

# Opportunistic predation and offspring sex ratios of cicada-killer wasps (*Sphecius speciosus* Drury)

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**Abstract.** 1. The way in which hunting of prey affects the sex ratio of the predator's offspring is not well understood. Female cicada-killer wasps are convenient for study because they specialise in capturing cicadas to provision their offspring. Cicada prey are nearly twice as heavy as the wasps that carry them, hence some degree of prey selectivity by the wasps is to be expected. It has been suggested that wasps bias their offspring towards females by foraging selectively for female prey, whereas there is some evidence that sex ratios are actually male-biased. This study was designed to establish the connection between foraging and offspring sex ratio.

2. Three, non-exclusive, hypotheses of selective predation were tested. The frequency of predation on different classes of prey in conjunction with their availability was estimated by intercepting the wasps on their way to their nests and by sampling cicadas in the environment. The hypothesis of selective predation was not supported; predation appears to be opportunistic and non-selective. Cicada prey weight was not a simple linear function of wasp weight, although the smallest wasps were constrained to carry small prey.

3. Wasp offspring (larvae) were excavated from subterranean nests and found to be male-biased (3 : 1 or 4 : 1) in 2 years. The observed ratios are close to expectation from Fisher's equal-investment model, taking account of sexual size dimorphism, and are evidently unrelated to the sex of the prey. A simple binomial probability rule of sex allocation provides a behavioural mechanism for producing the observed sex ratio of offspring.

**Key words.** Fisher's Equal Investment, nest provisioning, sex ratio, sexual dimorphism, wasp offspring.

## Introduction

Sex-allocation theory has been successful in predicting departures from a fundamental 1 : 1 Fisherian sex ratio (Fisher, 1930) in a variety of animals, mainly haplodiploid (arrhenotokous) insects (Charnov, 1982; King, 1993; Wrensch & Ebbert, 1993; Godfray, 1994; Hardy, 2002). The two most important influences on haplodiploid sex ratios of solitary and semisocial hymenoptera are local mate competition, when brothers compete for mates including their sisters (Hamilton, 1967), and variation in the relative fitness of males and females caused by variation in resource availability and use (Clausen, 1939; Flanders, 1939, 1942; Trivers & Willard, 1973; Charnov, 1982; King, 1987, 1993; Godfray & Hardy, 1993). Effects of seasonal and annual

variation in resources on sex ratios of solitary hymenoptera have been well documented (Torchio & Tepedino, 1980; Cowan, 1981; Strickler, 1982; Tepedino & Torchio, 1982; Frohlich & Tepedino, 1986; Bosch & Vicens, 2005). Less is known about geographical variation in salient environmental factors and the proximate behavioural mechanisms involved in the choice of food that results in sex ratio adjustments.

The sexually dimorphic, polygynous, univoltine and semisocial Eastern cicada-killer wasp, *Sphecius speciosus* (Hymenoptera), is a suitable species for studying the role of adult behaviour in modulating offspring sex ratios. Cicada killers nest in colonies throughout most of North America. Reports in the literature indicate that offspring sex ratios might be influenced by local mate competition, as in a few other solitary wasps (Cowan, 1981), because some predisposing conditions occur. These include close proximity of nests, male territoriality, protandry, competition for females who mate only once (Lin, 1963, 1979a; Lin & Michener, 1972), and greater genetic similarity of neighbours than non-neighbours (Pfennig & Reeve, 1993). Despite these conditions a

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prediction of the local mate competition hypothesis, that offspring sex ratios should be biased towards females, is not upheld. Instead sex ratios appear to be biased towards males (Lin & Michener, 1972; see also Dow, 1942). In the absence of local mate competition the expected sex ratio of sexually dimorphic species is the ratio produced when maternal investment in the two sexes is equal (Fisher, 1930; Trivers & Willard, 1973; Myers, 1978). As female wasps are larger than males, males should be produced in greater numbers than females.

By constructing a small or large cell to receive one or more cicadas, female wasps have the potential to bias their prey in relation to the sex of their offspring, before the prey are collected and the eggs are laid. Because (diploid) females are almost twice the size of (haploid) males (Coelho, 1997), they require much more food for growth. Therefore, to produce an excess of male offspring, a female could prey selectively on small prey. At variance with this expectation, however, wasps are believed to hunt selectively for large, and therefore usually female, prey and lay female eggs on them, because female prey outnumber male prey (Lin, 1979b). This would tend to yield a female-biased sex ratio. Thus it is not clear how adult female hunting behaviour is patterned in such a way as to result in the observed male-biased sex ratio of the offspring.

