiders caught by wasps.

dance, members of the *Lycosidae* remained the most commonly trapped spiders (Fig. 1). Spiders collected from *A. v. paganus* individuals or nests belonged almost exclusively to the *Lycosidae*. The most common host species were *Tarantula sulzeri* Pavesi, *Ta. cuneata* (Clerk), *Ta. fabrilis* (Clerk) and *Trochosa terricola* Thoreli. Most spiders found in the traps were juveniles or males (the most mobile categories) (Fig. 2). However, spiders captured by wasps belonged exclusively to the mature and premature (one stage before mature) stages (Fig. 2). Among premature hosts, the sexes were captured with equal frequencies ($\chi^2 = 2.06$, $P > 0.1$, $N = 257$), but captured mature spiders were almost exclusively female ($\chi^2 = 169.53$, $P < 0.001$, $N = 189$).

Wasps most commonly captured spiders with a body width of between 3 and 5 mm (Fig. 3; average body width = 4.19 ± 0.62 mm, $N = 457$; average body length = 10.58 ± 1.22 mm, $N = 456$). Spiders of this size category were very rare in the field, except in March just at the beginning of the wasps' period of activity (Fig. 3). Before and after the seasonal activity of the wasps the distribution of the spider size was skewed strongly toward the smaller sizes.

Spiders caught by wasps were on average twice as heavy as the wasps (33.28 ± 15.50 mg, $N = 87$ vs. 17.99 ± 5.06 mg, $N = 117$). Spiders caught by wasps of different size (dry weight) did not differ in terms of age and sex (Kruskal–Wallis test, $\chi^2_1 = 2.99$, $P > 0.2$, $N = 101$) but there was a positive correlation between the dry weight of wasps and the spiders they caught

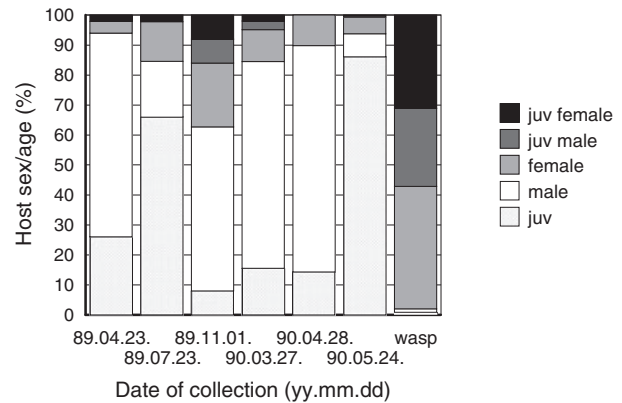


Figure 2. Sex and age distribution of Lycosid spiders from pitfall traps and wasp captures. Spiders were trapped before (November, $N = 75$; March, $N = 104$), during (April $N = 50$ and 49) and after (May, $N = 433$; July, $N = 92$) the wasps' period of hunting activity, which is generally from the very end of March to the beginning of May ($N = 450$). Juv, juvenile individuals where sex could not be identified; juv male and female, the last stage of the spider development before full maturation (underdeveloped sex organs are visible); wasp, spiders caught by wasps.

(Spearman's $\rho = 0.350$, $P < 0.01$, $N = 65$), suggesting that larger wasps preferred, or were able to subdue, larger spiders. Wasps that were smaller than average (dry weight < 18 mg) did not capture the same size of host as did the heavier individuals (Mann–Whitney $U = 291.5$, $P < 0.005$, $N = 65$, Fig. 4). Smaller wasps captured lighter hosts (dry weight = 27.59 ± 8.65 mg, $N = 28$), while larger wasps (dry weight ≥ 18 mg) captured heavier spiders (35.68 ± 10.59 mg, $N = 31$). The variance in the size of spiders captured by large wasps was more than twice that of those captured by small wasps, and the distribution of host sizes departed significantly from normality (Kolmogorov–Smirnov with Lilliefors significance correction = 0.179 , d.f. = 37 , $P < 0.005$; Fig. 4).

Focusing on spider species rather than size, we found that different sized wasps tended to catch different prey species. For example, *Ta. cuneata* was not as heavy as *Ta. sulzeri* (mean dry weight = 22.47 ± 5.39 mg, $N = 12$ vs. 32.10 ± 8.65 mg, $N = 45$) and was caught by significantly smaller wasps (mean dry weight = 14.57 ± 4.13 mg, $N = 23$) than was the most common medium-sized host (Mann–Whitney $U = 211.00$, $P < 0.001$, $N = 70$), whereas *Ta. sulzeri* was captured by wasps close to the average dry weight (19.48 ± 4.94 mg, $N = 47$). This result does not necessarily mean that smaller wasps were more host-species specific since the pattern may be a simple consequence of the fact that *Ta. cuneata* is one of the smallest hosts species and small spiders are captured by small wasps (see above).

