Oecologia (1997) 110:218–221

P. J. Mayhew · H. C. J. Godfray

Mixed sex allocation strategies in a parasitoid wasp

Received: 6 June 1996 / Accepted: 13 October 1996

Abstract The sex allocation strategy of the parasitoid *Laelius pedatus* (Hymenoptera: Bethylidae) on different-sized hosts was investigated. The wasp lays from one to five eggs, and clutch size increases with host size. On the smallest hosts, single male eggs are laid, while on slightly larger hosts single female eggs are laid. On still larger hosts, gregarious clutches are laid which nearly always consist of a single male and one or more female eggs. The sex ratio strategy of the wasp appears to be influenced by a combination of local mate competition and conditional sex expression based on host quality.

Key words Parasitoid · Sex ratio · Bethylidae · Clutch size · Reproductive strategy

Introduction

The two most important factors that lead to adaptive sex ratios among parasitoid wasps are local mate competition (Hamilton 1967) and conditional sex expression (Trivers and Willard 1973; Charnov 1979; Charnov et al. 1981). In the former, wasps are selected to produce a female-biased sex ratio if their sons are likely to compete among themselves for mates (including their sisters). The second factor applies chiefly to solitary wasps where only one individual develops in each host. Wasps are frequently observed to lay female eggs in large hosts and male eggs in small hosts. In these species, adult wasp size depends strongly on host size and it seems likely that females gain greater marginal benefits than males from increased adult size. Many parasitoid wasps are gregarious, with more than one larva (sometimes several hundred) developing on a single host and competing for fixed resources. As predicted by clutch size theory, female wasps normally lay more eggs on larger hosts, and tend to lay more eggs in circumstances where hosts are rare and so alternative oviposition sites are unlikely to be encountered (Charnov and Skinner 1984; Hardy et al. 1992; Vet et al. 1994).

Several authors have suggested that selection on clutch size and sex ratio may be interdependent (reviewed in Godfray 1994). Williams (1979) predicted that if the mating structure of the population is panmictic and males and females suffer to different degrees from resource competition, then as the available resources increased, the parent would produce a fixed sequence of brood combinations. Brood composition would thus depend critically on resource availability, leading to highly variable brood sex ratios. However, if mating is not panmictic but takes place solely between members of a single clutch, just enough males should be produced to fertilize all their sisters, leading to a low variance in brood sex ratio (Hamilton 1967; Green et al. 1982; Hardy 1992). As males are typically able to inseminate many females, the best strategy is often to lay a single male egg in each clutch (Griffiths and Godfray 1988). More than one male may be optimal in large clutches if there is a risk of immature-male mortality (Heimpel 1994; Nagelkerke and Hardy 1994), while less than one per clutch may occur if hosts are aggregated and mating occurs among the individuals developing on several hosts (Waage and Ng 1984).

Here we explore the relationship between clutch size and sex ratio in *Laelius pedatus* Say (Hymenoptera: Bethylidae), a parasitoid of dermestid beetles (Coleoptera: Dermestidae), whose clutch size ranges from one to about five (Mertins 1980; Klein and Beckage 1990, Klein et al. 1991; Morgan and Cook 1994). *L. pedatus* is an ectoparasitoid whose larvae feed with their heads embedded in the paralyzed body of their host. Other workers have shown that the clutch size laid by the wasp is strongly influenced by host size (Mertins 1980; Klein et al. 1991). Furthermore, in gregarious clutches, the wasp produces a sex ratio that is approximately equal to

---

P.J. Mayhew · H.C.J. Godfray (✉)

Department of Biology and NERC Centre for Population Biology,
Imperial College at Silwood Park,
Ascot, Berks SL5 7PY, UK
fax: 01344 294339; e-mail: c.godfray@ic.ac.uk

the reciprocal of clutch size, consistent with local mate competition occurring amongst the members of single broods (Mertins 1980; Morgan and Cook 1994). This pattern is typical across the Bethylidae as a whole (Griffiths and Godfray 1988). In *L. pedatus*, offspring from different mothers almost never develop on the same host because if a female encounters a host bearing a clutch of eggs, she destroys them prior to laying her own clutch (P.J. Mayhew, in preparation). Because the wasp lays both solitary and gregarious clutches there is the potential for interesting interactions between clutch size and sex ratio, but the sex allocation of the wasp in solitary clutches has never been investigated. Here we describe the sex allocation strategy of the wasp over the complete range of host and clutch sizes.

Materials and methods

The host used in this study was *Anthrenus flavipes* (Leconte) which we obtained from the Central Science Laboratories, Slough, UK. Our wasps came originally from the USDA (Hoboken, N.J.) and had been cultured for a number of generations in the U.K. by D.J.W. Morgan. Hosts were reared on a diet of fishmeal, yeast and cholesterol. Both cultures and experiments were maintained at 27°C and 70% humidity under a light:dark 14h:10h photoperiod.

