Two alternative strategies for spider egg parasitoids

Carlos E. Valerio
Escuela de Biología, Universidad de Costa Rica

(Received for publication December 7, 1983)

Abstract: Regulation of intensity of parasitism in spider-egg parasitoids is more complex than in most parasites, since spider eggs are tightly packed in sacs and factors controlling proportion of eggs parasitized per sac also regulate population densities. Both microhymenopterans *Baeus achaearaneus* (Scelionidae) and *Tetrastichus* sp. (Eulophidae), are egg parasitoids of the spider *Achaearanea tepidariorum* in Costa Rica. *B. achaearaneus* tends to locate a large number of sacs and to parasitize only a small proportion of eggs in each; *Tetrastichus* sp. locates a small proportion of the sacs available (typical of all parasites studied heretofore), but maximizes the utilization of eggs in each sac. The latter is intrinsically superior whenever both species attack the same sac (multiple parasitism).

A parasite must first find the general habitat in which the host is present, then locate the host itself (Laing, 1937); if the host is acceptable and suitable, some additional regulation of parasitism seems necessary (Vinson, 1976). In most cases the intensity of parasitism seems regulated by mechanisms controlling the ability of individual parasites to locate hosts (Nicholson, 1933 ; Nicholson and Bailey, 1935). However, spider-egg parasitoids encounter a group of hosts tightly enclosed in a sac and are faced with two alternative opportunities: to locate all sacs available and utilize a low proportion of the eggs within each sac, or locate a small proportion of the sacs available and utilize the totality of the eggs within these sacs.

These aspects are clarified by the present study on two microhymenopteran parasitoids on eggs of the spider *Achaeranea tepidariorum* (Araneae: Theridiidae) in Costa Rica.

MATERIAL AND METHODS

Baeus achaeraneus Loiacono (Scelionidae) and an undescribed species of *Tetrastichus* (Eulophidae) are both natural parasitoids on eggs of *A. tepidariorum* in the Central Valley of Costa Rica.

One individual of *Baeus* develops from each host egg (Valerio, 1971), with an average adult length of 0.7 mm (females wingless, males with four wings). In *Tetrastichus*, larvae develop inside the egg sac, feeding externally on the eggs, and every larva requires about three eggs to complete development (estimated, from numbers of wasps hatching and hostegg remains). The average length of adults is 2,0 mm.

Three parameters were used to determine their effect on utilization of host eggs: number of eggs per sac, age of eggs, and female parasitoid density. Several combinations of number of sacs and number of female parasitoids in the same container were tried (Table 2), utilizing freshly emerged wasps (24 hours or youger). The eggs used to estimate the effect of host age were stored in a constant temperature incubator (24.5 ± 0.3 °C) until the desired age was reached.

Female spiders were maintained in captivity to provide a stock of fresh eggs of known age.

The species of *Tetrastichus* also parasitizes another theridiid spider *(Tidarren sisyphoides)* ocupying similar microhabitats to those of *A. tepidariorum. Baeus achaerananeus* was not detected by a survey of the egg sacs of other theridiide, scytodid, pholcid and araneid spiders in the same area. These negative results include an intensive study of *Theridion rufipes,* a theridiid also found in buildings (Umaña, 1983).

