

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

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Interspecific host discrimination by adults, and larval competition among the endoparasitoids *Microplitis croceipes* (Cresson), *Microplitis demolitor* Wilkinson, *Cotesia kazak* (Telenga) and *Hyposoter didymator* (Thunberg) were investigated using *Heliothis virescens* (F.) as the host. In ovipositional choice tests, the mean number of encounters and ovipositions for unparasitized hosts was not significantly different from the mean number of encounters and ovipositions for parasitized hosts for each treatment combination ($P > 0.05$). Thus, none of the parasitoid species discriminated between host larvae recently parasitized once by a female of another species and unparasitized hosts. However, in all but two cases, females did discriminate between unparasitized hosts and hosts in which an early first instar of the first-attacking species was developing. *Cotesia kazak* and *H. didymator* did not discriminate between unparasitized hosts and hosts parasitized by an early first instar of *M. demolitor*.

Larval competition among these parasitoid species was studied for three time intervals between the first and second species parasitization : 1) second species attack immediately (5-15 sec) after the first ; 2) second species attack 24 h after the first ; and 3) second species attack 48 h after the first. Time until egg eclosion was shortest for *M. demolitor*, then *C. kazak*, then *M. croceipes*, and longest for *H. didymator*. When the second parasitoid species attacked a host immediately after the first species, the species in which egg eclosion occurred first was the victor more frequently, except when *M. demolitor* competed with *C. kazak* and *H. didymator*. With a 24 h delay between the first and second species to attack, the older first instar from the first parasitization usually outcompeted the younger first instar from the second attack. A first instar from the second species to attack generally outcompeted the second instar of the first species when the second parasitization had been delayed 48 h. Competitors were eliminated mainly by physical attack, but *C. kazak* and *M. croceipes* apparently also killed *H. didymator* eggs by physiological processes.

KEY-WORDS : Insecta, interspecific host discrimination, larval competition, parasitoids, *Heliothis virescens*.

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Microplitis croceipes (Cresson) is an important solitary endoparasitoid of *Heliothis virescens* (F.) and *Helicoverpa zea* (Boddie) (Snow *et al.*, 1966; Bottrell *et al.*, 1968; Lewis & Brazzel, 1968; Mueller & Phillips, 1983; King *et al.*, 1985) in the United States. This wasp is one of the most predominant parasitoids of *Heliothis/Helicoverpa* (Lewis & Brazzel, 1968; Mueller & Phillips, 1983; King *et al.*, 1985), and is noted to parasitize larger numbers of host larvae in more species of host plants and is active over a longer period than any other parasitoid species (Stadelbacher *et al.*, 1984). Field and laboratory studies (Powell & Scott, 1986; Powell *et al.*, 1986) indicate that *M. croceipes* is also tolerant of several insecticides.

In Australia, *Microplitis demolitor* Wilkinson is commonly found in high numbers attacking *Helicoverpa* spp. larvae in the field (Shepard *et al.*, 1983a), and was imported into the United States in 1981 (Shepard *et al.*, 1983b). This parasitoid species was imported from Australia into Egypt in 1940-1941 (Hafez, 1951) and to the United States in 1981 (Shepard *et al.*, 1983b). *Microplitis demolitor* has been released and recovered in grain sorghum in Arkansas, pigeon pea and soybean in South Carolina and cotton in Mississippi (Powell, 1989).

Cotesia kazak (Telenga) and *Hyposoter didymator* (Thunberg) were reported by Carl (1978) as important solitary endoparasitoids of *Helicoverpa armigera* Hubner in Greece and Bulgaria, respectively. *Cotesia kazak* was imported from Europe into New Zealand where it became successfully established (Johnson *et al.*, 1986). This parasitoid species then was imported into the United States from Europe in 1984 and from New Zealand in 1985 (Powell, 1989). *Hyposoter didymator* was imported from Europe into the United States in 1985 and released in unsprayed cotton in Mississippi in 1986, but was not recovered (Powell, 1989). Adult *C. kazak* from both countries were released in insecticide-free cotton infested with early instar *Heliothis* in Mississippi in 1985. While no recovery was made in 1985, *C. kazak* was recovered from *H. zea* in cotton and *H. virescens* in pigeon pea after adults from New Zealand were released in 1986.