A total of 181 hosts of different weight were placed individually in 3-cm petri dishes lined with filter paper. Single mated female wasps, 0–1 day old and with no prior experience of hosts, were introduced to each petri dish and checked daily until oviposition occurred. The female was then removed, the clutch size recorded, and the offspring left to develop. The date of emergence and size (thorax length) of all offspring were recorded. Fifteen broods were excluded from the analysis because all offspring died. However, even including these broods, total juvenile mortality was low (mean ± standard error: 13.2 ± 2.2%).

The data were analysed using generalized linear modelling techniques implemented in the GLIM statistical package. We assumed Poisson error variance for clutch size data, and binomial error variance for sex ratio data. We refer to sex ratio as the proportion of males.

Results

Clutch size increases with host weight. The relationship is highly significant ($n = 181$, $\chi_1^2 = 81.0$, $P < 0.001$) and explains 74.1% of the deviance about the mean. This significance level is, in fact, conservative, as the magnitude of the residual deviance is only 16% of that expected under the Poisson distribution. This indicates that the wasps are adopting a very precise clutch size strategy.

Fig. 1 shows the number of males per clutch as a function of host size. Broods in which there has been partial mortality are distinguished. Wasps tend to lay single male eggs on the very smallest hosts, single female eggs on slightly larger hosts, and clutches of one male and a variable number of females on larger hosts, although the host sizes on which the three categories of clutch are found overlap considerably. The probability of a male occurring decreases with increasing host size in solitary clutches (n = 55, $\chi_1^2 = 31.3$, $P < 0.001$, 42.7% deviance explained). The relationship is significant even when it is assumed that all individuals which died on hosts less than 0.6 mg were female, and greater than 0.6 mg were male ($\chi_1^2 = 16.63$, $P < 0.001$) (i.e. assuming the strongest possible differential mortality acting against the relationship). For gregarious clutches, the number of males in the brood is unrelated to either host weight or clutch size ($n = 111$; host weight: $\chi_1^2 = 0.13$, $P > 0.1$; clutch size: $\chi_1^2 = 0.05$, $P > 0.1$). The fact that male number is unrelated to clutch size in gregarious broods necessarily implies that the sex ratio decreases with clutch size ($\chi_1^2 = 7.86$, $P < 0.01$, 18.6% deviance explained). The same results are found if only those gregarious broods in which all wasps survived are included in the analysis ($\chi_1^2 = 6.77$, $P < 0.01$, 35.1% deviance explained). In an analysis of covariance, wasp size (measured as the cube of thorax length) increased with

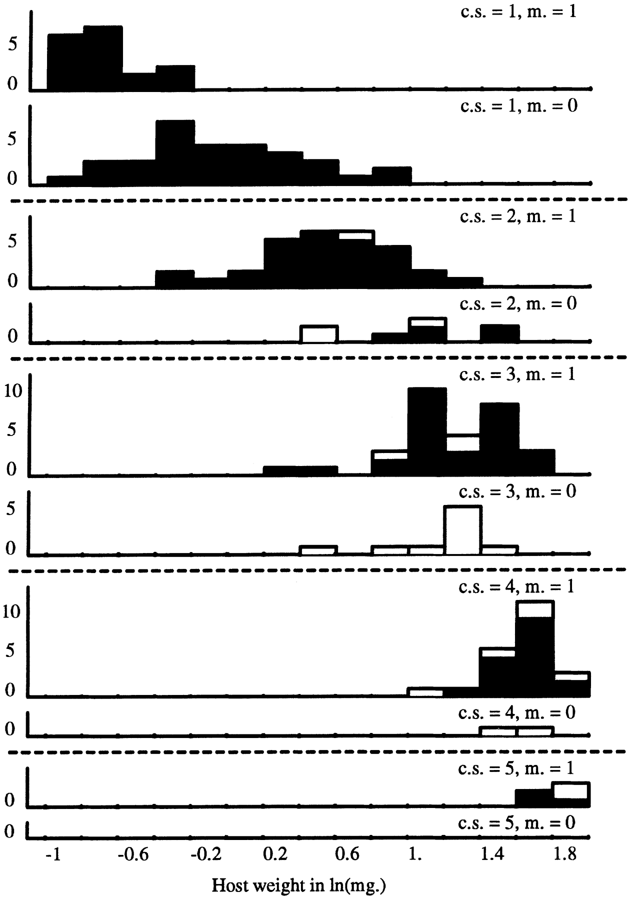

Fig. 1 The relationship between clutch composition and host weight. Clutches consisted of up to five wasps and the frequency distribution of host weights on which different clutch sizes were laid are displayed as five pairs of histograms separated by *dashed lines*. For each clutch size (*c.s.*), the top histogram represents hosts from which a single male emerged (*m = 1*) and the bottom histogram clutches from which no males emerged (*m = 0*). In only a single case did more than one male emerge from a brood – a clutch of three eggs laid on a host of 1.2 ln(mg) – and this is omitted from the figure. Clutches of eggs from which all wasps survived are shown in *black* while those that suffered partial mortality are shown in *white* (clutches where all wasps died are omitted)

host weight in solitary broods ($F_{1,54} = 30.4$, $P < 0.01$, $r^2 = 0.56$), but neither wasp sex nor the interaction between wasp sex and host size was significant.