The study reported here was designed to clarify the relationship between prey availability, predation, and offspring sex ratio. Three, non-exclusive, hypotheses of selective predation are tested. The first hypothesis is that wasps prey preferentially on one sex of their prey, the more valuable sex (Trivers & Hare, 1976; Charnov, 1982), without specifying a priori whether this is male or female; Lin's (1979b) argument implicitly assumes it is female. The second hypothesis is that wasps choose prey on the basis of the size of their prey (e.g. Kobayashi & Shimada, 2000). The third hypothesis is that wasps prey preferentially on larger, more conspicuous and hence easier to detect species of cicadas. Opportunistic predation, resulting in prey taken at random with respect to their traits, is the default hypothesis to account for data if they are not explained by selective predation.

Determining whether predation is selective or opportunistic requires estimating prey captured in relation to prey availability. This is difficult to achieve by direct observation because the attacks usually take place at the tops of tall trees. Successful attacks can be documented by study of prey brought to the wasps' nests, however (Coelho, 1997). The three hypotheses were tested with data on weights, sex, and species identity of cicadas (i) sampled in the environment, and (ii) captured by female wasps and carried to their burrows. Coelho (1997) tested the first two hypotheses using the same methods, and found no evidence of selective predation. The study reported here duplicates the first two tests in a different geographical location, where a different outcome is possible because the composition of the cicada community differs, and goes further by including the third test.

As a further extension, weights of individual wasps and of the cicadas they carried were used to test for a positive relationship between the two (Lin & Michener, 1972), as this has so far not been done. Such a relationship has been found for another sphecid wasp, *Palmodes laevis* Cresson, which preys upon Mormon crickets (Gwynne & Dodson, 1984). It is to be

expected with cicada killers because on average their prey burden is almost twice as heavy as the wasps (Coelho, 1997). Lin (1979a) found no relationship between the weights of *S. speciosus* and the weights of their prey (*T. resh*), but the sample size of wasps with prey was small (five).

At the conclusion of this study some of the burrows were excavated to determine the sex ratio of wasp larvae in relation to the sex ratio of the prey they were given, and to test the expectations of the equal-investment model of Fisher. This provides a link that has been missing so far between above-ground wasp behaviour and below-ground offspring production.

### *Behaviour and life history*

Relevant aspects of the life history of cicada-killer wasps have been well documented (Riley, 1892; Davis, 1920; Dambach & Good, 1943; Lin & Michener, 1972) and summarised by Evans (1966), Bohart and Menke (1976) and O'Neill (2001). Emergence coincides with the height of abundance of their prey, the so-called 'dog-day' cicadas (*Tibicen* spp.), but wasps do not begin to prey upon them until several weeks after emergence. After mating females excavate subterranean burrows, a complex system of branching chambers terminating in cells. In each cell the female deposits one, two, or rarely three cicadas, and lays a single egg on one of them before sealing the cell. Only females, and not the much smaller males, hunt for cicadas. They capture cicadas by flying into them, grasping, and stinging them. The cicadas quickly become paralysed and are then carried for up to 100 m or more to the burrows where they remain in deep paralysis and relaxed for up to 1 week. Wasp larvae rapidly devour the cicadas, remain quiescent over winter, pupate in May, and emerge as adults in June, July, or August. Evans (1966) lists nine species of *Tibicen* captured by the wasps. They include the five in the present study.

### **Materials and methods**

#### *Field samples*

The study was carried out on the Princeton University campus July–September 2004 and June–August 2005. In 2004 a colony of wasps in an area of 180 m<sup>2</sup> near the west entrance to McCosh Hall was monitored most days (mornings only) from 20 July to 25 August. A description of the habitat is given in Oberdörster and Grant (2006). Active nests were counted and the number of cicadas brought to them was recorded in observation periods of 20–75 min (average 45), one per day on 7 days between 22 July and 18 August for a total of 315 min. Wasps were not individually marked. Forty-one cicadas were obtained from the wasps by intercepting them and separating wasps from their prey with a stick as they were delivering the cicadas to their nests. Cicadas were weighed within 1 h of capture on an electronic balance (Denver Instruments, model TR64) to the nearest 0.01 g. A sample of 44 cicadas from the environment within 2 km of the colony was obtained by collecting them soon after dawn by hand on the ground (alive or dead) or with a net

on the vegetation. In the absence of an obvious bias they are assumed to reflect proportions in the trees. Those that were damaged or partly eaten by ants were not weighed. Cicadas were identified with information on the Michigan website (Cooley *et al.*, 2005) and confirmed by Kathy Hill and David Marshall (pers. comm.).

The procedures of sampling, observing, and capturing cicadas were repeated at the same site in the first half of the 2005 season to assess the consistency of results obtained in 2004 and to provide additional information. Data were collected from mid-June to early August when observations ceased for logistical reasons. Methods were the same except in minor respects. Counting of nests, wasps, and cicadas brought to nests was carried out in observation periods of 30–60 min (average 37) approximately every other day for a total of 520 min. To check that provisioning activity was not missed by restriction of observations to 09.00–12.00 hours, checks were made at the colony in early morning (06.15–06.45 hours), afternoon (15.15–15.45 hours), and evening (19.45–20.15 hours) 30–31 July. No captures were observed. Outside the census period male and female wasps were captured and weighed. A novel feature in 2005 was the capture of some of the females with their prey, by netting them, which allowed a single prey weight to be obtained for 27 predators of known weights. All wasps were released unharmed at the nesting area after being marked on the thorax with nail polish for subsequent identification.