Interspecific host discrimination refers to the ability of parasitoids to distinguish between unparasitized hosts and hosts parasitized by another parasitoid species. Failure to discriminate can result in multiple parasitism, and possible wasting of offspring, especially in solitary parasitoids which require the entire host for development. Parasitoids discriminate interspecifically by recognizing either external marking pheromones or an internal marker (Vinson, 1976). The internal marker may be a pheromone injected by the ovipositing females or may be induced by physiological changes in the host caused by the developing parasitoid (Vinson, 1976). In laboratory studies, Vinson & Ables (1980) demonstrated that hosts previously parasitized by *Chelonus insularis* Cresson were acceptable to *M. croceipes* as oviposition sites. They concluded that *M. croceipes* was unable to discriminate interspecifically in this case. Previous research on interspecific host discrimination has not been reported for the three imported species. Interspecific competition among parasitized larvae should be studied to ascertain the compatibility of introduced and native species for control of *Heliothis/Helicoverpa* spp.

This research was conducted to determine 1) if these parasitoid species discriminate between unparasitized hosts and hosts previously parasitized by each of the other three parasitoid species, 2) the influence of time of attack by a second species on host discrimination for the four species, and 3) the outcome of larval competition between *M. croceipes* and the three imported species. Timing of egg eclosion was determined for each parasitoid species, and larval competition was studied at three time intervals to determine the effect of relative age of the competitors on competitive ability and the method of elimination of competitors.

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 *H. virescens* larvae by procedures from **Powell & Hartley** (1987). The *M. croceipes* colony originated from cotton collected in the Mississippi Delta. *Microplitis demolitor* was imported from Australia, *C. kazak* was imported from Australia, *C. kazak* was imported from New Zealand and *H. didymator* was imported from Europe. 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). Host larvae were dissected to determine survival or mortality of immature parasitoids. Instars of each species were morphologically distinguishable from other species in the test. Voucher specimens have been deposited at the United States National Museum of Natural History in Washington, D.C.

INTERSPECIFIC DISCRIMINATION

Parasitized vs. unparasitized larvae

An experiment was conducted to determine if any difference in oviposition by a female occurred between hosts recently (within 1 h) parasitized once by a female of another species 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 100 × 4 mm Petri dish 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). Mated females with prior oviposition experience and from 3-6 days old were used. A female was given prior oviposition experience by allowing her to oviposit in 10 unparasitized late second instars of *H. virescens* both 1 and 2 days emergence. During a test, the behavior of a female was observed continuously, 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. 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 (no first instars were present) were detected more easily. A host was dissected in a small watchglass containing Ringer's solution and scored by the presence or absence of the egg(s). This test was replicated 4 times for each of 12 possible treatment combinations of first and second parasitoid species (table 1). Different individual females were used for each replication. Two-tailed paired sample t tests were used to analyze the data.

Time of attack

A second experiment was conducted to determine whether female parasitoids would discriminate against hosts which had been parasitized 48 h earlier by a first parasitoid species. Mated females with prior oviposition experience and from 3-6 days old were exposed in a 100 × 15 mm Petri dish to one host at a time up to a total of 20-25 hosts in

TABLE 1

Mean (\pm SE) number of encounters and ovipositions by *M. croceipes*, *M. demolitor*, *C. kazak*, and *H. didymator* females for unparasitized larvae and parasitized host larvae