Discussion

There have been few studies on how conditional sex expression and local mate competition operate simultaneously in the same species. Werren (1984a), Werren and Simbolotti (1989) and Ikawa et al. (1993) have considered species which attack hosts distributed in patches and where one parasitoid develops per host (solitary parasitoids). The sex ratio strategy of the female is influenced by both the probability of mating between siblings and by the fitness consequences of placing either sex in different-sized hosts. Such models have helped explain the reproductive strategies of a number of parasitoids of stored-product pests (Werren and Simbolotti 1989; Brault 1991; Ikawa et al. 1993).

In *L. pedatus*, local mate competition and conditional sex expression combine in a different fashion. The wasp is semi-gregarious (Werren 1984b), with some individuals developing as solitary parasitoids alone on the host and others developing gregariously in clutches of two to five (and possibly more on other hosts; Klein and Beckage 1990). Females from gregarious clutches appear always to be mated by their brothers soon after or even before emergence (Morgan and Cook 1994) and the host might thus be considered a patch in Hamilton's sense with a foundress number of one. Theory predicts that the parent should lay just enough males to inseminate the females in the brood, which in these small clutches is probably just a single male. However, wasps also develop alone where they are not guaranteed an opportunity to mate immediately after emergence. Females laying solitary eggs on a host deposit male eggs on the smallest hosts and female eggs on relatively larger hosts, probably because females gain proportionally more from large hosts (see below). As host size further increases and larger clutches are selected, the progression of sex ratio combinations predicted by Williams (1979) does not occur because it is overridden by the effects of local mate competition.

Charnov's (1979) explanation for the observation that many parasitoids lay male eggs on relatively small hosts (1) predicts a threshold host size below which only males, and above which only females are laid, and (2) assumes that the rate of gain of fitness with increasing host size is greater for females than males. Fig. 1 shows that while there is a reasonably sharp switch in behaviour at a host weight of about 0.6 mg, it is not a discrete threshold. In fact, sharp thresholds are exceedingly rare among parasitoids (Godfray 1994). Blurred transitions may occur if wasps use host cues that are subtly different from those measured by the experimenter, or if individual wasps that differ in size or in their past experience are selected to adopt slightly different strategies (Charnov et al. 1981). That male fitness is less influenced by host size than female fitness is widely assumed because male mating success is less likely to be influenced by size than are the factors that limit female fecundity (e.g. van den Assem et al. 1989). In *L. pedatus,* wasp size increases with host size, and longevity increases with wasp size in the laboratory (Mayhew 1996). However, at present, investigations have been limited to the laboratory which may not be representative of conditions in the field (e.g. Hardy et al. 1992; Visser 1994; West et al. 1996). There are as yet no field studies of the size/fitness relationship for both sexes of species with conditional sex expression.

An important question which arises from these results is how the wasp sex allocation strategy relates to mating structure in natural populations. The sex ratios in gregarious broods are typical of locally mating species. However, offspring from solitary broods must necessarily mate with individuals from other broods. This implies that the mating structure is a mixture of panmixis and local mating (Nunney and Luck 1988; Hardy 1994). Hinton (1943, 1945) showed that hosts tend to occur in discrete patches in the field, which suggests that mating might occur between members of different broods, but as yet there is no hard evidence. An understanding of the mating structure of *L. pedatus*, and of other parasitoids (Antolin and Strand 1992), under natural conditions must be the next step towards understanding their sex ratio strategies.

Acknowledgements We thank Dr. D. Morgan for donating the insect cultures, and Drs. J. Cook, I. Hardy, L. Kraaijeveld, C.M. Lessells and C. Müller for comments on the manuscript. P.J.M. was supported by a NERC studentship.