Several parts of the study area were excavated to a maximum depth of 20 cm from 16 to 23 September in 2005. The combined area excavated was  $\approx 30 \text{ m}^2$ , equal to approximately 17% of the study area. Wasp cocoons and associated cicadas were collected, mostly in the upper 10 cm, and cicadas were identified to sex and species. Wasp cocoons from the previous year (2004) were either empty, filled with earth or contained fully formed and desiccated adult wasps. Width of wasp cocoons was measured to 0.1 mm with callipers. Larvae were extracted, weighed, returned to their cocoons, which were re-sealed with candle wax, and kept over winter at 4 °C. Larvae were assigned to sex on the basis of the size and weight of the cocoon (Dow, 1942); females are larger than males. Ten cocoons containing larvae weighed much more (2.15–3.91 g) than 31 others (0.55–1.62 g). Widths (13–16.5 mm) of the 10 cocoons containing presumptive females were discretely larger than the others (10–12 mm), and the difference was used to identify the sex of larvae from cocoons that lacked weights.

### Statistical analysis

Analyses were performed with Statview version 5.0 (SAS Institute, 1998). Expected 1 : 1 sex ratios were tested with two-tailed binomial tests.  $\chi^2$  tests of sex ratios of captured prey in relation to available prey were corrected for continuity. All  $\chi^2$  tests of proportions have one degree of freedom unless otherwise stated. Size variation was analysed with one-way and two-way ANOVA of  $\ln$ -transformed data. The relationship between wasp weight and the weight of the cicada prey they carried was assessed with reduced major axis regression of untransformed data, and the 95% confidence range was calculated by the method given in Rayner (1985).

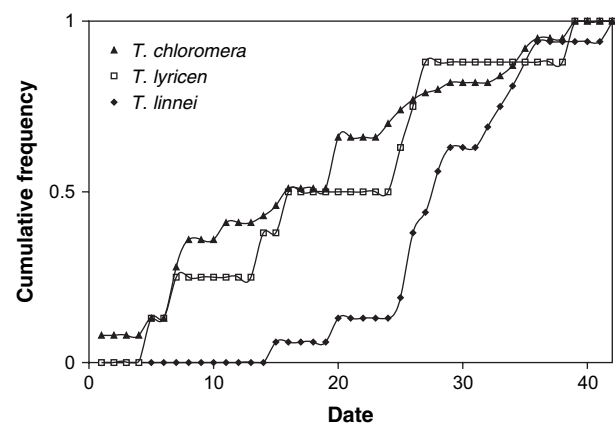
## Results

### Phenology

The main phenological patterns common to both years were relatively early emergence of the two larger cicada species *T. chloromera* (Walker) and *T. lyricen* (Deg.) (Fig. 1), and earlier emergence of males than females (protandry) in both cicadas and wasps. Protandry is demonstrated only with the largest sample of cicadas, *T. chloromera*, in 2005. Up to 3 August when observations ceased there were relatively few females in the environment (34.6%,  $n = 52$ ). Departure from an expected 1 : 1 sex ratio is too large to be attributed to chance (binomial  $P = 0.0376$ ). The first delivery of cicadas to nests was observed on 22 July in both 2004 and 2005. The smaller prey species *T. linnei* (Smith and Grossbeck) was first found on 30 July in 2004 and on 28 July in 2005. The main difference between years was a later emergence of *T. chloromera* and *T. lyricen* in 2004 (mid-July) than in 2005 (late June), which can possibly be attributed to nymphal interactions with the abundant periodical cicadas (*Magicicada* spp.) in 2004 (Oberdörster & Grant, 2006).

### Prey and predators

Five species of annual cicadas (*Tibicen*) and one periodical cicada (*Magicicada septendecim* Lin.) were brought to wasp nests (Table 1). Not all cicadas could be intercepted for weighing. Mean weights for samples are given in Table 2. On average female wasps were barely half as heavy (54%) as their two largest prey, *T. chloromera* and *T. lyricen*, and twice as heavy as male wasps (Table 2). They varied (0.50–1.37 g) more than males (0.31–0.56 g) and their coefficients of variation (0.228) were 66% greater than the coefficients of males (0.137) although not to a significant extent with weights transformed to  $\ln x + 1$  ( $F_{46,25} = 1.461$ ,  $P > 0.10$ ). Coefficients of variation of larval males (0.191) and females (0.195) were almost identical.



**Fig. 1.** Cumulative numbers of three species of prey during the nesting season of cicada-killer wasps in 2004. Killed and available prey numbers have been combined and then transformed ( $\ln x + 1$ ) to facilitate comparisons.

**Table 1.** Sex ratios of cicadas captured by wasps compared with those available in the environment and those excavated from nests. Numbers in italics are minima and the proportions are not considered reliable (see text).

