

This is an electronic version of an article published in *Oecologia*:

King, B.H. 1989. Host size-dependent sex ratios among parasitoid wasps: Does host growth matter? *Oecologia* 78:420-426.

Host-size-dependent sex ratios among parasitoid wasps: Does host growth matter?

B. H. King, Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221

Summary. Waage's (1982) hypothesis that host-size-dependent sex ratios will occur in parasitoids of nongrowing hosts and not in parasitoids of growing hosts is examined using published data on parasitoid wasps. Waage's hypothesis is supported as a general, but not absolute, rule: among solitary parasitoid wasps, a significantly greater proportion of parasitoids of nongrowing than of growing hosts show some evidence of host-size-dependent sex ratios (85% versus 45%, $G = 5.28$, $p < 0.05$). The premise of Waage's hypothesis--that for parasitoids which develop in a growing stage, host size at oviposition is not a good predictor of the amount of resources available to the developing parasitoid--is also examined. It is suggested that across host species Waage's premise will hold for some, but not all, parasitoids of growing hosts. Likely exceptions to Waage's premise, and thus his prediction, are discussed. Parasitoids of growing hosts which are expected to have evolved host-size-dependent sex ratios include parasitoids which utilize a narrow size range of host species, parasitoids which can distinguish among host species by some criterion other than size, and parasitoids which utilize host species whose susceptible instars do not overlap in size.

Key Words: sex ratio, parasitoid wasps, host size

The possibility that mothers may manipulate their offspring sex ratio (proportion sons) has been investigated in a variety of taxa (reviewed in Charnov 1982). One factor which mothers may manipulate in response to is resource availability. That such manipulation might be adaptive was first suggested for polygynous mammals in verbal arguments (Trivers and Willard 1973) and has since been modelled formally for parasitoid wasps (Charnov 1979; Charnov et al. 1981; Werren 1984). Most parasitoid wasps have haplodiploid sex determination whereby unfertilized eggs develop into males and fertilized eggs into females. Haplodiploidy provides a mechanism by which females can potentially manipulate their offspring sex ratio. In addition, it is generally easy to measure resource availability for parasitoid wasps by determining host size or age. Evolutionary models designed to explain maternal manipulation of offspring sex ratio in response to host size (referred to as host-size models) predict that a greater proportion of females will be oviposited in large than in small hosts. This prediction has been supported for most, but not all, species of parasitoid wasps examined (King 1987 and below). Host-size models assume that sex-ratio manipulation is an adaptation selected for by a differential effect of host size on the fitness of female versus male wasps (Charnov 1979; Charnov et al. 1981; Werren 1984). For example, wasps may be larger when they develop on larger hosts, and being large may have a more positive effect on the fitness of female wasps than of males.

This paper is an examination of Waage's (1982) hypothesis that sex ratio manipulation in response to host size is expected to occur only in species which develop in non-growing hosts. Specifically, Waage (1982) stated that, "size-dependent sex ratios are to be anticipated in parasitoids which attack a non-growing host stage (i.e. egg or pupa) or which paralyze their hosts (many larval ectoparasitoids), but not in parasitoids which develop in a growing stage (egg-larval or larval endoparasitoids), for which host size is not a good predictor of larval resources." Parasitoids which parasitize non-growing host stages--egg parasitoids, pupal parasitoids, and larval parasitoids which paralyze their hosts--are referred to as "idiophytic". Parasitoids which parasitize growing host stages--egg-larval parasitoids and larval parasitoids which do not paralyze their hosts--are referred to as "koinophytic" (Haeselbarth 1979). I examine the validity of the prediction of Waage's hypothesis as well as the basic premise--that for koinophytic parasitoids, host size at oviposition is not a good predictor of the amount of resources available to a developing wasp. I show that there are exceptions to the hypothesis, but that the available data suggest that a greater proportion of idiophytic than koinophytic species exhibit host-size-dependent sex ratios.

