



A synthesis of feeding habits and reproduction rhythm in Italian seed-feeding ground beetles (Coleoptera: Carabidae)

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Abstract. Many species of carabid beetles are important pre- and post-dispersal seed feeders of herbaceous plants. Here we summarise data from dissections, field observations, rearing and “cafeteria” experiments on 55 granivorous and 188 omnivorous species that occur in Italy. We tested the hypothesis that seed feeding carabids are restricted to taxa with pronounced morphological adaptations for manipulating and crushing seeds in both the larval and adult stages. The feeding guilds of carabids were rearranged into the following groups: (i) strict predators with long mandibles and predaceous larvae, often depending also on non-prey food; (ii) omnivorous species with stout mandibles and larvae of a seed-eating morphotype; (iii) granivorous species, feeding only on seeds with larvae sometimes of the scarabeoid c-form type. The seed feeding carabids in the Italian fauna belong to the tribe Zabritini (*Amara* and *Zabrus* genera) and to all the Harpalinae (sub)tribes, from Anisodactylini to Ditomina. The time of reproduction seems to be associated with habitat preference; wetland or dry open land, rather than true granivorous versus omnivorous habits, but in stenophagous seed feeders, a phenological coincidence with particular plants is sometimes recorded.

INTRODUCTION

Carabid beetles are polyphagous and their feeding behaviour ranges from complete zoophagy to complete phytophagy, with most granivorous species falling somewhere in the middle of this continuum (Zetto Brandmayr, 1976, 1978, 1990; Hengeveld, 1980a, b, c, 1981; Brandmayr et al., 1990; Laroche, 1990; Honek et al., 2003, 2006; Martinkova et al., 2006; Lundgren, 2009). Quantitative and qualitative studies on several carabid species involved in the biological control of several cropland pests (Luff, 1987; Lövei & Sunderland, 1996; Kromp, 1999; Holland & Luff, 2000) have shown their role as predators (Luff, 1987; Lövei & Sunderland, 1996; Kromp, 1999; Holland & Luff, 2000). In the temperate zone, these are the most important seed predators (Honek et al., 2003, 2005) in intensively managed agricultural landscapes (Saska et al., 2014). Granivorous carabids are important pre- and post-dispersal weed seed predators, and in terms of agricultural ecosystem services are biological control agents of weeds (Mauchline et al., 2005; Jacob et al., 2006; Gaines & Gratton, 2010; Kulkarni et al., 2015).

Many authors have studied the phytophagous habits of ground beetles. Forbes (1883) first recognized the granivorous preferences of many species and described three general feeding guilds based on morphological differences in

the mouthparts. Zhavoronkova (1969) divided adult carabids into three feeding guilds: (1) strict predators (obligate zoophages); (2) predominant zoophages (more predaceous than phytophagous); (3) predominant phytophages (predaceous omnivores that consume more plant material than animal tissue).

Thiele (1977) classified carabids into three categories according to their manner of food intake: oligophagous predators, polyphagous predators and phytophages. Granivory was subsequently confirmed by numerous authors (Burmeister, 1939; Lindroth, 1949; Davies, 1953; Skuhavy, 1959; Dawson, 1965; Burakowsky, 1967; Johnson & Cameron, 1969; Manley, 1971; Laroche, 1990; Hürka, 1992, 1998; Jørgensen & Toft, 1997a, b; for a more complete list see Forsythe, 1982; Acorn & Ball, 1991; Honek et al., 2003). Although adult feeding habits and food requirements are reasonably well known, little is known about granivory in larvae. Some morphofunctional studies have shown a relationship between morphology and feeding behaviour in the larval stage. Sharova (1960) defines some morpho-ecological types in the European temperate zone and places most Harpaline and Zabrine larvae with a phytophagous diet into the morpho-ecological types V, VI, VII and VIII. Zetto Brandmayr et al. (1998) reduced these types into two simpler categories: a – spermophaga-