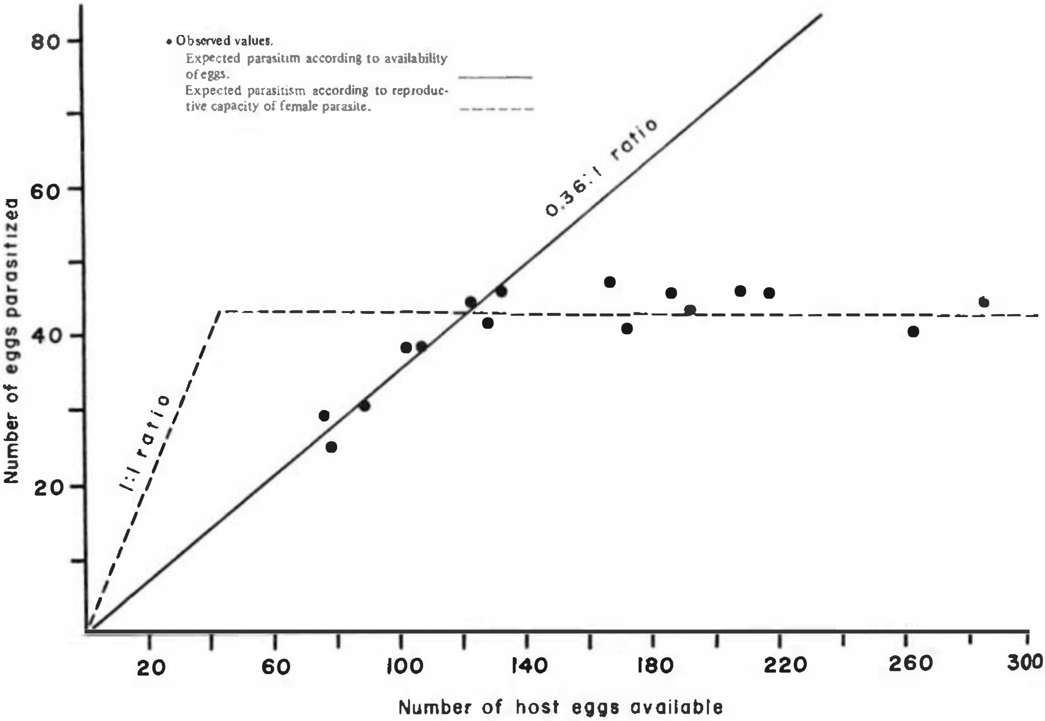

Fig. 1. Relationship between available and utilized numbers of eggs per sac by ***Baeus achaearaneus.*** Each sac exposed to only one female parasite.

RESULTS

Parasitism by *Baeus achaearaneus*

From a total of 841 sacs collected from field populations, 397 were parasitized by *Baeus* (47.2%) and of a sample of 28 parasitized sacs containing 3 669 eggs (Table 3), 989 eggs (27%) were utilized by these wasps.

The parasitizing strategy of *Baeus* is related to a very effective searching behavior by female parasites and a sophisticated mutualistic relationships with the spider at population levels between the spider offspring and the adult wasps, where survival of spiderlings increases when parasites are present (Valerio, (1975).

The considerable variation in number of eggs parasitized per sac observed in the field (Table 3) suggests that several factors may affect the oviposition behavior of *Baeus* females; these are clarified by the experiments under controlled conditions.

TABLE 1

Eggs parasitized per sac by Baeus achaearaneus *under controlled conditions. Each sac exposed to one female parasite only*

Number of eggs in sac	Number of eggs parasitized	Parasitism (%)
77	29	37.7
78	26	33.3
89	32	36.0
102	39	38.2
105	39	37.1
108	3	2.8*
114	17	1.5*
121	46	38.0
125	3	2.4*
127	43	33.9
132	47	35.6
167	48	28.7
173	41	23.7
185	47	25.4
186	47	25.3
191	45	23.6
207	47	22.7
219	47	21.5
228	47	20.6
262	41	15.6
284	46	16.2
TOTAL 3 280	754	23.1

*Eggs under 18 hours of age.

TABLE 2

Eggs parasitized per sac by Baeus achaeraneus *under controlled conditions. Each sac was exposed to from 4 to 10 females simultaneously*

Number of eggs in sac	Number of eggs parasitized	Parasitism (%)
66	42	63.6
119	28	23.5
120	120	100,0
123	29	23.6
125	48	38.4
129	20	15.5*
130	33	25.4
132	52	39.4
138	79	57.2
143	92	64.3
151	93	61.6
152	8	5.3*
152	102	67.1*
163	32	19.6*
172	91	52.9
183	104	56.8
186	181	97.3
188	59	31.4
191	159	83.2
193	142	73.6
209	82	39.2
212	113	53.3
229	170	74.2
229	185	80.8
TOTAL 3 835	2 064	53.8

* Eggs under 18 hours of age.

42; Table 1), except in three sacs recently built by the spider (18 hours or less, where few eggs were parasitized, other sacs were 24 to 30 hours old). This inhiting effect of the fresh eggs may be due to remanent fluids from the spider oviducts, that might disrupt the female parasite. This modified behavior on fresh eggs was also observed when several female parasites attacked simultaneously (Table 2).

Parasitoid reproductive capacity: In sacs of appropriate age (24 to 30 hours) the reproductive capacity of the parasitoid is a determining factor, since a female cannot parasitize more hosts than the number of eggs in her oviducts.

The reproductive capacity of an average parasitoid is estimated to be 48 eggs, based on the progenies obtained from sacs containing more than 132 host eggs (hence, showing no host scarcity; Table 1).

TABLE 3

Eggs parasitized per sac by Baeus achaearaneus *in natural populations. Random sample of 28 sacs*

Number of eggs in sac	Number of eggs patasitized	Parasitism (%)
63	33	52.3*
66	61	92.4*
73	1	1.4
77	23	29.9
82	21	25.6
89	46	51.7*
97	20	20.7
101	31	30.7
106	3	2.8
112	18	16.1
117	51	43.6
120	40	33.3
124	59	47.6*
124	115	92.7*
126	9	7.1
133	52	39.1
142	42	29.6
142	51	35.9
147	26	17.7
149	70	47.0*
164	8	4.4
165	49	29.7
176	7	4.0
182	36	19.8
195	58	29.7
197	8	4.1
188	50	26.6
212	1	0.5
TOTAL 3 669	989	26.9

*Probably attacked by more than one female parasite.

