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HYMENOPTEROUS PARASITOIDS OF BARK BEETLES [*SCOLYTIDAE*] IN ISRAEL : RELATIONSHIPS BETWEEN HOST AND PARASITOID SIZE, AND SEX RATIO*

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Information on parasitoids of bark beetles infesting conifers and broadleaves is presented to show the relations between host and parasitoid size, and parasitoid sex ratios. Sticky traps were employed to determine the sex ratios of parasitoid species operating on beetle-infested material. A wide range in body length was found for most species. Females of *Cerocephala eccoptogasteri* Masi, *Cheiropachus quadrum* Febr., *Eurytoma morio* Boheman, *Heydenia pretiosa* Forster, *Metacolus unifasciatus* Forster, *Rhaphitelus maculatus* Walker and *Roptrocerus xylophagorum* (Ratz.) were usually significantly longer than their males, whereas the males of all four *Dendrosoter* spp. were significantly longer than the females. Body lengths of the males and females were almost identical in *Entedon ergias* Walker and *Ecphylus caudatus* Rusch. The sex ratio varied markedly within most species ; the mean ratio for 5 of them differed significantly from 1:1. The sex ratio of *M. unifasciatus* and *E. morio* was significantly related to host size. The sex-ratio of parasitoids trapped on sticky traps varied with time in relation to the phenology of the host beetle. Females were more numerous during the larvae development while males were more abundant between the pupal stage and emergence of the host. Male courtship behaviour of *Dendrosoter caenopachoids* Rusch., *D. protuberans* (Nees), *M. unifasciatus* and *R. xylophagorum* is described. The effect of host size, the diversity in sex ratios, and possible interaction between parasitoid size and sex-ratio are discussed.

KEY-WORDS : *Hymenoptera*, bark beetles, *Scolytidae*, parasitoid size, sex-ratio.

Although hymenopterous parasitoids have received much attention from scientists engaged in research on bark beetles (*e.g.* **Russo**, 1938 ; **Chararas**, 1962 ; **Schvester**, 1957 ; **Bushing**, 1965 ; **Berisford** *et al.*, 1972 ; **Dahlsten**, 1982) little has been published about the relation between host - parasitoid size and sex ratios.

Bark beetle parasitoids are usually oligophagous attacking a wide range of Scolytids and, occasionally, also other xylophagous beetles (*e.g.* **Bushing**, 1965 ; **Chararas**, 1962 ; **Hedqvist**, 1963 ; **Mendel**, 1986 ; **Nuorteva**, 1957 ; **Pettersen**, 1976 and **Russo**, 1938). They can develop on different larval instars and pupae (*e.g.* **Ryan & Rudinsky**, 1962 ; **Mendel**, 1986). Consequently, bark beetle parasitoids usually show a wide range of adult body size (*e.g.* **Hedqvist**, 1963).

The positive correlation between host - parasitoid sizes is a well known phenomenon among parasitic Hymenoptera (*e.g.* **Sweetman**, 1958) ; however it was little investigated for bark beetle parasitoids (**DeLeon**, 1935 ; **Kaston**, 1937 ; **Ryan & Rudinsky**, 1962 ; **Hedqvist**, 1963).

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The sex ratio of bark beetle parasitoids has been little studied and is usually given in the literature as the number of males and females reared from field collections (*e.g.* **Schvester,** 1957 ; **Kennedy,** 1970), or obtained from sticky traps (*e.g.* **Stephen & Dahlsten,** 1976).

This study presents information on 13 bark beetle parasitoids to show the relationship between host and parasitoid size, and their sex-ratio.

MATERIALS AND METHODS

STUDIES IN SITU

The data were collected during 1980-1984 mainly in the Judean Hills (Eshthaol), the Shefela, coastal plain north of Tel-Aviv and Upper Galilee (Biriyya). Parasitoids of pine (*Pinus halepensis* Mill. and *P. brutia* Ten.), cypress (*Cupressus sempervirens.* L.), fig (*Ficus carica* L.), olive (*Olea europaea* L.) and almond (*Amygdalus communis L.*) bark beetles were studied. Bark beetle parasitoids of elm (*Ulmus canescens* Melv.) were studied in Wadi Naha'laot in the Menashe Hills.