gous (seed predators); b – c-shaped harpalines, excluding the Ditomines. These larvae all possess shorter and wider mandibles, enlarged heads and occasionally multiple teeth on the terebra. In the c-shaped harpalines, the entire body becomes physogastric, i.e., swollen as in scarabeoid larvae, the cerci are rudimentary and, in some cases, their food supply depends on the capacity of adults to accumulate seeds in subterranean nests (*Ditomus*, *Dixus*; see Brandmayr & Zetto Brandmayr, 1987). In the laboratory, such larvae prove to be omnivorous, spermophagous or carnivorous (Brandmayr Zetto & Brandmayr, 1975; Zetto Brandmayr, 1976; Luff, 1980; Brandi & Zetto Brandmayr, 1991; Jørgensen & Toft, 1997a, b; Saska & Jarošík, 2001; Saska & Honek, 2003). To date, true granivory in larvae is restricted to the “ophonoid” line of *Harpalus*, which have a characteristic larval morphology (Brandmayr et al., 1980). This line includes all species of *Ophonus* s. l. that are associated with Umbelliferae and the Mediterranean-Afroindian subgenus *Cryptophonus*. A comparative laboratory study of the larval stages of several Harpaline species has confirmed the existence of two categories of phytophagous carabids. The former is able to develop on a mixed diet (seeds, insects or meat) such as *Harpalus* s. str. and its subgenus *Harpalophonus*. The latter, including all the species of *Ophonus* s. str. and most of the *Metophonus*, feed exclusively on seeds (Zetto-Brandmayr, 1990). Moreover, the larvae of *Amara eurynota*, *A. similata* and *A. ovata* often require seeds of a particular species of plant for successful development (Saska & Jarošík, 2001; Saska, 2004), or they may require animal food (Saska, 2005). In the field, larvae of seed predators are occasionally observed feeding on seeds scattered on the soil surface or caching seeds in burrows (Kirk, 1972; Brandmayr Zetto & Brandmayr, 1975; Alcock, 1976; Luff, 1980).

This review aims to outline the extent of the knowledge on the seed eating ground beetles of Italy. Data for other European countries (except the Czech Republic) are scarce. All the experimental data on carabid species belonging to the Italian fauna were compared and updated using: (1) graduate theses produced during the past 25 years at the University of Calabria; (2) data on Italian species kept in the Zoocoenoses laboratory (DiBEST, University of Calabria) and used in rearing experiments or in “cafeteria” tests accumulated over about 35 years and (3) gut dissections performed on rare species found during field trips. In this study we redefine the concept of phytophagous by using the terms carnivorous, omnivorous and granivorous. The term seed feeder refers to range of feeding adaptations from omnivory to true granivory. Moreover, we estimate the number of species of seed feeders and higher taxa present in Italy, and their relationship between plant seasonality and their reproduction rhythm. The taxonomic arrangement of all the data presented follows the updated version of the family Carabidae in the Fauna Europaea by Vigna Taglianti (<http://www.fauna-eu.org>).

FOOD PREFERENCE

Several aspects of seed consumption are poorly understood, including the preferences of particular species of carabid for specific species of seed. Many species of granivorous carabids climb plant stems and feed on the ripening seeds of grasses, umbelliferous, composite and cruciferous plants (Thiele, 1977; Hürka, 1996; Martinkova et al., 2006). However, many less specialized carabids forage for seed mainly on the ground (“post-dispersal” seed predation, Honek et al., 2003; Mauchline et al., 2005). Some species of *Amara* prefer crucifer seeds and some *Harpalus* prefer seeds of composites (Lindroth, 1949; Thiele, 1977). Honek et al. (2007) studied the seed preferences of the adults of 30 species of carabids using the seeds of 28 common species of agricultural weeds in controlled laboratory experiments. The factors determining the preferences of carabids for particular species of seed are similar to that determining prey specificity in other predator groups. Body size of both predator and seed (“prey”) are also important, probably because of the problems associated with handling seed of different sizes (Honek et al., 2003). It is also well known that primarily carnivorous insects utilize plant material as a food source in some phases of their development (Norris & Kogan, 2000). Many species (Zabrini and Harpalini) are mainly granivorous as adults (Thiele, 1977; Zetto Brandmayr, 1990) and carnivorous species often supplement their diet of insects with seeds (Lund & Turpin, 1977; Hurst & Doberski, 2003; Fawki & Toft, 2005).

