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Temporal Relationship between the Prey Spectrum and Population Structure of the Weevil-Hunting Wasp *Cerceris arenaria* (Hymenoptera: Crabronidae)

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Carlo Polidori, Roberto Boesi, Carlo Pesarini, Cristina Papadia, Stefania Bevacqua, Matteo Federici, and Francesco Andrietti (2007) Temporal relationship between the prey spectrum and population structure of the weevil-hunting wasp *Cerceris arenaria* (Hymenoptera: Crabronidae). *Zoological Studies* **46**(1): 83-91. Specialized predators must face the problem of reductions in resources, and variations in the prey spectrum can be expected to be reflected in predator population traits. *Cerceris arenaria* L. (Hymenoptera: Crabronidae) is a solitary wasp that hunts weevils (Coleoptera: Curculionidae), with the individual range of prey sizes varying according to the size of the female wasp. A nest aggregation in Castiglione d'Adda, northern Italy was studied in 1997-1999, 2001, 2003, and 2005 in order to investigate variations in the prey spectrum across several years, while a 2nd aggregation in Castell'Arquato was investigated in 2001 to look for possible differences in prey selection between the 2 populations. The captured weevils belonged to 23 species. At both sites, the most often collected genera were *Otiorhynchus* Germar and *Sitona* Germar, which include several pests of cultivated plants. The prey spectrum (in terms of taxonomic identity and specimen frequency per species) varied among the years of study in Castiglione d'Adda, with *Sitona* spp. being more abundant in 1997-1999 and *Otiorhynchus* spp. in 2001, 2003, and 2005. According to this temporal shift in the prey spectrum, the annual average prey size increased from 1999 to 2005. Annual average prey size in Castiglione d'Adda was always lower than that in Castell'Arquato, where the frequency ratio of *Otiorhynchus*/*Sitona* was higher than that in Castiglione d'Adda. Prey size and the frequency ratio of *Otiorhynchus*/*Sitona* in Castiglione d'Adda were negatively correlated to the wasp population size, and the average wasp size increased when the frequency of larger prey increased. We concluded that interactions between extrinsic (prey availability) and intrinsic (wasp size distribution) factors may strongly influence fluctuations and persistence of specialized predatory wasp populations. http://zoolstud.sinica.edu.tw/Journals/46.1/83.pdf

Key words: *Cerceris*, Prey, Curculionidae, Population ecology.

Specialist feeders face the important problem of periodic drastic reductions in their resources. Specialized organisms cannot replace their exploited resource with a new one if the specialization is fixed genetically. For example, some oligolectic bees can shift from the preferred pollen source to another if the 1st becomes rare, but other more-specialized bees have co-evolved with only 1 plant and cannot survive without it (monolecty) (Wcislo1996). Parasites face the same problems if they are specialized in their host use (Frank 1993). Digger wasps (Hymenoptera: Apoidea and Vespoidea) are characterized, in most cases, by a specialized diet in the larval stage (O'Neill 2001). Mother wasps provide food for the larvae by preying upon restricted groups of arthropods, ranging from a single species (e.g., the beewolf, *Philanthus triangulum* F., hunting only

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honeybee workers) to several species of a single family (e.g., *Cerceris* spp., generally hunting members of a single coleopteran family), up to many species of various families of a single order or, rarely, to various orders (Bohart and Menke 1976). Digger wasps are thus good models for the study of the influence of prey selection on the population structure, but no studies have been carried out monitoring the prey spectrum and population traits across several nesting seasons.