1 st Species	2 nd Species	Hosts	Mean no. of encounters	Mean no. of ovipositions
<i>M. demolitor</i>	<i>M. croceipes</i>	Unparasitized	27.8 \pm 3.9	9.8 \pm 1.5
		Parasitized	24.5 \pm 4.0	8.0 \pm 1.7
		Calculated t	1.8 NS	0.6 NS
<i>C. kazak</i>	<i>M. croceipes</i>	Unparasitized	30.8 \pm 2.5	9.5 \pm 0.7
		Parasitized	30.0 \pm 3.6	7.5 \pm 0.9
		Calculated t	0.5 NS	2.7 NS
<i>H. didymator</i>	<i>M. croceipes</i>	Unparasitized	31.0 \pm 1.7	10.8 \pm 1.1
		Parasitized	29.5 \pm 3.1	7.0 \pm 0.4
		Calculated t	0.3 NS	2.6 NS
<i>M. croceipes</i>	<i>M. demolitor</i>	Unparasitized	14.8 \pm 1.5	8.3 \pm 0.9
		Parasitized	11.5 \pm 0.9	6.8 \pm 0.5
		Calculated t	2.9 NS	1.4 NS
<i>C. kazak</i>	<i>M. demolitor</i>	Unparasitized	18.5 \pm 1.3	9.3 \pm 1.1
		Parasitized	15.0 \pm 2.1	6.3 \pm 0.7
		Calculated t	1.1 NS	2.1 NS
<i>H. didymator</i>	<i>M. demolitor</i>	Unparasitized	12.3 \pm 1.0	9.0 \pm 0.7
		Parasitized	13.5 \pm 0.9	9.5 \pm 0.9
		Calculated t	0.8 NS	0.4 NS
<i>M. croceipes</i>	<i>C. kazak</i>	Unparasitized	16.5 \pm 1.0	8.3 \pm 0.9
		Parasitized	13.8 \pm 3.6	5.0 \pm 0.7
		Calculated t	2.9 NS	2.9 NS
<i>M. demolitor</i>	<i>C. kazak</i>	Unparasitized	12.5 \pm 0.7	9.8 \pm 0.8
		Parasitized	11.5 \pm 1.3	7.8 \pm 0.8
		Calculated t	0.9 NS	1.7 NS
<i>H. didymator</i>	<i>C. kazak</i>	Unparasitized	16.5 \pm 1.7	10.0 \pm 1.1
		Parasitized	13.5 \pm 2.1	7.5 \pm 1.0
		Calculated t	1.1 NS	2.2 NS
<i>M. croceipes</i>	<i>H. didymator</i>	Unparasitized	18.0 \pm 0.9	11.5 \pm 1.1
		Parasitized	15.0 \pm 1.4	7.8 \pm 1.1
		Calculated t	1.4 NS	1.8 NS
<i>M. demolitor</i>	<i>H. didymator</i>	Unparasitized	26.5 \pm 4.1	10.5 \pm 1.3
		Parasitized	24.5 \pm 5.4	7.3 \pm 1.3
		Calculated t	0.5 NS	1.4 NS
<i>C. kazak</i>	<i>H. didymator</i>	Unparasitized	41.5 \pm 8.9	10.3 \pm 0.5
		Parasitized	32.0 \pm 5.7	9.0 \pm 0.7
		Calculated t	2.4 NS	2.1 NS

NS, not significant, ($P > 0.05$); $df = 3$

each of three categories: 1) unparasitized hosts, 2) hosts recently (within 5-10 seconds) parasitized by the first parasitoid species and 3) hosts previously parasitized by the first parasitoid species 2 days earlier. Three females were exposed to each category of hosts. Different females were used for each host category. Each host was attacked only once, and insertion of the ovipositor was observed for each attack. Egg depletion was not a problem since in the above experiment females of each parasitoid species oviposited in 20 consecutive hosts within 15-30 min. Hosts were dissected 24 h after attack as described above. This test was repeated three times for each of 12 treatment combinations of first and second parasitoid species (table 2). All host instars used in these tests have been shown to be equally acceptable to these parasitoid species (Tillman & Powell, 1989), and thus, host

age was not considered a source of variance. Percent parasitization by the second female was calculated for each treatment combination. These data were subjected to analysis of variance and least significant difference tests (LSD ; P < 0.05) with the general linear model procedure of SAS (SAS Institute 1986).

