

Spatial distribution and niche partitioning in the *Ooencyrtus* spp. complex parasitizing the eggs of *Stenozygum coloratum*

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Received: 16 March 2015 / Accepted: 5 June 2015 / Published online: 12 June 2015
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Abstract The way in which species coexist is an important ecological question. Often, several parasitoid species may share a common host species. Five species of *Ooencyrtus* Ashmead (Hymenoptera: Encyrtidae) co-inhabit the egg clusters of *Stenozygum coloratum* Klug (Hemiptera: Pentatomidae), in the East Mediterranean region. Their relative abundance and spatial and seasonal occurrence were investigated. Parasitism and parasitoid male ratios gradually increased to about 50 and 26.8 %, respectively, from May to October. *O. telenomicida* Vassiliev was dominant in Mediterranean climatic regions and absent from arid areas, *O. fecundus* Ferrière and Voegelè dominated semi-arid areas, and *O. near nigerrimus* was the commonest in hot-arid areas. *O. near fecundus* occurred everywhere but was most abundant in the more extreme weather conditions. *O. pityocampae* Mercet was uncommon in most areas and

absent from arid ones. *O. telenomicida* abundance was positively, and that of *O. fecundus* negatively, correlated with annual rainfall. *O. near fecundus* and *O. near nigerrimus* abundance was positively correlated with temperature extremes. The results display a clear picture for climatic based spatial niche partitioning, although there is evidence that interspecific competition also plays a significant role in the frequency of occurrence of the studied *Ooencyrtus* spp.

Keywords Egg parasitism · Encyrtidae · Hymenoptera · Niche partitioning · Sex ratio · Variegated caper bug

Introduction

Several closely related species often share a common resource. There is, however, a limit to the similarity, and therefore also to the number, of competing species which can coexist on the same resource (MacArthur and Levins 1967). Gaining understanding of the factors that facilitate coexistence among multiple species remains an important quest in ecology (Hawkins 2000; Holt 2001).

There have been numerous studies on niche partitioning in insect communities, and there are many ways in which two or more insect species may share a common resource. Niche partitioning often occurs on a temporal or spatial basis (Albrecht and Gotelli 2001; Harvey et al. 2014; Moya-Raygoza et al. 2012;

Handling Editor: Stefano Colazza.

Electronic supplementary material The online version of this article (doi:10.1007/s10526-015-9683-2) contains supplementary material, which is available to authorized users.

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Trizzino et al. 2014; van Baaren et al. 2004). Partitioning may occur on a relatively small scale, e.g., the height of a tree (Harvey et al. 2014), or on a much larger scale such as elevation range (Moya-Raygoza et al. 2012; Trizzino et al. 2014). In parasitoids, coexistence may also be maintained by interspecific differences in various biological features related to host (common resource) exploitation, which might give each species an advantage over the others under specific conditions. Competition among parasitoids can be divided into extrinsic, i.e., among adults searching for hosts, or intrinsic, i.e., among juveniles, inside a host (Cusumano et al. 2012a). Adult features related to competitiveness include longevity, fecundity, oviposition behavior, host-seeking strategies, host acceptance and handling time, and coping with host defenses (for examples see Borer et al. 2004; van Baaren et al. 2004). Intrinsic competition may involve physiological suppression or physical attack on competing larvae (Godfray 1994). Tradeoffs between differing life traits may facilitate resource partitioning and coexistence (Bonsall et al. 2002). However, since parasitoids form part of complex food webs, which include other hosts, host plants, predators and hyperparasitoids, host partitioning is likely to be influenced also by combinations of direct and indirect interactions with other species (Müller et al. 1999). In general, it seems obvious that, because of the complexity of natural environments, isolating the effect of each factor on parasitoid species coexistence is difficult or even impossible.

Egg parasitoids comprise an important group of natural enemies of insect pests. In part, this is due to the fact that they kill their hosts before the latter can cause any damage (Bin 1994; Conti and Colazza 2012; Godfray 1994). The genus *Ooencyrtus* Ashmead (Hymenoptera: Encyrtidae) includes more than 300 known species worldwide (Noyes 2014), most of which are egg parasitoids attacking mainly Lepidopteran and Heteropteran hosts (Huang and Noyes 1994; Mizrachi 2006). Some *Ooencyrtus* species are also known as natural enemies of major agricultural and forest pests (Clarke 1990; Corrêa Ferreira and Moscardi 1995; Guerrieri et al. 2011; Halperin 1990b; Huang and Noyes 1994; Laraichi 1979a; Peri et al. 2011).

Ooencyrtus species frequently share a host species with other parasitoid species, often from a different taxonomic group (Amarasekare 2003; Conde and Rabinovich 1979; Corrêa Ferreira and

Moscardi 1995; Laraichi 1979a; Mohammadpour et al. 2014). In such cases interspecies competition and, consequently, also interference are likely to occur (i.e., the occurrence of one species may negatively affect the occurrence of others), and to have an effect on the relative abundance and parasitism rate of each species. In cases of biological control programs, intra-guild competition may also have an effect on the overall success of control efforts (Follett et al. 2000; Peri et al. 2011).

