Taxon-biased diet preference in the 'generalist' beetle-hunting wasp *Cerceris rubida* provides insights on the evolution of prey specialization in apoid wasps

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Opportunism and specialization appear to be widespread in apoid wasps, although the factors affecting the diet preference (and thus explaining the degree of specialization) are still largely unknown. Four hypotheses that stressed the importance of the size, sex, habitat, and taxonomic identity of prey of the beetle-hunting digger wasp, *Cerceris rubida*, were formulated and tested. The wasp population hunted for phytophagous beetles belonging to abundant families around the wasp nesting site. In practice, the prey appeared to be hunted only in two cultivated fields, thus habitat accounted for a majority of the observed diet. The size of wasps was furthermore correlated with the size of their prey, and thus this also accounted for the frequencies of hunted prey and the strong individual specialization for both taxa and size. However, in the exploited habitat, some species were significantly over-hunted than expected and some other significantly avoided by the wasps, causing an unexpected major role of prey taxon on the probability of being hunted, over the other explanatory variables (body size, body shape, sex, availability). This contrasts to that found in other wasp species, which appear to select prey basing essentially on their ecology and size or their relative abundance (opportunism). The results obtained in the present study show that even an apparent 'generalist' predator may turn out to be taxonomically specialized. Together with a re-evaluation of previous studies, our results further suggest that the effect of size constraints and the developmental plan of prey (holometaboulous versus hemimetabolous) may have promoted either taxonomic opportunism or specialization in different lineages of apoid wasps. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **99**, 544–558.

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INTRODUCTION

The 'diet preference' of a predator is the tendency to consume some prey more frequently than would be expected based on the relative abundances of alternative prey in the environment (Sih & Christensen, 2001; Huseynov, Cross & Jackson, 2005). Diet preferences are ecologically important because nonrandom predation has important effects on the relative impacts of predators on different prey (Paine, 1966; Sih *et al.*, 1985). Although the 'active predator choice' (i.e. the tendency to attack some prey more often than others, given an encounter with each prey type) (Tikkanen *et al.*, 1997; Lang & Gsödl, 2001) can be investigated only experimentally; it is possible to evaluate nonrandom preferences by comparing observed diets with patterns of prey abundance in the environment where predators hunt (Chesson, 1983). Diet preferences may provide a good indication of

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overall predator choice in particular if prey are immobile or scarcely mobile, so that prey that have lower escape ability should tend to be 'preferred' (i.e. over-represented in the diet; Sih & Christensen, 2001). Moreover, many generalist species consist of individual specialists (Bolnick *et al.*, 2003) and, even though all the mechanisms behind this pattern are not clear, both intraspecific competition and predation has been shown to influence individual diet specialization (Svanbäck & Persson, 2004; Eklöv & Svanbäck, 2006; Svanbäck & Bolnick, 2007).

If resource specialization is not phylogenetically determined at level of one or few single species, discrimination of a prey item should pass through a number of prey biological traits (apart availability), such as body size, body shape, age, sex, autoecology, escaping behaviour, and so on (Kaiser, Hughes & Gibson, 1993; Stamp & Meyerhoefer, 2004; Wohlfahrt *et al.*, 2006; Polidori *et al.*, 2007a).

It is thus possible, through the detailed evaluation of prey abundance and prey biological traits, to test a number of non-exclusive hypotheses, under the default hypothesis of prey taken at random with respect to their traits, but simply in accordance with their availability in the environment (opportunistic predation): (1) individuals choose prey on the basis of the size of their prey (the 'biomass-bias hypothesis', BHp; Polidori *et al.*, 2005); (2) individuals prey preferentially on particular taxa of prey, the 'taxon-bias hypothesis', THp (e.g. larger ones because they are more visible: Grant, 2006; ones recognized as prey via chemical cues: Anton & Gnatzy, 1998); (3) individuals prey only on those species which inhabit particular habitats and have similar autoecology (the 'ecology-bias hypothesis', EHp; Polidori *et al.*, 2007b); and (4) individuals prey preferentially on one of the two sexes of the targeted species (the 'sex-bias hypothesis', SHp; Lin, 1979) (i.e. generally the more valuable one; often the females).

Apoid wasps (Hymenoptera: Sphecidae and Crabronidae) are good models for testing these hypotheses for at least three reasons: (1) they are central-place foragers, in that they depart from a fixed place (nest) and come back with prey many times during their life-time (O'Neill, 2001), allowing the sampling of many prey by stealing them from home-returning wasps; (2) the potential and available taxa suitable as prey are restricted to few arthropod groups, generally up to a single insect order for each given wasp species (Bohart & Menke, 1976), allowing to an easier survey of such communities in the environment; and (3) females of Apoidea generally forage at relatively short distances from the nesting site, rarely at a distance of more than 1 km (Gathmann & Tscharntke, 2002; Greenleaf *et al.*, 2007), thus the survey of available prey in the environment may not be expansive in terms of time and adequately accurate.

Studies on the prey spectrum of digger wasps are numerous (Evans & O'Neill, 1988, 2007; O'Neill, 2001), although very few of them have compared actual prey with the environmental availability of the target taxa (Stubblefield *et al.*, 1993), and even fewer studies have considered the effect of prey biological traits on the probability of being hunted (Grant, 2006; Polidori *et al.*, 2007b). In these studies, prey preference of non-opportunistic wasp species was explained by factors that may be different for each species of predators. For example, size was the main factor determining the diet in the grasshopper-hunter *Sphex ichneumoneus* because females are constrained to shift to new prey species when the hunted ones become too large during the season (Brockmann, 1985). On the other hand, ecology of prey (e.g. their feeding habits or habitat) accounted for most of the variation between diet and availability in *Sceliphron* spider-hunting wasps and the grasshopper-hunter *Stizus continuus* Klug (Elgar & Jebb, 1999; Polidori *et al.*, 2007b; Polidori *et al.*, 2009). In some strongly specialized predatory species, the chemo-sensitivity system of wasps ('sensory window') was shown to determine the final acceptance of prey, so that prey preference depend primarily on taxonomic identity (taxon-bias hypothesis valid) (Anton & Gnatzy, 1998; Herzner *et al.*, 2005). However, for a few species, prey preference has not been detected and the species turned out to be opportunistic: females hunt for the most abundant species in the environment, regardless of sex, appearance and size (Stubblefield *et al.*, 1993; Grant, 2006).