TABLE 2

Influence of time of attack by a second parasitoid species on interspecific host discrimination for four species of parasitoids

1 st species	2 nd species	Mean (± SE) percent parasitization by 2 nd species		
		Alone (n)	Immediate attack (n)	Attack delayed 48 h (n)
<i>M. demolitor</i>	<i>C. kazak</i>	95.4 ± 0.05(66)xa	100.0 (42)xa	78.8 ± 0.07 (38)ye
<i>H. didymator</i>	<i>C. kazak</i>	86.7 ± 0.06(53)xa	90.6 ± 0.06(42)xa	20.1 ± 0.05(60)ybc
<i>M. croceipes</i>	<i>C. kazak</i>	90.4 ± 0.05(62)xa	94.6 ± 0.07(37)xa	12.2 ± 0.06(41)yab
<i>C. kazak</i>	<i>M. demolitor</i>	96.9 ± 0.05(63)xa	91.6 ± 0.06(46)xa	0.0 (41)ya
<i>H. didymator</i>	<i>M. demolitor</i>	95.1 ± 0.05(60)xa	100.0 (34)xa	19.3 ± 0.06 (52)yb
<i>M. croceipes</i>	<i>M. demolitor</i>	96.6 ± 0.05(58)xa	90.3 ± 0.07(31)xa	23.0 ± 0.05(57)ybc
<i>C. kazak</i>	<i>M. croceipes</i>	92.6 ± 0.05(55)xa	92.7 ± 0.06(39)xa	11.0 ± 0.05(56)yab
<i>H. didymator</i>	<i>M. croceipes</i>	94.7 ± 0.05(57)xa	100.0 (44)xa	23.8 ± 0.05(55)ybc
<i>M. demolitor</i>	<i>M. croceipes</i>	94.4 ± 0.05(54)xa	97.9 ± 0.06(47)xa	30.5 ± 0.06(52)ybc
<i>C. kazak</i>	<i>H. didymator</i>	95.1 ± 0.05(65)xa	89.6 ± 0.07(37)xa	34.0 ± 0.05 (62)yc
<i>M. demolitor</i>	<i>H. didymator</i>	98.3 ± 0.05(60)xa	100.0 (40)xa	92.5 ± 0.05 (65)xf
<i>M. croceipes</i>	<i>H. didymator</i>	93.5 ± 0.05(64)xa	92.9 ± 0.06(41)xa	53.8 ± 0.05 (56)jd

Means followed by the same letter (x,y) in a row or by the same letter (a-f) in a column were not significantly different (P < 0.05 ; LSD test [SAS 1986]) based on LSD comparisons.

INTERSPECIFIC LARVAL COMPETITION

Timing of eclosion

Timing of egg eclosion was determined by allowing a mated female 3-8 days old to oviposit one egg into each of 90 second instars of *H. virescens*, and then later dissecting these hosts in a small watchglass containing Ringer's solution to observe the immature parasitoid. Initially, a few hosts were dissected every 4 h from 28 to 60 h after oviposition until the appropriate range of egg eclosion was ascertained for each parasitoid species. Then, 20 hosts were dissected every 4 h within this range. Percent eclosion was calculated every 4 h-time interval for each species.

Host attack by two parasitoid species

Larval competition was studied by parasitizing a second instar of *H. virescens* with one species and then allowing a second species to attack the same host. This was accomplished for three different time intervals between the first and second species attack : a) second attack 0 h (within 5-15 sec) after the first, b) second attack 24 h after the first and c) second attack 48 h after the first. Females were mated and 3-8 days old. Three days after the attack

by the second species, each host was dissected as described above. Both the outcome of the competition between the two species and the method of elimination were recorded. This process was repeated for each treatment combination of first and second parasitoid species.

RESULTS

INTERSPECIFIC DISCRIMINATION

Parasitized vs. unparasitized larvae

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 treatment combination ($P > 0.05$) (table 1). Also, the mean number of ovipositions for unparasitized hosts was not significantly different from the mean number of ovipositions for parasitized hosts for each treatment combination ($P > 0.05$).

Time of attack

The 2 day time delay between the first and second species attack did influence the discriminatory ability of the second parasitoid species (table 2). There were no differences in the mean percent parasitism by the second species between hosts attacked by the second species alone and hosts attacked immediately by this second species for all treatment combinations. For example, *C. kazak* parasitized 95.4 % of the hosts parasitized by this species alone, yet also parasitized 100 % of the hosts previously parasitized by *M. demolitor* a few seconds earlier. Percent parasitization by the second parasitoid species, of hosts previously parasitized 2 days earlier by the first parasitoid species, was significantly different from that of both hosts parasitized by the second species alone, unparasitized hosts and hosts recently parasitized by a first species ($P < 0.05$), except when *H. didymator* parasitized hosts with first instars of *M. demolitor* ($P > 0.05$). The percent parasitism by *C. kazak* (78.8 %) on hosts previously parasitized by *M. demolitor* 48 h earlier was significantly different from all other mean percent parasitism for this category of hosts.