Underground nests of *Cerceris* spp. are provisioned with only 2 orders of insects (only adult individuals are hunted): Hymenoptera (a few species) and Coleoptera (in most cases) (Bohart and Menke 1976). However, Gess (1980) suggested that, originally, Hymenoptera was the unique prey for the genus. The recorded coleopteran families used as prey include the Anthicidae, Anthribidae, Apionidae, Attelabidae, Belidae, Bruchidae, Buprestidae, Cerambicidae, Chrysomelidae, Coccinellidae, Curculionidae, Dermestidae, Eucnemidae, Nitidulidae, Hydrophilidae, Phalacridae, Scarabeidae, and Tenebrionidae, while Hymenoptera chosen as prey are in practice always Apoidea, except for *Cerceris stratiotes* Schlett., that hunts only 1 species of Chalcidoidea, *Stilbula cynipiformis* Vor, and a few species (e.g., *Cerceris circularis* F.) that seem to hunt both apoid and non-apoid Hymenoptera (Grandi 1950, Balthasar 1972, Gess 1980, Evans and Hook 1986, Callan 1987, Polidori et al. unpubl. data). Some species of the genus seem to be more specialized than others: for example, *C. fumipennis* Say hunts 27 species belonging to 3 different families of Coleoptera, while *C. binodis* Spinola seems to provision the nest with only a few species of Clytrinae (Chrysomelidae) (Scullen and Wold 1969, Evans 1971, Callan 1990, Giovanetti 2005). It has been suggested that this resource partitioning arose to avoid competition for provisions, since many times *Cerceris* spp. were observed nesting in the same restricted areas (Scullen and Wold 1969, Stubblefield et al. 1993).

The digger wasp *C. arenaria* L., exclusively hunts weevils (Curculionidae), as do most of the Coleoptera-hunting species of the genus (Fabre 1856, Hamm and Richards 1930, Crevecour 1946, Callan 1987, Evans 2000). Females mass-provision their nests (Polidori et al. 2005). Nests are reused year after year and represent the main resource producing intraspecific competition (nest usurpation) (Field and Foster 1995, Polidori et al. 2006). Prey-predator dimensional relationships can be well clarified by observing this species, because we previously stated that different-sized females hunted different prey: smaller wasps use a smaller range of weevils (only small weevils are used) compared to larger females (both small and large weevils are used) (Polidori et al. 2005).

In the present study, we attempted to investigate 2 points: 1) to verify if the prey spectrum (prey species collected and their frequency) of *C. arenaria* varies across nesting seasons and between 2 different populations, and 2) to analyze possible temporal relationships of prey spectrum variations and prey size distribution with the wasp population structure. A variation in the prey spectrum may be reflected in a modification of some population traits, such as the wasp size distribution and population size. Since prey records for this wasp are scattered through the literature, we also include a review of previously recorded prey weevils to define the actual (larval) dietary breadth and thus the degree of specialization.

MATERIALS AND METHODS

Study area

Two nest aggregations were examined, one in Castiglione d’Adda (45°12'57"N, 9°41'42"E) and the other in Castell’Arquato (44°52'06"N, 9°52' 24"E). The 1st one is situated in the Regional Park of Adda Sud (Lombardy, northern Italy). This is a sub-continental climatic area. Rainfall occurs mainly in autumn (with an average of 700 mm/yr) and the hottest month is July (with a mean temperature of 24.5°C). The park is mainly composed of cultivated fields (maize, soybean, and tomatoes). The nest aggregation of *C. arenaria* was located on a farm (Cascina Castello) of the town.

Castell’Arquato (Emilia Romagna, northern Italy) is a small town located in the foothills of the Apennines. It is drier and during summer, comparably cooler (with a mean temperature in July of 23.5°C) than Castiglione d’Adda. Wasps nested along the streets of the village.

Prey collection, data from the literature, and statistical analysis

The study was carried out over 6 yr (1997-1999, 2001, 2003, and 2005) during the flight period of the wasps (June and July). Observations made in Castiglione d’Adda covered the periods 11 June-25 July in 1997, 9 June-24 July in 1998, 8 June-20 July in 1999, 18-19 July in 2001, 1-7 July in 2003, and 7-19 July in 2005; prey specimens from Castell'Arquato were collected only in 2001 (15-17 July).