Materials and methods

Data used to test the prediction and the premise of Waage's hypothesis were obtained primarily from published reports of laboratory studies. Only studies which had information on host size at the time of oviposition were included. Pupal and egg parasitoids were classified as idiophytic. Larval parasitoids were classified as idiophytic if the author noted that the host was paralyzed or killed at the time of oviposition or if parasitized hosts were not fed. Larval parasitoids were classified as koinophytic if the author mentioned that the hosts were provided with food after being exposed to parasitization or if the author stated that the hosts continued to grow.

In the studies discussed here, wasps parasitizing different-sized hosts may be parasitizing 1) different-sized hosts within a host species, 2) host species of different sizes, 3) sexes within a host species with sexual size dimorphism, or 4) different-aged hosts for larval and nymphal hosts. Larvae and nymphs feed and so increase in size and provide more resources with increasing age. Host-size models predict a negative relationship between host size and parasitoid sex ratio, and I took such a relationship as evidence of host-size-dependent sex ratio.

Host-size-dependent sex ratios have been considered to be a phenomenon of solitary species (one parasitoid completes development on a host) (e.g., Charnov et al. 1981; Werren 1984; Charnov and Skinner 1985). This is because in gregarious species (more than one parasitoid completes development per host) the relationship between wasp offspring size and host size may be confounded by a relationship between the number of eggs oviposited per host and host size (e.g., Abdelrahman 1974). Nevertheless, there may be selection for sex ratio manipulation in response to host size in gregarious species if host size affects wasp size or development time (King 1987). For this reason, in addition to solitary species, I have also considered gregarious species and facultatively gregarious species (sometimes one and sometimes more than one wasp completes development on a host).

Results and discussion

The Prediction of Waage's Hypothesis

Data on the relationship between host size and parasitoid offspring sex ratio were obtained for 11 solitary koinophytic parasitoids and 29 idiophytic parasitoids--20 solitary, 3 facultatively gregarious, and 6 gregarious (Table 1). There is some evidence of the predicted negative relationship between host size and wasp sex ratio for 5 of 11 (45%) of the koinophytic parasitoids, 17 of 20 (85%) of the solitary idiophytic parasitoids, 2 of 3 (67%) of the facultatively gregarious idiophytic parasitoids, and 2 of 6 (33%) of the gregarious idiophytic parasitoids. Results with the idiophytic parasitoids suggest that host-size-dependent sex ratios may be more common in solitary than in gregarious species, as expected (see Materials and methods); however, the number of gregarious species which have been examined is very small. Looking just at the solitary parasitoids, a significantly greater proportion of idiophytic than koinophytic species show some evidence of host-size-dependent sex ratio ($G = 5.28$, $P < 0.05$).

The presence of the predicted negative relationship between host size and wasp sex ratio by itself is not definitive evidence for sex ratio manipulation because such a relationship may be a result of differential mortality between the sexes rather than a result of maternal manipulation. Among the species for which differential mortality has been ruled out (and hence it is certain that females manipulate offspring sex in response to host size) are five idiophytic and three koinophytic parasitoids (Table 1). Exceptions to Waage's prediction include: *Heterospilus prosopidis*, a koinophytic solitary parasitoid which does manipulate sex ratio in response to host size, and *Spalangia endius*, an idiophytic solitary parasitoid which does not manipulate sex ratio in response to host size.

One might argue that the species examined are not all independent samples because of phylogenetic relationships. However, host-size-dependent sex ratios do not appear to be phylogenetically constrained. For example, within *Aphidius* and *Spalangia* some species do and others do not exhibit a negative relationship between host size and wasp sex ratio (Table 1).

The Premise of Waage's Hypothesis

The premise of Waage's hypothesis--that for koinophytic parasitoids, host size at oviposition is not a good predictor of the amount of resources available to a developing wasp--is incorrect on a within host species basis. Even for koinophytic parasitoid wasps, within a host species, host size at the time of oviposition seems to be a good indicator of the amount of resources available to a developing parasitoid. It is true that parasitization changes the growth rate of larval hosts even in the absence of host paralysis: solitary parasitoids generally reduce host growth rate, and gregarious parasitoids generally increase host growth (Slansky 1986). However, even though parasitization by solitary species decreases host growth, the ranking of final host size matches the host age (size) at parasitization, i.e., a host parasitized when young remains smaller than a host parasitized when older [*Ephosoma annulatum* (Bennet 1960), *Cardiochiles nigriceps* (Vinson and Barras 1970), *Microplitis croceipes* (Jones and Lewis 1971), *Campoletis sonorensis* (Vinson 1972), *Hyposoter exiguae* (Smilowitz and Iwantsch 1973)].