In the present study we investigated the coexistence of five *Ooencyrtus* spp. associated with the variegated caper bug (CB) *Stenozygum coloratum* Klug (Heteroptera: Pentatomidae). The CB is common in the east Mediterranean region, and was found on several caper species (*Capparis* spp., Capparaceae) in various areas in Israel and southern Turkey (Samra et al. 2015). The CB is also known as a minor pest of various agricultural species (Bodenheimer 1930). However, the overall damage caused by this bug is usually low (Samra et al. 2015; Swirski et al. 2002), probably because of its inability to reproduce on these agricultural plants (Samra et al. 2015), therefore, hitherto, this bug did not draw much attention. However, this lack of interest recently changed when it was discovered that the eggs of CB are parasitized by several closely related *Ooencyrtus* spp. (Samra et al., personal observation). Five species were identified: *Ooencyrtus pityocampae* Mercet, *O. telenomicida* Vassiliev, *O. fecundus* Ferrière & Voegelè, *O. near nigerrimus* and *O. near fecundus*. The latter two species may have been previously mistakenly identified as *O. nigerrimus* Ferrière & Voegelè, and *O. fecundus*, respectively. Therefore any literature data on the latter species may be relevant for *O. near nigerrimus* and *O. near fecundus* as well (Samra et al., personal observation). *Ooencyrtus near fecundus* and *O. near nigerrimus* may be new to science (Guerrieri and Noyes, personal communication). The above species and their close congeners are known natural enemies of several insect pests: *O. pityocampae* is considered an important natural enemy of the pine processionary moth (PPM) *Thaumetopoea pityocampa* Denis & Schiffer-Müller/*T. wilkinsoni* Tams (Lepidoptera: Notodontidae) species complex (Battisti 1989; Halperin 1990b) and *O. telenomicida*, *O. fecundus* and *O. nigerrimus* attack the eggs of *Nezara viridula* L. and *Aelia* spp. (Heteroptera: Pentatomidae) (Laraichi 1979a; Peri et al. 2011) and also those of

other, less significant heteropteran pests (Noyes 2014). These *Ooencyrtus* spp. were recorded from various species of both Lepidoptera and Heteroptera (Noyes 2014). The CB seems to be a common host for this parasitoid group in the East Mediterranean region, and may be important for their conservation in the area. It may be especially important for *O. pityocampae*, because the eggs of its main host, the PPM, are found only from late summer to early winter (Halperin 1990a), whereas those of CB are laid from April through September (Samra et al. 2014). Thus, seasonal alternation between these two hosts is likely to occur (Samra et al. 2014). This knowledge led us to consider using this bug population for biological control against PPM and other pest species. This could be done, for example, by planting caper plants inside pine forests, in order to increase the CB abundance and that of its parasitoids, which will result in increased parasitism rates of the PPM eggs (Samra et al. 2015). Nonetheless, the significance of CB as an alternative host for *O. pityocampae* and the other *Ooencyrtus* spp., their seasonal and spatial occurrence patterns, their relative abundance on CB eggs, and the way in which their coexistence is maintained on this host, are all unknown.

In the present study, we investigated the parasitism on CB eggs collected in various seasons and areas in Israel and southern Turkey, and the relative contribution of each of the *Ooencyrtus* species. Furthermore, the relatively small part of the whole CB distribution range sampled and studied in the present study is, nonetheless, highly diverse, including varied climatic regions, i.e., arid, semi-arid and Mediterranean weather regimes. The various regions are characterized mainly by differing amount of precipitation and differing temperature regimes, and it was suspected that these two factors—rainfall and temperature—in particular, might affect the spatial distribution of occurrences of the various studied *Ooencyrtus* spp. Therefore, our main objectives were to determine parasitism rates of CB eggs by each *Ooencyrtus* species, to supply a picture of their spatial distribution ranges, and to test whether some environmental factors are related to the observed spatial pattern. Concerning the latter, we examined the possible effects of the above mentioned climatic conditions on the occurrence patterns of the studied *Ooencyrtus*

spp. in the studied area. We considered our findings as related to the known global distribution boundaries of each species.

Materials and methods

Insect sampling

Caper bug egg clusters were sampled in 2007 and in 2010–2013 from caper plants located at various sites in Israel and southern Turkey (Table 1; Fig. 1). The spatial distribution of the CB is highly aggregative (Samra et al. 2014), meaning that in any given moment only a small number of plants are infested with CB, but with large number of CB individuals. This fact, together with the general difficulty in locating egg clusters, meant that often many (and up to a about 10–15) egg clusters had to be collected on each infested plant in order to have a reasonable sample size, and this prevented any option of random sampling. All egg clusters collected in each site on each date were placed together in a separate (15 × 100)-mm glass tube closed with cotton wool and kept in the laboratory at 25 °C and 40–60 % RH. The emerging parasitoids were collected almost daily, transferred to 96 %-ethanol-filled, 1.5-ml Eppendorf tubes, and stored at –20 °C pending detailed identification. About one month after collection, tubes containing egg clusters were placed outdoors in the shade for 6–10 months, until the following spring (around the end of May). This exposure to winter ambient temperatures was expected to hasten diapause termination of the parasitoids and to maximize the emergence of any diapausing individuals (Anderson and Kaya 1975; Battisti et al. 1990). These diapausing individuals emerged in the following year, and were also collected and treated as described above.

Egg parasitism rates

About one month after termination of emergence of individuals, i.e., around May, egg clusters were examined under a stereomicroscope in order to determine the condition of each egg, i.e., host hatching, parasitoid emergence, or unhatched.