Cut branches 4-10 cm in diameter were used to induce attack by beetles on broadleaves. In the case of pine and cypress, 25-year-old trees were felled of various dates in the 4 seasons (**Mendel,** 1984 ; **Mendel** *et al.*, 1985). The trap trees were placed in semi-shade ; the branches were suspended in the tree canopy to prevent direct radiation. Weekly checks were made to determine the onset of beetle infestation and these were followed by laboratory investigations, when the beetle brood reached the pupal stage and before the start of parasitoid emergence. The sample unit for each trap tree or branch was at least 1 500 cm^2 of bark surface.

Sticky traps were employed to determined the sex ratio of parasitoid species operating on infested stems. Sex ratios were obtained for parasitoid complexes of pine and cypress bark beetles. Three cypress trees (*C. sempervirens*) were felled at Ilanot in early April 1983, and 3 pine trees at Eshtha'ol in June 1983. Three sticky traps made of transparent polyethylene (28×28 cm) coated with Rimi-Foot® (a non-drying glue) were attached to the trap trees at 1.2 m from the base, mid-length, and at about 2-3 m from the top. The traps were replaced on cypress and pine at 1-3-day intervals, and at one-week intervals, respectively. The procedure was continued for about 2 months for pine, and about 3 months for cypress. Parasitoids on sticky traps were counted directly on the trap under a binocular lens or a $\times 10$ magnifying glass, paraffin oil being used to dissolve poorly defined specimens. Observations were made *in situ* on adult parasitoid behaviour at specific sites, mainly at Ilanot, with trap-trees or trap branches.

LABORATORY STUDIES

Branches and stem sections infested with bark beetles were placed into wooden emergence boxes under controlled temperature ($25° \pm 1°C$) and photoperiod (12L:12D) conditions. A flow of CO_2 was applied twice daily to collect the emerging individuals, in order to minimize additional parasitism by the emerging individuals and to record the exact sex-ratio and proportion of parasitoid species in the complex. The sex ratio for any specific parasitoid was determined in samples of at least 20 individuals. Body length was measured under a binocular microscope at $\times 40$ and $\times 80$ magnifications of 20-40 specimens of each sex of each parasitoid. Ovipositor length was measured for *Dendrosoter caenopachoides, D. protuberans* and *Metacolus unifasciatus.*

RESULTS

Relation between host beetle and parasitoid size

A distinct positive correlation was obtained between parasitoid and host sizes (table 1). The data also indicate the existence of a wide range in body length for most of the species. For example, the body length of *Metacolus unifasciatus* females ranged from 1.4 mm in a small larva of *Carphoborus minimus* to 5.7 mm in a mature larva of *Phloeosinus armatus*. The length of *Dendrosoter protuberans* males varied between 1.8 and 6.6 mm. There was also a wide range in parasitoid length for all host beetles, except for *Entedon ergias* (table 1). The females of *Pteromalidae* and of *Eurytoma morio* were significantly longer than the males. In the case of *M. unifasciatus* and *Rhaphitelus maculatus* the differences between the mean body lengths of the male and female were not always significant. However, the trend for females of these species to be larger than the males was also shown by the ranges in their body lengths. Different results were obtained for the *Braconidae* and for *Entedon ergias*. The mean body lengths of *Ecphylus caudatus* and of *Entedon ergias* and their ranges, were almost identical in both sexes. However, in all 4 *Dendrosoter* spp., the males were significantly longer than the females in all host populations. Data of body length of *Dendrosoter middendorffi* (obtained from a population of *Tomicus minor*) by **Nuorteva** (1957) from Finland also show that the males were significantly longer (3.4 mm) than the females (2.8 mm). Longer males were also recorded from a small sample of *Dendrosoter* sp. (obtained from *Orthotomicus erosus*) from South Africa (mean length of male 2.6 mm, female 2.3).