Prey were collected by 2 different methods: 1) directly from the wasps returning to the nest after hunting flights (in 1997-2005), and 2) when abandoned (often close to the nest entrances in the soil) (in 1997, 2001, 2003, and 2005) by the wasps. The 2nd case was common, since often before entering the nest after a provisioning flight, a wasp lost her prey. This could have been due to any disturbing event, such as the presence of a parasitic conspecific in the nest (during a nest usurpation attempt) or simply to difficulties of entering the nest, e.g., the combined width of the wasp and weevil being larger than the entrance width.

The size of the prey was roughly calculated from the literature (Porta 1932, Hoffman 1950 1954, Tempère and Pericart 1989), averaging the minimum and maximum 3rd power of body length therein found for each species, and for all *Sitona*, *Otiorhynchus*, and a few other species (17 of 23), we also weighed a sample of individuals to the nearest 0.002 g. A strong correlation between the (body length)^3 and the weight per prey species (Pearson correlation test, $n = 17$, $r = 0.82$, $p < 0.001$) was observed, justifying our use of literature data on prey size of species for which we did not have actual weights (the weight of the non-weighed 6 species was obtained from the regression equation of length^3 vs. weight obtained from the other 17 species, i.e. $y = 6^{-5}x + 0.0078$). From 18 to 87 (depending on the year) females were measured (head width) with calipers to the nearest 0.01 mm in 1997, 1998, 2001 (both sites), and 2003.

In all years of the study, the total number of nests was recorded in both aggregations. In 1997, we identified the most common plants around the Castiglione d'Adda site, and compared these plant species with those reported in the literature as hosts of weevils hunted by the wasps. In 2005, during the period of prey collection, we established a number of pit-fall traps in the area surrounding the wasp nesting site, to look for weevil species hunted by *C. arenaria*.

Statistical comparisons between the observed prey species frequencies were performed with the test for the equality of multinomial distribution (Kanji 1993). This method tests the equality of *n* independent multinomial distributions, using a modified χ^2 where the expected frequencies are calculated, in case of 2 groups and df = 1, as $(\text{observed}_1 + \text{observed}_2)/2$), and the critical values (0.05) is 9.48. Relationships between average prey sizes or wasp size and the variables, site and year, were evaluated using the general linear model (GLM). Linear correlations were tested with the Kendall test. In the text, average numbers are given ± SD.

Voucher specimens of prey and wasps were deposited in the Museo Didattico di Zoologia, Dipartimento di Biologia, Università di Milano.

RESULTS

Curculionids were collected during all 6 yr of the study at Castiglione d'Adda ($n = 1827$ specimens) and in 2001 at Castell'Arquato ($n = 188$ specimens). Prey belonged to 23 species (both sites and all years combined) (Tables 1, 2).

Weevils collected at Castiglione d'Adda belonged to 21 species and 6 subfamilies (Table 1). *Otiorhynchus* (5 species) and *Sitona* (5 species) were the most often represented genera. Only 3 species (*O. rugosostriatus*, *O. sulcatus*, and *S. hispidulus*) were present every year, with the most hunted prey (all years combined) being *S. hispidulus*, *O. rugosostriatus*, *S. nigriclavis*, and *O. appeninus salicicola*. The other species accounted for only a small percentage of the total (< 5% for all species, including 10 species that did not reach 1%) (Table 1).

Prey collected from Castell'Arquato are listed in table 2. Two of 9 species (*O. crataegi* and *O. frescati*) were only collected at this site, while 7 other species were collected at Castiglione d'Adda as well. At Castell'Arquato, > 95% of individuals belonged to the genus *Otiorhynchus* (Table 2).

The frequency of prey species varied through the 6 yr at Castiglione d'Adda ($\chi^2 = 335$, df = 15, $p < 0.01$) (only prey species with a frequency exceeding 5% were considered). The frequency ratio between the most abundant genera (*Otiorhynchus*/*Sitona*) was < 1 (more *Sitona* were hunted) in 1998 and 1999 and > 1 (more *Otiorhynchus* were hunted) in 1997, 2001, 2003, and 2005 (Fig. 1).