These different results do not suggest any common evolutionary process that lead to specialization in prey use by apoid wasps and, from this point of view, it may be helpful to study groups which hunt for other taxa. A good candidate would be the digger wasp genus *Cerceris*, comprising a large group that includes mainly Coleoptera-hunting wasps (Gess, 1980). In this genus, few generalist species (many families of beetles are hunted) and many specialized ones (only one family of beetle is hunted) have been recorded (Bohart & Menke, 1976; Evans & Hook, 1986).

In the present study, we investigated the relationship between the digger wasp *Cerceris rubida* Jurine 1807 and their beetle prey, testing the four mentioned hypotheses with respect to prey preference. Because of the non-obvious relationships between individuals' and population's diet preference (see above), we also investigated individual specialization of females.

Cerceris rubida is a small (approximately 1.7–2.3 mm in head width) digger wasp confined to

southern Europe, and its biology is remarkable in that it is the only European species of the genus known to be social (Polidori *et al.*, 2006). Females dig nests in compact soils and fill them with previously paralysed Coleoptera as food for the developing offspring (Grandi, 1961). This species is of interest for studying diet preference dynamics because, in contrast to most *Cerceris* spp., it is one of the few species that hunt for many beetle families (Chrysomelidae, Curculionidae, Nitidulidae, and Phalacridae) (Aptel, 1931; Grandi, 1961). Coleoptera-hunting *Cerceris* are also an advantageous model for testing diet preference in the field because their prey are generally scarcely mobile and, thus, to some extent, the results may also indicate the predator's 'choice' (see above).

MATERIAL AND METHODS

STUDY AREA

The study was conducted in the Maremma Regional Park (Grosseto Province, Tuscany, Central Italy) (42°40′5″N, 11°6′23″E), during the summer of 2005 (from June to August), consisting of most of the period of the year when the wasps were actively provisioning their nests (Polidori *et al.*, 2006). This Park is characterized by the Uccellina Mountains (a chain of hills parallel to the coast and covered by the thick Mediterranean maquis), Mediterranean pine-woods, and extended cultivated fields (in particular maiz, tomatoes, olives and sunflowers).

The nesting area of *C. rubida* consisted of a trail bounded by two cultivated fields (Field 1: alfa-alfa *Medicago sativa*; Field 2: wheat *Triticum* sp.). The

nests of *C. rubida* were intermixed with nests of at least other five species of ground-nesting bees and wasps, including other *Cerceris* (Polidori *et al.* 2006; Polidori C., unpubl. data).

SAMPLE OF BEETLES

To make a comparison between the beetles actually hunted by the wasps and those potentially available as prey, we collected them both from flying wasps returning to the nest (stealing the prey from the females after netting them) and around the nest aggregation (named, respectively, 'hunted' and 'available'). A sample of available beetles in the environment was made aiming to collect the highest number of beetle species (i.e. placing pitfall traps, netting on the plants with sweeping net of the fields and shaking the branches of trees to provoke the fall of the arboreal species on a tray beneath: knockdown sampling) (Southwood, 1978). The combination of these methods was previously shown to be successful in sampling beetle fauna in agro-ecosystems (Standen, 2000; Batáry *et al.*, 2007). The area chosen for the beetle sampling included the two fields bounding the path housing the nest aggregation and the bushed, shrubed, and wooded hedgerows bounding them, for a total of five sub-zones (Fig. 1), in an area of approximately 1 km². Careless, Marshall & Gill (2007) calculated a maximum flight distance for *Cerceris fumipennis* Say of approximately 1 km; such a value should be still lower for *C. rubida*, which is smaller then *C. fumipennis*, because, in Apoidea, a positive relationship between body size and maximum flight
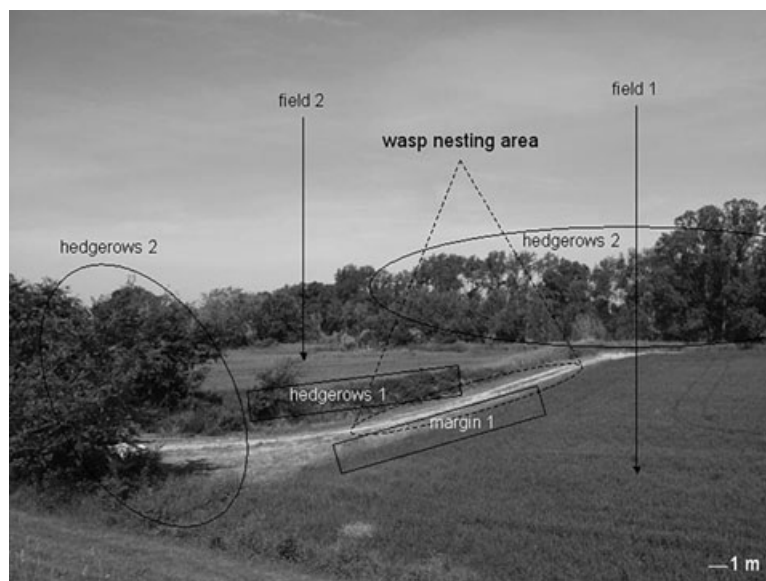

Figure 1. View of the nesting area of *Cerceris rubida* and the sub-zones where beetles were sampled during the present study.

distance was reported (Guédot, Bosch & Kemp, 2009). The five sub-zones differed in their main vegetation type: field 1 was an alfalfa field; field 2 was an abandoned crop field; margin 1 was bounding the field 1 and presented a mix of invasive and non-invasive grasses; hedgerow 1 included small to medium-sized arbusts; and hedgerow 2 included mainly trees and large arbusts. Thus, each sub-zone was not necessary a different patch (see hedgerow 2).

Beetles were collected from the wasps and in the environment from 1 June to 10 August at intervals of 15 days, and covering the daily period of provisioning of the wasps, from approximately 10.00–16.00 h (Polidori *et al.*, 2006).

With these data, we calculated the sample similarity between the frequency distribution of resources used by the wasps relative to the environment, to determine to what extent the niche of wasps is a subset of the available prey. We used Czekanowsky's proportional similarity index (Feinsinger, Spears & Poole, 1981):

$$PS = 1 - 0.5 \sum_j |p_j - q_j|$$

where p_j is proportion of jth prey in the population diet and q_j is the proportion of the resource in the environment. Note that, despite $PS = 1$ if the diet totally overlaps with availability, its value may still be very high also in case of wasps hunting for only one or few dominant species in the environment.