These data suggest that within a host species, size at oviposition is a good indicator of resources available to a developing wasp even for parasitoids of growing hosts. However, these data are not definitive. An alternative explanation of these data is that female parasitoids may oviposit a greater proportion of sons in young than in old hosts, and young and old hosts may provide the same amount of resources, but sons may make less efficient use of hosts than daughters. This alternative explanation would be discredited 1) if the parasitoid under investigation did not manipulate offspring sex ratio in response to host size or 2) if when hosts parasitized by just one sex of parasitoid offspring were examined, there still existed the pattern of

hosts parasitized when young exhibiting lower final weights than hosts parasitized when older. This information is not available for the above wasps.

Also relevant to whether host size at oviposition is a good indicator of resources available to a developing wasp is the effect of host size on wasp size. It is important to have wasp size separately for females and males. Otherwise smaller wasps on small hosts may just reflect that a greater proportion of males develop on small than on large hosts: in most parasitoid wasps, males are smaller than females (Hurlbutt 1987). The effect of host size at oviposition on wasp size has been examined primarily within host species. For all of the koinophytic species and most of the idiophytic species of parasitoid wasps which have been examined, within a host species both male and female wasps are larger when they are oviposited on larger hosts (Table 2). Thus even for parasitoids of growing hosts, within a host species, host size at oviposition is a good indicator of the amount of resources which will be available to a developing wasp.

I have shown that the premise of Waage's hypothesis is not valid on a within host species basis; however, many parasitoid wasps utilize multiple host species. Whether or not Waage's premise is valid across host species will depend on the range of sizes of host species utilized by a parasitoid. If there is a wide range in size (at maturity) of a parasitoid's host species, then across all host species there may not be a consistent relationship between host size at oviposition and amount of resources available to a developing wasp. For example, if a female of a koinophytic species encounters two hosts--a young instar of a large host species and an old instar of a small species--the former, though smaller, may actually provide more resources to a developing wasp in the long run. Across host species, a consistent, positive relationship between host size at oviposition and resources available to a developing koinophytic wasp is expected only for wasps which parasitize a small range of sizes of host species. Therefore, I suggest 1) that among koinophytic species, host-size-dependent sex ratio will evolve primarily in parasitoids with narrow ranges of host species sizes and 2) that for koinophytic species with wide host species size ranges, there will not be selection for females to manipulate offspring sex ratio in response to host size unless females can distinguish among host species or host species do not overlap in the size of susceptible instars. In contrast, in idiophytic parasitoids, a positive relationship between host size and amount of resources available to a developing wasp is expected even across a range of sizes of host species (although differences among host species in host quality may complicate this relationship (Charnov et al. 1981)).

A hypothesis identical to Waage's, that host-size-dependent offspring sex ratios are unlikely to evolve in koinophytic parasitoids, was also proposed independently by Wellings et al. (1986). Wellings et al. made a logical error in defending the hypothesis. They stated that in order for koinophytic parasitoids to evolve manipulation of primary sex ratio in response to host size, females would have to be able to assess, at oviposition, the host's future rate of resource acquisition. Wellings et al. felt that it was unlikely that females would have this knowledge. However, there is no reason that females need this knowledge. What is necessary is a consistent relationship between host size at oviposition and resources available to the developing parasitoid. (See Dawkins (1979) for discussion of a similar misunderstanding about kin selection).

Table 1. The relationship between host size and the sex ratio of emerging wasps.

An asterick (*) before the species name indicates that differential mortality has been ruled out as the cause of the relationship between host size and wasp sex ratio.