The definition of phytophagy in carabids is not unequivocal. Lundgren (2009) considers feeding on “non-prey food” or feeding vegetable material in the gut as seed predation. However, “true” seed feeders are easily recognizable by their unmistakable morphological characters: large or at least a broad head, short and stout mandibles (Forbes, 1883; Zhavoronkova, 1969; Forsythe, 1982; Acorn & Ball, 1991), shorter terebral length, wider incisor tip and larger molar width (Evans, 1965; Forsythe, 1982; Evans & Forsythe, 1985; Frank, 2007).

Most carabids that feed on seeds belong to the tribes Harpalini (e.g. *Harpalus*, *Ophonus*, *Pseudophonus*) and Zabrini (*Amara*, *Zabrus*) (Zetto Brandmayr, 1990), with a few belonging to the Trechini, Platynini and Pterostichini (Goldschmidt & Toft, 1997; Honek et al., 2003) (Appendix 1). Exceptions include the Scaritine, *Clivina fossor*, a single Trechine species, *Trechus quadristriatus*, scattered taxa in the Pterostichinae, such as Molopina (*Abax parallelepipedus*), Poecilina (*Poecilus cupreus*), Pterostichina (*Pterostichus melanarius*) and some Platyninae (*Calathus fuscipes* and *Agonum mülleri*) (Johnson & Cameron, 1969; Laroche, 1990; Goldschmidt & Toft, 1997; Honek & Martinkova, 2001; Toft & Bilde, 2002; Honek et al., 2003, 2007, 2009; Mauchline et al., 2005; Saska et al., 2008; Lundgren et al., 2009). The latter two species are often “reluctant” to accept seeds in no choice experiments (Honek et al., 2003) or accept the soft seeds of *Capsella bursa pastoris* in large quantities (*Calathus ambiguus*, *T. quadristriatus*). In *Abax parallelepipedus*, phytophagous behaviour is recorded,



Fig. 1. A female of *Zabrus costae* Heyden, 1891, feeding on *Poa bulbosa*. Matese Mts, Molise, Southern Italy, June 14, 2007.



Fig. 2. A male of *Ditomus calydonius* (P. Rossi, 1790) feeding around midnight on *Daucus carota* umbels. The forelegs are holding a carrot fruit. Abandoned cropland in Calabria, Rende, June 1992.

e.g. attacks on germinating seeds included under the well documented “non-prey food consumption” investigated by Lundgren (2009). All other cases studied belong to the phylogenetically easily identified Zabrine and Harpalinae (tribe Harpalini of other authors). Within these two taxa, we have distinguished four different feeding strategies (for a complete list of references view Appendix 1).

(1) **Omnivorous (carnivorous + partly granivorous)** species: most *Harpalus* s.l., *Pseudoophonus*, *Anisodactylus*, *Scybalicus*, *Trichotichnus*, *Parophonus*, *Bradycellus*, *Acupalpus*?, *Amara* (most species), *Zabrus* (Fig. 1), *Acinopus* and *Daptus*. The species in this feeding group are in the laboratory either predatory or zoophagous and eat a large spectrum of different kinds of seeds. A number of at least partly granivorous species of carabid specialize on weeds and are common in intensively managed agricultural landscapes (Saska et al., 2014; Kulkarni et al., 2015).

(2) **Plant specialist omnivorous**, i.e. partially carnivorous, but highly specialized in feeding on the seeds of just one plant genus; such as *Tetraplatypus ganglbaueri*, which feeds only on *Satureja* seeds or *T. ruficollis*, which only feeds on *Calluna* seeds. *Tetraplatypus ganglbaueri* occurs only in calcareous grasslands on Dinaric Karst, from Trieste to southern Dalmatia, where *Satureja* bushes form dense mats, similar to those of *Calluna* or *Erica* in heathland. It feeds on seeds both on the ground and on plants, by opening the flower calyx laterally (Zetto Brandmayr & Brandmayr, 1978a). *Tetraplatypus ruficollis* possibly feeds in the same way on *Calluna* heaths.

(3) **Imaginal omnivorous**. Carabids that are omnivorous as adults but the larvae are strictly granivorous: *Amara aulica* and perhaps some other species/subgenera of *Amara*.