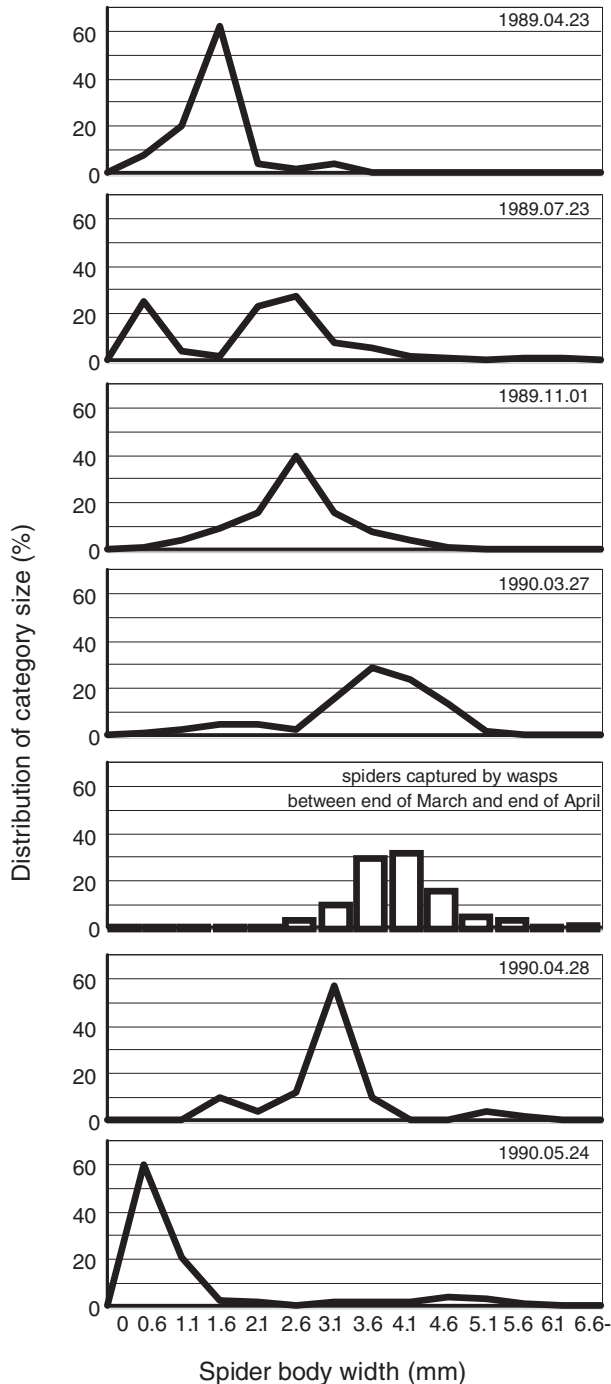


Figure 3. Size (body width) distribution of Lycosid spiders on different sampling dates. Lines show the sizes of spiders trapped in Barber traps before (November, $N = 75$; March, $N = 104$), during (April, $N = 50$ and 49) and after (May, $N = 433$; July, $N = 92$) the wasps are active in the field (wasps generally hunt spiders from the very end of March to the beginning of May). Columns show the sizes of spiders captured by wasps between late March and late April 1990 ($N = 240$).

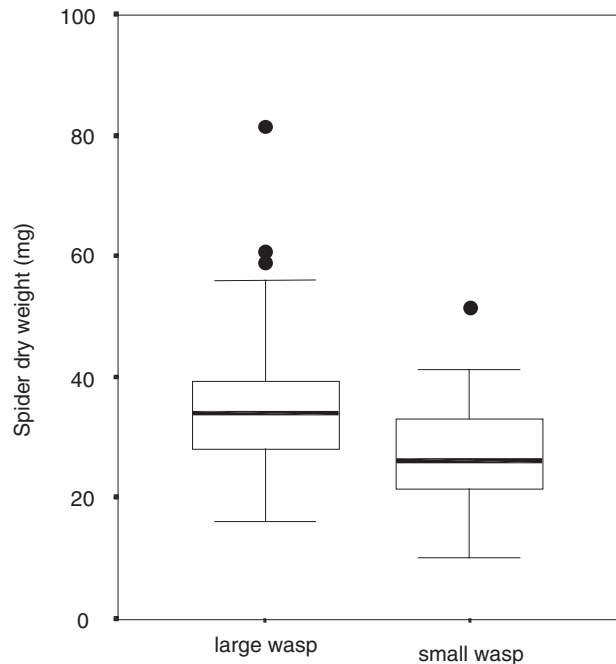


Figure 4. Boxplot of distribution of the dry weight of spiders caught by small (dry weight < 18 mg, $N = 28$) and large (dry weight ≥ 18 mg, $N = 37$) wasps. Outliers are shown by black circles.