Relationship: + = positive relationship, - = negative relationship, nd = nondirectional. S = significant, NS = nonsignificant. When statistics were not reported in a study but sufficient data were presented, the data were analyzed with nonparametric tests. Pooling decisions were based on log linear analysis (Brown 1977).

Idiophytic or Koinophytic Parasitoid: I = idiophytic, K = koinophytic, ? = unknown

Host Stage Parasitized: a = adult, e = egg, l = larva or nymph, o = ootheca, p = pupa, s = scale

Wasp Family: Ae = Aphelinidae, Ai = Aphidiidae, Be = Bethylinidae, Br = Braconidae, C = Chalcidae, D = Diapriidae, En = Encyrtidae, El = Eulophidae, Er = Eurytomidae, I = Ichneumonidae, P = Pteromalidae, S = Scelionidae, To = Torymidae, Ti = Tiphiidae, Tr = Trichogrammatidae

Measure of Host Size: age = age or instar within a host species, size = size within a host species, sex = size of males and females within a host species, species = size of different host species

Wasp Species	Relationship	Idiophytic/ Koinophytic	Host Stage Parasitized	Wasp Family	Measure of Host Size	Reference
Solitary Parasitoids						
<u>Coccophagus bartletti</u>	NS	K *	s	Ae	size	Walter (1988)
<u>Aphidius ervi</u>	- S	K	l	Ai	age	Wellings et al. (1986)
<u>Aphidius nigripes</u>		K	la	Ai	age	Cloutier et al. (1981)
female given 60 hosts every 24 hours	nd S					
female allowed to attack each host only once	- S					
<u>Aphidius sonchi</u>	NS	K	l	Ai	age	Liu Shu-sheng (1985)
<u>Ephedrus cerasicola</u>	none	K	la	Ai	age	Hagvar and Hofsvang (1986)
<u>Cotesia melanoscela</u>	NS	K	l	Br	age	Kolodny-Hirsch (1988)
<u>Heterospilus prosopidis</u>		K *1	l	Br	age	
host species:						
* <u>Callosobruchus chinensis</u>	- S					Jones (1982)

<u>Zabrotes subfasciatus</u>	-						Kistler (1986)
* <u>Leiophron uniformis</u>	S *2	K	l	Br	age		Debolt (1981)
<u>Macrocentrus ancyllivorus</u>	+	K	l	Br	size		Finney et al. (1947)
<u>Microplitis croceipes</u>	NS	K *3	l	Br	age		Hopper and King (1984)
<u>Opius concolor</u>	- S *4	K	l	Br	age		Avilla and Albajes (1984)
* <u>Tiphia popilliavora</u>	- S *5	K	l	Ti	age		Brunson (1938)
<u>Coeloides brunneri</u>	- S	I	l	Br	size		Ryan and Rudinsky (1962)
<u>Brachymeria intermedia</u>	- S	I	p	C	size		Barbosa and Frongillo (1979)
<u>Phaenopria occidentalis</u>	- S *6	I	p	D	size		Legner (1969)
* <u>Coccygomimus turionellae</u>	- S *7	I	p	I	size		Sandlan (1979)
* <u>Dolichomitus sp.</u>	-	I	p	I	size		Kishi (1970)
	- S *8				species		Kishi (1970)
<u>Echthromorpha hyalina</u>	-	I	p	I	species		Seyrig (1935)
							in Clausen (1939)
<u>Itoplectis conquisitor</u>	NS	I	p	I	sex		McGugan (1955)
	-						Mumma et al. (1974)
<u>Itoplectis cristatae</u>	-	I	p	I	size		Nozato (1969)
<u>Phaeogenes gilvilabris</u>	-	I	p	I	sex		Mumma et al. (1974)
<u>Pimpla instigator</u>	-	I	p	I	species		Chewyreu (1913)
							in Charnov et al. (1981)
<u>Pimpla maculiscaposa</u>	-	I	p	I	species		Seyrig (1935)
in Clausen (1939)							
<u>Pimpla turionellae</u>	- S *9	I	p	I	species		Arthur and Wylie (1959)
<u>Anisopteromalus calandrae</u>	- S	I *10	l	P	age		van den Assem et al. (1984)
	-						Kistler (1986)
	- S *11						Shimada and Fujii (1985)
* <u>Lariophagus distinguendus</u>	- S *12	I	l	P	size		van den Assem (1971)
	-						Charnov et al. (1981)
	- S *13				age		van den Assem (1971)
<u>Muscidifurax raptor</u>	NS	I	p	P	size		Wylie (1967);
	NS *14						Legner (1969)
<u>Spalangia cameroni</u>		I	p	P	size		
host (house fly)							
density:							Legner (1969)
high	NS *15						
low	+ S *16						