BIOLOGICAL TRAITS OF PREY

Once collected, all the hunted and available beetles were measured in the laboratory under a dissection microscope. Maximum length and width (to the nearest 0.01 mm) of the beetles were recorded and, from these measures, the length/width ratio (shape) was calculated as an additional morphometric parameter. This was carried out because individuals of different beetle species with a similar length can be more or less wide (Vogel, 1994). Once all these data were recorded, we converted the prey body length into weight according to regression equations, *sensu* Hódar (1996), to obtain the mean individual biomass that we will call 'size'.

After the measurement of all the available beetles, we selected for the subsequent analyses only those individuals that were revealed to have a size suitable to be hunted by the wasp. The chosen size-limit was the highest weight recorded for an actually hunted prey. No lower bound was chosen because, in principle, wasps would be able to carry very small beetles, but not very large ones.

The sex was assessed only for a sub-sample of beetles (210 prey and 62 beetles from environment).

Finally, all specimens were pinned and determined to the species level and, when not possible, to the genus or family level.

Through a survey of the literature (Grandi, 1951; Hoffmann, 1958; Center & Johnson, 1974; Audisio, 1993), we associated the typical habitat to each species of beetles: (1) litter (species living at the soil level, often detritivourous); (2) herbaceous plants (all the species living and feeding on pollen, nectar or other plant tissues of herbs and grasses); (3) bushes/shrubs (species living on bushes and shrubs generally feeding on leaves); and (4) trees (species living on the trunks or on leaves of trees).

INDIVIDUAL PREDATOR–PREY RELATIONSHIPS

To determine individual relationships between the wasps and their prey, we marked a total of 31 females with individual combinations of colours using non-toxic water proof paints. The head width (to the nearest 0.02 mm with a digital calliper) was used an estimate of wasp body size (Ohl & Thiele, 2008). A total of 241 prey items was collected from the individually marked wasps, which were measured and determined as explained above.

To measure individual specialization, we used two different indices: one to evaluate size specialization and one to evaluate taxonomic specialization. These indices were calculated for 13 wasps from which we obtained at least two prey items.

For size (length) specialization, we used the Roughgarden's index ($R'sI$) (Roughgarden, 1972) for continuous data, applied at the individual level (Bolnick *et al.*, 2002):

$$R'sI = \frac{WIC}{TNW}$$

where WIC is the variation in resource use within individuals and TNW (which represents the total niche width of the population) is given by WIC added to BIC, which is the variance in resource use between individuals. This index varies from 0 (maximum individual specialization, with all TNW explained by BIC) to 1 (no individual specialization).

To measure individual taxonomic specialization, for each individual, we used the proportional similarity index (PS; see above) adapted by Bolnick *et al.* (2002) to individual-level analyses (PS_i), because it follows:

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j|$$

where q_j represents the proportional abundance of jth prey item in population's diet, not in the environment, as for PS (see above). The measure of

individual specialization in prey taxa for the population is expressed as *IS*:

$$IS = \overline{PS_i}$$

STATISTICAL ANALYSIS

A table of contingency was built to test for diet preference, comparing the observed number of individuals per family or species stolen from the wasps with the expected ones taking account the environmental abundance of each genus. Chi-square values and residuals were calculated from the table. The same kind of analysis was performed to test for abundances of the beetle species in the sub-zones (and thus habitats because sub-zones were discriminated depending on vegetation types) (observed number of individual per species in a sub-zone versus the expected one taking account the abundance in the other sub-zones); this comparison was carried out to determine the type of habitat in which the beetle species are more common, and thus to infer where the wasps were more likely to hunt. A table of contingency was also built to compare sex ratios of beetles between those hunted and those collected in the environment (observed number of female and male individuals among the prey versus the expected ones taking account their numbers in the environment).

Linear correlations were tested with Pearson test. Differences between average values of two sets of data were tested with Student's *t*-test for unpaired data or, if variances resulted nonhomogeneous (significant *F*-test), with the Aspin–Welch test.

Data were then fitted using simple and multiple logistic regression models and the logit (log odds ratio; OR) link function was used to estimate various probabilities (Agresti, 2002).

The logit is the natural logarithm (ln) of odds of a successful response (hunted prey) compared to a failure (a coleopteran available but not hunted). When an odds ratio is significantly greater than 1, individuals in one group are more likely to have a success (to be hunted) than individuals from another group. An OR can be considered statistically significant if its confidence interval does not include 1 (because OR = 1 indicates no association between the predictor factor considered and the probability of being hunted). Because there was collinearity between width and length and because of the scarce variability of the ecology (feeding habitat, as obtained from literature) variable, the variables associated with each beetle were the species, size, and length/width ratio (see Results). Sex was not used as variable in the model because it was only determined for a subset of data.

The indices of individual specialization, *R′sI* and *PS*_i were calculated using INDSPEC1 (Bolnick *et al.*, 2002). INDSPEC1 uses a nonparametric Monte Carlo procedure to generate replicate null diet matrices drawn from the population distribution, from which *P*-values can be computed (Bolnick *et al.*, 2002). We used 10 000 replicates in Monte Carlo bootstrap simulations to obtain *P*-values for these different indices.

All the other statistical analyses were performed using the SAS statistical package (SAS Institute, 1989). Data are given as the mean ± SD.

RESULTS

GENERAL PREY SPECTRUM, PREY AVAILABILITY, AND SPATIAL–TEMPORAL VARIATIONS

Females of *C. rubida* provisioned their nests with adult beetles of six families, whereas a total of 14 beetle families were sampled in the environment (Fig. 2; see also Supporting Information, Appendix S1); five out of these 14 families were also present among the wasp prey, whereas Scolytidae were only found among the hunted beetles, not in the environment (see Supporting Information, Appendix S1). The absence of Scolytidae in our environmental sampling may be a result of their extreme rarity (only 1.28% of actual prey belonged to this family), and also suggests either the wasps were hunting in not sampled patches or that these beetles were missed by sampling, as all sampling schemes have inherent limitations.

Chrysomelidae, Curculionidae, and Phalacridae altogether represented almost the 95% of all the hunted beetles (with the sole Chrysomelidae reaching approximately 50%). These three families were also the most abundantly sampled in the environment (63.55%, with Chrysomelidae covering 39.26%); however, the Coccinellidae (i.e. not hunted by the wasp) also comprised an abundant group of the available beetles (27.46%). Chrysomelidae, Curculionidae, Phalacridae, Nitidulidae, and Scolytidae were significantly over-hunted when taking into account their relative abundance in the environment, whereas Coccinellidae and Corylophidae were significantly ignored by the wasp females (Fig. 2).