(4) **True granivorous species**: all *Ophonus* subgenera, *Cryptophonus*, all Ditomina so far tested, such as *Ditomus*, *Dixus* and *Carterus*. This category is easy to determine in the laboratory because meat is always refused. The only exception is *Ophonus azureus*, which sometimes accepts small pieces of beef. In this group, hyper specializations are known, such as the storing of seed in paedotrophic nests (brood care) by *Ditomus calydonius* (Fig. 2) and *Dixus clypeatus*. Many taxa restrict their choice of food to one or few

plant genera. *Carterus* Dejean & Boisduval specialises on the seed of umbellifers, *Ditomus* Bonelli (*Sabienus* Gozis,) on those of *Daucus carota* or *D. gingidium* (Brandmayr, 1974; Brandmayr & Zetto Brandmayr, 1974, 1987; Laroche, 1990; Brandmayr et al., 1994; Zetto Brandmayr et al., 1994) and *Dixus clypeatus* Rossi (*Ditomus* auctt.) on plantain seeds (Schremmer, 1960). In this the last group of species, a “main nursing plant” is often easily identifiable, as recorded for *O. ardosiacus* by Zetto Brandmayr (1983), or for *Ditomus* and *Dixus*.

SEED FEEDING CARABIDS IN ITALY

Vigna Taglianti (2005) records 1313 species of carabids in the Italian fauna and among these 243 (18.50%) are seed feeders. This includes all the Zabrine and Harpaline taxa and the tentative inclusion of Amblystomina (seven species belonging to the genus *Amblystomus*), for which there is currently no data on food choice. Only 55 (4.2%) of these can be considered to be true granivores and the inclusion of *Graniger* and *Oedesis* is tentative due to the current lack of data on their food preferences (Fig. 3).

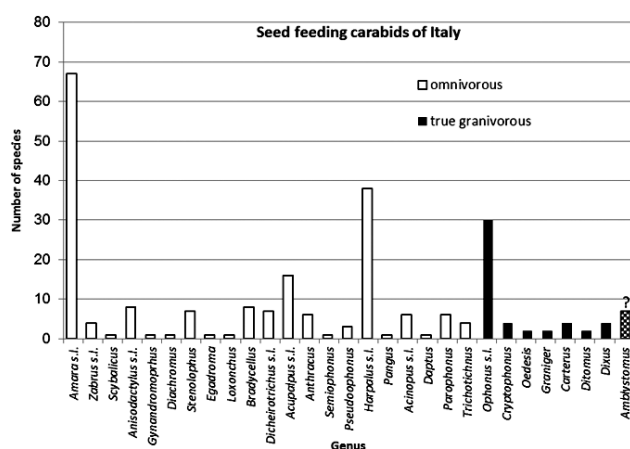


Fig. 3. The genera to which the 243 seed feeding species of carabids recorded in Italy belong. Black columns are the strictly granivorous taxa, the feeding habits of the Amblystomines are still unknown.

PLANT SEASONALITY AND REPRODUCTION RHYTHM

Even though the importance of ground beetles as seed feeders is recognized (Luff, 1987; Kromp, 1999; Tooley & Brust, 2002; Mauchline et al., 2005), little is known about the omnivorous/granivorous taxa in other European countries, such as Spain, Greece and Southern Russia. In Central and Western Europe, ground beetles are the most important invertebrates that feed on the seeds of herbaceous plants (Honek et al., 2003; Martinkova et al., 2006). The granivorous species typical of arable land belong mainly to the tribes Harpalini (e.g., the genera *Anisodactylus*, *Har-*

palus, *Parophonus*, *Pseudophonus* and *Stenolophus*) and Zabrinini (*Amara*, *Zabrus*) (Lindroth, 1949; Thiele, 1977; Hürka, 1996). In northern temperate agricultural areas some studies report seasonal fluctuations in the intensity of predation of weed seeds by carabid beetles (Tooley & Brust, 2002; Honek et al., 2003; Saska et al., 2010). This variation, however, cannot always be attributed to changes in the activity/density of these predators (Honek et al., 2003; Mauchline et al., 2005; Saska et al., 2010). This incongruence may be attributed to intrinsic seasonal variation in consumption (Honek et al., 2006), but temperature variation may also contribute to the seasonal variation in

Table 1. Number of species, habitat, diet, main nursing plant, reproduction rhythm and possible phenological coincidence of all the genera (subgenera) of Italian seed feeding ground beetles. OL – open land; SUMMER – reproduction in spring or summer, with summer larvae; WINTER – reproduction in autumn or late autumn with winter larvae; BIENNIAL – species that have a two year life cycle. * – *Hesperophonus azureus* in the laboratory will also eat small pieces of meat.

