ENTOMOPHAGA 37 (2), 1992, 229-237

INTRASPECIFIC HOST DISCRIMINATION AND LARVAL COMPETITION IN *MICROPLITIS CROCEIPES, MICROPLITIS DEMOLITOR, COTESIA KAZAK* (*HYM.: BRACONIDAE*) AND *HYPOSOTER DIDYMATOR* (*HYM.: ICHNEUMONIDAE*), PARASITOIDS OF *HELIOTHIS VIRESCENS* (*LEP.: NOCTUIDAE*)

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Intraspecific host discrimination and larval competition were studied for *Microplitis croceipes* (Cresson), *Microplitis demolitor* Wilkinson, *Cotesia kazak* (Telenga), and *Hyposoter didymator* (Thunberg), solitary endoparasitoids of the tobacco budworm, *Heliothis virescens* (F.). In ovipositional choice tests between unparasitized and parasitized hosts, the mean number of ovipositions for unparasitized hosts was significantly higher than the mean number of ovipositions for hosts parasitized once by a conspecific female for *C. kazak* and *H. didymator,* demonstrating that females of these 2 species discriminate against hosts recently (within a few seconds) parasitized by a conspecific female. No significant difference in oviposition occurred between these 2 kinds of hosts for *M. croceipes* and *M. demolitor*. Mean percent parasitization by a 2nd conspecific female was determined at 24, 48, and 72-h delays in time between the 1^{rst} and 2nd female attack, and with no delay. Except for the 0 h time delay for *C. kazak* and *H. didymator,* percent parasitization by a 2nd conspecific female generally decreased as the delay in time between the 1^{rst} and 2nd female attack increased. When the 2nd parasitization immediately followed the 1^{rst}, one parasitoid larva always eliminated the other by physical combat. With a 24 or 48 h delay between the 1^{rst} and 2nd parasitization, the younger larva was the victor over the older larva for *M. croceipes, M. demolitor* and *C. kazak* in at least 50 % of the cases. Elimination of older larvae by younger larvae was by physical attack. However, for *H. didymator,* the older instar was the victor, and elimination of younger larvae by older larvae was probably through physiological processes. Further, older larvae of *H. didymator* apparently killed the eggs of the 2nd female by physiological processes.

KEY-WORDS : *Heliothis virescens,* endoparasitoids, intraspecific host discrimination, larval competition.

The ability to discriminate between unparasitized and parasitized hosts and to refrain from ovipositing in the latter has been shown for many parasitoid species in most families of parasitic Hymenoptera (**Lenteren,** 1981 ; **Alphen** *et al.*, 1987). Parasitoids discriminate by detection of either external marking pheromones (**Vinson & Guillot,** 1972 ; **Bosque & Rabinovich,** 1979 ; **Klomp** *et al.,* 1980 ; **Strand,** 1986) or some kind of internal mark or change in the condition of the host (**Jackson,** 1966 ; **Fisher & Ganesalingam,** 1970 ; **Greany & Oatman,** 1972 ; **Klomp** *et al.,* 1980, **Strand,** 1986). Failure to discriminate can result in superparasitism. The function of host discrimination and superparasitization in parasitoids was discussed by **Bakker** *et al.* (1985). Competitors are eliminated by physical attack or physiological suppression via toxins, anoxia or nutritional deprivation (**Salt,** 1961 ; **Fisher,** 1971 ; **Vinson & Iwantsch,** 1980).