A total of 61 species of beetles were collected during the study. In the five families both collected from the wasps and in the environment, a total of 50 species of beetles were sampled (30 species hunted by the wasps, 20 only in the environment, and nine in both categories) (see also Supporting Information, Appendix S2). Most hunted species belonged to Chrysomelidae, with species of the genus *Chaetocnema* representing approximately half of all the specimens (47.6%); the next abundant hunted species were *Protapion trifolii* (Curculionidae) (23.8%) and *Olibrus*
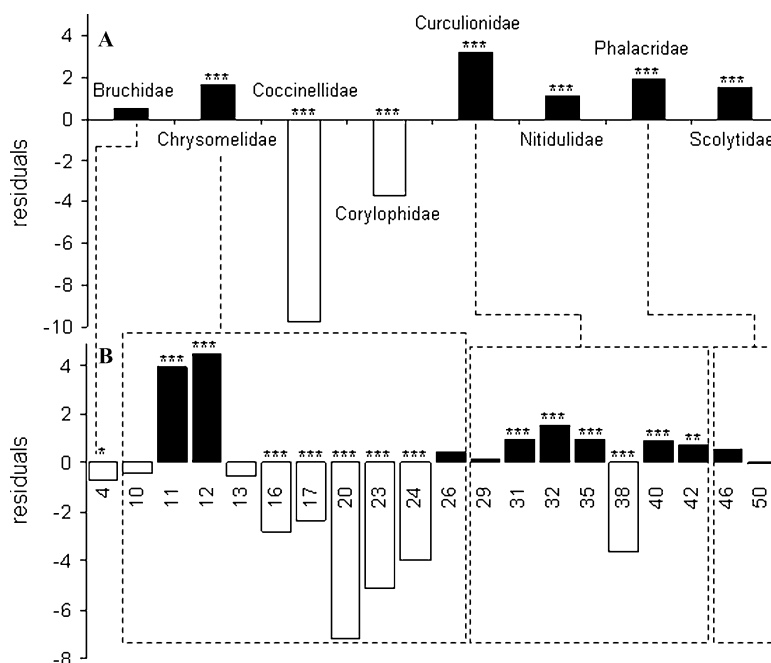
Figure 2. Taxonomic selective predation by *Cerceris rubida*, viewed as the distribution of standardized residuals obtained by the contingency table analysis at the family level (A) and the species level (B). The dashed lines connect the families in (A) to the group of species belonging to them in (B). Only the families and species for which the sample was adequate to perform a chi-square test are shown. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. The identity of the species is indicated in the Supporting Information (Appendix S2).

affinis (Phalacridae) (9.11%). No other species represented more than 5% of beetles. Eight species were significantly over-hunted when taking into account their relative abundance in the environment (one in the Bruchidae, two in the Chrysomelidae, and four in the Curculionidae), whereas six species were significantly ignored by the wasp females (five in the Chrysomelidae and one in the Curculionidae) (Fig. 2). Czekanowsky's PS) was 0.36.

There was a correlation between the frequency of the hunted families and those available (Pearson correlation test, $r = 0.79$, $N = 15$, $P < 0.001$), although Coccinellidae strongly departed from the trend line (Fig. 2; see also Supporting Information, Appendix S2). A positive, but weaker, correlation was found also between the frequency of the hunted species and those available (using only the families both hunted and available) (Pearson correlation test, $r = 0.32$, $N = 50$, $P = 0.023$) (Fig. 2). This comprised the chrysomelid species of *Phyllotreta* (very abundant in the environment but ignored by the wasps) and *Chaetocnema* (very abundant among hunted specimens but rarely found in the environment) that considerably departed from the regression line (Fig. 2).

The overall sex ratio (females/males) of prey was 1.8 (female-biased: $\chi^2 = 8.57$, d.f. = 1, $P = 0.003$), whereas that of beetled collected in the environment was 1.3 (no bias: $\chi^2 = 0.51$, d.f. = 1, $P = 0.47$). These values did not differ from the expected under the hypothesis of 'equal sex ratios' between the diet and the available prey (SHp) ($\chi^2 = 3.02$, d.f. = 1, $P = 0.08$).

BIOLOGICAL TRAITS OF PREY

Ecology (feeding habitat)

The groups of beetles targeted by the wasps were not equally distributed among sub-zones, with most of them being collected in the fields bounding the nest aggregations (159 in Field 1 and 187 in Field 2); the other 123 individuals were sampled in the field margin, and 67 and 30, respectively, in the two hedgerows ($\chi^2 = 575.31$, d.f. = 4, $P < 0.0001$). Species belonging to the genera *Chaetocnema*, *Olibrus*, *Stilbus*, *Protapion*, and *Gymnetron*, which were abundantly found among prey, were essentially collected in the two fields, and also most of the ignored or rarely hunted species, such as *Sitona lineatus* and all the *Phyllotreta*, were collected mostly there (see Supporting Information, Appendix S3). From the available literature, it emerged that the 95% of species collected both from wasps and the environment are typically associated with herbaceous plants or flowering grasses, feeding on leaves, fluids, or pollen (Grandi, 1951; Hoffmann, 1958; Center & Johnson,
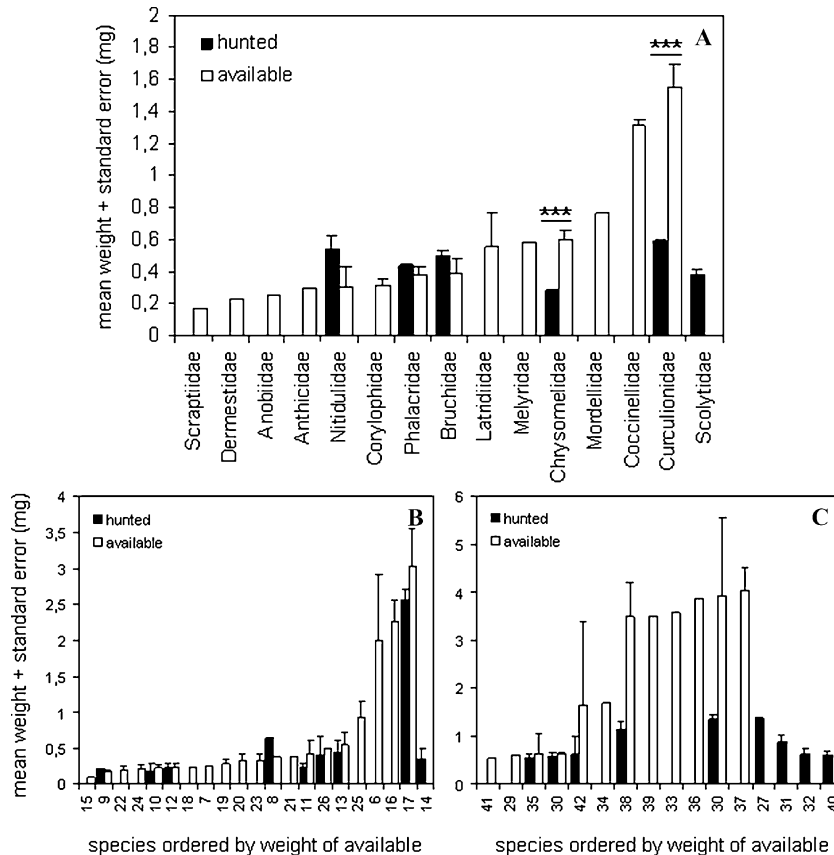
Figure 3. Mean weight and standard error (mg) of the 15 families of beetles sampled in the present study (A) and of the sampled species of the families Chrysomelidae (B) and Curculionidae (C). Statistical test for difference in mean weight between the hunted and available samples was performed for samples ≥ 7. ***$P < 0.001$. The identity of the species is indicated in the Supporting Information (Appendix S2).