The minimum number of host eggs that allow the wasp to ovoposite at its full capacity (48 eggs) not utilizing more than 33,3% of this resource (see below) would be 144. Consequently, in sacs with more than this number of eggs the wasp ovarian load is expected to be the main regulating factor.

Number of host eggs per sac: However, it seems that a female does not always deposit all her egg load in those sacs containing unusually low number of host eggs, since the intensity of parasitism is lower (Table 1).

A sac with one of the lowest number of eggs recorded (78 eggs) produced the least parasite progeny obtained from a suitable sac (26

TABLE 4

Eggs utilized per sac by Tetrastichus *sp.*

Number of parasites attacking	Parasite progeny	Number of eggs not utilized	Number of eggs utilized *	Total number eggs per sac*	Eggs utilized (%)
1	8	79	24	103	23,4
1	9	15	27	42	64,2
1	11	102	33	135	24,3
1	15	126	45	171	26,4
2	24	70	72	142	50,7
3	32	109	96	205	46,8
3	33	53	99	152	65,1
4	37	182	111	293	37,8
4	39	0	117	117	100,0
5	61	10	183	193	94,8
6	32	0	96	96	100,0
6	55	3	165	168	98,1
7	36	11	108	119	90,6
7	47	24	141	165	85,5
7	56	7	168	175	96,0
7	59	8	177	185	95,7
8	54	15	162	177	91,5
8	71	0	213	213	100,0
TOTAL	679	814	2 037	2 851	71,5

* Estimated assuming that each parasitic larva consumed three eggs during development.

parasites), representing a utilization of 33.3% of the eggs available. All other sacs with a small number of eggs (132 or less; Table 1) had percentages of parasitism higher than 33, suggesting that, in all these cases, the low number of available host eggs was affecting the ovipositing behavior of the female parasite. How this controlling factor might operate is not clear in the present study, but is easily detected as illustrated in Figure 1. Then in those sacs containing less than 144 eggs the controlling factor would be the relative scarcity of hosts.

Avoidance of previously parasitized sacs: In natural populations most of the sacs are attacked by only one female judging from the number of the parasite progeny (Table 3). Females were observed to avoid in the laboratory the already parasitized sacs, presumably marked by a contact pheromone at the time of oviposition by the first female. Conditions permiting the few recorded cases of multiple parasitism in the field were not determined.

In other hymenopterans that also mark food sources with chemical materials, breaking down of the repellent effect may result due to unusual aggregations of females at the same site (Frankie and Vinson, 1977).

Under experimental conditions, isolated females always behaved according to the proposed regulating mechanisms, but four or more females in contact with the same sac simultaneously alter their behavior and overparasitism (utilization of more than one third of eggs present) was observed. In these circumstances the ultimate factor controlling progeny size was the capacity to produce only one parasite per host egg. This extreme case was met only in 4% of the cases (Table 2).

Agressivity of the female spider: Another factor effecting the utilization of the eggs by the parasite in the field is the defensive attitude of the female spider guarding the sac. This effect is not detectable when one female wasp attacks alone, but it seems to play an important role when two or more parasites attack simultaneously, since the aggresive behavior of the spider increases in relation to the number of parasites on the surface of the sac. In one case, a guarding spider was observed to locate and capture a wasp.

Peripheral eggs: In a few cases, wasps were found inside a fresh egg sac, which indicates their ability to penetrate the sac, but it was not determined if they can move freely among the eggs. Table 2 shows that, under crowded conditions, all eggs present were parasitized, implying that either the wasp penetrated to the center of the egg masses or that larvae hatched outside the host eggs and moved around freely (it could also be that this species in ovoviviparous). These possibilities were not investigated, but it is clear that female wasps were not limited by physical barriers to the pheripheral eggs.

Parasitism by *Tetrastichus* sp.

Of the total sacs collected (841) only 18 were parasitized by *Tetrastichus* (2.1%), and over 70% of the eggs in these sacs were parasitized (Table 4).

The ovipositing capacity of the parasite seems to be the main factor controlling the proportion of host eggs that are utilized. Whenever more than three female parasites simultaneously attacked a sac during the laboratory experiments, a high proportion (nearly 100%) of the available eggs was utilized by the resulting larval progeny.

Under natural conditions in the field, four or five female *Tetrastichus* are usually found in the web of one of the host spiders (this also occurs in the related species *Tidarren sisyphoides*). This cumpling of females might function in assuring maximum utilization of the available resources and had been detected in other parasitoid species (Vinson 1976), but it is not well documented.

This strategy would be considered stable by May and Hassell (1981), since they conclude that stability requieres the evolution of aggregative behavior in parasites. On the other hand, *Baeus* seems very effective doing precisely the opposite, but controlling the proportion of egg utilized per sac.