Table 1 Site-specific data on the 22 sites sampled in the present study

Site code	Country	General area	Site	Co-ordinates	Altitude (m)	Annual rainfall (mm)	Mean min. Jan. temp. (°C)	Mean max. Aug. temp. (°C)	Mean temp. difference (°C)
1	Israel	Jordan Valley and Negev Desert	Avdat	30°79'N; 34°77'E	537	97	5.5	33.0	27.5
2	Israel	Jordan Valley and Negev Desert	Bet-Shean	32°48'N; 35°56'E	-150	281	8.2	38.3	30.1
3	Israel	Jordan Valley and Negev Desert	Eyn-Gev	32°79'N; 35°64'E	-200	372	8.4	38.0	29.6
4	Israel	Jordan Valley and Negev Desert	Kfar Haruv	32°77'N; 35°68'E	313	534	5.9	33.7	27.8
5	Israel	Southern Judean Hills	Yatir	31°20'N; 35°05'E	650	258	6.2	31.6	25.4
6	Israel	Southern Judean Hills	Lahav	31°22'N; 34°51'E	480	278	7.3	32.4	25.1
7	Israel	Southern Judean Hills	Haruvit	31°45'N; 34°55'E	135	479	6.0	31.8	25.8
8	Israel	Southern Judean Hills	Rogalit	31°65'N; 35°01'E	337	338	9.5	33.5	24.0
9	Israel	Costal plane, Galilee, Samaria and Judea	Eshat 'ol	31°48'N; 35°00'E	260	560	9.5	33.5	24.0
10	Israel	Costal plane, Galilee, Samaria and Judea	Gilboa	32°31'N; 35°22'E	170	460	7.7	33.6	25.9
11	Israel	Costal plane, Galilee, Samaria and Judea	Ma'alul	32°41'N; 35°14'E	229	520	6.0	32.6	26.6
12	Israel	Costal plane, Galilee, Samaria and Judea	Ofer	32°62'N; 34°98'E	108	607	11.4	30.8	19.4
13	Israel	Costal plane, Galilee, Samaria and Judea	Carmel, Oren Stream	32°71'N; 34°98'E	60	576	11.4	30.8	19.4
14	Israel	Costal plane, Galilee, Samaria and Judea	Nesher	32°76'N; 35°04'E	173	549	11.4	30.8	19.4
15	Israel	Costal plane, Galilee, Samaria and Judea	Segev	32°52'N; 35°14'E	270	538	6.9	31.3	24.4
16	Israel	Costal plane, Galilee, Samaria and Judea	Kabri	33°03'N; 35°15'E	61	606	7.6	30.4	22.8
17	Israel	Costal plane, Galilee, Samaria and Judea	Biriya	33°00'N; 35°29'E	780	678	5.1	30.2	25.1
18	Israel	Costal plane, Galilee, Samaria and Judea	Rosh Pinna	32°57'N; 35°32'E	380	408	7.1	34.4	27.3
19	Israel	Costal plane, Galilee, Samaria and Judea	Kfar HaNassi	32°98'N; 35°59'E	273	518	7.1	34.4	27.3
20	Turkey	Hatay	Antakya	36°12'N; 36°10'E	140	1146	4.0	31.0	27.0
21	Turkey	Adana	Karatag-Bebeli village	36°33'N; 35°32'E	26	756	5.0	30.0	25.0
22	Turkey	Mersin	Tarsus	36°57'N; 34°54'E	50	640	4.0	33.0	29.0

Geographical locations are shown in Fig. 1. Data on egg cluster numbers, parasitism and parasitoid species abundances in each sample is given in Appendix S1