INTERSPECIFIC LARVAL COMPETITION

Timing of eclosion

Percent egg eclosion over time for each parasitoid species is shown in fig. 1. Although egg eclosion began at 36 h after oviposition for both *M. demolitor* and *C. kazak*, a greater percentage of first instars for *M. demolitor* than *C. kazak* was found at this time. Thus, development of the egg is faster for *M. demolitor* than for *C. kazak*. Egg eclosion began later (at 40 h after oviposition) for *M. croceipes*. Some overlap in time of egg eclosion occurred among these three species. Egg eclosion began at 44 h after oviposition for *H. didymator*. There was very little overlap in time of egg eclosion between this species and the other three species.

Host attack by two parasitoid species

When parasitization by the second species followed immediately (0 h) after parasitization by the first species, the species in which egg eclosion occurred first usually

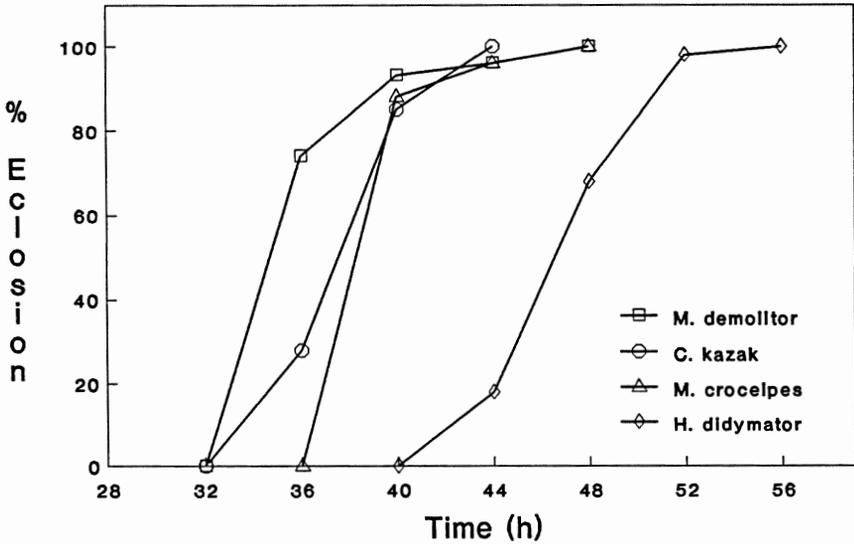


Fig. 1. Percent egg eclosion over time (h) for *M. croceipes*, *M. demolitor*, *C. kazak*, and *H. didymator*.

TABLE 3

Results of larval competition among *M. croceipes*, *M. demolitor*, *C. kazak* and *H. didymator* in *Heliothis virescens* with an immediate parasitization by a second species

Competitors		n	% victory of 1 st to eclose
1 st to eclose	2 nd to eclose		
<i>M. demolitor</i>	<i>C. kazak</i>	72	11.1
<i>M. demolitor</i>	<i>M. croceipes</i>	76	61.8
<i>M. demolitor</i>	<i>H. didymator</i>	57	12.3
<i>C. kazak</i>	<i>M. croceipes</i>	65	87.7
<i>C. kazak</i>	<i>H. didymator</i>	87	85.1
<i>M. croceipes</i>	<i>H. didymator</i>	87	72.4

outcompeted the other parasitoid species (table 3). *Microplitis demolitor* was exceptional in this regard, with *C. kazak* and *H. didymator* usually outcompeting *M. demolitor* even though *M. demolitor* eclosed earlier. In every case, a competitor was eliminated by physical combat. Sometimes a first instar was observed biting the competitor (first instar) with its mandibles, but more often, a healthy individual and a moribund, punctured first instar were found.