WASP BEHAVIOUR IN THE LABORATORY

There was no significant between-wasp difference in the time individuals spent between paralyzing the spider and filling in the nest (mean = 133.53 ± 55.97 min, $N = 60$, Kruskal–Wallis, $\chi^2_{14} = 17.92$, $P > 0.2$). The time wasps took to detect the presence of the spider in the cage was highly variable and was positively correlated with the duration of the attack (Table 1). Attack duration was, in turn, positively correlated with the duration of paralyzation (Table 1). Wasps started to dig nests an average of 20 min after paralyzing the spider. During this interim period, wasps rested and searched for nesting locations: the length of this period was uncorrelated with the timing of other behaviours. Both digging and filling the nest took about an hour, and the durations of the two behaviours were positively correlated (Table 1). Wasps most commonly dug nests in the driest sand (66%, $N = 65$) but showed no preference for medium-wet over wet sand (each type was used in 17% of the 65 cases). None of the measured times depended on the wetness of the sand (Kruskal–Wallis test, d.f. = 2, $P > 0.05$, $N = 20$). The times required to dig a nest and to fill it were positively correlated with spider width (digging: Spearman's $\rho = 0.302$, $P < 0.05$, $N = 70$; filling: Spearman's $\rho = 0.303$, $P < 0.05$, $N = 67$). Two differences were found between the situations when wasps

Table 1. Time schedule of host handling and correlations between the times allocated to different behaviours

	ToAttack (min)	Attack (s)	Paral (s)	Startdig (min)	Dig (min)	Digfill (min)
ToAttack	1.00	0.388*	0.108	-0.155	0.141	0.128
Attack		1.00	0.504*	0.172	0.008	0.432
Paral			1.00	0.102	0.051	-0.036
Startdig				1.00	0.188	0.192
Dig					1.00	0.336**
Digfill						1.00
Average	14.94	11.41	2.95	19.79	63.19	50.03
SD	21.71	8.64	0.95	32.26	31.94	19.03
N	83	29	39	78	70	67

ToAttack, time from introducing the spider into the cage to the first attack by the wasp; Attack, duration of the attack; Paral, duration of paralyzation; Startdig, time from paralyzation until the wasp started to dig a nest; Dig, time between the wasp starting to dig the nest and pulling the spider into it; Digfill, time spent egg-laying and filling the nest with sand, terminating when the wasp left the vicinity of the nest. Values of Spearman rho coefficients are in the cells above the diagonal (* $P < 0.05$, ** $P < 0.01$).

were provided with vigorous or previously paralyzed spiders: the time between introducing the spider and the first attack was shorter if the spider was vigorous (Mann–Whitney $U = 537$, $P < 0.01$, $N = 83$) and the wasp started to dig a nest earlier if the spider was already paralyzed (Mann–Whitney $U = 452.5$, $P < 0.01$, $N = 78$).

OFFSPRING SEX RATIO

Laboratory data

The sex ratio of offspring departed significantly from equality (i.e. 0.5) (mean = 0.638, S.E. = ± 0.06 , $N = 60$, likelihood ratio test, $G_1 = 5.48$, $P > 0.05$). The numerical ratio may not, however, reflect the investment sex ratio. The mean body width of host spiders may provide an indication of maternal investment since it may require more energy to subdue and transport larger spiders, and it took more time to prepare a nest when spiders are larger (see above). The mean width of spiders on which male wasps developed was 3.682 ± 0.488 mm ($N = 39$) and for female wasps the mean host width was 4.48 ± 0.537 mm ($N = 21$). If, overall, there was an equal investment in male and female offspring, we would expect the numerical sex ratio to be biased in accordance to the ratio of host spider sizes, i.e. $3.68 : 4.48 = (60 - X) : X$, $X = 33$. In other words, 27 female and 33 male offspring would be expected; our observation of 21 female and 39 male offspring does not differ significantly from this (likelihood ratio test, $G_1 = 2.47$, $P > 0.05$).