	Environment		Captured		Nests	
	Males	Females	Males	Females	Males	Females
2004						
<i>T. chloromera</i>	13	15	18	14	44	8
<i>T. lyricen</i>	3	3	1	1	0	0
<i>T. linnei</i>	4	6	5	1	4	2
<i>M. septendecim</i>	0	0	0	1	0	0
2005						
<i>T. chloromera</i>	34	18	22	12	38	20
<i>T. lyricen</i>	11	8	1	2	3	5
<i>T. linnei</i>	6	2	3	0	5	11
<i>T. pruinosa</i>	1	1	0	0	0	0
<i>T. canicularis</i>	0	0	0	1	0	0

### Sex-biased predation

The possibility of disproportionate predation on one sex of prey was tested by comparing the proportions of males and females in the samples from wasp captures and from the environment. Each prey species was analysed separately because their phenologies differed to some extent. In 2004 there was no sex bias in the prey, either for *T. chloromera* ( $\chi^2 = 0.418$ ,  $n = 59$ ,  $P = 0.5178$ ) or *T. linnei* (Fisher's exact probability 0.3348,  $n = 17$ ). The small samples of *T. lyricen* give no indication of a sex bias either. Results in 2005, with larger samples, were the same; there was no difference in proportions of the two sexes in the samples of *T. chloromera* ( $\chi^2 = 0.000$ ,  $n = 86$ ,  $P = 0.9999$ ), *T. lyricen* ( $\chi^2 = 0.029$ ,  $n = 22$ ,  $P = 0.8649$ ) and *T. linnei* (Fisher's exact probability 0.9999,  $n = 11$ ). These results provide no support for the hypothesis of sex-selective predation.

As a second test, proportions of male and female prey in the samples from wasp nests in 2005 were compared with those from the environment; proportions of the sexes of prey excavated from 2004 nests (in 2005) are unreliable owing to extensive and variable deterioration. There was no difference in proportions of the two sexes in the samples of *T. chloromera* ( $\chi^2 = 0.000$ ,  $n = 110$ ,  $P = 0.9999$ ), *T. lyricen* ( $\chi^2 = 0.316$ ,  $n = 27$ ,  $P = 0.5739$ ) and *T. linnei* ( $\chi^2 = 2.538$ ,  $n = 24$ ,  $P = 0.1111$ ).

Predation occurred in proportion to prey availability under contrasting conditions in the two years. In 2004 the sex ratio of prey in the environment and in captures was approximately 1 : 1, whereas in 2005 males predominated in the sample of *T. chloromera* in the environment (0.65), in captures (0.65) and in nests (0.66). The ratios depart significantly from 1 : 1 in the sample from the environment (binomial test,  $z = 2.08$ ,  $P = 0.0376$ ) and in nests ( $z = 2.23$ ,  $P = 0.0258$ ) but not in the sample of captures ( $z = 1.54$ ,  $P = 0.1236$ ) owing to the smaller sample size.

### Species-biased predation

Wasps captured the three main cicada species, *T. chloromera*, *T. lyricen* and *T. linnei* (Table 1), in proportion to their frequencies in the environment, both in 2004 ( $\chi^2 = 3.083$ , d.f. = 2,  $P = 0.2140$ ) and in 2005 ( $\chi^2 = 3.630$ , d.f. = 2,  $P = 0.1629$ ).

### Size-biased predation

Independent of prey species and sex wasps may capture large cicadas preferentially. Because the *T. chloromera* sample is much larger than the rest it was used to test for a difference between

**Table 2.** Mean weights (g) of *Tibicen* and *Magiccada* prey and *Sphex* predators, with standard deviations (SD) and sample sizes ( $n$ ).

	Males			Females		
	$n$	Mean	SD	$n$	mean	SD
<i>T. chloromera</i>	56	1.66	0.155	46	1.80	0.225
<i>T. lyricen</i>	5	1.67	0.170	8	1.63	0.174
<i>T. linnei</i>	11	1.27	0.122	5	1.26	0.108
<i>T. canicularis</i>	–	–	–	1	1.10	–
<i>T. pruinosa</i>	–	–	–	1	1.43	–
<i>M. septendecim</i>	–	–	–	1	0.96	–
<i>S. speciosus</i> adults	25	0.44	0.060	36	0.91	0.207
<i>S. speciosus</i> larvae	31	0.61	0.117	10	1.55	0.302

early and late season (2004) weights of males and females in the environment. A two-way ANOVA showed no effect of time ( $F_{1,12} = 0.0535$ ,  $P = 0.4787$ ) when controlling for a difference between the sexes, therefore early and late season samples were combined. A possible difference in weights between cicadas found dead and captured alive was tested with the 2005 *T. chloromera* samples for an independent test. There was no difference between the samples ( $F_{1,25} = 1.067$ ,  $P = 0.3114$ ) after controlling for a sex difference, therefore the samples were combined.