The frequency of the most abundant shared prey species (*O. rugosostriatus*, *O. armadillo*, and *O. appeninus salicicola*) varied between the 2 populations ($\chi^2 = 78.7$, df = 2, $p < 0.01$). This difference was due to *O. rugosostriatus* being more abundant at Castiglione d'Adda and *O. armadillo* being more abundant at Castell'Arquato. The frequencies of *O. appeninus salicicola* did not significantly vary between the 2 sites.

Overall, a difference in the average body weight of prey was observed across the 6 yr at Castiglione d'Adda (Fig. 2), as well as a difference in the average body weight of prey between the 2 populations, with prey hunted at Castiglione d'Adda being smaller (0.038 ± 0.026 g) than those hunted at Castell'Arquato (0.071 ± 0.019 g). A GLM considering the prey weight as the dependent variable and the year, site, and interaction between year and site as independent variables, confirmed these variations ($R^2 = 0.4193$, df = 2, $F = 176.59$, $p < 0.0001$).

Table 1. The 21 species of prey collected at Castiglione d'Adda in 1997-1999, 2001, 2003, and 2005, their dimensions, and frequencies. Data on the most abundant (> 10%) species are given in boldface

Subfamily	Genus	Species	Weight (mg)	1997	1998	1999	2001	2003	2005	Total
Baridinae	*Baris*	*Baris scolopacea* Germ.	2.00	0.00%	0.00%	0.00%	0.42%	0.00%	0.00%	0.05
Brachyderinae	*Sitona*	*Sitona cylindricollis* (Fahrs.)	4.00	0.00%	0.00%	0.00%	0.42%	0.00%	0.00%	0.05
		S. hispidulus (F.)	5.38	**11.86%**	6.99%	**43.08%**	7.56%	5.78%	3.88%	**13.08**
		S. humeralis Stephens	20.00	0.00%	1.04%	0.00%	0.84%	0.00%	0.00%	0.33
		S. sulcifrons (Thunb.) *argutulus* Gyll.	2.00	0.85%	0.26%	0.92%	0.84%	0.18%	0.00%	0.44
		S. nigriclavis Marsham	8.71	**17.80%**	**43.01%**	0.00%	5.88%	**24.01%**	4.37%	**18.77**
	Polydrusus	*Polydrusus sericeus* (Schaller)	8.64	0.00%	4.15%	0.00%	0.00%	0.00%	0.00%	0.88
Cleoninae	*Larinus*	*Larinus turbinatus* Gyll.	6.00	0.00%	0.00%	0.31%	0.42%	0.00%	0.00%	0.11
Hylobinae	*Lepyrus*	*Lepyrus capucinus* Schaller	62.33	2.54%	5.18%	0.00%	2.52%	7.40%	4.37%	4.32
Hyperinae	*Neglamis*	*Neglamis salviae* Schrank	48.63	0.00%	0.00%	6.15%	6.72%	9.21%	0.97%	4.87
	Donus	*Donus intermedius* Boheman	8.83	3.39%	2.07%	7.38%	0.00%	0.00%	0.00%	1.97
		D. zoilus (Scopoli)	8.89	5.93%	5.44%	0.00%	0.00%	3.43%	0.00%	2.57
	Hypera	*Hypera postica* Gyll. (sub*variabilis*) (Herbst)	8.48	0.00%	0.26%	0.92%	0.00%	0.00%	0.00%	0.22
		H. rumicis (L.)	8.51	0.00%	0.00%	0.92%	0.00%	0.00%	0.00%	0.16
		H. adspersa (F.)	8.51	0.00%	0.00%	0.31%	0.42%	1.44%	0.49%	0.60
		H. nigrirostris (F.)	8.25	0.00%	0.00%	0.00%	0.00%	0.18%	0.00%	0.05
Otiorhynchinae	*Otiorhynchus*	*Otiorhynchus rugosostriatus* (Goeze)	34.60	**16.95%**	8.03%	**24.31%**	**43.70%**	**19.13%**	**48.54%**	**24.08**
		O. armadillo (Rossi)	82.18	0.00%	0.00%	3.69%	2.94%	0.00%	0.00%	1.04
		O. appeninus Stierlin, *salicicola* Heyden	75.73	**35.59%**	**21.76%**	0.00%	**22.27%**	**24.91%**	**33.98%**	**21.18**
		O. ovatus (L.)	14.00	0.00%	0.00%	9.54%	2.94%	0.00%	0.00%	2.08
		O. sulcatus (F.)	71.63	5.08%	1.81%	2.46%	2.10%	4.33%	3.40%	3.12
Number of specimens collected				**118**	**386**	**325**	**238**	**554**	**206**	**1827**