Significant correlations ($r > 0.9$) were calculated for the relationships between body length and ovipositor length for *Dendrosoter caenopachoides*, *D. protuberans* and *Metacolus unifasciatus*. The mean ovipositor lengths were 44 %, 69 % and 61 % of the body lengths for *D. caenopachoides*, *D. protuberans* and *M. unifasciatus*, respectively.

Sex ratio and male behaviour

The sex ratio of the brood in the investigated species varied markedly but in most cases the mean ratio did not differ significantly from 1:1 ; Five species, viz., *Cephalonomia hypobori*, *Dendrosoter caenopachoides*, *Ecphylus caudatus*, *Heydenia pretiosa* and *Roprocerus xylophagorum*, had a male:female ratio lower than 1:1, in *Entedon ergias* the ratio was higher than 1:1 (table 2). Sex ratios of *Metacolus unifasciatus* and *Eurytoma morio* as related to host size, showed that the male:female ratio of the brood was higher than 1:1 when the parasitoids developed on small host species, and lower than 1:1 when the parasitoids developed on small host species, and lower than 1:1 when the parasitoids developed on large host species (table 3).

The sex ratio of parasitoids trapped on sticky traps varied with time in relation to host phenology. Figures 1 and 2 show the changes in sex-ratio of parasitoid complexes of the pine and the cypress bark beetle, respectively. During the early stages of beetle infestation, between mass arrival and development of larval stages of the host, the female parasitoids were dominant, while in the last developmental stages, between pupation and emergence of the host, male parasitoids were more numerous. Table 4 shows the dominance of females over males for each investigated parasitoid from the arrival of the beetle on the trap tree to the onset of parasitoid brood emergence. Later, from the onset of parasitoid brood emergence the situation was reversed. **Stephen & Dahlsten** (1976) showed similar results for trapped *R. xylophagorum* on pine infested with *Dendroctonus ponderosae*.

TABLE 1

Length of male and female parasitoids (mean ± s.d. in mm) as related to size (body length and pronotum breadth) of the adult host beetle. Host species are arranged according to increasing size.

HOSTS		*Hypoborus ficus* Erichson	*Carphoborus minimus* Fabr.	*Pityogenes calcaratus* Eich.	*Phloeotribus scarabaeoides* (Bern.)	*Scolytus rugulosus mediterraneus* (Ratz.)	*Scolytus multistriatus orientalis* (Egg.)	*Phloeosinus aubei* Perris	*Orthotomicus erosus* (Woll.)	*Tomicus destruens* (Woll.)	*Phloeosinus armatus* Reiter
		1.39 0.59*	1.88 0.66	2.39 1.08	2.43 1.06	2.84 0.92	2.61 1.04	2.77 1.25	3.27 1.08	4.47 1.61	4.19 2.00
PARASITOIDS		x ± s.d.	x ± s.d.	x ± s.d.	x ± s.d.	x ± s.d.	x ± s.d.	x ± s.d.	x ± s.d.	x ± s.d.	x ± s.d.
Cerocephala	♂	1.25 ± 0.23			1.60 ± 0.19		1.82 ± 0.26				2.04 ± 0.31
eccoptogasteri	♀	1.60 ± 0.27			2.21 ± 0.19		2.26 ± 0.15				2.42 ± 0.26
Masi		0.05**			0.01		0.001				0.001
Cheiropachus	♂				2.03 ± 0.29		2.15 ± 0.33				
quadrum	♀				2.49 ± 0.26		2.83 ± 0.32				
Febr.					0.01		0.001				
Entedon	♂					1.66 ± 0.09	1.90 ± 0.12				
ergias	♀					1.63 ± 0.15	1.90 ± 0.14				
Walker						n.s.	n.s.				
Dendrosoter	♂		2.08 ± 0.24	2.28 ± 0.43					3.07 ± 0.71	5.15 ± 0.45	
caenopachoides	♀		1.68 ± 0.22	1.85 ± 0.26					2.41 ± 0.55	4.06 ± 0.51	
Rusch.			0.001	0.001					0.01	0.001	
Dendrosoter	♂			2.41 ± 0.46							
hartigii	♀			1.87 ± 0.30							
(Ratz.)				0.001							
Dendrosoter	♂								4.30 ± 0.21	4.93 ± 0.55	
middendorffi	♀								3.54 ± 0.76	4.13 ± 0.56	
Ratz.									0.05	0.05	
Dendrosoter	♂				2.93 ± 0.48		3.57 ± 0.50				5.40 ± 0.60
protuberans	♀				2.40 ± 0.43		3.29 ± 0.42				4.67 ± 0.45
(Nees)					0.001		0.05				0.001