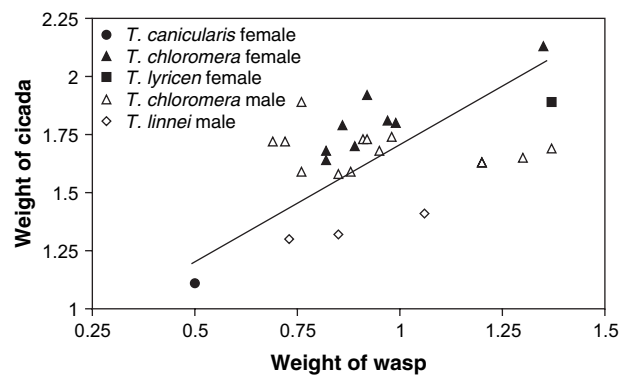
In 2004 weights of *T. chloromera* captured by wasps did not differ from those in the environment ( $F_{1,41} = 1.495$ ,  $P = 0.2285$ ) after controlling for a significant difference between the sexes ( $F_{1,41} = 6.908$ ,  $P = 0.012$ ; females heavier than males), and there was no significant interaction between sex and capture ( $F_{1,41} = 0.040$ ,  $P = 0.9508$ ). This result was duplicated in 2005, with a significant effect of sex ( $F_{1,53} = 9.531$ ,  $P = 0.0032$ ), but not capture ( $F_{1,53} = 0.396$ ,  $P = 0.532$ ) or an interaction between sex and capture ( $F_{1,53} = 0.931$ ,  $P = 0.3390$ ). Therefore the hypothesis of size bias in prey captured by wasps is not supported. Moreover it is not supported by the small samples of weights of the other species. The data are insufficient for sex-specific analysis. Tests of *T. lyricen* (2005) and *T. linnei* (both years) were negative ( $P > 0.1$ ) with one-way ANOVA.

#### Prey loads of individual wasps

In the absence of an overall size-bias in the prey there may none the less be a non-random tendency for small wasps to capture small prey and large wasps to capture large prey. If predators seek the maximum size of prey they can carry, variation in prey size should correlate with variation in predator size. This is supported by the result of an analysis of data from all prey species (Fig. 2). Support, however, is dependent on the inclusion of extreme values of prey weights. When the smallest prey individual (1.10 g) and its predator are excluded the slope of the relationship (0.93) does not differ from zero (95% confidence range;  $-0.305$  to  $2.55$ ). Similarly, when the largest prey individual (2.12 g) and its predator are excluded the slope of the relationship (0.97) does not differ from zero (95% confidence range;  $-0.597$  to  $2.34$ ). Weights of *T. chloromera* prey considered separately do not vary in proportion to the size of the wasps that carry them; slope = 0.64, confidence range is  $-2.07$ – $3.352$ .

Therefore, there is almost no support to the hypothesis of size-selective predation in relation to the predator's weight. Prey weights varied greatly, from 1.17 to 2.50 times heavier than their carriers (Fig. 3). Small predators appear to be constrained by their size more than large ones. Predators with the heaviest prey load relative to their own body size were the lightest ones. At the other end of the predator size spectrum only one of the four heaviest wasps carried a cicada above the mean weight of prey.

A second possible non-random tendency is for small and large wasps to differ in the sex of their prey. Wasps that carried male prey ( $n = 17$ ), however, were no different in average weight ( $0.911 \pm 0.210$  SD) from those that carried female prey ( $0.949 \pm 0.210$  SD,  $n = 10$ ;  $t_{25} = 0.452$ ,  $P = 0.6552$ ). The same applies to the subset that carried only the larger species *T. chloromera* and *T. lyricen* ( $t_{21} = 0.081$ ,  $P = 0.9364$ ).



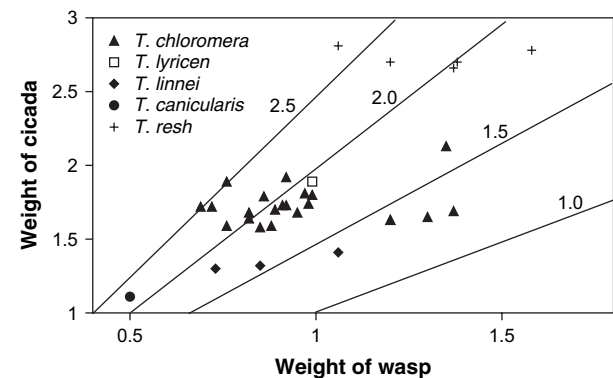
**Fig. 2.** Cicada prey weight in relation to the weight of their wasp predators. The reduced major axis regression has a slope of 1.00 and a 95% confidence range (0.11–1.89) entirely above zero. The relationship is no longer significantly different from zero when extreme values of prey weights are excluded (see text).