With a 24 h delay between parasitization by the first and second species (table 4), competition was between late first instars of the first parasitoid species and early first instars of the second species. When *M. croceipes* was the first parasitoid species to parasitize the host, this wasp outcompeted *M. demolitor* and *H. didymator*, but was inferior

TABLE 4

Percent of first attacks that resulted in possession of the host larvae when the second attack was 24 h after the first attack ; n = number

		2 nd species to attack							
		<i>M. demolitor</i>		<i>C. kazak</i>		<i>M. croceipes</i>		<i>H. didymator</i>	
		(n)	%	(n)	%	(n)	%	(n)	%
1 st species to attack	<i>M. demolitor</i>	—	—	(52)	11.5	(42)	35.7	(41)	0
	<i>C. kazak</i>	(24)	66.7	—	—	(18)	16.7	(42)	52.4
	<i>M. croceipes</i>	(22)	68.2	(22)	13.6	—	—	(46)	67.4
	<i>M. didymator</i>	(22)	90.9	(25)	92.0	(25)	80.0	—	—

to *C. kazak*. As the second parasitoid species, *M. croceipes* outcompeted *M. demolitor* and *C. kazak*. *Microplitis demolitor* was outcompeted by all the other species, regardless of whether this was the first or second species which attacked the host. *Hyposoter didymator* outcompeted all species except when it was the first species in the hosts. When *H. didymator* was the second species to attack the host, it only outcompeted *M. demolitor*. Except for two cases, elimination of competitors was accomplished by physical attack. When *C. kazak* and *M. croceipes* were the first species, they were also able to kill eggs of *H. didymator* more often than not (table 4). *Hyposoter didymator* eggs were assumed to be killed by physiological suppression since the eggs were black and not developing. Normally the eggs of each species are white and have developed into first instars (second species) by the time the hosts are dissected. Also, some of these black, dead eggs were encapsulated.

The second parasitoid species usually outcompeted the first parasitoid species when the second parasitization was delayed 48 h (table 5). In these cases, the second instars of the first parasitoid species were eliminated by the first instar of the second parasitoid species. There were three exceptions to this general trend. When *M. croceipes* was the first species and *M. demolitor* and *H. didymator* were the second species, neither parasitoid species was intrinsically superior to the other one. Another exception was the competitive superiority of *H. didymator* second instars over *M. demolitor* first instars. Generally, elimination of competitors was accomplished by physical attack. These *H. didymator* eggs were black and

TABLE 5

Percent of first attacks that resulted in possession of the host larvae when the second attack was 48 h after the first attack ; n = number

		2 nd species to attack							
		<i>M. demolitor</i>		<i>C. kazak</i>		<i>M. croceipes</i>		<i>H. didymator</i>	
		(n)	%	(n)	%	(n)	%	(n)	%
1 st species to attack	<i>M. demolitor</i>	—	—	(40)	15.0	(64)	32.8	(69)	5.8
	<i>C. kazak</i>	—	—	—	—	(6)	16.7	(20)	15.0
	<i>M. croceipes</i>	(22)	45.5	(20)	0	—	—	(29)	51.7
	<i>H. didymator</i>	(11)	81.8	(17)	11.8	(14)	28.6	—	—

not developing. Larval competition did not occur between *C. kazak* and *M. demolitor* because *M. demolitor* does not oviposit in hosts containing first instars of *C. kazak* (table 2).

DISCUSSION

The results of our ovipositional choice tests in this study demonstrate that none of these species discriminate between unparasitized hosts and hosts recently (within one hour) parasitized once by a female of a different species, thus, a high degree of multiple parasitism occurred in laboratory situations. However, female parasitoids usually could distinguish between unparasitized hosts and hosts in which an early instar of another parasitoid species was developing (hosts previously parasitized by first species 48 h earlier). Nevertheless, some multiple parasitism still occurred. Since only one individual parasitoid can develop to maturity with these solitary parasitoid species, the result of multiple parasitism is larval competition. Supernumerary larvae are eliminated by: a) selective starvation, b) physiological suppression, and c) physical attack (Salt, 1961; Fisher, 1971; Vinson & Iwantsch, 1980). However, most of the parasitoid species did show evidence of discriminating between recently parasitized hosts, and hosts previously parasitized 2 days earlier by another parasitoid species. Thus, interspecific host discrimination is time-dependent for these 4 parasitoid species.