Ecphylus	♂	1.52 ± 0.17									
caudatus	♀	1.51 ± 0.18									
Rusch.		n.s.									
Eurytoma	♂			1.27 ± 0.13	1.76 ± 0.14			1.79 ± 0.34			3.06 ± 0.24
morio	♀			1.62 ± 0.29	2.14 ± 0.26			2.63 ± 0.33			3.98 ± 0.32
Boheman				0.01	0.001			0.001			0.001
Heydenia	♂			2.19 ± 0.33					2.29 ± 0.40		3.62 ± 0.61
pretiosa	♀			2.54 ± 0.42					2.81 ± 0.39		3.91 ± 0.62
Forster				0.05					0.01		n.s.
Metacolus	♂		1.70 ± 0.51	2.05 ± 0.32				2.13 ± 0.35	3.08 ± 0.47	4.99 ± 0.55	4.52 ± 0.31
unifasciatus	♀		1.82 ± 0.42	2.59 ± 0.26				2.73 ± 0.35	3.16 ± 0.62	5.08 ± 0.34	4.83 ± 0.27
Forster			n.s.	0.01				0.001	n.s.	n.s.	0.001
Rhaphitelus	♂	1.67 ± 0.13			2.18 ± 0.49	2.00 ± 0.38	2.10 ± 0.45				2.73 ± 0.28
maculatus	♀	1.77 ± 0.12			2.22 ± 0.29	2.22 ± 0.23	2.16 ± 0.24				2.78 ± 0.24
Walker		0.01			n.s.	n.s.	n.s.				n.s.
Roptrocerus	♂			2.09 ± 0.23					1.63 ± 0.42	1.92 ± 0.28	
xylophagorum	♀			2.16 ± 0.17					2.63 ± 0.23	3.66 ± 0.37	
(Ratz.)				n.s.					0.001	0.001	

* Beetle body length and pronotum breadth.

** Level of significance for two- tailed t-test between male and female lengths

TABLE 2

Ratio of males to females (average and range) of bark beetle parasitoids obtained from infested material

	Number of samples	Number of parasitoids	Sex ratio
Cephalonomia hypobori	2	340	(0.1-)0.1(-0.2)*
Cerocephala eccoptogasteri	9	1121	(0.4-)0.9(-1.7)
Cheiropachus quadrum	4	764	(0.5-)1.0(-2.0)
Dendrosoter caenopachoides	6	3073	(0.6-)0.8(-1.1)*
D. protuberans	8	2934	(0.6-)0.9(-1.3)
Ecphylus caudatus	2	828	(< 0.3-)0.3(-0.4)*
E. silesiacus	1	996	0.9
Entedon ergias	3	842	(0.4-)2.5(-3.3)*
Eurytoma morio	13	1299	(0.2-)1.0(-2.5)
Heydenia pretiosa	6	231	(0.4-)0.7(-1.0)*
Metacolus unifasciatus	13	3764	(0.5-)0.9(-2.5)
Rhaphitelus maculatus	4	765	(0.7-)0.9(-5.0)
Roptrocerus xylophagorum	4	267	(0.3-)0.6(-1.7)*

* Sex ratio significantly different from 1:1 ($P < 0.05$)