1974; Audisio, 1993); indeed, they were collected in the two fields and/or on their margins. In addition, none of the species associated with the litter and the soil surface (collected in the pitfall traps) were hunted by the wasps, and only extremely rarely did a wasp hunt a beetle associated with trees (Scolytidae) or shrubs (1 species of Bruchidae). Thus, it may be inferred that almost all the prey were hunted by the wasps in the two fields around the nesting site.

Body size and length/width ratio
Beetles collected in the environment weighed approximately twice as much as those hunted by the wasps (0.927 ± 0.943 mg versus 0.471 ± 0.250 mg) (Aspin–Welch, $t = 12.82$, d.f. = 616.68, $P < 0.0001$). Furthermore, the maximum and minimum weights recorded were found among the beetles in the environment (0.048 mg and 5.084 mg, whereas the range of hunted prey was 0.111–2.664 mg).

Analysing the size distributions for each beetle family, the Mordellidae, Coccinellidae, Latritidae, and

Melyridae weighed more than the other families collected (Fig. 3). Confining the analysis to the families both hunted and available (i.e. those with samples adequately large for the statistics), the weight of Bruchidae and Phalacridae did not differ between the two categories (Bruchidae: *t*-test, $t = 1.25$, d.f. = 29, $P = 0.22$; Phalacridae: Aspin–Welch, $t = 1.11$, d.f. = 47.47, $P = 0.26$), whereas Chrysomelidae and Curculionidae collected in the environment were heavier than those that were hunted (Chrysomelidae: Aspin–Welch, $t = -6.19$, d.f. = 240.30, $P < 0.001$; Curculionidae: Aspin–Welch, $t = -6.43$, d.f. = 98.14, $P < 0.001$) (Fig. 3). However, considering the weight of the single species collected in the environment, it appeared that the heaviest individuals of Chrysomelidae and Curculionidae belong to species not hunted by the wasps (or only rarely hunted, as for *Oulema duftschmidi* and *S. lineatus*) (Fig. 3). In general, it appears that the weight limit that decreases considerably the probability of being hunted is in correspondence with the species *Catapion seniculus* (0.63 g): all

the hunted species (with exception of the two cases highlighted above) weighed less than this value (Fig. 3).

The average weight of the actual prey differed among beetle families [analysis of variance (ANOVA): $F = 106.3$, d.f. = 8, $P < 0.001$] and among species in the two more hunted families [only those species with at least six items were included in the analysis (Curculionidae: ANOVA: $F = 14.4$, d.f. = 5, $P < 0.001$; Chrysomelidae: ANOVA: $F = 60.03$, d.f. = 4, $P < 0.001$].

The length/width ratio (shape) of the hunted beetles was lower (1.99 on average) than the available ones (slightly longer, 2.18 on average) (considering only the families collected using both methods) (Aspin–Welch, $t = 9.7$, d.f. = 516, $P < 0.01$).

INDIVIDUAL PREDATOR–PREY RELATIONSHIPS

Wasp head width was linearly and positively correlated with average prey length (Peason correlation test: $r = 0.41$, $N = 31$, $P = 0.02$). PS_i was in the range 0.147–0.509 per female ($N = 13$), so that IS was 0.399 for the population, which revealed specialization ($P < 0.001$).

The variation in resource length use within individuals (WIC) and the variance in resource length use between individuals (BIC) were, respectively, 0.141 and 0.07, so that the total size (body length) niche width of the population (TNW) was 0.211 and the resulting value of $R'sI$ was 0.668, which also revealed specialization ($P < 0.001$).

LOGISTIC REGRESSION MODEL

Frequencies for prey weight, shape, and prey species are shown in Table 1 for the 1356 beetles included in this analysis (prey hunted: $N = 804$; beetles available: $N = 551$).

Out of the morphological variables associated with the beetles, we selected shape and weight because of the strong correlations between weight and both length and width as well as the strong correlation between length and width. Moreover, all the species poorly represented both among prey and in the environment were pooled as 'other species', sometimes dividing by family. The variable 'ecology' of beetles was also omitted in this analysis because most of the collected species had the same type (living on grass/flowers, see above).

The size and shape were categorized according to the whole sample quartiles, aiming to better analyse any potential differences between the two groups. Prey with an intermediate weight (range 1.86–2.22 g) were more frequently hunted compared to the lightest ones (OR ~1.6 after adjustment for length/width ratio), whereas the heaviest had no major risk of

being hunted compared to the light ones. The role of shape as predictor for a prey to be hunted is marked for the second category (approximately 1.9 mm) compared to the first one (the OR adjusted for weight was significant and equal 4), whereas the largest ones were significantly protected against hunting compared to smallest ones (OR = 0.3).

Species differed markedly in their probability of being hunted, also after adjustment for size and shape. *Chaetocnema scheffleri* (Chrysomelidae) had the major risk of being hunted (OR = 38) followed by *Chaetocnema tibialis* (OR = 15), whereas the other Chrysomelidae were not hunted (OR = 0.01) (this also may be a result of their major length/width ratio).

DISCUSSION

Because we recorded several morphological and ecological data from the beetles sampled in the present study, we had a unique chance to look for the relative importance of beetle biological traits on the probability of being hunted by the wasps (i.e. in shaping the prey spectrum of the wasp population). We now discuss our results in relation to the four hypotheses tested.