Interspecific host discrimination is relatively rarely reported, and in studies where rejection of hosts parasitized by another parasitoid species has been shown, this discrimination is time-dependent (Steinberg *et al.*, 1987; Strand, 1986; Vinson, 1972; Wylie, 1970, 1971; van Alphen & van Strien-van Liempt, unpubl. data). Other endoparasitoids of *H. virescens* have been reported not to discriminate interspecifically. *Cardiochiles nigriceps* Viereck, *Campoletis sonorensis*, and *M. croceipes* were not capable of distinguishing between unparasitized hosts and *Chelonus insularis* Cresson parasitized hosts (Vinson & Ables, 1980). *Campoletis perdistinctus* (Viereck) did not discriminate against hosts recently parasitized by *C. nigriceps* and vice-versa (Vinson, 1972). However, *C. perdistinctus* did not oviposit eggs in hosts parasitized by *C. nigriceps* 5 days earlier. Thus, without consideration of the time-dependency of discrimination, the results of discrimination tests may not give the whole picture. Research on interspecific host discrimination should therefore include experiments to determine the ability of females to discriminate between recently parasitized hosts and hosts previously parasitized some time earlier.

In cases where rejection of hosts parasitized by another parasitoid species has been shown, this rejection is more likely to be due to a severely changed physiological condition of the host, rather than to the recognition of a specific mark (Steinberg *et al.*, 1987; Strand, 1986; Vinson, 1972; Wylie, 1970, 1971; van Alphen & van Strien-van Liempt, in preparation). An exception was reported by Vet *et al.* (1984) who determined that *Asobara tabida* (Nees) and *Asobara rufescens* (Foerster) were capable of discriminating against hosts recently parasitized by females of the other species. The ability of these parasitoids to discriminate interspecifically was due to the recognition of a specific mark. Apart from this exception, results of previous studies suggest that the species we studied do not detect marks (since they failed to discriminate early on), but for the most part, they may be using altered host physiological condition as cue for interspecific discrimination. Something interesting is going on when *M. demolitor* attacks a host since *H. didymator* does not discriminate against it and *C. kazak* barely does so. Thus, there is a need to study host-induced changes in *M. demolitor* in comparison with the other species. In conclusion, our research shows that interspecific host discrimination is dependent not only on the

second species and its ability or inability to detect a mark, but also on the first species and the changes it may or may not induce in the host.

These studies on competitive interactions between the native parasitoid *M. croceipes* and the three imported species may be particularly pertinent to release strategies. The greatest opportunities for competitive interactions (especially at the 0-24 h interval) occur when large numbers are released at the same time in the same area. Our laboratory studies indicate that intrinsic competition between *M. demolitor* and the other two imported species, *C. kazak* and *H. didymator*, is intense and unfavorable to *M. demolitor*. Therefore, it may be better to release *M. demolitor* early in the growing season before the other two imported species to give it a greater chance to become established. Even though *M. croceipes* would also be present at this time, competition between the two species probably would not be intense since our laboratory results showed that neither species dominates the other one. Also, both adult and larval competition between *M. croceipes* and *M. demolitor* may be avoided to some extent in the field since *M. croceipes* accepts older instars of *H. virescens* while *M. demolitor* accepts younger instars of this host (Tillman & Powell, 1989).

In our studies, rarely did one species completely outcompete the other. Even though one species may dominate, other species should be able to maintain populations as long as field conditions are conducive to their survival. Also, competition between these parasitoids may not be as intense in the field as in the laboratory since other factors such as differences in efficiency of host finding and host and/or host preferences are also involved.