Microplitis croceipes (Cresson), *Microplitis demolitor* Wilkinson, *Cotesia kazak* (Telenga), and *Hyposoter didymator* (Thunberg) are solitary parasitoids of *Heliothis/Helicoverpa* spp. The braconid *M. croceipes* was one of the most predominant native parasitoids of *Heliothis virescens* (F.) and *Heliothis zea* (Boddie) in the United States (**Lewis & Brazzel,** 1968 ; **Mueller & Phillips,** 1983 ; **King** *et al.,* 1985). In Australia, *M. demolitor* was commonly found in high numbers attacking larvae of *Heliothis armigera* Hubner, so was imported (**Shepard** *et al.,* 1983). The braconid *Cotesia kazak* and the ichneumonid *H. didymator* were reported by **Carl** (1978) as important endoparasitoids of *H. armigera* in Greece and Bulgaria. For use in these studies, *C. kazak* was imported from cooperators in New Zealand, and *H. didymator* was received through the USDA-ARS European Parasite Laboratory in France. All 3 imported species were propagated in the laboratory, then released in the field in the United States (**Powell,** 1989). Developmental times (**Tillman & Powell,** 1991) and acceptance of larval instars (**Tillman & Powell,** 1989) for *M. croceipes, M. demolitor, C. kazak,* and *H. didymator* were evaluated in related studies. In this study, we looked at intraspecific host discrimination and larval competition in each of these 4 species.

MATERIALS AND METHODS

Parasitoids used in these studies were reared in the laboratory at 25 °C, 60-70 % RH, and a 14 : 10 (L : D) photoperiod, from larvae of the tobacco budworm, *H. virescens,* using the procedures of **Powell & Hartley** (1987). The *M. croceipes* colony originated from cotton in the Mississippi delta. The *M. demolitor* colony was imported from Australia, *C. kazak* from New Zealand, and *H. didymator* from Israel. Adult parasitoids were maintained in the laboratory on a solution of honey and water (1 : 1). All host larvae were reared on an agar soybean flour-wheat germ diet (**King & Hartley,** 1985) at 26.7 $\pm$ 2 °C, 50 $\pm$ 5 % RH and a 15 : 9 (L : D) photoperiod. Voucher specimens have been deposited at the United States National Museum of Natural History, Washington, D.C.

All females used in experiments were 3 to 6 days old, mated, and had prior ovipositional experience. A female was given oviposition experience by allowing her to oviposit in 10 unparasitized late second instars of *H. virescens,* both 1 and 2 days after emergence.

All hosts which had been attacked were dissected to ascertain whether or not the female had oviposited in these hosts. Hosts were dissected 24 h after being attacked, at which time eggs were more easily detected, yet no first instars were present. A host was dissected in a small watchglass containing Ringer's solution and scored by the presence or absence of the eggs.

Host discrimination

Ability of females to discriminate between hosts parasitized by a conspecific female and unparasitized hosts was evaluated in two different experiments.

Experiment 1

The first experiment was conducted to determine if any difference in oviposition by a female occurred between hosts recently (within 1 h) parasitized once by conspecific females and unparasitized hosts when the female was given an equal choice of ovipositing in either kind of host. One female of one species was introduced into a Petri dish (100 × 4 mm) in which 5 unparasitized and 5 parasitized hosts had been randomly placed. Late second instars of *H. virescens* were used as hosts. Parasitized hosts were marked with liquid Day-Glo paint (Day-Glo Color Corp., Cleveland, Ohio) for easy identification. Females show no preference for Day-Glo paint marked or unmarked hosts (**Tillman & Powell,** unpubl. data).

The behavior of a female was observed continuously during a test, and the number of encounters with each kind of host was recorded. Antennation of a host (either followed or not followed by an ovipositional attack) was considered to be an encounter with a host. An ovipositional attack occurred when a female inserted her ovipositor into a host. To maintain a total of 10 hosts at all times during the experiment, hosts were removed immediately after an ovipositional attack and replaced with another host in the same category until 20 hosts were attacked. The test was replicated 5 times using a different female for each replication. Two-tailed, paired-sample t tests were used to analyze the data. This experiment was repeated for each of the 4 parasitoid species.