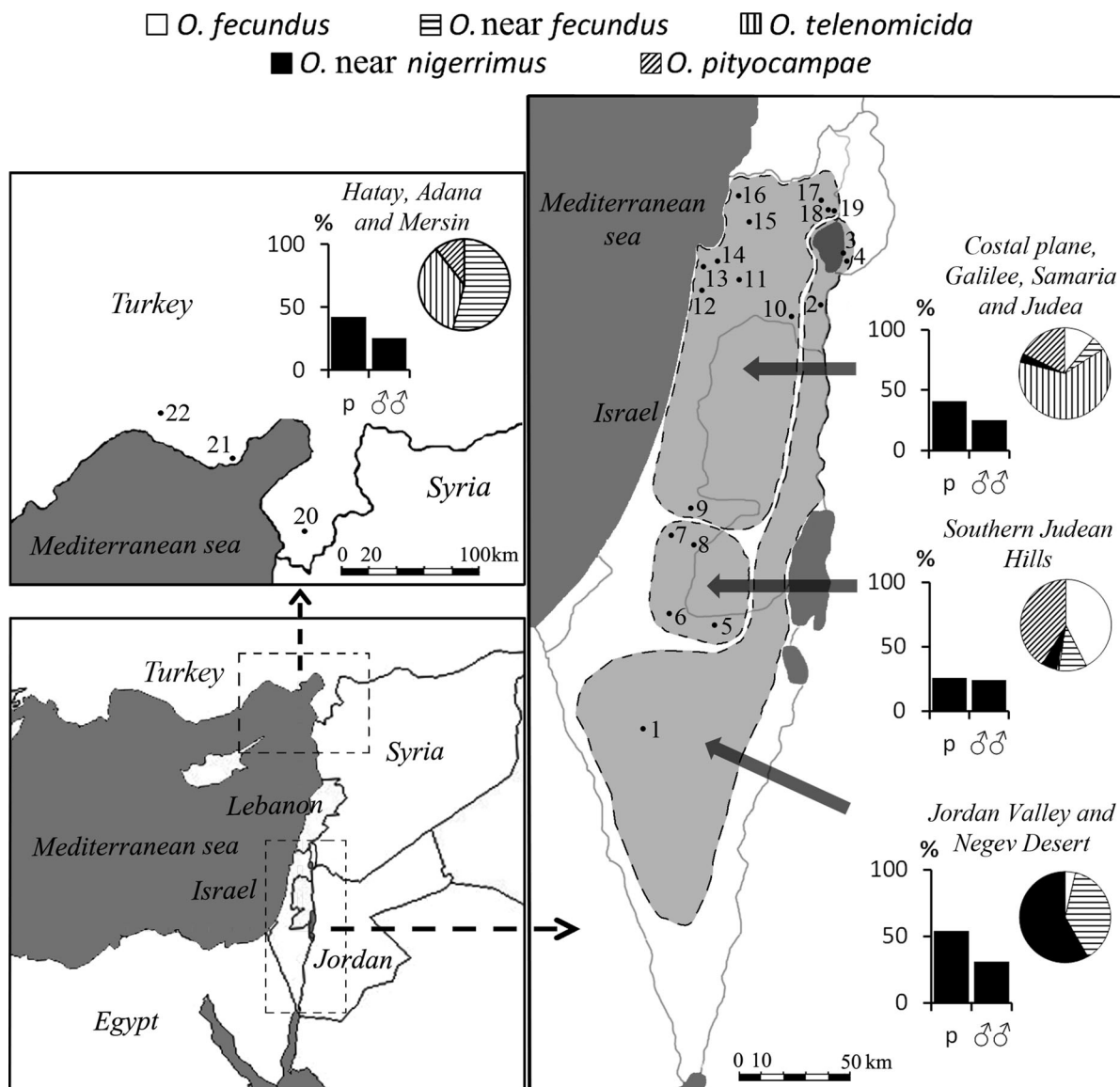


Fig. 1 *Stenozygum coloratum* egg parasitism in the four studied regions in the East Mediterranean region: percentage parasitism (p), percentage of males among emerging individuals (♂♂), and relative abundances of the various *Ooencyrtus* spp. in

each area. Site names and site-specific data are given in Table 1. Data of parasitism and of relative species abundances in each site and sample excursion are given in Appendix S1

Parasitoid species identification, sex ratios and relative abundances

Most parasitoids which emerged from egg clusters collected in 2010–2013 were identified to species level. Species were initially distinguished by molecular methods, i.e., sequencing of COI and ITS2 DNA fragments (Samra et al., personal observation).

Later we identified morphological features that enabled identification of most species, without the need for further molecular work (Samra et al., personal observation). However, morphological distinction between males of the various species was impossible at the time. Therefore, for calculating the relative number of each species, we first identified all the females in each sample, and then divided the

total number of males among the species according to the relative number of females of each species. *O. pityocampae* is parthenogenetic and deuterotokous (i.e., both male and female offspring are obtained without mating; for further information on these terms see Douth 1959). Males of *O. pityocampae* are rare (Halperin 1990b), therefore all males in the samples were attributed to the other species, all of which were shown to reproduce sexually (Samra, personal observations). The rarity of *O. pityocampae* males also was confirmed by molecular identification: only one out of 55 tested males belonged to this species. However, the above calculation of species relative abundances assumed that similar sex ratios of the other species occurred in the field, which requires further validation. Nevertheless, we suggest that this method is the most accurate way to evaluate relative species abundances, pending availability of reliable morphological distinction between males of different species.

A total of 1499 egg clusters were sampled. 3304 parasitoids were examined and sexed, of which 2658 were identified to species level (for site-specific data see Appendix S1), although about 25 % of this number comprised males that were arbitrarily categorized into species as explained above. The data on relative species abundances, parasitism rates and sex ratios, were grouped according to four geographical regions, three in Israel and one in southern Turkey (Fig. 1), and also according to three time periods, May–June, July–August, and September–October (designated as early, middle and late season, respectively; Fig. 2).

Effects of whether conditions on species abundance

We also tested for possible effects on the relative abundance of each species of mean annual precipitation, mean maximum summer (August) and minimum winter (January) temperatures, and mean temperature differences, as calculated from the latter two. All of these were based on ($n=$) 50 sampled events at each site on each date. Climatic data for the Israeli and Turkish sites were obtained from the archives of the Israel Meteorological Service (<http://www.ims.gov.il>) and from <http://www.weatherbase.com>, respectively.

Statistics

Statistical analyses were performed using the JMP software, version 7.0.7 (SAS Inc., Cary, NC, USA). Linear regression was used to evaluate the effects of precipitation and temperature on the relative abundance of each species. The measurements values were \log_{10} transformed and the normality of the data was confirmed, prior to the analysis.

Results

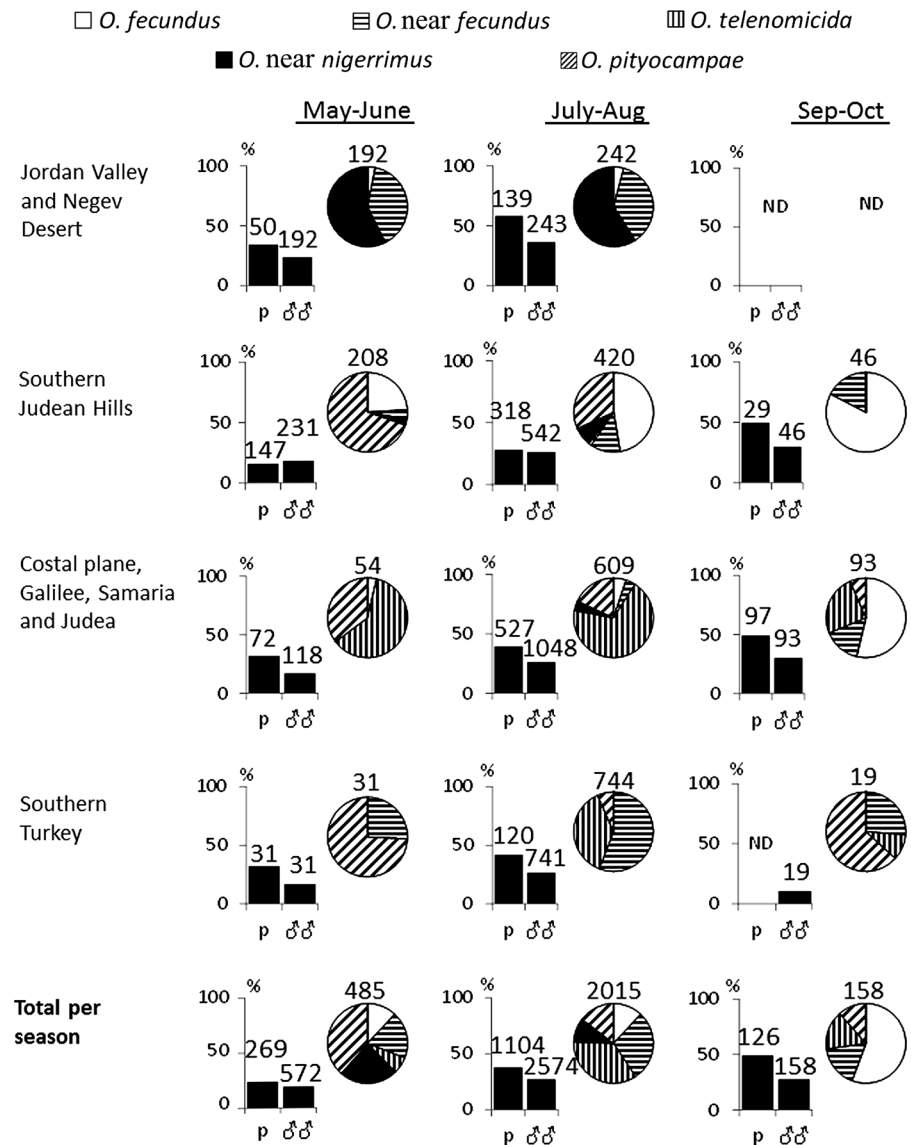
Seasonal parasitism rates of *S. coloratum* eggs