Jalali *et al.* (1988) studied the competitive interaction between *C. kazak* and *H. didymator* on *H. armigera*. Hosts were parasitized by first one species then the other at 0 h, 24 h and 48 h intervals between the first and second species parasitization. For each of these treatments, they determined a measure of « percent parasitism » based on cocoons recovered. Since these authors did not determine whether or not one species oviposited into hosts parasitized by the other species, they actually obtained a measure of the outcome of the competitive interactions, both indirect (adult competition) and direct (larval competition) between these two species, and not a measure of percent parasitism for each species. « Percent parasitism » at the 0 h interval is mainly a measure of larval competition, and their results are similar to ours for larval competition, and their results are similar to ours for larval competition at this time interval. At the 24 h interval, « percent parasitism » is a measure of both the ability of these parasitoids to discriminate against hosts previously parasitized by the other species and larval competition. Results of our host discrimination studies demonstrated that *C. kazak* will oviposit into only 29 % of the hosts previously parasitized by *H. didymator* 24 h earlier (unpubl. data). Furthermore, *H. didymator* outcompeted *C. kazak* 23 out of 25 times with a 24 h delay in parasitism by *C. kazak* (table 4). Therefore, we suggest that the « percent parasitism » for *H. didymator* when parasitization by *C. kazak* was delayed 24 h, should be higher than the 20 % found by Jalali *et al.* (1988) unless there are host-induced differences. « Percent parasitism » at the 48 h interval is a better measure of actual parasitization. These authors found that *H. didymator* parasitizes only ca. 10 % of the host parasitized by *C. kazak* 48 h earlier and *vice versa*. Their results are similar to those determined in our host discrimination studies where *H. didymator* parasitized 34 % and *C. kazak* parasitized 20 % of the hosts previously parasitized 48 h earlier by *C. kazak* and *H. didymator*, respectively (table 2). Jalali *et al.* (1988) erroneously attributed « percent parasitization » at the 48 h interval to larval competition between the two species. These authors stated that *H. didymator* could not survive in competition with *C. kazak* since a suppression of the *H. didymator* population by ca. 70 % in the 24 h interval was recorded, and suggested that the intrinsically inferior species, *H. didymator*, should be released before *C. kazak*.

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RÉSUMÉ

Discrimination interspécifique et compétition larvaire chez *Microplitis croceipes*, *Microplitis demolitor*, *Cotesia kazak* (Hym. : Braconidae) et *H. didymator* (Hym. : Ichneumonidae), parasitoïdes de *Heliothis virescens* (Lep. : Noctuidae).

La discrimination interspécifique au niveau des adultes et la compétition au niveau des larves entre les parasitoïdes *Microplitis croceipes* (Cresson), *Microplitis demolitor* Wilkinson, *Cotesia kazak* (Telenga) et *Hyposoter didymator* (Thunberg) ont été étudiées sur l'hôte *Heliothis virescens* (F.). Au cours de tests de choix lors de la ponte, le nombre moyens de rencontres et de pontes n'était pas significativement différent sur des hôtes sains et sur des hôtes parasités ($P > 0.05$) pour chaque combinaison de traitements. Ainsi, aucune des espèces de parasitoïdes n'a distingué entre des larves d'hôtes récemment parasitées à une seule reprise par une femelle d'une autre espèce et des larves d'hôtes saines. Cependant, dans tous les cas sauf deux, les femelles ont distingué d'hôtes sains des hôtes dans lesquels une jeune larve de premier stade de l'espèce attaquant la première était présente. *C. kazak* et *H. didymator* ne distinguent pas des hôtes sains et des hôtes parasités par une jeune larve de premier stade de *M. demolitor*. La compétition larvaire entre ces parasitoïdes a été étudiée sur trois intervalles de temps entre l'attaque de deux espèces : 1° la seconde espèce attaque immédiatement (5 à 15 sec après la première) ; 2° la seconde espèce attaque 24 h après la première ; 3° la seconde espèce attaque 48 h après la première. La durée nécessaire à l'éclosion est la plus courte chez *M. demolitor*, puis *C. kazak*, puis *M. croceipes* et la plus longue pour *H. didymator*. Lorsque la seconde espèce de parasitoïde attaque un hôte immédiatement après la première, l'espèce dont l'œuf éclôt le premier est en général vainqueur, excepté lorsque *M. demolitor* est en compétition avec *C. kazak* et *H. didymator*. Avec un délai de 24 h entre l'attaque des deux espèces, la larve de premier stade la plus âgée qui provient du premier parasitisme vient généralement à bout de la plus jeune larve de premier stade qui provient de la deuxième attaque. Une larve de premier stade de la deuxième espèce vient généralement à bout d'une larve de deuxième stade de la première espèce lorsqu'il y a un écart de 48 h entre les deux attaques. Les compétiteurs sont principalement éliminés par attaque physique mais il semble que *C. kazak* et *M. croceipes* tuent également les œufs de *H. didymator* par des processus physiques.

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