Experiment 2

This experiment was conducted to determine the effect of delay in time between the 1rst and 2nd female attack on discrimination by the 2nd female. The parasitoids were exposed in a Petri dish (100 × 15 mm) to 20-25 hosts in each of four categories : 1) hosts recently (within 5 to 15 sec.) parasitized by the 1rst female, 2) hosts parasitized by the 1rst female 24 h earlier, 3) hosts parasitized by the 1rst female 48 h earlier and 4) hosts parasitized by the 1rst female 72 h earlier. This test was repeated 3 times for each category of hosts for each parasitoid species. Different individuals were used for each trial. Each host was attacked only once, and insertion of the ovipositor was observed for each attack. Egg depletion was not thought to be a problem since females of each parasitoid species were observed to oviposit in 20 consecutive hosts within 15-30 min in Experiment 1. All host instars used in these tests have been shown to be equally acceptable to these parasitoid species (**Tillman & Powell,** unpubl. data), and thus host age was not considered a source of variance. Percent parasitization by the 2nd female was calculated for each host category for each parasitoid species. These data were subjected to analysis of variance and least significant difference tests (LSD ; $P < 0.05$) with the general linear models procedure of SAS (SAS Institute 1986). The use of transformations was unnecessary.

LARVAL COMPETITION

Larval competition was studied by parasitizing a 2nd instar of *H. virescens* with a female parasitoid and then allowing a 2nd female of the same species to attack this host. This was accomplished for 3 different time intervals between the first and second attack : 1) second attack immediately (within 5 to 15 sec.) after the first, 2) second attack 24 h after first and 3) second attack 48 h after first. Each host was dissected as above 3 days after the second attack. Both the outcome of the competition between the 2 immature parasitoids and the method of elimination were recorded. This process was repeated for each of the 4 parasitoid species.

RESULTS

Host discrimination

Experiment 1

In the ovipositional choice tests, the mean number of encounters for unparasitized hosts was not significantly different from the mean number of encounters for parasitized hosts for each parasitoid species ($P > 0.05$) (table 1). The mean number of ovipositions for unparasitized hosts was significantly higher than the mean number of ovipositions for parasitized hosts for *C. kazak* ($P < 0.01$) and *H. didymator* ($P < 0.005$). No significant difference in oviposition occurred between these 2 kinds of hosts for *M. croceipes* and *M. demolitor* ($P > 0.05$). The mean number of ovipositor insertions was significantly different from the mean number of ovipositions for only *H. didymator* ($P < 0.005$) and *C. kazak* (P. < 0.01).

Table 1

Mean (± SE) number of encounters, ovipositor insertions, and ovipositions by M. croceipes, M. demolitor, C. kazak, *and* H. didymator *females for unparasitized and parasitized hosts*

Species	Host condition	Mean no. of encounters	Mean no. of ovipositor insertions	Mean no. of ovipositions	Calculated t value : insertions vs. ovipositions
M. croceipes	Unparasitized	25.8 ± 3.8	9.8 ± 0.3	8.5 ± 0.6	2.6 NS
	Parasitized	24.0 ± 6.8	10.3 ± 0.3	8.0 ± 1.5	2.0 NS
	Calc. t value	0.5 NS	1.0 NS	0.3 NS	
M. demolitor	Unparasitized	14.5 ± 2.0	10.0 ± 0.9	8.3 ± 0.9	2.3 NS
	Parasitized	15.3 ± 1.4	10.0 ± 0.9	8.0 ± 0.5	2.2 NS
	Calc. t value	0.8 NS	0 NS	0.5 NS	
C. kazak	Unparasitized	12.5 ± 1.0	11.3 ± 0.9	8.8 ± 1.3	1.9 NS
	Parasitized	13.0 ± 1.5	8.8 ± 0.9	3.3 ± 0.3	6.5*
	Calc. t value	0.2 NS	1.7 NS	6.5*	
H. didymator	Unparasitized	29.3 ± 5.8	11.0 ± 0.8	10.3 ± 0.8	1.6 NS
	Parasitized	29.3 ± 3.4	9.0 ± 0.8	1.8 ± 0.6	11.2**
	Calc. t value	0 NS	1.4 NS	8.9**	

* $P < 0.01$; $t > 5.84$; ** $P < 0.005$; $t > 7.45$; NS = not significant ; df = 3.