Genus (subgenus)	Sp N	Habitat	Diet	Main nursing plant	Reproduction rhythm	Phenological coincidence
<i>Amara</i> s. str.	9	OL, open forest	OMN	No, except for the association between <i>A. montivaga</i> and <i>T. officinalis</i>	SUMMER	
<i>Zezea</i>	2	OL, river gravels	OMN	No	SUMMER	
<i>Bradytus</i>	2	OL	OMN	No	WINTER	
<i>Percosia</i>	2	OL	OMN	No	WINTER	
<i>Curtonotus</i>	2	OL	OMN	No	WINTER	
<i>Celia</i>	6	OL, abandoned fields, heaths	OMN	<i>Artemisia?</i> <i>Polygonum aviculare?</i>	WINTER: 4 SUMMER: 2	
<i>Leiromorpha</i>	1	Alpine OL	OMN	No	WINTER	
<i>Zabrus</i>	2	OL, pasture	OMN	No	WINTER	
<i>Anisodactylus</i>	3	Wetlands	OMN	No	SUMMER	
<i>Scybalicus</i>	1	OL, clay soils	OMN	No	WINTER	
<i>Bradycellus</i>	2	OL, meadows	OMN	No	WINTER	
<i>Tetraplatypus</i>	2	OL, heaths	OMN	<i>Satureja</i> , <i>Calluna</i>	WINTER	YES
<i>Acupalpus</i>	2	Wetlands	OMN	No	SUMMER	
<i>Pseudophonus</i>	2	OL, crops, riparian forests	OMN	No	WINTER	
<i>Harpalus</i> s. str.	14	OL, crops, pastures	OMN	No	SUMMER	
<i>Semiophonus</i>	1	OL, sandy soils	OMN	No	SUMMER	
<i>Harpalophonus</i>	1	OL, clay soils	OMN	No	SUMMER	
<i>Acinopus</i> s. str.	1	OL, pastures	OMN	No	WINTER	
<i>Osimus</i>	1	OL, pastures	OMN?	<i>Medicago minima?</i> Other plant species?	WINTER	YES
<i>Daptus</i>	1	Salt marshes	OMN	No	SUMMER	
<i>Trichotichnus</i>	1	Forests	OMN	No	BIENNIAL	
<i>Parophonus</i>	2	OL, croplands	OMN	No	SUMMER	
<i>Ophonus</i> s. str.	4	OL, aband. fields	GRAN	<i>Daucus carota</i>	WINTER	YES
<i>Hesperophonus</i>	1	OL, pastures, cropland	GRAN*	<i>Daucus</i> , other	WINTER, som. SUMMER	YES
<i>Metophonus</i>	5	OL, pastures	GRAN	<i>Daucus</i>	WINTER	YES
<i>Incisophonus</i>	1	OL, pastures	GRAN	<i>Foeniculum</i>	WINTER	YES
<i>Cryptophonus</i>	1	OL, cropland	GRAN	<i>Daucus</i> , <i>Foeniculum</i>	WINTER	YES
<i>Ditomus</i> (<i>Sabienu</i> s)	2	OL, garigues	GRAN	<i>D. gingidium</i> , <i>D. carota</i>	SUMMER	YES, brood care in summer
<i>Dixus</i>	2	OL, garigues	GRAN	<i>Plantago</i> spp.	SUMMER	YES, brood care in summer
<i>Tschitscherinellus</i>	1	OL, aband. fields	GRAN	<i>D. gingidium</i> , <i>D. carota</i>	SUMMER	YES, presumably brood care in summer
<i>Carterus</i>	2	OL, aband. fields and umbel plant seed crops	GRAN	<i>Daucus</i> spp., anise and celery seed crops	SUMMER	YES, presumably brood care in summer