Table 2. The 9 species of prey collected at Castell'Arquato in 2001 and their frequencies. Data on the most abundant (> 10%) species are given in boldface

Subfamily	Genus	Species	Weight (mg)	2001
Brachyderinae	*Sitona*	*S. hispidulus* (F.)	5.38	1.60%
Hyperinae	*Neglamis*	*N. salviae* Schrank	48.63	1.60%
Otiorhynchinae	*Otiorhynchus*	*O. crataegi* Germ.	9.00	1.06%
		O. frescati Boheman	8.00	1.06%
		O. rugosostriatus (Goeze)	34.60	**10.64%**
		O. armadillo (Rossi)	82.18	**48.40%**
		O. appeninus Stierlin, *salicicola* Heyden	75.73	**30.85%**
		O. ovatus (L.)	14.00	0.53%
		O. sulcatus (F.)	71.63	4.26%
Number of specimens collected				188

The frequency ratio of *Otiorhynchus*/*Sitona* per year was negatively correlated with the corresponding number of *C. arenaria* nests counted in the aggregation in the different years (a rough measure of population size, see Polidori et al. 2006) (Kendall correlation test, $n = 6$, $\tau = -0.73$, $p = 0.038$). The number of nests was negatively correlated with annual prey weight (Kendall correlation test, $n = 6$, $\tau = -0.68$, $p = 0.014$). The ratio of *Otiorhynchus*/*Sitona* per year was positively correlated with the average prey weight per year at Castiglione d'Adda (Kendall correlation test, $n = 6$, $\tau = 0.86$, $p = 0.014$), and the relationship was also significant when we added data from Castell'Arquato (Kendall correlation test, $n = 7$, $\tau = 0.90$, $p = 0.004$).

The average wasp size (head width) varied among all categories (4 yr at Castiglione d'Adda and 2001 at Castell'Arquato, see Fig. 2): females were smaller in 1998, when fewer *Otiorhynchus* (the larger prey) were hunted, and larger (in 2001, 2003, and 2001 at Castell'Arquato) when more *Otiorhynchus* were collected. A GLM considering wasp head width as the dependent variable and the year, site, and interaction between year and site as independent variables, showed that these variations were significant ($R^2 = 0.0966$, df = 2, $F = 13.5$, $p < 0.0001$).

Finally, from a literature survey, it seems that *Otiorhynchus* spp. prefer to live on the leaves of trees and shrubs, while *Sitona* spp. commonly feed on a wide range of forbs (Table 3), and we located several plants recorded as hosts of the most abundant weevil species at Castiglione d'Adda (Table 3). However, from pitfall traps located in 2005, the only weevil species (also hunted by the wasps) collected was *Lepyrus capucinus* (5 individuals).