In general, a clear spatial pattern and some temporal patterns in the relative rate of parasitism by each species emerged, and the data were grouped according to these spatial and temporal differences. Substantial egg parasitism rates were observed throughout the sampling area, ranging from 25.7 to 54.0 %, for an average of 36.8 ± 24.7 % for all data combined (Fig. 1). Parasitism rates generally increased throughout the CB activity period, and leveled at approximately 50 % from September onward (Fig. 2). However, in the Jordan Valley and Negev Desert higher parasitism rates (58 %) were observed at midseason (Fig. 2), indicating that even higher rates were to be expected in late season, for which no data were available.

Relative abundances and spatial differences of the various *Ooencyrtus* species

Clear geographical differences between the various *Ooencyrtus* species were observed, manifested as differences in relative abundance of the respective species in the various studied areas (Fig. 1). *O. telenomicida* was found in Israel's north and center and in southern Turkey, and generally was the dominant species in moderate (humid) climatic regions, i.e., the coastal plain, Galilee, Samaria and Judea in Israel, and the Hatay region in Turkey (Fig. 1). However, in some sampled locations, particularly in relatively warm regions that included open, unshaded patches, the contributions of other species, and especially of *O. near fecundus*, usually increased, and the latter occasionally even outnumbered *O.*

Fig. 2 Seasonal changes in *S. coloratum* egg parasitism in the four main studied regions: percentage parasitism (p), percentage of males among emerging individuals ($\delta\delta$), and relative abundance of each parasitoid species (pie charts). Sample sizes, i.e., the number of egg clusters included in the calculation of parasitism rates, and numbers of adult wasps tested for male percentages and for species relative abundances are given above the bars/pie charts. ND: no data



telenomicida, e.g., in Tarsus, Turkey. *O. near nigerrimus*, followed by *O. near fecundus*, dominated the warmest and driest regions in Israel, i.e., the Jordan Valley and the Negev Desert. However, *O. near fecundus* was also found in all other sampled areas, and was the dominant species in open areas in southern Turkey, whereas *O. near nigerrimus* was absent from Turkey and also very rare in northern Israel. *O. fecundus* occurred in low relative frequencies in almost all areas in Israel and, like *O. near nigerrimus*, was absent from the northernmost Israeli sites and from Turkey. However, *O. fecundus* was the dominant species in semiarid pine afforested areas of the

southern Judean Hills, although in this region it was often outnumbered by *O. pityocampae* in early season (Fig. 2). Furthermore, as the season progressed, the relative abundance of *O. fecundus* in the northern Israeli sites generally increased. However, most late-season data from this region were obtained from Gilboa, which is a relatively dry area, with 460 mm annual rainfall (Table 1). *O. fecundus* was relatively common in this location, but probably absent from most of the more humid areas.

Ooencyrtus pityocampae was relatively uncommon on CB eggs in most samples, but was found in all areas except for the warmest and driest ones—the Jordan Valley

and Negev Desert (Fig. 1). It is worth mentioning that these two areas are the only sampled areas that generally lack pine stands, and that the PPM is either absent (Negev) or rare (Jordan Valley). The relative abundance of *O. pityocampae* generally decreased throughout the season, which also was indicated by a gradual increase in parasitoid male ratios. However, male ratios, which averaged 26.8 % (all data combined), generally increased along the season, also in areas from which *O. pityocampae* was absent.

Only three out of the five *Ooencyrtus* spp. were found in Turkey (Fig. 1). There were, however, large differences among the various Turkish samples. *O. pityocampae* and *O. near fecundus* were found in all Turkish samples, the former mostly in relatively low numbers, whereas the latter was dominant in the sample taken from a warm unshaded area, i.e., around Tarsus. *O. telenomicida* was found only in two samples from Hatay, which were taken in a forested area on the margins of Antakya. In these two samples it substantially outnumbered *O. near fecundus* by about 20:1. The small sample sizes—31 and 19 individuals in early and late seasons, respectively—in southern Turkey did not enable us to form any solid conclusions regarding seasonal changes in sex ratio

and relative species abundance in this area (but see “Discussion” section).