the amount of seed predation by carabid beetles. To obtain a better insight into the factors influencing the reproduction rhythm of granivorous carabids in Italy, a table (Table 1) was constructed, which contains data on habitat and, if available, “main nursing plant”. With reference to the omnivorous genera/subgenera, reproduction may occur in spring (summer larvae) or autumn (winter larvae); *Amara montivaga* is defined as a “dandelion specialist” (Honek et al., 2005) because this species aggregates in stands dominated by *Taraxacum officinale*. *Zabrus* species are autumn breeders, feeding on a wide range of graminaceous plants. In the omnivorous Anisodactylines, the breeding season depends more on soil moisture, with xerophilic taxa (*Scybalicus*) reproducing in autumn and the more hygrophilic *Anisodactylus* in spring/late spring. In the Stenolophini, we know of a xerophilic genus with winter larvae (*Bradycellus*) and a hygrophilic taxon (*Acupalpus*) with summer larvae. In the xerophilous *Tetraplatypus ganglbaueri* and *T. ruficollis*, carnivory is associated with strictly specialized seed feeding. They are associated with autumn disseminating plants, such as *Satureja* and *Calluna* (Zetto Brandmayr & Brandmayr, 1978a), which seems to account for their phenological coincidence. In the taxa around *Harpalus*, the larvae of some lineages (*Harpalus* s. str., *Harpalophonus*, *Semiophonus*) occur in summer and others in winter (*Pseudoophonus*), depending mainly on climate or phylogenetic constraints, as reported by Larsson (1939), Paarmann (1979) and Hürka (1986) for *Carabus*, with no evident association with a particular nursing plant.

In granivorous taxa, a phenological coincidence with autumn ripening umbelliferous plants is widespread in the genus *Ophonus* (Zetto Brandmayr, 1983), but in some Ditomines (*Ditonus*, *Dixus*, *Machozetus*?) the evolution of brood care in paedotrophic nests enabled a shift to summer breeding (Sharova & Makarov, 1983; Brandmayr & Zetto Brandmayr, 1987). Thus, different granivorous taxa have different adaptive strategies associated with the same nursing plant. In contrast, the free-living winter larvae of *Ophonus* are “post-dispersal seed predators”, whereas *Ditonus* and probably *Carterus* and *Dixus* care for their summer larvae by feeding them with *Daucus carota* or *Plantago* seeds. The associations between plant seasonality and reproduction rhythm of granivorous carabids are in need of further research.

DISCUSSION

The findings of this study indicate that it would be appropriate to rearrange the three feeding guilds of Forbes (1883) and Zhavoronkova (1969) in the following way:

(1) carnivorous, species with long mandibles and predaceous larvae, that are sometimes also dependent on non-prey food. There are a wide variety of morphotypes of larvae in this category of species (Zetto Brandmayr et al., 1998): soil pore walkers, surface runners, surface walkers, sand diggers, parasitoids, etc. Many taxa show a more or less pronounced prey specialization (Thiele, 1977), which is not discussed here;

(2) omnivorous species with stout mandibles, capable of crushing hard seeds and with larvae that are of a seed-eating morphotype (“spermophagous”), with wide mandibles and terebra often with supernumerary teeth. All Zabrinines and most Harpalines belong to this category, including the subtribes Anisodactylines and Selenophorines;

(3) granivorous species, found only in some of the Harpalines (*Ophonus*, Ditomina), all the larvae of which have strongly enlarged heads, short mandibles and some genera have a characteristic c-shaped scarabeoid larva. This last characteristic may be associated with the parent providing the larva with seeds.

The new categorization means that sensu stricto only the Zabrinini and Harpalinae are seed feeders and that the few cases of seed feeding in other taxa are due to non-prey food intake (Lundgren, 2009).

Considering all the carabids characterized as seed feeders, we identified four levels of granivory: omnivorous (carnivorous + partly granivorous); omnivorous, but highly specialized in feeding on the seeds of just one plant genus; imaginal omnivorous and true granivorous species.

Moreover, there is a large body of evidence that seed feeding also occurs in the tropics, where many phylogenetically ancient harpaline stocks (*Notiobia*, *Trichotichmus*, *Platymetopus*) are known to be both carnivorous and small seed predators of several tree fruits: *Ficus*, *Bellucia*, *Loreya*, *Miconia* (Paarmann et al., 2001, 2002, 2003, 2006).