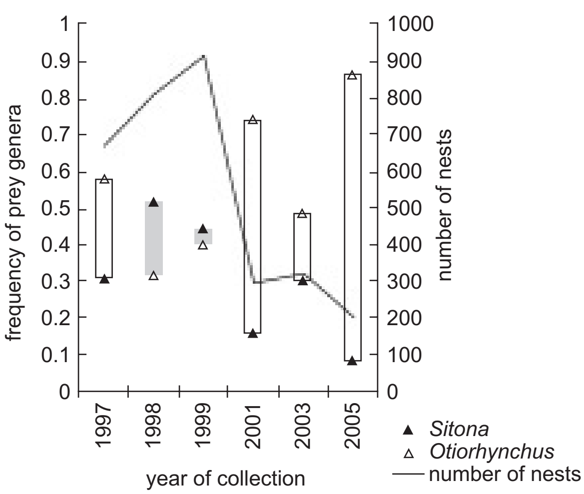

Fig. 1. Frequencies of the most abundant prey genera collected (*Sitona* and *Otiorhynchus*) and *Cerceris arenaria* population size (using the number of nests as the parameter) at Castiglione d'Adda in 1997-2005. Gray bars indicate that *Sitona* frequency was higher than *Otiorhynchus* frequency; white bars indicate that *Otiorhynchus* frequency was higher than *Sitona* frequency.

DISCUSSION

Prey spectrum in Europe

The collection of prey led to the identification of 23 species of weevils, belonging to 9 different genera. Hamm and Richards (1930), in a review of the prey hunted by *C. arenaria* by different authors in mainland Europe and the UK including their own records, listed 13 genera, while other authors observed 5 additional genera during prey collection (Table 4). In the present work, 5 new genera and 20 new species of prey records are added, bringing to 23 the total number of different weevils genera recorded (Table 4). The greatest number of prey genera belonged to the Brachyderinae, Hyperinae, and Otiorhynchinae. Female *C. arenaria* primarily confines her choice to a restricted range of weevil subfamilies, but can use other groups, probably if they are locally more abundant or accessible. Given insufficient information on the diet of the prey (which are often polyphagous), it was not possible to correlate specific plant-host associations with prey choice.

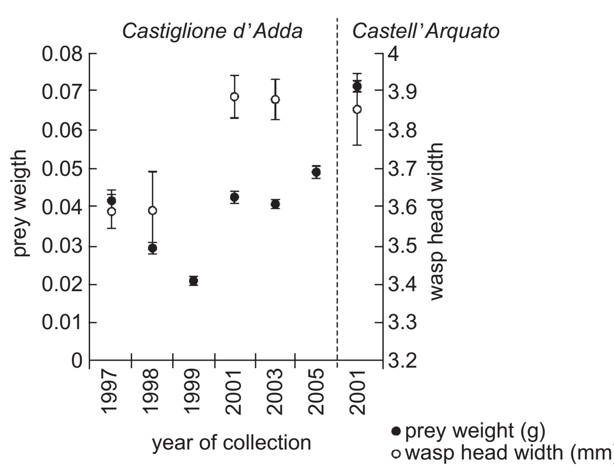

Fig. 2. Average weight (± standard error) of prey and average head width (± standard error) of wasps collected at Castiglione d'Adda and Castell'Arquato.

In general, *Otiorhynchus* and *Sitona* were abundantly hunted probably for their good availability in nature, the 1st one often being polyphagous on various trees and shrubs, and the 2nd often associated with plants which are very common on fence rows between crop fields and also on waste land, such as *Medicago* and *Lotus* (Table 3). The same could be said for some other collected prey genera such as *Donus*, which commonly feeds on plants like *Mentha*, well represented in the area surrounding the Castiglione d'Adda nest aggregation.

Intra- and interpopulational prey spectrum variations

Our results show that the prey spectrum varied across the years in Castiglione d'Adda, in terms of prey species (only a few species were collected in all years), prey specimens per species, and average prey weight. Moreover, it seemed that the average of prey size increased as the frequency ratio of *Otiorhynchus*/*Sitona* increased. An increase in size is primarily related to a shift in prey spectrum toward larger prey species, i.e., the ones belonging to the genus *Otiorhynchus*. Why did the Castiglione d'Adda population shift its prey spectrum toward *Otiorhynchus*? Variations in the prey hunted may depend on the availability of prey species: if for any reason in the area surrounding the nest aggregation, *Sitona* spp. populations decreased, this change could affect the prey spectrum of the wasp. However, this shift in prey selection should also have important effects on the wasp population structure. In fact, it was previously shown that *C. arenaria* females hunt prey according to their size: smaller wasps are confined to preying upon small weevils, while the larger ones