Effect of climatic conditions on species relative abundances

Apparently, climatic conditions affected the relative abundance of some of the species. The relative abundance of *O. fecundus* seemed to be negatively, and that of *O. telenomicida* positively related to the annual rainfall in the area (linear regression: $R^2 = 0.17$, $p < 0.002$ for *O. fecundus*; $R^2 = 0.16$, $p < 0.003$ for *O. telenomicida*, Table 2). Temperature did not have a significant effect on most species, except for *O. near nigerrimus* whose abundance seemed to be positively related to the mean maximum summer (August) temperature ($R^2 = 0.31$, $p < 0.0001$, Table 2). However, temperature differences between winter and summer, which correspond to extreme weather conditions, seemed to have a significant positive effect on both *O. near fecundus* and *O. near nigerrimus* ($R^2 = 0.08$, $p = 0.04$ for *O. near fecundus*; $R^2 = 0.31$, $p < 0.0001$ for near *O. nigerrimus*, Table 2).

Table 2 Linear regressions for the relationships between the relative abundance of the various *Ooencyrtus* species parasitizing the CB eggs (log transformed) and the annual rainfall,

mean minimum daily winter temperatures (in January), mean maximum daily summer temperatures (in August), and mean differences between the latter two

Species	Annual rainfall (mm)	Min. daily winter temp. (°C)	Max. daily winter temp. (°C)	Temp. differences (°C)
OF	y = -0.0x + 0.1 R² = 0.17 p < 0.002	y = 0.0x + 0.0 R ² = 0.01 p = 0.43	y = -0.0x + 0.1 R ² = 0.00 p = 0.64	y = -0.0x + 0.1 R ² = 0.03 p = 0.25
ONF	y = -0.0x + 0.0 R ² = 0.00 p = 0.95	y = -0.0x + 0.1 R ² = 0.03 p = 0.13	y = 0.0x - 0.1 R ² = 0.01 p = 0.47	y = 0.0x - 0.2 R² = 0.084 p = 0.04
OT	y = 0.0x - 0.0 R² = 0.16 p < 0.003	y = 0.0x + 0.1 R ² = 0.02 p = 0.27	y = -0.0x + 0.1 R ² = 0.01 p = 0.61	y = -0.0x + 0.1 R ² = 0.04 p = 0.14
ONN	y = -0.0x + 0.0 R ² = 0.02 p = 0.13	y = -0.0x + 0.0 R ² = 0.00 p = 0.91	y = 0.0x + 0.6 R² = 0.31 p < 0.0001	y = 0.0x - 0.3 R² = 0.31 p < 0.0001
OP	y = -0.0x + 0.1 R ² = 0.00 p = 0.63	y = -0.0x + 0.1 R ² = 0.01 p = 0.47	y = -0.0x + 0.2 R ² = 0.07 p = 0.06	y = -0.0x + 0.2 R ² = 0.03 p = 0.19

Data on relative abundances are based on a total of 2658 adult parasitoids that emerged from *S. coloratum* egg clusters collected in 50 different sampling events (location/date). Significant regressions are indicated in bold, $p < 0.05$

OF *O. fecundus*, ONF *O. near fecundus*, OT *O. telenomicida*, ONN *O. near nigerrimus*, OP *O. pityocampae*

There was relatively extensive distribution overlap at the transition zones between hot/dry and moderate/humid regions, e.g., in the Lahav, Gilboa, and Rosh-Pinna sites, where all five species co-inhabited CB eggs. For example, a single sample of 20 individuals from Rosh-Pinna, collected in August 2011, yielded individuals of all five *Ooencyrtus* species.

Occurrence of diapausing *Ooencyrtus* individuals

Relatively few individuals emerged from CB eggs after diapause, all of them from egg clusters collected from mid-August onward. Fifteen egg clusters collected in Yatir in August 2010, and 29 in Lahav and 29 in Gilboa in September 2012 yielded a total of 16 diapausing adults (three, six, and seven, respectively), all of which were *O. near fecundus* and they emerged at the beginning of April of the following year. Egg clusters collected in Eshta'ol in August 2013 also yielded a few diapausing adults (three females and one male). These may have been of *O. telenomicida*, but the adults died before being preserved in ethanol and could not be identified for certain.

Discussion

In the present work we discovered clear differences in the geographical distribution between the various *Ooencyrtus* species, which may also help to explain their coexistence. In recent years, several studies referred to intra-guild interactions that involved one or more *Ooencyrtus* species sharing a common host species (Amarasekare 2003; Avci 2003; Cusumano et al. 2012b; El Bouhssini et al. 2004; Mainali and Lim 2012; Mohammadpour et al. 2014; Peri et al. 2014). However, the present case of CB, with five *Ooencyrtus* species coexisting sympatrically on the same host, is somewhat unique. Their spatial occurrence seems to be governed by climatic conditions—at least in few of the species. It seems that *O. telenomicida* prefers moderate climatic regions, while *O. fecundus* and *O. near nigerrimus* are most abundant in semi-arid and arid areas, respectively. Nonetheless, other factors, and especially interspecies competition, may also shape the ecological boundaries and affect the abundance of the studied species, and may give a false impression of climatic influence. We suspect that *O. telenomicida* simply cannot survive in the somewhat

extreme environments, whereas *O. near nigerrimus*, *O. fecundus* and, especially, *O. near fecundus* can survive in both extreme and moderate climatic areas, but are outcompeted in the latter areas by *O. telenomicida*. This scenario is supported by the finding that all species were observed in the moderate (Mediterranean) regions, whereas *O. telenomicida* was never found in the areas of more extreme weather.