CONCLUSIONS

Baeus achaearaneus examplifies the specialist in searching for egg sacs and, consequently, the utilization of the eggs in each sac is restricted by a combination of factors. *Tetrastichus* represents the less specialized parasite locating only a low proportion of the sacs available and with no mechanisms restricting the utilization of eggs inside the sacs located. These two alternative strategies allow the two parasites to exploit the same host population simultaneously (Valerio, 1971) and allows the *Baeus* type of parasite to maintain a more intimate and sophisticated interaction with the host at population level (Valerio, 1975).

Price (1980) indicates that specificity for host had been often atributed to absence of potential alternate hosts or to close adaptation of life histories between parasite and host. In the case here discussed the remarkable specificity seems due mostly to coadaptation, since three theridiid spiders (*Tidarren sisyphoides, Theridion rufipes* and one species of *Achaearanea*), that could act as alternate hosts, occupy similar habitats as the host *A. tepidariorum* and are equally abundant.

In *Baeus*, the individuals emerging from a sac are brothers and sisters that mate before dispersing in a strict inbreeding system (Valerio, 1976) while in *Tetrastichus* the groups are probably genetically diverse and subject to a very different selective pressure. Levin and Pimentel (1981) argue that parasite-host interactions might be good examples of altruistic behavior and group selection, which might be the case in *Tetrastichus* but certainly not in *Baeus*.

ACKNOWLEDGMENTS

I wish to express my gratitude to W.G. Eberhard for valuable comments and revision of the manuscript, and to B.D. Burks (Systematic Entomomogy Laboratory, U.S. National Museum), L. De Santis (Facultad de Ciencias y Museo, Universidad de La Plata, Argentina) and H.W. Levi (Museum of Comparative Zoology, Harvard University) for species identifications.

RESUMEN

El control de la densidad de parasitismo en parasitoides de huevos de arañas requiere de mecanismos naturales más complejos que en la mayoría de los parásitos, ya que los

huevos de araña se encuentran en grupos empacados en sacos de seda por lo que se requieren factores adicionales para regular la proporción de huevos que han de ser parasitados en cada saco atacado por los parasitoides.

Las avispitas *Baeus achaearaneus* (Hymenoptera: Scelionidae) y *Tetrastichus* sp. (Hymenoptera: Eulophidae), ambos parasitoides de los huevos de la araña *Achaearenea tepidariorum* (Araneae: Theridiidae) en Costa Rica, utilizan estrategias de parasitismo muy diferentes una de la otra. El sceliónido encuentra aproximadamente el 50% de los sacos disponibles en su ambiente natural, pero parasita solamente un promedio de 32% de los huevos en cada uno de los sacos atacados. Por el contrario, el eulófilo localiza una bajísima proporción (cerca de 2%) de los sacos disponibles, y utiliza casi todos (más del 70%) de los huevos en cada saco. Cuando ocurre parasitismo múltiple en el mismo saco, el eulófido es intrínsicamente superior y puede utilizar huevos parasitados previamente por *Baeus*.

REFERENCES

Frankie, G.W., & S.B. Vinson. 1977. Scent marking of passion flowers by females of *Xylocopa virginica texana*. J. Kansas Entomol. Soc., 50: 613-625.

Laing, J. 1937. Host finding by insect parasites. J. Anim. Ecol., 6: 298-397.

Levin, S., & D. Pimentel. 1981. Selection of intermediate rates of increase in parasite-host systems. Amer. Nat., 117: 308-315.

May, R. M., & M.P. Hassell. 1981. The dynamics of multiple parasitoid-host interactions. Amer. Nat., 117: 234-261.

Nicholson, A.J. 1933. The balance of animal populations. J. Anim. Ecol., 2: 132-178.

Nicholson, A.J., & V.A. Baily. The balance of Natural Populations. Proc. Zool. Soc. London, 2: 551-598.

Price, P.W. 1980. Evolutionary Biology of Parasites. Princenton University Press. 237 p.

Umaña, Gina M. 1983. Ciclo de vida y biología de la reproducción de la araña *Theridion rufipes* (Araneae, Theridiiae) en Costa Rica. Tesis de Licenciatura, Escuela de Biología, Universidad de Costa Rica.

Valerio, C.E. 1971. Parasitismo en huevos de la araña *Achaearanea tepidariorum* (C.L. Koch) en Costa Rica. Rev. Biol. Trop., 18: 99-106.

Valerio, C.E. 1975. A unique case of mutualism. Amer. Nat., 109: 235-238.

Valerio, C.E. 1976. Significance of all-male progenies in some microhymenopteran parasites. Brenesis, 9: 25-29.

Vinson, S.B. 1976. Host selection by insect parasitoids Ann. Rev. Entomol. 21109-132.