Experiment 2

The mean percent parasitization by a 2nd female over time is shown for each parasitoid species in table 2. Percent parasitization decreased significantly with a 24 h delay between the 1rst and 2nd female attack for *M. croceipes* ($P < 0.05$). A significant decrease in percent parasitization by a 2nd female also occurred for this species from 24 to 72 h in delay of time of the 2nd attack ($P < 0.05$). Percent parasitization by a 2nd female decreased significantly between each time interval (except the last two) for *M. demolitor* ($P < 0.05$). For *C. kazak* and *H. didymator*, percent parasitization by a 2nd female significantly decreased from 24 to 72 h in delay of time of the second attack. In comparison between species, percent parasitization by a 2nd female at 0 h time delay for the 2nd attack was significantly higher for *M. croceipes* and *M. demolitor* than for *C. kazak* and *H. didymator* ($P < 0.05$).

TABLE 2

Mean percent parasitization (± SEM) by second parasitoid female over time for M. croceipes, M. demolitor, C. kazak, *and* H. didymator

Time (h)	Mean percent parasitization (± SEM)			
	M. croceipes	*M. demolitor*	*C. kazak*	*H. didymator*
0	94.1 ± 13.3 a,x	93.7 ± 13.3 a,x	38.2 ± 6.4 a,y	19.2 ± 6.4 a,z
24	63.0 ± 7.6 b,x	44.7 ± 6.4 b,xy	27.2 ± 6.4 a,y	90.4 ± 7.6 c,z
48	40.1 ± 7.6 bc,x	19.0 ± 6.4 cd,y	7.8 ± 6.4 bc,y	79.6 ± 6.4 c,z
72	37.3 ± 9.4 c,x	0.4 ± 9.4 d,y	0.4 ± 9.4 c,y	50.0 ± 7.6 b,x

Means followed by the same letter within a (a-d) column and in a row (x-z) are not significantly different ($P > 0.05$); LSD test [SAS 1986].

LARVAL COMPETITION

Results of intraspecific larval competition for each of the 4 parasitoid species are shown in table 3. When the second parasitization immediately followed the first, one 1^rst^ instar always eliminated the other 1^rst^ instar by physical combat. We could not determine from visual observations whether the 1^rst^ or 2^nd^ individual was the victor in this case. With a 24 h delay in time between parasitization by the 1^rst^ and 2^nd^ female, the younger instar eliminated the older instar in ca. 60 % of the cases for *M. croceipes, M. demolitor* and *C. kazak*. Percent victory was even greater after a 48-h delay for *M. croceipes* and for *C. kazak*. For these 3 parasitoid species, elimination of older competitors by younger larvae was by physical attack ; while elimination of younger competitors by older larvae, when it did occur, apparently was through physiological processes. It was assumed that the younger larvae were killed by older larvae by physiological processes since these former larvae had turned brown and did not appear to be wounded or mutilated. With *H. didymator,* the older immature parasitoid generally outcompeted the younger one. The older instars of *H. didymator* could kill the eggs of the 2^nd^ immature, presumably by physiological processes ; but even if the egg of the 2^nd^ female survived, the older instar eliminated the younger one by physical attack. It was assumed that the eggs were killed by physiological processes since they were black and not developing, but determining the actual cause of death was beyond the scope of this study. Normally the eggs are white and have developed into 1^rst^ instars (progeny of second female) by the time the hosts were dissected. Also, some of these black, dead eggs were encapsulated, although none of the dead larvae were observed to be encapsulated.