TABLE 3

Ratio of males to females (average and range) of Metacolus unifasciatus *and* Eurytoma morio *obtained from hosts of 2 size groups (for beetle dimensions see table 1)*

Parasitoid species	Host size (species)	Number of samples	Number of parasitoids	Sex ratio
Metacolus unifasciatus	small (**C.m., O.e., P.au., P.c.*)	7	1610	(1.1-)1.3(-2.5)
	large (*P.ar., T.d.*)	6	2154	(0.5-)0.7(-0.8)
Eurytoma morio	small (*P.c., P.s., S.m., S.r.*)	6	646	(0.7-)1.7(-2.5)
	large (*P.ar.*)	7	653	(0.2-)0.6(-0.8)

* *C.m.* - *Carphoborus minimus*, *O.e.* - *Orthotomicus erosus*, *P.au.* - *Phloeosinus aubei*, *P.ar.* - *Phloeosinus armatus*, *P.c.* - *Pityogenes calcaratus*, *P.s.* - *Phloeotribus scarabaeoides*, *S.m.* - *Scolytus multistriatus orientalis*, *S.r.* - *Scolytus rugulosus mediterraneus*, *T.d.* - *Tomicus destruens*.

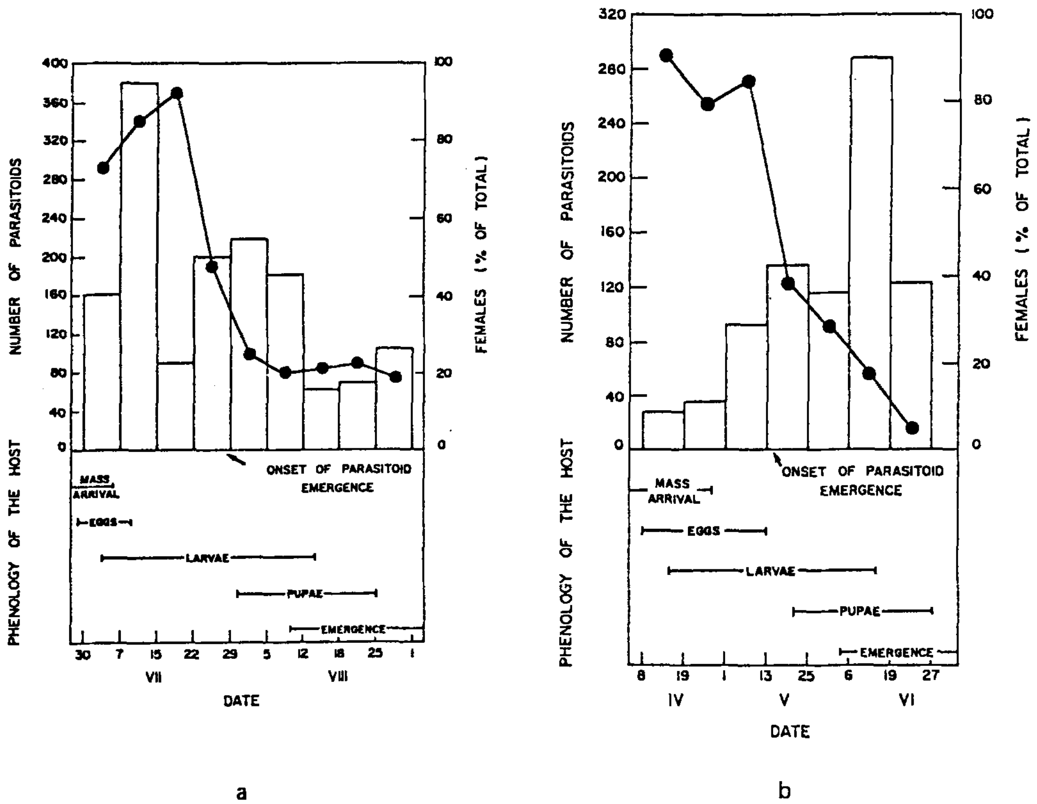

Fig. 1. Number of parasitoids (histogram) and percentage of females (line graph) trapped on sticky traps attached to (a) *Pinus halepensis* stems, as related to *Orthotomicus erosus* phenology, (b) *Cupressus sempervirens* stems as related to *Phloeosinus armatus* phenology.