in the field:							
	NS				species	King MS	
stable fly	+ S				size	King (1988a)	
house fly	- S						
in the lab:							
* house fly	- S				size	King (1988b)	
<u>Spalangia drosophilae</u>	NS *17	I	p	P	size	Legner (1969)	
<u>Spalangia endius</u>	NS	I	p	P	size	Donaldson and Walter (1984)	
<u>Spalangia nigra</u>	- S *18	I	p	P	size	Legner (1969)	
<u>Roptrocercus xylophagorum</u>	- S	I	l	To	age	Samson (1984)	
<u>Eurytoma morio</u>	- S *19	?	lp	Er	species	Mendel (1986a,b)	
<u>Metacolus unifasciatus</u>	- S *20	?	l	P	species	Mendel (1986a,b)	

Facultatively Gregarious Parasitoids

* <u>Aphytis lingnanensis</u>	- S	I	s	Ae	size	Luck and Podoler (1985)	
<u>Trichogramma minutum</u>	- S *21	I	e	Tr	species	Houseweart et al. (1983)	
<u>Trichogramma semifumatum</u>		I	e	Tr	species	Taylor and Stern (1971)	
sizes of host species (length X width, mm ²): 0.24, 0.26, 0.30, 0.48 0.18, 0.26	nd *22 + *23						
<u>Metaphycus helvolus</u>	-	?	s	En	size	Flanders (1946)	

Gregarious Parasitoids

<u>Goniozus emigratus</u>	NS	I *24	l	Be	size	Green et al. (1982)	
---------------------------	----	-------	---	----	------	---------------------	--

<u>Dahlbominus fuscipennis</u>		I *25	l	El	size	Wilkes (1963)
experiment 1	- S					
experiment 2	NS					
<u>Tetrastichus hagenowii</u>	-	I	o	El	size	Narasimham (1984)
	-				species	
<u>Gregopimpla himalayensis</u>	NS	I	p	I	sex	Shiga and Nakanishi (1968)
<u>Nasonia vitripennis</u>	NS	I	p	P	size	Wylie (1967)
<u>Pteromalus puparum</u>	NS	I	p	P	sex	Lasota and Kok (1986)

Solitary or Gregarious Parasitoids?

<u>Apechthis ontario</u>	-	I	p	I	sex	McGugan (1955)
<u>Phaeogenes hariolus</u>	-	I	P	I	sex	McGugan (1955)

*1 Wellings et al. (1986)

*2 $G = 8.98$, $P = 0.03$; a posteriori G-tests (Sokal and Rohlf 1969) show that sex ratio increases from host instar 4 to 2 to 1 to 3, but at $\alpha = 0.05$ the difference was significant between instars 4 and 3. only

*3 Jones and Lewis (1971)

*4 $G = 184.99$, $P < 0.001$

*5 young and old hosts presented simultaneously: $G = 251.38$, $P = 0.00$;

on alternate days: $G = 171.55$, $P = 0.00$

*6 high host density: $G = 4.58$, $P = 0.03$; low host density: $G = 22.61$, $P < 0.001$

*7 $G = 12.65$, $P < 0.001$

*8 $G = 79.27$, $P < 0.001$

*9 $G = 53.72$, $P < 0.001$; $r_s = 0.89$, $P < 0.01$

*10 van den Assem, personal communication

*11 larval hosts: $G = 18.12$, $P < 0.001$

*12 $G = 77.64$, $P < 0.001$

*13 $G = 172.90$, $P < 0.001$; $r_s = -0.70$, $P < 0.01$ (data from Table II (van den Assem 1971));