For size-related variables, there were significant differences between hosts of male or female wasps but not for variables related to spider age or sex (Table 2). To identify the most important influences on sex ratio, we further explored the sex of the offspring emerging

from the host in relation to characteristics of the host presented to the adult wasp: host species, sex, developmental stage, whether the host was already paralyzed and host size [estimated as both wet weight (at time of presentation) and body width] using logistic analysis (binary data, 0 = female, 1 = male offspring). Offspring sex was not significantly related to any host characteristic except for size, with more female offspring developing on larger hosts (backwards stepwise logistic analysis of covariance: $N = 58$; species, $G_6 = 6.44$, $P > 0.1$; age (juvenile or adult), $G_1 = 0.01$, $P > 0.1$; sex, $G_1 = 0.12$, $P > 0.1$; state (paralyzed or unparalyzed), $G_1 = 0.67$, $P > 0.1$; wet weight, $G_1 = 4.16$, $P < 0.05$, %Dev = 5.5; width, $G_1 = 12.01$, $P < 0.001$, %Dev = 15.8). The significant variables, host width and host wet weight, were correlated (standard regression of width on wet weight: $F_{1,56} = 34.7$, $P < 0.001$, $r^2 = 0.38$, regression equation: width = $0.0095 \times$ wet weight + 2.775).

FIELD DATA

Offspring sex ratio was close to equality in the field (mean = 0.513, S.E. = ± 0.08 , $N = 38$, $G_1 = 0.12$, $P > 0.1$). There were no significant differences between the sex ratios of offspring collected in different years ($G_2 = 2.3$, $P > 0.1$) and no significant sex-ratio trends with date during the field season ($G_1 = 1.02$, $P > 0.1$). Field sex-ratio data were thus combined with respect to sample date. The mean width of spiders on which males developed was 3.97 ± 0.41 mm ($N = 20$) and for females this was 4.68 ± 0.69 mm ($N = 18$). As above, for equal material investment in the sexes we would expect a numerical sex ratio of $3.97 : 4.68 = (38 - X) : X$, $X = 21$, or 21 male and 17 females. The observation of 20 males and 18 females did not differ

Table 2. Characteristics of spiders (mean \pm SD) from which male and female wasps developed

Variable	Males	Females	Test
LABORATORY	(<i>N</i> = 39)	(<i>N</i> = 21)	
Spider length (mm)	9.93 \pm 0.93	11.67 \pm 1.28	MW: 94.0, <i>P</i> < 0.001
Spider live weight (mg)	109.62 \pm 26.62	156.71 \pm 45.57	MW: 133.0, <i>P</i> < 0.001
Spider width (mm)	3.68 \pm 0.49	4.48 \pm 0.54	MW: 94.0, <i>P</i> < 0.001
Spider age (1 = adult, 0 = premature)	0.5385	0.6190	CH: 0.107, <i>P</i> > 0.1
Spider sex (1 = m, 0 = f)	0.3333	0.1429	CH: 1.65, <i>P</i> > 0.1
Wasp offspring dry weight (mg)	6.23 \pm 1.78	14.12 \pm 5.67	MW: 36.0, <i>P</i> < 0.001
Wasp offspring development time (days)	53.43 \pm 16.5	75.4 \pm 25.35	MW: 77.0, <i>P</i> < 0.01
FIELD	(<i>N</i> = 19)	(<i>N</i> = 18)	
Spider length (mm)	10.03 \pm 0.72	11.16 \pm 1.32	MW: 75.5, <i>P</i> < 0.05
Spider width (mm)	3.97 \pm 0.41	4.68 \pm 0.69	MW: 57.5, <i>P</i> < 0.001
Spider age (1 = adult, 0 = premature)	0.2000	0.6666	CH: 6.66, <i>P</i> = 0.01
Spider sex (1 = m, 0 = f)	0.4000	0.1111	F: <i>P</i> > 0.05
Offspring dry weight (mg)	7.41 \pm 2.12	11.51 \pm 2.42	MW: 9.5, <i>P</i> < 0.001
Offspring development time (days)	37.74 \pm 3.11	41.44 \pm 6.52	MW: 103.0, <i>P</i> = 0.10

Spider age and sex are binary variables, therefore the means are computed from zeros and ones. This value shows the proportion of spiders from which wasps of the specified gender developed. CH, chi-square test with Yates correction; f, female; F, Fisher's exact test; m, male; f, female; MW, Mann–Whitney test.

significantly from this expectation ($G_1 = 0.04$, $P > 0.1$). Logistic analysis of covariance further showed that females tended to develop on adult hosts and males on juvenile hosts ($G_1 = 6.25$, $P < 0.05$, %Dev = 12.2). Females also tended to develop on wider hosts ($G_1 = 12.55$, $P < 0.001$, %Dev = 24.5). Wasp offspring sex was not significantly related to spider sex ($G_1 = 1.54$, $P > 0.1$) but there were significant differences in wasp sex ratio between the host species ($G_5 = 12.29$, $P < 0.05$, %Dev = 23.9). By aggregating factor levels of the host species variable (Crawley, 1993: 190), we found that sex ratio was not significantly related to host species within the genus *Tarantula* ($G_4 = 7.47$, $P > 0.05$, %Dev = 14.57). A comparison between sex ratio on *Tarantula* hosts and the remaining host species (*Tr. terricola*) found no significant difference ($G_1 = 3.82$, $P > 0.05$, %Dev = 7.4). It should, however, be noted that *G*-values of 12.29 and 3.82 were close to the 5% critical values in χ^2 tables (11.07 for 5 d.f. and 3.84 for 1 d.f.) and that there is no firm theory on the precision of the probability estimates for significance testing when binomial errors are specified (Crawley, 1993: 278).