Table 3. Most common prey species of the 2 most hunted genera (*Otiorhynchus* and *Sitona*), and their preferred host plants

Species	Host plants	Plant found at Castiglione d'Adda
Sitona hispidulus	*Galega* sp.[1]	no
	Lotus sp.[1]	yes
	Trifolium pratense[2]	yes
	Centaurea sp.[2]	yes
Sitona nigriclavis	*Vicia* sp.[1]	yes
	Pisum sp.[1]	yes
	Medicago sativa[1]	yes
	Galega sp. [1]	no
	Trifolium sp[2]	yes
Otiorhyncus rugosostriatus	*Ciclamen* sp.[3]	no
	Rubus sp.[1]	yes
	Crataegus monogyna[1]	no
	Aucuba japonica[1]	no
	Senecio erraticus[2]	no
Otiorhyncus appeninus salicola	Polyphagous on various trees and shrubs[1]	yes
Otiorhyncus sulcatus	*Vitis vinifera*[3]	no
	Fragaria sp.[1]	no
	Taxus sp.[2]	no
	Azalea sp.[2]	no
	Rhododendrum sp.[2]	no
	Begonia sp.[2]	no
	Vaccinum sp.[2]	no
	Rubus sp. [2]	yes
	Ciclamen sp.[2]	no
Otiorhyncus ovatus	*Picea excelsa*[3]	no
	Fragaria sp.[2]	no
	Carduus nutans[2]	no
	Centaurea sp.[2]	yes

References: [1]Hoffmann (1950); [2]Campobasso et al. (1999); [3]Grandi (1951).

are able to prey upon a wider size range of prey (Polidori et al. 2005). If smaller prey becomes less abundant in the environment, smaller wasp females would have a reduced prey spectrum to exploit, risking and reducing their fitness because of the fewer number of larvae successfully fed. The negative correlation between prey size (as expressed by the frequency ratio of *Otiorhynchus*/*Sitona*) and wasp population size (as expressed by the number of nests) may support this hypothesis, as well as the observed difference in wasp size between years when abundant large species (*Otiorhynchus* spp.) were used as prey and those when exploitation of large species was scarce (Fig. 2).

The reduction in *Sitona* spp. populations around the wasp nesting site could have been due, however, to factors either independent of or dependent on the presence of the wasp population. Weevil populations may gradually decline because of biological or chemical control of fields, and their presence might not coincide with that of *Otiorhynchus* spp., which can live on different plants (see next paragraph), but they also may suffer a reduction because of intense foraging activity by wasps. This hypothesis may be supported by the fact that smaller *C. arenaria* females make more provisioning trips per day than do larger

Table 4. Comparison between the prey genera of *Cerceris arenaria* collected in the literature and in the present work

Subfamily	Genus	Published work 1815-1995	Present work
Brachyderinae	*Cneorrhynus* (see *Atactogenus*)[4,8,15,30]	x	
Brachyderinae	*Atactogenus*[22]	x	
Brachyderinae	*Brachyderes*[4,8,9,11,12,21,25,29]	x	
Brachyderinae	*Caulostrophus*[18,23]	x	
Brachyderinae	*Geonemus*[4,8,30]	x	
Brachyderinae	*Neliocarus*[24]	x	
Brachyderinae	***Polydrusus*		x (1)
Brachyderinae	**Sitona*[4,8,10,18,23,29]	x	x (5)
Brachyderinae	*Strophosomus*[2,3,6,7,11,12,15,18,20,22,23,25,29]	x	
Hylobinae	*Hylobius*[29]	x	
Hylobinae	**Lepyrus*[15]	x	x (1)
Hyperinae	***Donus*		x (2)
Hyperinae	***Neglamis*		x (1)
Hyperinae	**Hypera*[26]	x	x (3)
Hyperinae	*Phytonomus* (see *Hypera*)[5]	x	
Otiorhynchinae	**Otiorhynchus*[1,5,6,8,11-17,19,22,27-29]	x	x (5)
Otiorhynchinae	*Peritelus*[19]	x	
Cleoninae	***Larinus*		x (1)
Curculioninae	*Curculio*[29]	x	
Curculioninae	*Balaninus* (see *Curculio*)[6,20]	x	
Baridinae	***Baris*		x (1)
Tanymecinae	*Tanymecus*[11,22,29]	x	
Molytinae	*Pissodes*[29]	x	
Chrysomelidae	*Bromius*[5]	x	
Total new prey species recorded			20