Male behaviour was observed in 4 parasitoid species. *Dendrosoter caenopachoides* on pine, and *D. protuberans* on cypress, moved slowly on the bark of the infested tree searching for preemerging females. They usually formed a circle around a spot on the bark, from which a female emerged within minutes to more than an hour. *Dendrosoter caenopachoides* males were usually restless and showed intraspecific aggressive behaviour while waiting for the female to emerge. *Dendrosoter protuberans* males usually formed a tight circle of 2-8 individuals, pressing on each other with their legs, antennae and wings, and remained motionless, unless the female began to emerge or a new male tried to join the circle. Similar behaviour of braconid males was observed by **Dix & Franklin** (1983) on pines infested with *Dendroctonus frontalis*. The males of *Metacolus unifasciatus* usually run on the bark, chasing the newly emerging females. The males of *Roptrocerus xylophagorum* usually swarmed over the infested material, resting on the bark for only a few seconds or minutes ; encounters between the sexes were never observed under field conditions in the present study.

TABLE 4

Ratio of male to female parasitoids, before and after emergence of parasitoid brood, obtained from sticky traps on bark-beetle infested stems of pine and cypress

Species	Pine		Cypress	
	before	after	before	after
Calosota aestivalis	0.14	0.55	0.50	2.0
Cerocephala eccoptogasteri	–	–	0.11	1.67
Dendrosoter caenopachoides	0.12	3.33	–	–
D. protuberans	–	–	0.14	3.33
Eurytoma morio	0.20	0.91	0.04	5.00
Heydenia pretiosa	0.31	2.50	0.5	2.5
Metacolus azureus	0.5	3.33	–	–
M. unifasciatus	0.33	5.00	0.17	3.33
Rhaphitelus maculatus	–	–	0.08	2.50
Roptrocerus xylophagorum	0.42	5.00	–	–
Overall ratio	0.29	3.33	0.22	3.33
Numbers	777	650	165	671

DISCUSSION

Positive correlations between parasitoid size and host size have been well established for both sexes of bark beetle parasitoids for each species studied (table 1). The wide range in parasitoid length in most of the investigated species is probably due to parasitization of different larval stages of the beetle. Differences between mean body lengths of males and females were significant for most of the species considered (table 1). **Ryan & Rudinsky** (1962) studied the effect of hosts larvae size on *Coeloides brunneri* and showed the tendency of the female to lay fertile eggs (*i.e.* to produce female progeny) on larger hosts. **Flanders** (1939) stated that "the production of males is assured in solitary parasitoids by oviposition on unpreferred individuals of the normal host". It is very common among insects for the fecundity of larger females to be greater than that of small specimens. This may explain why female parasitoids select the larger host for production of female progeny. The positive correlation between body length and ovipositor length of 3 investigated species suggests that a large-sized female can attack the host under a relatively thick bark, which is otherwise inaccessible to small-sized females because of the shorter ovipositor. Production of females that are larger than males is therefore a distinct advantage for parasitoids of bark beetles. The larger female was a phenomenon seen in most of the investigated species. The identical length of the sexes in *Entedon ergias* is probably related to its being an egg-larva parasitoid (**Beaver,** 1965). The female is unable to differentiate between large and small larvae, and a long ovipositor is not necessarily an advantage because parasitization occurs inside the egg tunnel. Except for a reference by **Mickel** (1928), the fact that males are larger than females, as shown for *Dendrosoter* spp. (table 1), was never recorded for any hymenopterous parasitoid. It is logical to assume that this phenomenon may be related to the specific sex-ratio of the parasitoid population. However, on the one hand, in species with a low male : female ratio, such as *Roptrocerus xylophagorum, Ecphylus caudatus* or *Heydenia pretiosa,* the mean length of the males is smaller than or equal to that of the female. On the other hand, the sex ratio of *Dendrosoter* spp., whose males are larger than the females, was close to 1:1. It may be assumed that production of larger males in *D. caenopachoides* and *D. protuberans* is related to their specific courtship behaviour. Assuming that a larger male is also stronger, it will be easier for it to compete for the emerging female in the typical courtship circle on the infested tree. Male dimensions are probably less important in species whose males are looking for the females after the latter have emerged from the bark, due to the fact that unmated females will mate with any male of her kind when it manages to mount her, while a mated female usually refuses to mate (*e.g.* **Doutt,** 1964 ; **Dix & Franklin,** 1981).