#### Offspring sex ratios

In both 2004 and 2005 three to four times as many male as female wasp larvae were produced (Table 3). Males predominated at all four nests with 10 or more offspring. There was no evidence of individual mothers specialising in the production of daughters. Only one of 51 cells with prey lacked a cocoon, therefore larval mortality was negligible and the observed ratio is a good estimate of the primary sex ratio.

The hypothesis that two female prey are required for the production of female offspring was not supported by the data. Three of 11 female wasp larvae were provisioned with only males. The remaining eight had one male and one female (five), one male and two females (one), two females (one), and one female prey (one).

The hypothesis that females require, and are provisioned with, more prey than males was supported. In the three nests in 2005



**Fig. 3.** Cicada prey weight in relation to the weight of their wasp predators, as in Fig. 2 but with the inclusion of five data points (crosses) from a study of *S. speciosus* and *T. resh* in Louisiana (Lin, 1979a). Slopes are drawn for prey-loadings of 1.0, 1.5, 2.0, and 2.5. Note that both predator and prey weights are larger at the Louisiana locality, but are largely confined to the zone of prey-loads bounded in the New Jersey study.

**Table 3.** Sex ratios of cicadas in excavated wasp nests, ranked by numbers per nest. It is assumed that each nest is owned by a different female, and that laying of eggs in more than one nest (Dambach & Good, 1943; Lin, 1963; Pfennig & Reeve, 1989), if it occurs, is rare and can be ignored.

Nests	2004			2005			
	Males	Females	Total	Males	Females	Total	Total
1	1	0	1	1	0	1	1
2	1	0	1	1	0	1	1
3	1	1	2	1	0	1	1
4	2	0	2	1	0	1	1
5	3	1	4	1	0	1	1
6	5	0	5	0	1	1	1
7	5	1	6	2	0	2	2
8	7	4	11	3	0	3	3
9	11	2	13	3	3	6	6
10				10	1	11	11
11				12	6	18	18
Total	36	9	45	35	11	46	46
Mean			5.1				4.1
SD			4.54				5.5
CV			0.89				1.33

SD, standard deviation; CV, coefficient of variation.

where both sexes of larvae were present nine of 10 female larvae were provided with two or more cicadas (mean  $\pm$  SD =  $2.0 \pm 0.47$ ), in contrast to 10 of 25 males ( $1.5 \pm 0.65$ ). The difference in proportions is significant (Fisher's Exact probability = 0.0098). There was no difference in species composition of prey given to male and female larvae. Both female (75%) and male larvae (61%) were provisioned predominantly with *T. chloromera*.

## Discussion

### Predation

Individual female wasps were estimated to visit the nesting grounds with prey on average once every 1.5 h at maximum in both 2004 and 2005 seasons, and usually much less frequently, which suggests that either they had difficulty finding or capturing prey (Hastings, 1986), or they were spending a long time hunting selectively. The basis of selectivity could be the size, sex and species of prey, either as independent or interacting factors. For example, choice of the largest prey could result in sex-biased and species-biased prey. Results of several statistical analyses, however, were consistent in showing that cicadas of different sizes, sexes and species were apparently captured in the same proportion in which they were encountered in the environment, in other words not selectively. The same results were obtained in two successive years. Therefore predation was, in general, random with respect to these three properties of the prey as a result of opportunistic, non-selective, hunting.

The acceptance of the default hypothesis must be qualified by acknowledgement that some prey samples (*T. lyricen* and *T. linnei*) were small, therefore some tests had relatively low statistical power. This limitation does not affect the main conclusion because samples of *T. chloromera*, and of the species combined, were large enough to detect small non-random effects. Moreover none of the

tests gave marginal, ambiguous, results, as all probability values were greater than 0.1, and most exceeded 0.5. A particularly striking result was a 1 : 1 sex ratio in the prey captured when the ratio in the environment was 1 : 1, but when the proportion of males in the environment was 0.65 it was also 0.65 in the captures. A similar conclusion of non-selective predation was reached by Coelho (1997) in a different geographical location (Indiana) and with a different prey composition. Apart from three very large *T. superba* (Fitch) the prey were all relatively small (*T. pruinosus* Say).

Random predation is qualified with 'in general' because some members of the wasp population may prey selectively. Wasps appear to be constrained to some extent in maximum prey load by their size-related power of flight because they sometimes drop their prey (Lin & Michener, 1972), and they have been observed to climb trees with their prey to gain height before flying back to the colony (Davis, 1920; Dambach & Good, 1943). Lin and Michener (1972) suggested that large wasps carry heavy prey, and are more successful foragers than smaller ones (Lin, 1963; Hastings, 1986; Pfennig & Reeve, 1989), whereas intermediate ones carry only light prey, and small ones carry neither. Data from the present study are not entirely consistent with these suggestions; both large and small females carried small prey items. Actual prey weights in excavated nests could not be determined, but none of the nests were filled predominantly with female prey, which would have indicated specialisation by large wasps. Nevertheless, the data on prey weights are consistent with the idea that small wasps are constrained by their size to prey on small cicadas.