DISCUSSION

Cotesia kazak and *H. didymator* were able to discriminate between unparasitized hosts and hosts recently parasitized once by a conspecific female, whereas *M. croceipes* and *M. demolitor* were not. The fact that the mean number of ovipositor insertions was significantly different from the mean number of ovipositions for *C. kazak* and *H. didymator* indicates that these 2 species were discriminating between unparasitized and parasitized hosts by the recognition of an internal mark due to the action of the attacking parasitoid. This phenomenon has been reported for other parasitoid species (**Jackson,** 1969 ; **Wylie,** 1971 ; **Greany & Oatman,** 1972 ; **Guillot & Vinson,** 1972).

TABLE 3

Mean percent victory 1st attacking female : 2nd attacking female for M. croceipes, M. demolitor, C. kazak, *and* H. didymator *in intraspecific larval competition for* Heliothis virescens

Species	Delay between parasitizations			
	n	24 h	n	48 h
M. croceipes	30	40 : 60	17	12 : 88
M. demolitor	42	40 : 60	6	50 : 50
C. kazak	31	35 : 65	5	20 : 80
H. didymator	36	75 : 25	40	73 : 27

M. croceipes and *M. demolitor* do not discriminate between unparasitized hosts and hosts recently parasitized once by a conspecific female. Using choice tests for unparasitized vs. parasitized hosts, **Vinson & Guillot** (1972) also determined that *M. croceipes* does not distinguish between these 2 kinds of hosts. However, they did ascertain that *M. croceipes* discriminates against hosts superparasitized by conspecific females.

Between 24 h and 72 h, percent parasitization by a 2nd conspecific female decreased as the delay in time between the first and second female attack increased. These results suggest that second-attacking females may have detected an internal mark induced by physiological changes in the host due to the developing immature parasitoid, and thus, discriminated against the host accordingly. Internal discrimination due to physiological changes within the host is frequently latent (**Klomb** *et al.*, 1980 ; **Cloutier** *et al.*, 1984 ; **Chow & Mackauer,** 1986 ; **Strand,** 1986).

For *C. kazak* and *H. didymator,* the 2nd female may be discriminating against hosts in the 0 h time delay category by detecting an internal marking pheromone injected by the 1rst attacking female. Shortly after the 1rst attack, this marking pheromone probably is gone and the 2nd female then later begins discriminating against parasitized hosts by detecting physiological changes in the host due to the developing parasitoid. **Chow & Mackauer** (1984, 1986) described patterns of host discrimination and larval competition in an aphid parasite, and compared their model (**Chow & Mackauer,** 1986) with that proposed by **Klomp** *et al.* (1980) for *Trichogramma embryophagum* Hartig.

Since the decrease in percent parasitization by *H. didymator* and *M. croceipes* was slower than that for *C. kazak* and *M. demolitor,* respectively, we hypothesize that the trend of increased discrimination against the internal mark induced by changes over time is a function of developmental rate. The greatest percent of eclosion from eggs occurs between 36-40 h after oviposition for *M. demolitor* and *C. kazak,* between 40-44 h for *M. croceipes,* and between 48-52 h after oviposition for *H. didymator* (**Tillman & Powell,** unpublished). The increase in percent parasitism for *H. didymator* at 24 h (90 %) relative to 0 h (19 %) corresponds to a hypothesis of two marks — a short-lived one deposited by the adult female, and one produced by the developing larva. An interim period occurs in which a 2nd parasitoid fails to recognize the host as previously parasitized, and the mark produced by the parasitoid larva is never as effective as that produced by the adult at oviposition. *Cotesia kazak* does not behave in a similar manner (table 2) ; the initial mark apparently is as effective at 24 h as at 0 h, and the ability of this parasitoid to discriminate increases with each time interval.

In these experiments, superparasitism occurred to some extent for each of the 4 parasitoid species, resulting in intraspecific competition. The 2 *Microplitis* spp. were unable to recognize recently parasitized hosts, but *M. demolitor* was significantly better than *M. croceipes* at recognizing hosts that had been parasitized 48 or more hours earlier. *Hyposoter didymator* was capable of avoiding superparasitism in recently parasitized hosts, but not in hosts parasitized 24 h earlier. *Cotesia kazak* was not quite as successful as *H. didymator* at recognizing a host recently parasitized by a conspecific, but their ability to detect a previously parasitized host increased with the time after the 1rst oviposition.