$G = 63.70$, $P < 0.001$ (data from Table III (van den Assem 1971))

*14 $G = 0.43$, $P = 0.51$
*15 $G = 1.35$, $P = 0.25$
*16 $G = 5.14$, $P = 0.02$
*17 $G = 3.34$, $P = 0.07$
*18 high host density: $G = 11.14$, $P < 0.001$; low host density: $G = 19.06$, $P < 0.001$
*19 $G = 69.53$, $P < 0.001$
*20 $G = 60.00$, $P < 0.001$
*21 $G = 15.97$, $P < 0.001$
*22 Experiment Va (Taylor and Stern 1971)
*23 Experiments Ia and Ib (Taylor and Stern 1971)
*24 Gordh and Hawkins (1981)
*25 Ulllyett (1936)

Table 2. The relationship between host size and size of parasitoid wasp at adult or pupal stage. Wasp Sex: m = males, f = females, mf = males and females examined separately. Other symbols as in Table 1.

Wasp Species	Wasp Sex	Relation	Idiophytic/ Koinophytic	Host Stage	Wasp Family	Measure of Host Size	Reference
Solitary Parasitoids							
<i>Aphidius smithi</i>	mf	+	K	l	Ai	size	Henkelman (1979 in Mackauer 1986)
<i>Aphidius sonchi</i>	mf	+ S	K	l	Ai	age	Liu Shu-sheng (1985)
<i>Apanteles rubecula</i>	mf	+	K	l	Br	age	Nealis et al. (1984); pers. comm.
<i>Cotesia melanoscela</i>	f	+	K	l	Br	age	Kolodny-Hirsch pers. comm.
<i>Heterospilus prosopidis</i>	mf	+	K	l	Br	age	Shimada and Fujii (1985)
<i>Brachymeria intermedia</i>	f	+ S	I	p	C	size	Greenblatt et al. (1982)
<i>Coccygomimus turionellae</i>	f	+ S	I	p	I	size	Greenblatt et al. (1982)
<i>Dolichomitus</i> sp.	mf	+	I	p	I	size	Kishi (1970)
<i>Hyposoter exiguae</i>	mf	+	I	l	I	age	Jowyk and Smilowitz (1978)
<i>Itopectis cristatae</i>	mf	+	I	p	I	size	Nozato (1969)
<i>Mutilla glossinae</i>	mf	+ S	I	p	Mu	size	Heaversedge (1967)
<i>Anisopteromalus calandrae</i>	mf	+	I	l	P	age	Shimada and Fujii (1985)
<i>Lariophagus distinguendus</i>	mf	+	I	l	P	age	van den Assem (1971)
<i>Spalangia cameroni</i>	mf	+	I	p	P	size	King (1988b)
<i>Spalangia endius</i>	f	NS	I	p	P	size	Donaldson and Walter (1984)
<i>Roptrocercus xylophagorum</i>	mf	+	I	l	To	age	Samson (1984)
Bark beetle parasitoids:	mf		?			species	Mendel (1986a,b)
<i>Cerocephala eccoptogasteri</i>		+		lp	P	(size	
<i>Cheirpachus quadrum</i>		+		l	P	as	
<i>Entedon ergias</i>		+		e	El	adults)	
<i>Dendrosoter caenopahcoides</i>		+		l	Br		
<i>Dendrosoter middendorffi</i>		+		l	Br		
<i>Dendrosoter protuberans</i>		+		l	Br		
<i>Eurytoma morio</i>		+		lp	Er		
<i>Heydenia pretiosa</i>		+		l	P		
<i>Metacolus unifasciatus</i>		+		l	P		
<i>Rhaphitelus maculatus</i>		+		l	P		
<i>Roptrocercus xylophagorum</i>				lp	To		
	m	nd					
	f	+					
Facultatively Gregarious Parasitoids							
<i>Aphytis melinus</i>	f	+	I*	s	Ae	size	Opp and Luck (1986)