At the lowest weights wasps are constrained to carry prey that are no more than 2.5 times their weight (Fig. 2). With rare and minor exceptions the 2.5 'rule' holds in another geographical location (Lin, 1979a) where both wasp and cicada weights are on average higher (Fig. 3) presumably as a result of an evolutionary adjustment of wasp size to larger prey (see also Coelho, 1997).

The smallest female (0.50 g) in the study reported here carried a *T. canicularis* (Harr.) individual weighing 1.10 g, which is close to the maximum prey size of 1.25 g for a wasp of this weight. Of the total of 131 cicadas weighed, only seven (5.3%), all *T. linnei*, had weights below 1.25 g and were thus available to this wasp. By the same calculations the next two heaviest female wasps, both weighing 0.58 g, could have carried only 20.6% of available prey. Neither of them was recorded carrying prey. The only other small wasp without prey weighed 0.65 g and could have carried most (58.8%) of the available prey. All these small wasps were at a selective disadvantage. As judged by their weights the full range of cicadas were potential prey for the remainder, 26 of 36 (72.2%) females that were weighed.

Thus some degree of prey selectivity was shown by some of the wasp population, forced on them by mechanical constraints, but it was not pronounced or common enough to generate an overall bias in the prey. Sex ratios of offspring are not biased through selective hunting and provisioning, either on the basis of size or sex of the prey.

#### *Geographical variation in predation*

Biases in species of prey, and size independent of sex, have not been reported, but sex-biased predation has been inferred at other locations (Riley, 1892; Davis, 1920; Dow, 1942; Dambach & Good, 1943; Hastings, 1986). According to Evans (1966, p. 104) 'nearly everyone who has worked on the cicada killer has noted that more females than males are taken.' Dambach and Good (1943) found 204 males and 499 females among the prey recovered by digging up a colony at the end of the nesting season in Ohio, and Dow (1942) found 24 males and 44 females by the same method in Massachusetts. These values of 71% and 65% females respectively, deviate from an expected 50% too much to be explained by sampling error (binomial  $P < 0.001$  and  $P = 0.0208$  respectively; my calculations). Eight of 10 cicadas captured by wasps in a study in Louisiana were females (Lin, 1979a). Prey availability was not known in any of these studies. The consistent results stand in marked contrast to the unbiased or male-biased ratios of cicadas found in the present study, and requires an explanation.

First, there may be a truly biased sex ratio in some prey populations but not in others. Second, sexual size dimorphism in prey may be greater at some locations (e.g. Ohio and Massachusetts) than at others (e.g. New Jersey), and the potential for sex-preferential predation may vary correspondingly. Third, wasp emergence may be relatively late at some locations, and in some years (e.g. Hastings, 1986, 1989), with predation then falling most heavily on female prey because they tend to emerge later than males. There are 'good' years and 'bad' years for wasps (Lin, 1979a), and these do not necessarily coincide with 'good' years and 'bad' years for cicadas (Hastings, 1986). Fourth, at some locations female cicadas may be more vulnerable to predators than males because they are generally larger on average than males, although not in all species (Table 2; see also Hastings, 1986), more nutritious (Coelho, 1997), live longer, fly less (Dow, 1942) and are necessarily restricted in movement when ovipositing on thin branches of trees (Dambach & Good, 1943).

#### *Male-biased offspring sex ratio*

The proportion of males in the total samples of wasp larvae was 0.80 (2004) and 0.76 (2005). Male bias can be explained by Fisher's equal investment hypothesis, taking account of sexual size dimorphism and the reasoning that numbers of offspring of each sex are produced in proportion to their respective costs (Charnov, 1982; Frank, 1987; Crozier & Pamilo, 1993). Costs are approximated by weights in the absence of direct measurements such as energy expended in hunting for cicadas, digging burrows and constructing cells, and carrying cicadas of varying weights and for varying distances to the burrows (Danforth, 1990; Helm, 1994; but see Visscher & Danforth, 1993; Strohm & Linsenmaier, 1999). The numerical ratio of male to female offspring should be inversely proportional to their respective weights (Paini & Bailey, 2002).

In the present study, the proportion of males should be 0.68 on the basis of adult weights, 0.72 on the basis of larval weights, or slightly less than both if costs are overestimated by weight more in the (larger) females than males (Helm, 1994). Observed proportions of 0.80 and 0.76 are similar to these expectations. A more detailed study with much larger samples would be required to establish whether the small deviations from expectation are significant, but it is notable that, as in several other aculeate hymenoptera (Strohm & Linsenmaier, 1999), they are in the direction of male bias. To account for such observations it has often been suggested that equal investment may be modified by a facultative response to seasonal scarcity of food resources (Trivers & Willard, 1973; Torchio & Tepedino, 1980; Tepedino & Torchio, 1982; Charnov, 1982; Strickler, 1982; Frohlich & Tepedino, 1986; Frank, 1987, 1995; Strohm & Linsenmaier, 1997; Kim, 1999; Paini & Bailey, 2002; Bosch & Vicens, 2005). When resources are scarce, or rearing conditions are poor, females should tend to overproduce the smaller and energetically less-demanding sex (Myers, 1978), which is usually, but not always, the male (O'Neill, 2001; Paini & Bailey, 2002). This may have happened in the present study because cicada numbers declined in the second half of the season, and so did average weights as the smaller species (*T. linnei*) increased in frequency (Fig. 1). Thus, some degree of environmental dependence is to be expected in offspring sex ratios.