Comparison of laboratory and field data

We compared the relationship between offspring sex, host width and age between the laboratory and field datasets using logistic analysis of covariance ($N = 98$). Offspring sex was not significantly related to whether the data derived from the laboratory or the field ($G_1 = 0.02$, $P > 0.1$), but more females developed on older ($G_1 = 5.36$, $P < 0.05$, %Dev = 4.1) and wider hosts

($G_1 = 49.0$, $P < 0.001$, %Dev = 37.4). The relationship between offspring sex and host size and age is shown in Figure 5.

OFFSPRING SIZE

There was no significant difference between the dry weights of offspring deriving from the field and from the laboratory ($F_{1,77} = 0.068$, $P > 0.05$) so laboratory and field data were combined for further analysis. Female offspring were significantly heavier (dry weight) than were males ($F_{1,77} = 23.04$, $P < 0.01$, $r^2 = 0.21$). There was a weak but significant relationship between offspring dry weight and host width ($F_{1,77} = 4.25$, $P < 0.05$, $r^2 = 0.028$) with no significant sexual difference in the slope of the relationship (host width \times offspring sex interaction: $F_{1,76} = 0.16$, $P > 0.05$). These relationships are shown in Figure 6.

OFFSPRING DEVELOPMENTAL TIME

Examination of laboratory and field data combined showed that, overall, males developed significantly faster than did females ($F_{1,60} = 5.89$, $P < 0.05$), but only a small proportion of the variance was explained ($r^2 = 0.07$) and the measured developmental time of both males and females was significantly shorter in the field than it was in the laboratory ($F_{1,60} = 21.15$, $P < 0.01$, $r^2 = 0.34$ (see also Table 2). Because there were field data for only few individuals and the field temperature varied uncontrollably, we carried out further exploration of developmental times using

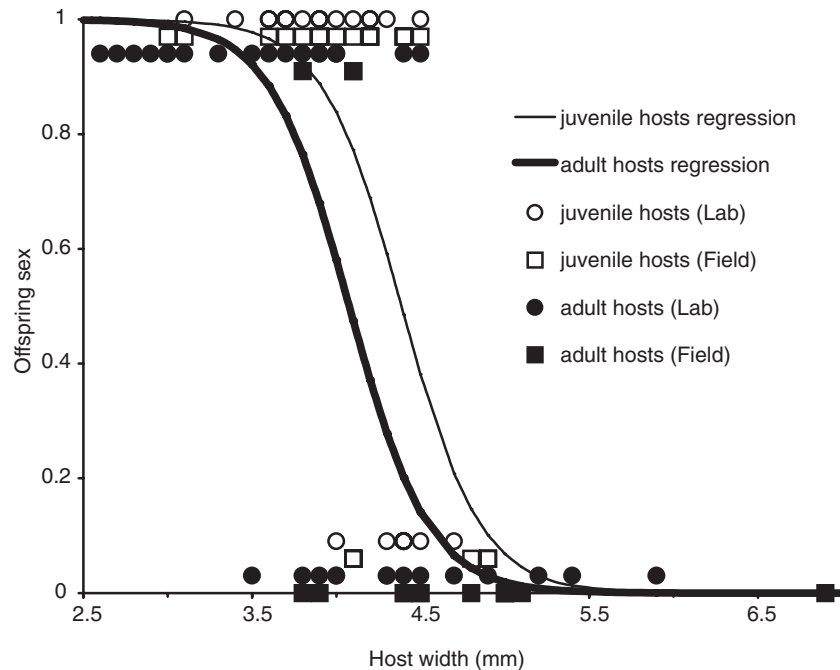


Figure 5. Relationship between offspring sex, host size and host age. Offspring sex data are binary (0 = female, 1 = male) but have been vertically displaced for visual clarity. Some data points represent multiple observations. The fitted regression lines represent the most parsimonious model to explain the combined laboratory and field data: offspring sex = $1/[1 + \{1/(\exp(-4.263 \times \text{host width} + \text{intercept}))\}]$; the intercept is 18.70 for juvenile hosts and 17.378 for adult hosts.