EXPLORING THE ENVIRONMENT: DO *C. RUBIDA* FEMALES CONFORM TO THE 'ECOLOGY-BIAS HYPOTHESIS'?

The results obtained suggest that females of *C. rubida* hunt basically only on fields near the nest aggregation where grass-associated phytophagous beetles are common, rarely patrolling different microhabitats, such as bushes or trees. The exploitation of fields over the other habitats is not a result of their proximity to the nesting site because trees and shrubs are neighbouring the fields. This is evidently the first step that restricted the prey groups used by the wasps, and explains why some families were rare or even absent from the diet. Corylophidae, for example, are typically associated with fungi on the litter (Bowestead, 1999), where *C. rubida* females do not hunt. The same may be said for Scolytidae, which are wood-burrowing in trunks of trees. The 'ecology-bias hypothesis' (EHp) should not be rejected at a large scale (see below).

The persistence of a wasp in returning many times to the same sub-zone to hunt for an abundant prey until the reduction of its availability was suggested in previous studies as a possible factor accounting for a 'temporary' specialization (Stubblefield *et al.*, 1993; O'Neill, 2001; Polidori *et al.*, 2005), and probably accounts for the recorded values of taxonomic index of individual specialization (PS_i and IS). Individual diet specialization is evident in many different animal species (Bolnick *et al.*, 2003) and has been shown to be

Table 1. Distribution and odds ratio (OR) estimates of prey hunted and available according to selected characteristics considered as predictors of prey selection

	Hunted		Available		Total		OR	95% confidence intervals*
	Frequency ($N = 804$)	%	Frequency ($N = 551$)	%	Frequency ($N = 1356$)	%		
Weight (g)								
1.33–1.85	170	21.1	163	29.5	333	24.5	1†	
1.86–2.00	225	28.0	113	20.5	338	24.9	1.68	1.22–2.32
2.01–2.21	223	27.7	109	19.8	332	24.4	1.69	1.22–2.33
2.22–3.94	186	23.1	167	30.2	353	26.0	1.10	0.80–1.49
Length/width								
1.34–1.90	201	25.0	139	25.2	340	25.0	1†	
1.91–1.99	284	35.4	47	8.5	331	24.4	4.19	2.87–6.11
2.00–2.08	206	25.6	131	23.7	337	24.8	1.09	0.80–1.48
2.09–3.39	112	14.0	235	42.6	347	25.5	0.33	0.24–0.45
Species‡								
Chaetocnema tibialis	224	27.9	10	1.8	234	17.2	14.9	7.61–29.23
Chaetocnema scheffleri	144	17.9	2	0.4	146	10.7	38.1	9.25–157.31
Chrysomelidae – others	47	5.9	208	37.8	255	18.8	0.09	0.06–0.13
Protapion trifolii	188	23.4	57	10.3	245	18.0	5.48	3.75–7.99
Curculionidae – others	66	8.2	37	6.7	103	7.5	2.42	1.48–3.95
Coccinellidae sp.	.	.	155	28.1	155	11.4	–	–
Olibrus affinis	72	9.0	23	4.2	95	7.0	2.48	1.48–4.15
Phalacridae – others	33	4.1	17	3.1	50	3.6	1.14	0.60–2.15
Others	30	3.7	42	7.6	72	7.6	0.33	0.19–0.55

*OR adjusted for biomass (in quartiles) and length/width ratio (in quartiles); for biomass, the OR were adjusted for length/width ratio only and, for length/width ratio, the OR were adjusted for biomass only.
†Reference category.
‡The OR were calculated considering each species compared to all the others (as a reference category) (e.g. the probability of being hunted for *C. tibialis* compared to all other species).

affected by both competition (Svanbäck & Persson, 2004; Svanbäck & Bolnick, 2007) and predation (Eklöv & Svanbäck, 2006). In the case of *C. rubida*, the ability to discriminate the hunting areas on the basis of chemical and physical cues provided by the prey may help wasps to learn the position of those areas (Raveret Richter, 2000). However, if we take this bias into account by dividing the data collected by sub-zones, we can discuss prey preference by referring to the more-exploited sub-zones, which likely decreases the effect of an habitat-linked specialization.

EXPLORING THE HUNTING PATCH: DO *C. RUBIDA* FEMALES FOCUS ON A SUBSET OF AVAILABLE PREY?

When the wasps arrive at the hunting site, they encounter different beetles that may be referred as 'potential' prey. Although we could not assess the rate of encounter in a precise and quantitative way, we could approximately consider that, if in a field the abundance of a beetle species is high, the probability of encounter also should be high because most of the beetles found belong to groups that are generally scarcely mobile (compared to wasps): some groups have fused elytrae, and the others have weak flying abilities; an extreme case of non-escaping behaviour in such coleopterans is that of Curculionidae, which are known to enter thanatosis if attacked (Grandi, 1951).

At a family-level and for many beetle species, a general correspondence was found between the prey and environment frequencies. The importance of environmental availability on the probability of being hunted was shown in the wasps *Philanthus sanbornii* Cresson, 1865 (Stubblefield *et al.*, 1993), *Sphecius speciosus* (Drury, 1773) (Grant, 2006), *Sphex ichneumoneus* (Linnaeus 1758) (Brockmann, 1985), and two *Ammophila* spp. (Rosenheim, 1987; Field, 1992), which were all defined as generalist predators in these studies.

However, on the basis of availability in the more exploited sub-zones (the fields), *C. rubida* should encounter more often chrysomelid species of *Phyllotreta* and Coccinellidae. By contrast, these two groups were completely ignored by the wasps. On the other hand, chrysomelids species of *Chaetocnema* were extremely abundant among prey, but rarely sampled in the environment.

It is thus evident that some biological traits associated with these species, and not abundance, determine the probability of being hunted.

DETERMINING THE SUBSET OF PREY: DO *C. RUBIDA* FEMALES CONFORM TO THE 'BIOMASS-BIAS HYPOTHESIS'?

Size is an important factor in prey choice of digger wasps, and many studies have revealed a positive correlation between wasp size and their prey (Coelho & Ladage, 1999; Polidori *et al.*, 2005; Grant, 2006); this often produces a partitioning in prey use by females of a population (Gwynne & Dodson, 1983; Polidori *et al.*, 2005), and probably, to some extent, this happened in our case, as revealed by the recorded value of the index of size individual specialization ($R'sI$) together with the values of the taxonomic indices.