#### *A behavioural model of sex allocation*

Part of the environmental dependence of offspring sex ratios derives from the uncertainty that female wasps experience in how long it will take them to find a cicada prey, and the size of it. A female has two binary choices; first, collect only one cicada (and lay a haploid egg) or two cicadas, and second, if two cicadas are collected then lay a haploid or diploid egg. In the face of resource uncertainty an equal probability rule at each choice would meet the need of a female to provide a minimum of two cicada prey for the development of female offspring in this sexually dimorphic system. It would yield a sex ratio ( $\approx 3 : 1$ ) that reflects approximately equal investment at the population level while allowing for variation among families.

Female cicada-killer wasps have been reported to construct a cell before they hunt (Dambach & Good, 1943). Thus, a simple rule would be to construct a small cell with a 50% probability; if it is a small cell it will be supplied with one cicada on which a haploid egg will be laid. For the large cell supplied with two or more cicadas the rule is to lay a haploid egg with 50% probability. Though individual ratios will vary through sampling variation the population's proportion of males should approximate 0.75. This value is close to the observed values of 0.80 and 0.76.

The binary choice model is supported by the larval sex frequencies when analysed in association with prey numbers. In 2005, half of 46 cells with cicadas had a single prey (0.50), as expected, and all but one had male larvae. Thirteen of the remainder (0.57) with two or more cicadas had male larvae; the frequency is close to an expected 0.50. The only other complete study of offspring sex ratios, by Dow (1942) in Massachusetts, gives similar results. Twenty-one of 39 cells (0.54) had a single cicada, from which only males emerged, and nine of the remaining 18 cells (0.50) with at least two cicadas had male larvae. The proportion of males in total was 0.77. In Dambach and Good's (1943) study, 49 cells were supplied with a single cicada, and as expected approximately half this number (24) of cells with two cicadas produced female offspring. Unfortunately, the number of cells with two or more cicadas that produced male offspring was not reported so the total is unknown.

Thus, aside from this incomplete report values close to 0.75 were observed in two studies, one (Dow's) with a female bias in the prey and the other two in a study with no sex bias in the prey in one year (2004) and a male bias in another (2005). Prey sex ratios vary geographically, whereas wasp offspring sex ratios apparently do not. This implies that the binary choice mechanism operates independently of variation in prey sex ratios. The calculations ignore the minor complication that occasionally (< 5%) a diploid egg is laid on a single cicada; one of 23 (present study) and two of 49 (Dambach & Good, 1943).

The first eggs laid by cicada-killer wasps are apparently haploid, as inferred from the relatively peripheral position of small cells in the burrows (Lin & Michener, 1972). Further research is needed into mechanisms governing the switch from haploid to diploid egg production. An external cue such as rate of prey capture or prey size might activate an internal, neurohumoral, switch mechanism, causing or inhibiting fertilization, which is known to occur as the egg moves past the spermatheca before oviposition (Flanders, 1956) or during oviposition itself (Gerber & Klostermeyer, 1970). Size of prey could be assessed by weight in relation to the carrier's weight (Fig. 3) and hence ability to carry the prey. Given temporal variation in resources, the proportion of male wasps produced will not be fixed but will vary as a joint function of predator weights and prey weights (e.g. Cowan, 1981; Freeman, 1981; Molumby, 1997; Strohm & Linsenmaier, 1999; see also Frohlich & Tepedino, 1986).

The binary choice model may be usefully applied to other species of solitary bees and wasps because many are known to provision young sex-specifically with pollen or arthropod food (O'Neill, 2001). The choice rule itself is expected to vary because different species experience different temporal patterns of resource availability and predictability. This variation should

lead to different optimal rules of allocation, which could be exploited in comparative tests of the model. Two candidates for tests are *Ammophila* and *Philanthus*, as they show contrasting non-random patterns of haploid and diploid egg laying in relation to food quantity. Female *Ammophila sabulosa* (L.) lay haploid and diploid eggs with equal probability (0.50) when cells are provided with one, always large, caterpillar, and predominantly haploid eggs (0.94) in cells with two to five caterpillars of varying size (Field, 1992). In contrast European bee wolves (*Philanthus triangulum* F.) lay only haploid eggs in cells with one or two honeybee prey (*Apis mellifera* L.), and a high frequency of diploid eggs in cells with three (0.55) or four (0.84) bees (data in Strohm & Linsenmaier, 1999).

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