Related studies include in depth observations on interspecific host discrimination and larval competition among these same 4 parasitoid species (**Tillman & Powell,** unpublished). This information on discrimination and competition gives us insight into development of release strategies because each species prefers a different host size. However, information on relative searching efficiencies at various host densities would be useful in predicting field efficacy. The greatest opportunity for competition probably occurs when a large number of parasitoids is released simultaneously in the same area. Releasing lower numbers of parasitoids over a longer period in a uniform distribution over a treatment area may be more effective than releasing large numbers from fewer release sites. Further studies are needed on the effects of different release strategies.

ACKNOWLEDGEMENTS

We thank **S. Gray** for technical assistance, **D. L. Boykin** for statistical expertise, and **W. J. Lewis** and **J. C. van Lenteren** for reviewing the manuscript. For shipping parasitoids to the U.S., we thank **M. Shepard** and **R. Lawn** for *M. demolitor* ; **P. Cameron** for *C. kazak* and **Dr. Bar** and **D. Perkins** for *H. didymator*.

RÉSUMÉ

Discrimination intraspécifique de l'hôte et compétition larvaire chez *Microplitis croceipes, Microplitis demolitor, Cotesia kazak* [*Hym. : Braconidae*] et chez *Hyposoter didymator* [*Hym. : Ichneumonidae*], parasitoïdes de *Heliothis virescens* [*Lep. : Noctuidae*]

La discrimination intraspécifique de l'hôte et la composition larvaire des parasitoïdes ont été étudiées chez *Microplitis croceipes* (Cresson), *M. demolitor* Wilkinson, *Cotesia kazak* (Telenga) et *Hyposoter didymator* (Thunberg), endoparasitoïdes solitaires de *Heliothis virescens* (F.).

Dans les tests de choix lors de la ponte entre les hôtes parasités et sains, le nombre moyen de pontes dans des hôtes sains était significativement plus élevée que le nombre moyen de pontes dans les hôtes parasités une fois par une femelle de la même espèce pour *C. kazak* et *H. didymator,* ce qui montre que les femelles de ces 2 espèces reconnaissent des hôtes parasités récemment par une femelle de la même espèce (quelques secondes auparavant). Aucune différence significative ne s'est produite entre la ponte de ces 2 types d'hôtes pour *M. croceipes* et *M. demolitor*. Le pourcentage moyen de parasitisme par la seconde femelle de la même espèce a été déterminé avec un écart entre deux piqûres consécutives de 0, 24, 48 et 72 heures. A l'exception de l'écart nul pour *C. kazak* et *H. didymator,* le pourcentage de parasitisme par la 2e femelle conspécifique décroît généralement quand l'écart entre les piqûres augmente. Quand la seconde piqûre suit immédiatement la première, une larve de parasitoïde élimine toujours l'autre par combat physique. Lorsque l'écart est de 24 ou 48 heures, la larve la plus jeune l'emporte dans au moins 50 % des cas chez *M. croceipes, M. demolitor* et *C. kazak*.

L'élimination de la larve la plus âgée par la plus jeune se fait par attaque physique. Cependant, en ce qui concerne *H. didymator,* la larve du stade le plus âgé est victorieuse et l'élimination des larves les plus jeunes par les plus âgées se fait probablement par des processus physiologiques. De plus, les larves les plus âgées de *H. didymator* tuent apparemment les œufs de la seconde femelle également par des mécanismes physiologiques.

MOTS CLÉS : *Heliothis virescens,* endoparasitoïde, discrimination intraspécifique de l'hôte, compétition larvaire.

Received : 27 April 1989 ; Accepted : 18 June 1991.

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