Within the omnivorous taxa, there are some interesting variations. Despite their predatory habits, both on seeds and animal food, some species may specialize on a restricted group (genus) of plants, which may influence their choice of habitat (*Tetraplatypus ganglbaueri*, *T. ruficollis*). In some species, such as *Amara montivaga*, an evident preference for species-specific seeds is recorded, (Honek et al., 2005) which is not congruent with their choice of habitat. Finally, some species may be omnivorous in the adult stage but more dependent on seeds during the larval stages (Saska, 2005). According to our data, the provision of fresh meat in cafeteria or no-choice experiments should be used as a preliminary test to distinguish omnivorous from granivorous taxa.

The number of species that can be classified as seed feeders in the Italian fauna is 243 out of a total of 1313 (18.5%), 55 of which (4.2%) are true granivores. On the Iberian Peninsula, a total of 1255 carabid species are recorded (Serrano, 2003, 2013), of which 276 (22%) are seed feeders and 57 (4.5%) are true granivores. In continental countries, e.g. in Central Europe (Koch, 1989), there are 179 (23.2%) seed feeders, and 21 (2.7%) true granivores out of a total of 770 species. In Russia and adjacent countries (Krizhanowskij et al., 1995), 630 taxa of seed feeders occur (20.5%), of which 79 (2.6%) are true granivores out of a total of 3075 species. In Fennoscandia (Lindroth, 1945, 1985–1986) there are 73 (18.1%) seed feeders and 7 (1.7%) true granivores out of a total of 403 species. Summing up, in Western Palearctic countries the percentage of seed feeders varies from 18 to 23%, and constitutes an important component of the faunas. The percentage of true

granivores ranges from 1.7 to 4.4%, and they occur mainly in Mediterranean countries, such as Spain and Italy.

When the granivorous carabids breed is known only for a small fraction of the European fauna and very little is known about those in the Mediterranean area. For omnivorous carabids, when they breed depends mainly on climate and habitat factors (e.g. wet versus dry soil), and “phenological coincidence” is frequently recorded between breeding in granivorous species and seed production of a “main nursing plant”. The reproductive rhythms of the Ditomines are exceptional, and currently summer reproduction in paedotrophic nests is only suggested for several genera living within and outside Europe.

In the last two decades seed-feeding carabids have been re-evaluated in terms of ecosystem services in the agricultural environment, as potential auxiliary agents for weed control in sustainable cropland management (Honek et al., 2003, 2005; Westerman et al., 2003; Mauchline et al., 2005; Jacob et al., 2006; Gaines & Gratton, 2010; Kulkarni et al., 2015). Nevertheless, the precise species traits and habitat associations of this feeding guild are poorly known, especially in southern European countries. Further research on this topic should also take into account changing scenarios driven by global warming, particularly as there have been recent reports of mass occurrences of Ditomines (*Carterus*) in carrot, anise and celery seed crops (Koçak et al., 2007; Fabbri & Contarini, 2009). This clearly shows us that the ecology of seed-feeding carabids in Mediterranean countries is still poorly investigated and that some species that are considered harmless today could become the “pests” of tomorrow.

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Appendix 1. Summary of the food preferences of larvae and adults of Italian seed feeding ground beetles, with an indication of the source of the data. lpe – laboratory preference essay; fo – field observation; d – dissection.