How *O. telenomicida* might outcompete the other species is uncertain. Intrinsic competition and the outcome of multiparasitism events were not investigated in the present study. However, *O. telenomicida* was previously shown to outcompete *O. fecundus* and *O. nigerrimus* Ferrière & Voegelè in multiparasitism events in the eggs of another pentatomid host, *Solenostethium lynceum* Fabricius (Heteroptera: Pentatomidae) (Laraichi 1978). In another work (Laraichi 1979b) the same author studied the effect of temperature on the fecundity of the above three species, i.e., *O. telenomicida*, *O. fecundus* and *O. nigerrimus*, and concluded that the former was the most susceptible to high temperatures. Furthermore, there is evidence of *O. telenomicida* females using an as yet unknown physiological suppression mechanism against the developing larvae of other parasitoid species (Cusumano et al. 2012b), and this might give this species a substantial advantage when overall parasitism rates are high. These data fit well with our present field data, and with our hypothesis of *O. telenomicida* being the dominant species among its congeners on CB eggs. Laraichi (1978) also reported the superior survivability of *O. fecundus* over *O. nigerrimus* in multiparasitism events. The possible inferior survivability of *O. near nigerrimus* (which is probably most closely related to *O. nigerrimus* mentioned in Laraichi's works, or may in fact be the same species) compared with both *O. telenomicida* and *O. fecundus* may explain why, on the one hand, the latter species is dominant on CB eggs in the harshest climatic areas but, on the other hand, extremely rare in or absent from all other areas.

Similarly to our findings in Israel, the *O. telenomicida* population in Turkey seemed to be confined to cooler and more humid environments, in which it outnumbered the other species. Unfortunately, we were able to obtain parasitoids from only three locations in Turkey, scattered over a relatively wide area (Fig. 1). This rather limited sampling does not enable us to draw conclusions about the consistency of

the differences among the relative abundances observed in each of the sampled Turkish areas. However, in light of the general picture emerging from all sampled areas we suggest that it is very likely that both *O. near fecundus* and *O. telenomicida* are common in all of these areas, but that their abundance changes drastically according to the conditions in the specific location, with the latter species outcompeting the former where conditions favor the occurrence of both.

Interestingly, *O. pityocampae* was relatively uncommon on CB eggs in most sites, in both Israel and Turkey, apart from the relatively dry area of the southern Judean pine forests, where *O. telenomicida* is rarely found. The rarity of *O. pityocampae* seems somewhat surprising, since it has some apparent advantages over the other species. First, it is the only one which also parasitizes PPM eggs (Samra et al. 2014). The PPM is very common in the studied area, its eggs are laid later in the season (Sep–Nov), and are parasitized by *O. pityocampae* until November (Halperin 1990b) and occasionally as late as early December (Samra, personal observations). Thus, *O. pityocampae* exhibits a longer activity period than the other species, although it should be noted that we cannot exclude the additional possibility of its congeners switching to eggs of other hosts in autumn. Secondly, *O. pityocampae* is uniparental, and thus has the potential to increase its numbers faster than the other congeners, which are all biparental (see Bell 1982). These two features, i.e., longer activity period and uniparental reproduction, may enable *O. pityocampae* populations to expand quickly before entering winter hibernation, and this may also explain its high early-season relative abundance. However, in the present study, we found that as the season progressed, the relative abundance of *O. pityocampae* decreased, probably because of increased competition from the other *Ooencyrtus* species. Yet again, this hypothesis could be tested through experimental studies on interspecific competition. The complete absence of *O. pityocampae* from the southern and eastern areas in Israel, i.e., the Negev and the Jordan Valley, could be attributed either to unfavorable weather conditions, or to the absence of its main host, PPM from these areas. However, regarding the latter hypothesis, it is still unknown whether *O. pityocampae* is indeed unable to survive in areas where PPM is not found. In fact, there is a record of *O. pityocampae* being found in Iran

(Mohammadpour et al. 2014) (Fig. 3), outside the distribution range of PPM. Nevertheless, the high male ratio in the Iranian population means that other *Ooencyrtus* species may have been present, therefore the occurrence of *O. pityocampae* in Iran remains questionable. Furthermore, identification of members of this species-rich genus is often difficult, and many mistakes were made in the past (Prinsloo 1987). One also needs to consider that many new *Ooencyrtus* species are constantly being recognized (for recent examples see Ebrahimi et al. 2015; Hayat 2014; Zhang et al. 2014), and it is likely that many others, possibly cryptic ones, still remain unidentified. Therefore, any record should be considered with care. In light of our own experience and that of others, we suggest that identification of *Ooencyrtus* specimens should not rely solely on morphological examination, but further should be validated by means of molecular tools. The introduction of molecular tools easily may uncover the occurrence of cryptic species in a studied population (Bickford et al. 2007).

The reports of *O. pityocampae* in Poland also are somewhat puzzling, because of the absence of PPM from this country. However, a closely related *Thaumetopoea* species, *T. pinivora*, is found in northern Europe (Larsson et al. 2006), and is known as a host of *O. pityocampae* (Noyes 2014).

Local patterns of occurrence of the various *Ooencyrtus* species on CB eggs generally fit their known global distribution ranges (Fig. 3). The widespread distribution of *O. telenomicida* mostly includes temperate and Mediterranean climatic regions. The distribution of *O. pityocampae* largely matches that of its main host, the PPM, around the Mediterranean basin. The distribution of *O. nigerrimus* (which probably represents also the distribution of *O. near nigerrimus*, at least partially) is probably more southerly biased, as also was observed in the present study. It was previously recorded in Morocco, Israel, and Iran. Nevertheless, it also was recorded in Norway (Japoshvili and Hansen 2013). However, because of the difficulty in identifying this species (Guerrieri and Noyes, personal communication), one cannot exclude the possibility that this record is of a closely related, currently unidentified congener. In fact, two distinct COI haplotypes were found in this species in different areas (Samra et al., personal observation), and they may represent two spatially differentiated cryptic species.