References: [1]Kirby in Kirby and Spencer 1815; [2]Westwood 1836; [3]Dahlbom 1843; [4]Fabre 1856; [5]Lucas 1858; [6]Smith 1858; [7]Thomson 1874; [8]Fabre 1879; [9]Kohl 1880; [10]Sickmann 1891; [11]Alfken 1899; [12]Adlerz 1903; [13]Hallet 1914; [14]Feytaud 1918; [15]Alfken 1915; [16]Fahringer 1922; [17]Perkins 1923; [18]Grandi 1926; [19]Chevalier 1927; [20]Hamm and Richards 1930; [21]Minkiewicz 1933; [22]Crèvecoeur 1946; [23]Grandi 1961; [24]Bonelli 1969; [25]Eck 1971; [26]Hoffmann 1954; [27]Willmer 1985; [28]Field and Foster 1995; [29]Lomholdt 1976; [30]Friese, 1926, quoted in Lomholdt 1976. References 1-3, 5-17, and 19 are quoted in Hamm and Richards (1930). *Shared results; **new host genera records, in parentheses the number of new species records.

females (Polidori et al. 2005), thus they might exert a stronger pressure on weevil populations compared to that of the larger wasps. Moreover, it has been suggested (Polidori et al. 2005) that the positive correlation between prey (divided by wasp biomass) and wasp biomass does not favor size stability, since the larger prey biomass collected by larger wasps could produce still-larger wasps (or maybe a larger number of wasps). Since the wasp population decreased through the years of study (Polidori et al. 2006), it is possible that larger wasps became the major component of the population, as shown, at least partially, by our data on wasp size. Although we did not record wasp sizes in all years, it seemed to increase according to *Otiorhynchus* abundances rather than to *Sitona* abundances (Figs. 1, 2), because the former genus can be only hunted by larger females, while the latter genus can be hunted by both smaller and larger females (Polidori et al. 2005).

A 2nd hypothesis is that the wasp population is responsible for the prey size shift through the years, with a minor role being played by variations in prey availability. In fact, during nest usurpation events, it was observed that larger wasps won more frequently than smaller ones in cases of direct fighting (Polidori and Andrietti 2006), as occurs also in other *Cerceris* species (Mueller et al. 1979). Over a long period of time, this size-dependent competition could have negative effects on the reproductive success of smaller females, which would spend more time successfully occupying a nest, and consequently a shorter time provisioning it. Unfortunately, we have no evidence on prey availability in the environment which may support one or the other of the, possibly non-exclusive, hypotheses.

CONCLUSIONS

It seems that even if prey selection is essentially related to a limited number of weevil subfamilies, the generic or specific prey choices depend on their local and temporal availability and probably also on the wasp population structure. The present results confirm that which was established by Linsley and MacSwain (1956), who showed that the prey population structure affected a population of the buprestid-hunter, *Cerceris californica* Cress. Long-term studies are necessary to understand predator-prey relationships in digger wasps, since observed prey selection may be a product of non-obvious interactions between extrinsic (prey availability) and intrinsic (intraspecific competition and size distribution) factors within predator populations. Prey palatability might even be another important factor, never before considered in digger wasps prey exploitation studies, since predators can become better adapted to using unpalatable prey, resulting in a diet breadth subject to dynamic evolutionary change (Rana et al. 2002). And finally, a molecular approach may also be of interest, since prey specialization may influence gene flows in predator populations, as suggested by Carmichael et al. (2001).

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