In *C. rubida*, the influence of size on prey use is clear. At a population level, beetle families such as Mordellidae and Coccinellidae probably are too large for the wasp females, and perhaps are not hunted for this reason. The curculionid *S. lineatus* and the chrysomelid *O. duftschmidi* were rarely hunted probably because their average weight was high and individuals may be hunted only by a few large wasp females. At an individual level, larger wasps hunted for larger prey. The 'biomass-bias hypothesis' (BHp) should be not rejected completely. By contrast, shape of beetles did not appear to have an effect on the frequency of their occurrence among prey. In any case, size could only partially account for the observed prey preference: indeed, if prey really matters regardless of the taxa of the beetles, the size of hunted prey belonging to different taxa would be expected to be very similar, although this was not the case. In addiction, *Chaetocnema* are not likely to be more visible than *Phyllotreta*, with both having an approximate same size and appearance.

Thus, we could exclude that taxonomic bias in prey preference by the wasps depends on the size of the species.

DETERMINING THE SUBSET OF PREY: DO *C. RUBIDA* FEMALES CONFORM TO THE 'SEX-BIAS HYPOTHESIS'?

Sex of the beetles may probably have a low effect on the probability of being hunted. Indeed, females were actually more hunted than males, although the sex ratio of prey did not differ from that found in the environmental sample. The 'sex-bias hypothesis' (SHp) may be rejected. No effect of sex on the prey preference was reported by Grant (2006) on *S. speciosus*, nor was it reported by Stubblefield *et al.* (1993) on *Philanthus sanbornii*.

DETERMINING THE SUB-SECTION OF PREY: DO *C. RUBIDA* FEMALES CONFORM TO THE 'TAXON-BIAS HYPOTHESIS'?

The most important question arising from the present study concerns the over-hunting and the avoidance of some beetle species in the fields compared to their availability. This result differs from that found previously in other wasp species, where either no prey
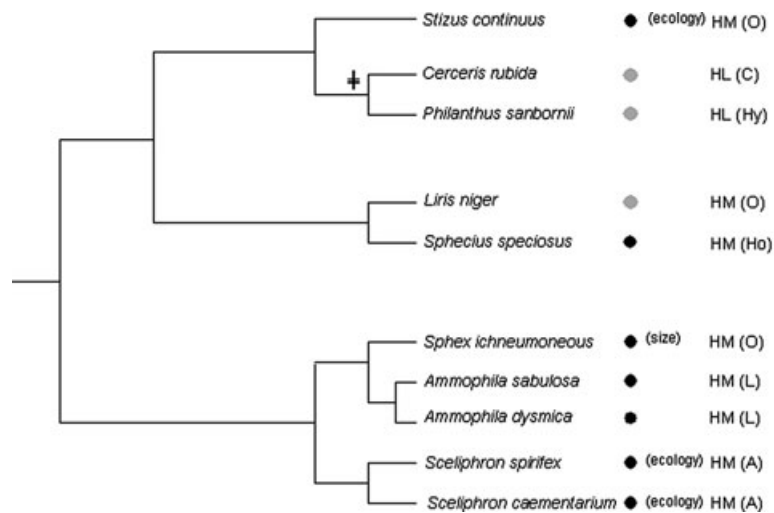
Figure 4. Phylogenetic relationships among species of digger wasps for which prey preference (i.e. comparison between actual and potential prey) and/or prey selection (i.e. laboratory experiments) were studied (phylogeny modified from Melo (1999)). Black circles, species was assessed as taxonomic opportunistic; grey circles, species was assessed as taxon-biased selective. When other kinds of selectivity were assessed in taxonomically opportunistic species, they were specified (factor spelled in brackets). HL, holometabolous; HM, hemimetabolous; O, Orthoptera; Hy, Hymenoptera; C, Coleoptera; Ho, Homoptera; L, Lepidoptera larvae; A, Arachnida. ✦, lineage where monophagy evolved. References: Polidori *et al.* (2009) (*S. continuus*), Stubblefield *et al.* (1993) (*P. sanbornii*), Anton & Gnatzy (1998) (*L. niger*), Grant (2006) (*S. speciosus*), Brockmann (1985) (*S. ichneumoneous*), Field (1992) (*A. sabulosa*), Rosenheim (1987) (*A. dysmica*), Polidori *et al.* (2007b) (*Sceliphron* spp.). Note that *Philanthus sanbornii* presents the symbol of taxon-biased selectivity despite it being assessed as opportunistic by Stubblefield *et al.* (1993), after our re-evaluation of the published data (for additional details, see text).

preference was detected (opportunism) or the size and ecology of prey explained most of the prey preference (Stubblefield *et al.*, 1993; Grant, 2006; Polidori *et al.*, 2007b). The reasons behind the exclusion of abundant beetle species such as *Phyllotreta* as prey remain unknown, and alternative hypotheses have to be experimentally tested. At least one hypothesis, invoking particular behavioural adaptations that give a high escape capability to the beetles, may be probably discarded. Indeed, both *Chaetocnema* and *Phyllotreta* are able to jump rapidly if a danger is detected (Jolivet, 1997). Whatever the factors producing the observed frequency distribution, however, the 'taxon-bias hypothesis' (THp) appears to be most probably true when attempting to explain selective predation by *C. rubida*.

In conclusion, *C. rubida* is not a generalist predator: females frequently hunted, or almost ignored, relative to their availability in the environment, an important number of beetle species, resulting in a low value of intersection between the actual diet and the available taxa.

Wasps would first select, at a large spatial scale, valuable microhabitats where to hunt ('ecology-bias hypothesis'), then, once within a patch, they would select prey based on taxon ('taxon-bias hypothesis'), eventually selecting further those individuals of valuable size ('biomass-bias hypothesis').

WHAT *C. RUBIDA* SELECTIVE PREDATION SUGGESTS ABOUT THE EVOLUTION OF OPPORTUNISM AND SPECIALIZATION IN APOID WASPS?