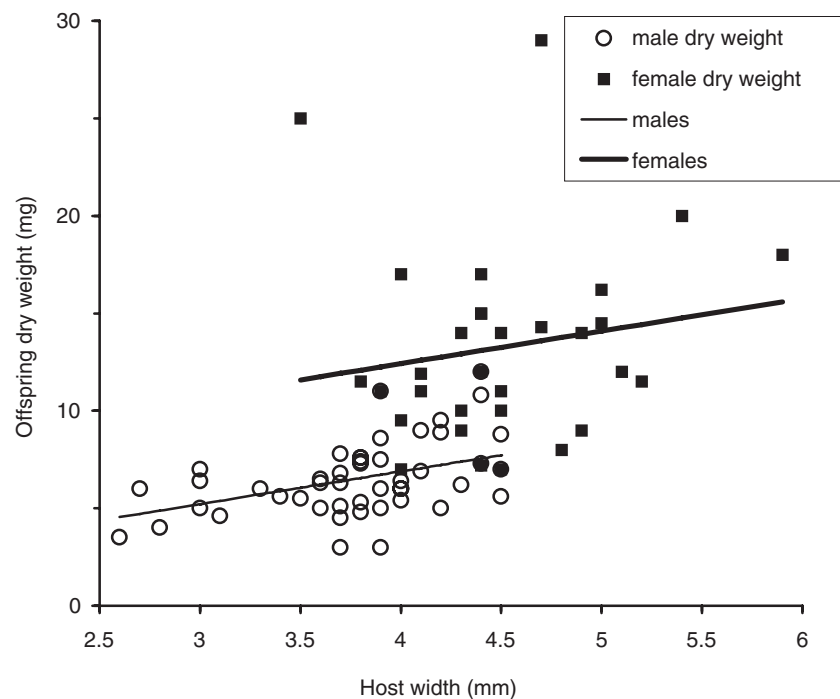


Figure 6. Relationship between offspring weight, sex and host size. Fitted lines are from stepwise analysis of covariance of combined laboratory and field data: offspring dry weight sex = $1.67 \times \text{host width} + \text{intercept}$; the intercept is 0.2051 for males and 5.74 for females.

laboratory data only. In the laboratory, males generally developed faster than did females ($F_{1,39} = 5.69$, $P < 0.05$, $r^2 = 0.12$ (see also Table 2). The relationship between development time and dry weight was different for males and for females (size \times sex interaction: $F_{1,38} = 5.07$, $P < 0.05$, $r^2 = 0.16$): larger males developed more quickly than did smaller males, while larger females developed more slowly than did smaller females (Fig. 7). These relationships were, however, found to rely on the developmental time of one exceptionally heavy female. With the data from this individual removed, the above relationships were not significant (size: $F_{1,38} = 0.69$, $P > 0.05$, $r^2 = 0.02$, sex: $F_{1,39} = 4.01$, $P > 0.05$, $r^2 = 0.10$, size \times sex interaction: $F_{1,37} = 3.55$, $P > 0.05$, $r^2 = 0.08$) and developmental time was most parsimoniously described by the overall mean (64.18 days, S.E. = 4.443, Fig. 7).

DISCUSSION

Female *A. v. paganus* are selective hunters: the types and the sizes of prey that they captured were only a small subset of the range of potential hosts available. Hosts belonging to the *Lycosidae* were clearly favoured (as found for *A. viaticus*, Field, 1992a, b) and among those, wasps preferred juveniles (of either sex) or adult females, and also captured spiders at the larger end of the size range. The activity of the wasps in the field was restricted to the period between the end of March and the end of April when, due to

individual growth, average spider size reached a maximum. Although our trapping method selectively caught the actively moving spiders and rarely captured those that 'sit-and-wait', this selectivity matched the foraging strategy of *A. v. paganus*. Field (1992a) showed that *A. viaticus* phenology is different from that of other pompilids, which mostly emerge during the later, and warmer, months of the year. In general, larger insects can become active at lower temperatures than can small ones (Willmer & Unwin, 1981; Gilbert, 1985; Willmer, 1985). Field (1992a) concluded that the unusual phenology of *A. viaticus* could be an adaptation unrelated to interspecific competition. Our field data appear to support this claim. The wasps need to be active early in the season, because this is when large *Lycosidae* spiders are most available. Later in the season subadult male spiders lose weight and width, and gain agility after the last moult, and females lose most of their weight and width when they deposit their eggs in early May (I. Karsai, pers. observ.). The size distribution of caught spiders and the size distribution of available spiders just before the active nesting period of the wasp corresponded almost perfectly.