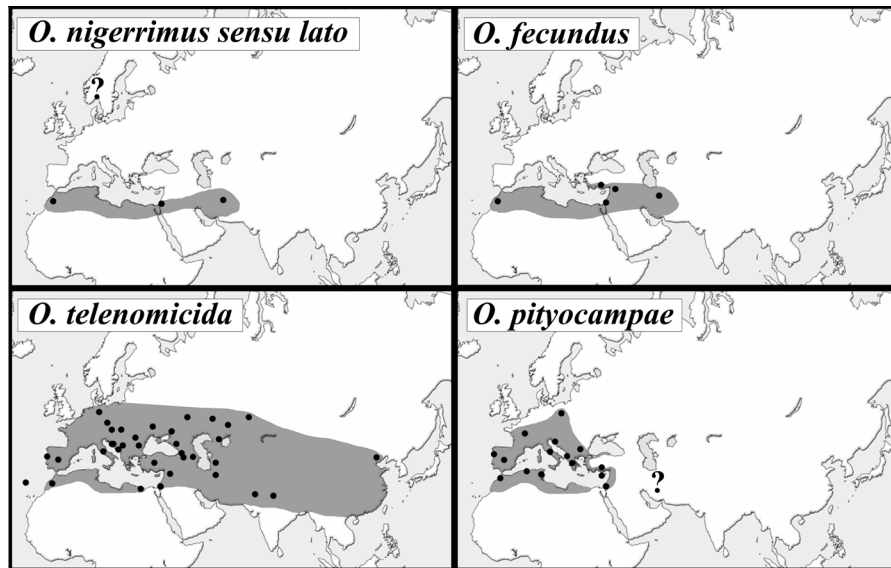


Fig. 3 Global distribution maps of four *Ooencyrtus* species that were collected from *S. coloratum* eggs in the present study. For *O. near nigerrimus* distribution, we used the literature data on *O. nigerrimus*. These two species are highly similar (E. Guerrieri and J. Noyes. Personal communications) and thus any previous mention of *O. nigerrimus* may in fact be relating to *O. near nigerrimus*. For this reason it is also impossible to differentiate the distribution of the two species at this point. Geographical ranges are based mostly on data taken from Noyes (2014), as well as data from the present study. The occurrence of *O.*

Interestingly, *O. fecundus*, which was previously recorded in Turkey (Melan 1994), was completely absent from the Turkish samples in the present study. However, genetically, *O. fecundus* and *O. near fecundus* are the most closely related (Samra et al., personal observation), and are extremely difficult to distinguish morphologically (Noyes et al., personal communication). The latter species was common in the Turkish samples (data confirmed by both molecular and morphological identification). Taken together, these data suggest that it is likely that *O. near fecundus* previously may have been mistakenly identified as *O. fecundus*, which could account for the apparent records of the latter species in Turkey, and possibly in other areas as well.

Parasitoid male ratios, which averaged approximately 25 % over all species in the present study, increased throughout the activity season, and this pattern was observed also in areas from which *O. pityocampae* was absent. Therefore, the increase in the number of males could not be explained simply in terms of a decrease in *O. pityocampae* abundance. The

fecundus in Iran was mentioned in Fallahzadeh and Japoshvili (2013). “?” symbols indicate recorded locations that do not seem to fit the distribution range of the species, i.e., the occurrence of *O. nigerrimus* in Norway (Japoshvili and Hansen 2013), and of *O. pityocampae* in Iran (Mohammadpour et al. 2014). These records may represent the occurrence of morphologically similar, closely related congeners (see “Discussion” section). The global distribution of *O. near fecundus*, which was recorded in Israel and southern Turkey in the present study, is currently unknown

increase in male progeny abundance corresponded with an increase in seasonal parasitism rates. This is consistent with the Local Mate Competition theory (Hamilton 1967), which predicts that increased competition with non-siblings should favor increases in male ratios within offspring of haplodiploid populations. The late-season increased parasitism rates are related to intensification of interspecies competition and thus, according to the theory, an increase in male ratios is to be expected. However, contributions of other factors, such as differing mortality rates of males and females, via competition for local resources, cannot be excluded (Godfray 1994).

Substantial egg parasitism rates were usually observed in all studied areas, mostly toward the end of the CB activity season. They reached about 50 % or more, and about 90 % in some locations. These data suggest that the CB is an important alternative host for these egg parasitoids in the East Mediterranean region, which means that increased CB populations may lead to significant increases in populations of these studied *Ooencyrtus* species. This could be achieved by

planting caper plants or through encouragement of caper establishment (reviewed by Samra et al. 2015).

To conclude, all the above data suggest that a balance among several factors maintain the coexistence of the studied parasitoid species on CB eggs: the superior survivability of *O. telenomicida* that springs from intrinsic competition mechanisms, the ability of the other species to survive in more extreme environments, and the higher population growth rate and longer activity period (on PPM eggs) of *O. pityocampae*, which otherwise is most likely inferior to most of the other studied species with respect to intrinsic competitiveness.

Our present findings suggest that, despite their seemingly generalist nature, each species does have some level of specialization, which is reflected in life traits other than host range, e.g., climate adaptations and intrinsic competitive capabilities. There is evidence that other traits, such as adult fecundity and longevity, and larval performance, i.e., development and survival, may further differentiate among species in this group, and thereby help to maintain their coexistence (Samra et al., personal observation). These *Ooencyrtus* species also co-inhabit several other host species. Therefore, future field and laboratory studies on the occurrence and multiparasitism scenarios of these species on other hosts may yield a broader understanding of their coexistence.

Acknowledgments We would like to thank Emilio Guerrieri, John Noyes, and George Japoshvili for helping with the challenging task of identifying the various *Ooencyrtus* species. We are also grateful to Mikat Doğanlar, Ahmet Yildirim, Muharrem Kamberoglu, Feza Can Cengiz (Turkey), and Carlos Jorge Carvalho (Israel) for their assistance in sampling *Ooencyrtus* populations. This study was supported by the Keren Kayemeth LeIsrael/Jewish National Fund (Project 131-1619-13), and is a part of the Ph.D. dissertation of S. Samra at the Hebrew University of Jerusalem.

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