Little is known concerning the sex-ratio of bark beetle parasitoids. **Gargiullo & Berisford** (1981) indicated that among 8 parasitoid species of *Dendroctonus frontalis, R. xylophagorum* was the only parasitoid whose sex-ratio was significantly different from 1:1. The present study shows that in bark beetle parasitoids the sex-ratio usually differs from 1:1 (table 2). In some cases, *e.g. Cephalonomia hypobori,* the males are present at very low rates in the population. There is little doubt that sex-ratio may change according to different environmental conditions. **Doutt** (1964) discussed intrinsic and extrinsic factors affecting the sex-ratio of parasitic Hymenoptera. In our study the sex-ratio of *Metacolus unifasciatus* and *Eurytoma morio* was reduced when parasitization occurred on large-sized hosts (table 3). Apparently this fact is related to the possibility that larger males may survive longer than smaller ones, and may mate with more females.

The sex-ratio of parasitoids present on infested material changed according to the course of beetle infestation (figures 1 and 2). Female parasitoids were more numerous during larvae development and males were more abundant between the pupal stage and host emergence. This may be due to the different behaviour of the sexes. The females tend to leave the tree, on which they had developed, for a newly infested tree where they will find available host stages. The females occur in greater numbers than the males during the 1st development stages of the host, as males tend to remain on the original tree to locate newly emerging unmated females. Thus, males are more numerous than females during emergence of the parasitoids.

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RÉSUMÉ

Hyménoptères parasitoïdes des scolytides en Israël :
relations entre les dimensions de l'hôte et du parasitoïde et rapport entre les sexes

Des données sont présentées sur les parasitoïdes des scolytides de conifères et de feuillus pour montrer les relations existant entre les dimensions de l'hôte et celles du parasitoïde, et le rapport entre les sexes des parasitoïdes. Sur du matériel infesté par des scolytides, la grandeur des parasitoïdes varie considérablement dans la plupart des espèces. Les femelles de *Cerocephala eccoptogasteri* Masi, *Cheiropachus quadrum* Febr., *Eurytoma morio* Boheman, *Heydenia pretiosa* Forster, *Metacolus unifasciatus* Forster, *Rhaphitelus maculatus* Walker et *Roptocerus xylopagorum* Ratz. sont en général plus longues que leurs mâles ; par contre, les mâles des 4 espèces de *Dendrosoter* spp. sont nettement plus longs que leurs compagnes. La longueur des 2 sexes est presque la même chez *Entedon ergias* Walker et *Ecphylus caudatus* Rusch. Le rapport des sexes diffère dans la plupart des espèces ; il est très différent de 1:1 chez 5 d'entre elles. Chez *M. unifasciatus* et *E. morio* ce rapport est en relation avec la dimension de leur hôte. Le rapport entre les sexes chez les parasitoïdes recueillis sur des pièges englués varie selon l'évolution des scolytides. Les femelles sont plus abondantes pendant le développement larvaire des scolytides, tandis que les mâles sont plus nombreux pendant la pupaison et l'émergence de ces derniers. Le comportement avant la copulation de *Dendrosoter caenopachoides* Rusch., *D. protuberans* Nees, *M. unifasciatus* and *R. xylophagorum* est décrit. L'effet de la grandeur du scolytide, la variation du rapport entre les sexes, et les interactions possibles entre grandeur et rapport entre sexes des parasitoïdes sont discutés.

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