While females were able to capture spiders much larger than themselves, relatively small females appeared to be limited in terms of the size of the spider they could subdue, since larger wasps caught larger spiders. There was thus a 'host-handling ability' component of the female size–fitness relationship when

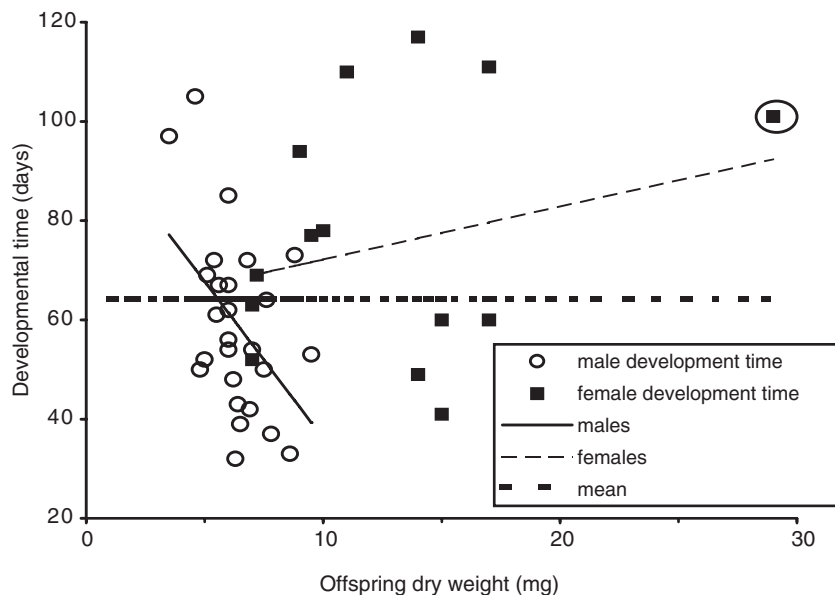


Figure 7. Relationship between development time, offspring dry weight and sex. Fitted lines are from stepwise analysis of covariance of laboratory data: male development time = $-6.308 \times \text{dry weight} + 99.25$; female development time = $1.065 \times \text{dry weight} + 61.51$. If, however, the circled point is removed these relationships are not significant and developmental time is best described by its mean (see main text).

females foraged naturally, and for this component, larger females had greater fitness. Host-handling ability has relatively seldom been studied in relation to parasitoid body size, but several studies have shown that prey size, or other components of handling ability, is related to the size of the foraging female in other pompilid wasps (Kurczewski & Kurczewski, 1968; Field, 1992a and references therein) and, for instance, at least one sphecoid wasp (e.g. Strohm & Linsenmair, 1997).

Nest construction by *A. v. paganus* took about 1 h, in close agreement with data on *A. viaticus* reported by Field (1992b). The average time to start digging after spider capture (~20 min) was longer in *A. v. paganus* than it was in *A. viaticus* (5–8 min), although this difference could be due to environmental conditions during observations or to the disparate samples sizes from which data in the two studies derived ($N=78$ and $N=3$, respectively). Despite being apparently preferred prey items, larger hosts required longer handling times, in terms of attack time, time to paralyze, nest digging and filling. This is likely to constitute a disadvantage but we cannot provide a detailed cost–benefit analysis to calculate the net gain associated with large hosts. We would, however, expect this cost to be small (although it could include a higher probability of the hosts being stolen during the next digging phase) because the additional time need to dig a nest for large hosts was tiny in proportion to the time wasps spent resting and searching for hosts.

Once hosts had been found and handled and placed into nests, there was a clear tendency for female offspring to be produced on larger hosts and male offspring on smaller hosts. Similar results have been found for numerous parasitoid species (e.g. King, 1993; Godfray, 1994), with the strongest relationships among idiobionts (West & Sheldon, 2002) like *A. v. paganus*. Because the hosts of idiobiont parasitoids stop growing upon being parasitized, the quality of the host (in terms of the amount of resource it provides for offspring) is highly predictable relative to that for koinobiont parasitoids (for which the host continues to develop). Together with the haplodiploid genetic mechanism of sex determination, which affords a high degree of control of offspring gender at oviposition (e.g. Hardy, 1992; Godfray, 1994), this means that the sex allocation decisions of *A. v. paganus* mothers should be essentially unencumbered by informational or mechanistic constraints. To evaluate this we used the MetaWin statistical calculator (Rosenberg, Adams & Gurevitch, 2000) to obtain the ‘effect size’ (Pearson’s r) of the relationship between offspring sex and host size. The resulting value of 0.707 was very close to the top of the range of effect sizes for this relationship in the 28 idiobiont

parasitoid species considered in the meta-analytic study of West & Sheldon (2002; their fig. 2), indicating that this relationship to be particularly strong in *A. v. paganus*. Indeed, only three of the 28 previously studied parasitoid species showed stronger relationships, with effect sizes of c. 0.75 (West & Sheldon, 2002: fig. 3).