References

Antolin MF, Strand MR (1992) Mating system of *Bracon hebetor* (Hymenoptera: Braconidae). Ecol Entomol 17: 1–7

Assem J van den, Iersal JJA van, Los-den Hartogh RL (1989) Is being large more important for female than for male parasitic wasps? Behaviour 108: 160–195

Brault S (1991) Host choice and offspring sex allocation in a solitary parasitic wasp. Behav Ecol Sociobiol 29: 353–360

Charnov EL (1979) The general evolution of patterns of sexuality: Darwinian fitness. Am Nat 113: 465–480

Charnov EL, Skinner SW (1984) Evolution of host selection and clutch size in parasitoid wasps. Folia Entomol 67: 5–21

Charnov EL, Los-den Hartogh RL, Jones WT, Assem J van den (1981) Sex ratio evolution in a variable environment. Nature 289: 27–33

Godfray HCJ (1994) Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton

Green RF, Gordh G, Hawkins BA (1982) Precise sex ratios in highly inbred parasitic wasps. Am Nat 120: 653–665

Griffiths NT, Godfray HCJ (1988) Local mate competition, sex ratio and clutch size in bethylid wasps. Behav Ecol Sociobiol 22: 211–217

Hamilton WD (1967) Extraordinary sex ratios. Science 156: 477–488

Hardy ICW (1992) Non-binomial sex allocation and brood sex ratio variances in the parasitoid Hymenoptera. Oikos 65: 143–158

Hardy ICW (1994) Sex ratio and mating structure in the parasitoid Hymenoptera. Oikos 69: 3–20

Hardy ICW, Griffiths NT, Godfray HCJ (1992) Clutch size in a parasitoid wasp: a manipulation experiment. J Anim Ecol 61: 121–129

Heimpel GE (1994) Virginity and the cost of insurance in highly inbred Hymenoptera. Ecol Entomol 19: 299–302

Hinton HE (1943) Natural reservoirs of some beetles of the family Dermestidae known to infest stored products, with notes on those found in spider webs. Proc R Entomol Soc Lond A 18: 33–42

Hinton HE (1945) A monograph of the beetles associated with stored products, vol 1. British Museum (Natural History), London

Ikawa T, Shimada M, Matsuda H, Okabe H (1993) Sex allocation of parasitic wasps: local mate competition, dispersal before mating and host quality variation. J Evol Biol 6: 79–94

Klein JA, Beckage NE (1990) Comparative suitability of *Trogoderma variabile* and *T. glabrum* (Coleoptera: Dermestidae) as hosts for the ectoparasite *Laelius pedatus* (Hymenoptera: Bethylidae). Ann Entomol Soc Am 83: 809–816

Klein JA, Ballard DK, Lieber KS, Burkholder WE, Beckage NE (1991) Host developmental stage and size as factors affecting parasitization of *Trogoderma variabile* (Coleoptera: Dermestidae) by *Laelius pedatus* (Hymenoptera: Bethylidae). Ann Entomol Soc Am 84: 72–78

Mayhew PJ (1996) Ecological studies of insect reproductive behaviour. PhD thesis, University of London

Mertins JW (1980) Life history and behaviour of *Laelius pedatus*, a gregarious bethylid ectoparasitoid of *Anthrenus verbasci*. Ann Entomol Soc Am 73: 686–693

Morgan DJW, Cook JM (1994) Extremely precise sex ratios in small clutches of a bethylid wasp. Oikos 71: 423–430

Nagelkerke CJ, Hardy ICW (1994) The influence of developmental mortality on optimal sex allocation under local mate competition. Behav Ecol 5: 401–411

Nunney L, Luck RF (1988) Factors influencing the optimal sex ratio in structured populations. J Theor Biol 33: 1–30

Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. Science 179: 90–92

Vet LEM, Datema A, Janssen A, Snellen H (1994) Clutch size in a larval pupal endoparasitoid – consequences for fitness. J Anim Ecol 63: 807–815

Visser ME (1994) The importance of being large – the relationship between size and fitness in females of the parasitoid *Aphaereta minuta* (Hymenoptera, Braconidae). J Anim Ecol 63: 963–978

Waage JK, Ng SM (1984) The reproductive strategy of a parasitic wasp. I. Optimal progeny allocation in *Trichogramma evanescens*. J Anim Ecol 53: 401–415

Werren JH (1984a) A model for sex ratio selection in parasitic wasps: local mate competition and host quality effects. Neth J Zool 34: 123–143

Werren JH (1984b) Brood size and sex ratio regulation in the parasitic wasp *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae). Neth J Zool 34: 123–143

Werren JH, Simbolotti G (1989) Combined effects of host quality and local mate competition on sex allocation in *Lariophagus distinguendus*. Evol Ecol 3: 203–213

West SA, Flanagan KE, Godfray HCJ (1996) The relationship between parasitoid size and fitness in the field, a study of *Achrysocharoides zwoelferi* (Hymenoptera, Eulophidae). J Anim Ecol 65: 631–639

Williams GC (1979) The question of adaptive variation in sex ratio in out-crossed vertebrates. Proc R Soc Lond B 205: 567–580