The results obtained in the present study may promote experimental studies aiming to investigate whether diet preference is shaped by a sensory window, which would exclude some beetle species from the diet. This has been shown in another apparently 'generalist' digger wasp, *Liris niger*: females readily accept prey of several species of crickets, but attack a nonhunted species only after ablation of their antennal flagellomers (Anton & Gnatzy, 1998). By contrast, females of the grasshopper-hunting *S. continuus* and *S. ichneumoneous* accept nonhunted prey presented at nests (Asís, Tormos & Jiménez, 1988). It would be important, at this point, to carry out comparative studies that may explain why some groups evolved taxonomic opportunism (but sometimes they evolved 'ecology-bias' or 'size-bias' selectivity) and other ones evolved taxonomic specialization. From the data available in the literature together with the results obtained in the present study, at least, we could try to find out some links between the kind of prey and this dichotomy. In Figure 4, a simplified phylogeny illustrates the relationship between the species for which data on prey preference (i.e. a comparison between the actual and the potential prey

was performed) and/or on prey choice (i.e. a experimental study was performed) are available. Re-evaluating the results of such studies, we defined the kind of selectivity for each species (ecological, taxonomical, dimensional, and opportunism; Fig. 4). Taxonomic opportunism (i.e. concordance between actual and potential prey frequencies) was found in three species, taxon-biased selectivity in three species, ecology-biased selectivity in three species, and size-biased selectivity in one. Note that *P. sanbornii* was now defined as taxon-biased specialist and no more as a generalist, as in the study of Stubblefield *et al.* (1993). The opportunism of *P. sanbornii* appears to be apparent. This wasp is reported to hunt all the size-valuable bees and wasps around the nests (Stubblefield *et al.*, 1993), although it was noted that a few abundant species, with size and feeding ecology comparable to actual prey, were ignored by the wasps, and at least two species were greatly over-utilized despite being quite rare in the environment. This situation is very similar to what we found on *C. rubida* (i.e. general concordance between prey and environmental frequencies but with few important exceptions), so that we think that *P. sanbornii* would be better defined as a taxon-biased selective predator rather than a generalist one.

As shown in Figure 4, no apparent effect of phylogeny on the kind of selectivity is visible. By contrast, taxonomic selectivity was found more often in species hunting for holometabolous prey (and monophagy evolved much more often in these lineages; Bohart & Menke (1976); O'Neill (2001), whereas all the other species, which are taxonomically opportunistic, hunt for hemimetabolous insects or spiders. Is there some interesting information in this pattern? In apoid wasps, the positive relationship between wasp size and prey size is widespread; such a relationship could be expected to be more linked to taxonomic selection if prey belong to holometabolous groups (e.g. beetles or bees) than if they are hemimetabolous (e.g. grasshoppers). In the first case, prey size did not change with time (so that too large species can never be hunted), whereas, in the second case, prey size increases with time (so that a species could be hunted; e.g. at the nymphal stage but not at adult stage) (Brockmann, 1985). Figure 5 gives a schematic representation of this idea. Consider two species of wasps: one hunting for holometaboulous prey (wasp A) and the other one for hemimetabolous prey (wasp B). A total of two species belonging to the hunted taxa (e.g. family) are present in the hunting site of each wasp. Wasp A can readily hunt for species 4 because its size stays permanently under their maximum load possible to carry across the foraging period, whereas species 2 is excluded from the diet because of its large size, above the loading capacity of wasp. Wasp B,
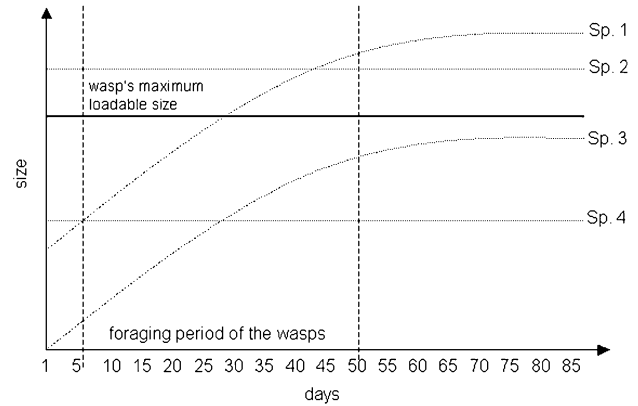

Figure 5. Schematic representation of size limitations on prey preference in case of hemimetabolous (species 1 and 3) and holometabolous (species 2 and 4) prey. Species 1 is hunted by the wasps until it become so large that it is no longer possible to handle and carry to the nest; when this happens, wasps have to shift to another prey (species 3), which has a size that permits them to be hunted. In this case, it may be not advantageous to the wasps to develop a 'taxon-biased' selectivity. By contrast, species 2 is never available to be hunted because of its large size, whereas species 4 is always available to wasps. In this case, it may advantageous to the wasps to develop a 'taxon-biased' selectivity.

by contrast, hunts preferentially for species 1 but, because this becomes too large at a certain moment of the foraging period, it is excluded from the diet; at this point, wasp B has to shift to another prey (species 3), which, either because it has a slower growth or because it appears at the hunting site in these days, has a size that permits it to be hunted. Note that the loading capacity sometimes may be surpassed: *S. ichneumoneous* and *S. continuus* females, for example, may hunt for very large grasshoppers and then descend to the nests by planning (Coelho & Ladage, 1999; C. Polidori *et al.*, 2009); however, still in these cases, a further increase in prey size would exclude the prey species from the diet.

Which consequences come from these different situations? If wasp of species B has to shift prey during the nesting season, it may not be advantageous to have any 'taxon-biased' selection: if the target taxon becomes too large, wasps have to change prey to successfully feed the offspring. On the other hand, wasps in the species A may be advantaged by a 'taxon-biased' specialization because, in no cases, a particular, large species could be hunted; this, in turn, may favour recognition systems that increase the efficiency of prey finding. Two possible exceptions to this picture concern *Sceliphron* wasps and *L. niger*. In the first case, the size of spider prey is always smaller than their own size (Polidori *et al.*, 2007b), so that

both adults and young may be hunted. However, this does not result in a taxon-biased selectivity, wasps hunting all the abundant spider species that build two-dimensional webs in the foraging area. This case might be explained by a particular and fine capacity for identifying webs rather than spiders. In the second case, taxonomic selectivity may be possible because *L. niger* does not carry its large cricket prey in flight, but grasps them on the ground (Anton & Gnatzy, 1998), so that size constraints may be not so important. Further studies are necessary to test this hypothesis.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of beetle families found among the prey of *C. rubida* (hunted) and in the environment (available). Total numbers, relative frequencies and statistics for comparison between hunted and available families frequencies (only when total number in the sample > 10) are shown.

Appendix S2. List of beetle species in the 5 families both hunted and found in the environment collected among the prey of *C. rubida* (hunted) and in the environment (available). Total numbers, relative frequencies and statistics for comparison between hunted and available species frequencies (only when total number in the sample > 10) are shown. The morphospecies (undetermined species but different from the determined ones) are named as genus or family + sp.

Appendix S3. List of beetle species found in the 5 sub-zones of sample in the environment for which the statistical comparison between habitats was possible (total number in the sample > 10). The morphospecies (undetermined species but different from the determined ones) are named as genus or family + sp. * indicates the hunted species.

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