The major functional explanation for host-size-dependent sex allocation patterns is that the amount of resource provided by the host affects the fitness of female offspring more greatly than it does male offspring (‘host quality model’, Charnov *et al.*, 1981; see also Trivers & Willard, 1973). More specifically, it is assumed that a given increase in host size has a greater, and more positive, effect on female fitness than it does on male fitness. It is predicted that maternal fitness is maximized by laying male eggs on small hosts and female eggs on large hosts. The body size of male and female *A. v. paganus* offspring increased equally with a given increase in host size (i.e. the male and female relationships in Fig. 6 have equal slopes). While we found that at least one component of female fitness, host handling (capture) ability, was positively correlated with body size, we have little evidence for the relationship between male size and fitness. A number of studies of other parasitoid species has shown that body size has a positive influence on the number of females that a male can successfully mate (reviewed in Hardy, Ode & Siva-Jothy, 2006) but such relationships are not found in all parasitoid species studied (e.g. King & King, 1994; Napoleon & King, 1999) and have not been assessed in *A. v. paganus*. In at least one species of sphecoid wasp, male size does not affect reproductive success in the field (Strohm & Lechner, 2000).

Furthermore, our analysis equivocally suggests that development time is either unaffected by body size, or that larger males develop faster. It is conceivable that more rapid development could be advantageous to males if early emergence leads to enhanced mating success before the mated females overwinter (Field, 1992b; see also King, 1993). Even if development time and mating constitute components of the male size–fitness relationship, we have insufficient information to compare male and female size–fitness relationships and hence cannot adequately evaluate the key assumption that male and female fitness are differentially affected by increasing host resources. This is a common problem in evaluating observed relationships between sex allocation and host quality (e.g. King, 1993; Godfray, 1994). While some laboratory studies have assessed the relationship for males and for females (e.g. van den Assem *et al.*, 1989; Heinz, 1991; King & King, 1994; King & Lee, 1994; Ode, Antolin & Strand, 1996; Napoleon & King, 1999), field information on sexually differential fitness relationships is

largely lacking (Kazmer & Luck, 1995; West, Reece & Sheldon, 2002).

Our study also encountered another common problem with estimating the size–fitness relationship: the relationship may have multiple (and unmeasured) components. For instance, at a relatively high population density, *A. viaticus* is reported to engage commonly in interspecific female–female competition for hosts (Field, 1992b). Such behaviour is also likely between adults in *A. v. paganus* females, although we never observed this species at high density. Field (1992b) reported that ‘nest parasites’ (conspecific females attempting to usurp hosts already in nests) were always repelled by the owner female on discovery, but when such conspecifics engaged prey-laden owner females (i.e. before the prey was placed in the nest), it was not always the initial owner that won. Field (1992b) did not provide body-size data to accompany his observations, but a body-size-related outcome to such fights is the most obvious candidate explanation and could be an important component of the size–fitness relationship when females often encounter each other (Petersen & Hardy, 1996; Mesterton-Gibbons & Hardy, 2004). In summary, our empirical results are entirely congruent with the assumed and predicted relationships that constitute the host-quality model, as illustrated schematically by King (1993: 421), but lack information on male fitness relationships. Since the predicted pattern of host-size-dependent sex allocation was clearly observed, we would tentatively expect the assumption of sexually differential size–fitness relationships to hold under empirical scrutiny but we must remain open to the possibility of a nonadaptive explanation (see related discussion by King & King, 1994; King & Lee, 1994).

While a plethora of previous studies have examined sex allocation in response to host quality (King, 1993; Godfray, 1994; West & Sheldon, 2002), very few of these have provided field data on the relationship. Encouragingly for the value of laboratory studies, which has been debated (Hardy *et al.*, 1995), we found no difference in sex allocation with respect to host size between sets of data collected in the laboratory and in the field. Previous laboratory and field studies of this relationship in parasitoids in the genus *Spalangia* have, however, found inconsistent and complex results (Donaldson & Walter, 1984; King, 1991a, b; Napoleon & King, 1999). Despite the consistency of the sex allocation with respect to host size in our laboratory and field data, we found inconsistent patterns in the overall sex ratio: the laboratory population of *A. v. paganus* showed a male bias in sex ratio but the field data, and all data combined, did not. Under host-quality-dependent sex allocation behaviour, a small numerical bias toward males may be expected in the

population sex ratio (although such predictions are not straightforward, Frank & Swingland, 1988; Pen & Weissing, 2002).

CONCLUSIONS

The biology of *A. v. paganus* has been little described. We have shown that foraging females are able to select larger host spiders from the field and the activity period of the wasps coincides with the season in which large Lycosid spiders are most available. Larger offspring develop from larger hosts and, in agreement with the prediction of the host-quality model of sex allocation, are generally female. This is one of few field studies of both a component of the female size–fitness relationship and the relationship between host quality and sex ratio.

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