Tribe	Genus/ subgenus	Species	Diet larvae/ references	Diet adults/ references	Diet adults/ unpubl. data	References
Scaritinae, Clivinini, Clivinina	<i>Clivina</i>	<i>C. fossor</i>		<i>Z. mays</i>		Lundgren, 2009
Trechinae, -ni, Trechina	<i>Trechus</i> , subg. <i>Trechus</i>	<i>T. quadristriatus</i>		<i>C. bursa-pastoris</i>		Honek et al., 2003; Honek & Martinkova, 2001; Lundgren et al., 2009
Pterostichinae, -ni, Poecilina	<i>Poecilus</i> , subg. <i>Poecilus</i>	<i>P. cupreus</i>		<i>Taraxacum</i> , <i>P. annua</i> , <i>C. arvense</i> , <i>C. bursa-pastoris</i>		Goldschmidt & Toft, 1997; Honek et al., 2003, 2009
Pterostichinae, -ni, Molopina	<i>Abax</i> , subg. <i>Abax</i>	<i>A. parallelepipedus</i>		Germinating seeds		Larochelle, 1990
Pterostichinae, -ni, Pterostichina	<i>Pterostichus</i> , subg. <i>Morphnosoma</i>	<i>M. melanarius</i>		Grass seeds		Johnson & Cameron, 1969; Larochelle, 1990; Honek et al., 2003
Pterostichinae, Zabrinii	<i>Amara</i> , subg. <i>Zezea</i>					Toft & Bilde, 2002; Mauchline et al., 2005; Honek et al., 2007
		<i>Z. plebeja</i>		<i>Poa</i> , <i>Festuca</i> , <i>Alopecurus geniculatus</i> , <i>Deschampsia caespitosa</i> , cereals		Lindroth, 1945; Saska et al., 2008
	subg. <i>Leiromorpha</i>	<i>L. uhligi</i>			vegetable remains (d)	
	subg. <i>Curtonotus</i>	<i>C. aulica</i>	<i>Artemisia vulgaris</i> , <i>Tripleurospermum inodorum</i> , <i>Urtica dioica</i> , <i>Cirsium arvense</i>	<i>T. molitor</i> , <i>C. arvense</i> , <i>C. heterophyllum</i> , <i>C. oleraceum</i> , <i>C. palustre</i> , <i>Carduus crispus</i> , <i>C. nutans</i> , <i>Taraxacum</i> , <i>Solidago virgaurea</i> , <i>Centaurea jacea</i> , <i>C. nigra</i> , <i>Achillea millefolium</i> , <i>Arctium</i> , <i>Leontodon</i> , <i>Tussilago</i> , <i>Inula</i> , <i>Fagopyrum</i> , <i>Capsella</i> , <i>Alopecurus pratensis</i>	vegetable remains (d) refuses <i>Daucus</i> (lpe)	Lindroth, 1945 Saska, 2005 Lundgren, 2009
		<i>C. convexiuscula</i>	<i>A. vulgaris</i> , <i>T. inodorum</i>	<i>T. molitor</i> , <i>U. dioica</i> , <i>C. arvense</i> , <i>Salicornia</i> , ripening seeds of <i>Hordeum</i> and <i>Fragaria</i> , a seed mixture		Lindroth, 1945; Saska, 2005; Honek et al., 2005; Lundgren, 2009
	subg. <i>Bradytus</i>	<i>B. fulva</i>		Grass seeds, potato stems <i>Persicaria maculosa</i>		Lindroth, 1945 Kolesnikov & Malueva, 2015
		<i>B. apricaria</i>		Prefers <i>Hyperodes</i> larvae to seeds		Johnson & Cameron, 1969 Lundgren, 2009
	subg. <i>Amara</i>	<i>A. communis</i>		Principally granivorous, <i>Z. mays</i>	vegetable remains (d)	Burakowski, 1967; Brandmayr, 1972; Larochelle, 1990; Hürka & Jarošik, 2001
		<i>A. aenea</i>	<i>Triticum</i> , <i>Zea mays</i> , <i>Glycine max</i> , <i>C. arvense</i> , <i>Poa annua</i> , mixed diet (seeds and insects)	<i>C. bursa-pastoris</i> , <i>S. media</i> , <i>Plantago major</i> , <i>Tussilago farfara</i> , <i>U. dioica</i> , <i>Potentilla argentea</i>		Saska & Jarošik, 2001; Hürka & Jarošik, 2003; Honek et al., 2003, 2005; Klimes & Saska, 2010; Lundgren, 2009; Saska et al., 2010
		<i>A. anthobia</i>		Seed mixture		Honek et al., 2005
		<i>A. eurynota</i>	<i>A. vulgaris</i> , <i>T. inodorum</i> , <i>U. dioica</i>	Principally granivorous, stamen of <i>Scabiosa</i> , <i>Anthriscus silvestris</i> , <i>C. bursa-pastoris</i> , a seed mixture		Lindroth, 1945; Brandmayr, 1972; Saska, 2004; Honek et al., 2005; Zavoronkova, 1969
		<i>A. similata</i>	<i>Capsella bursa-pastoris</i> , <i>T. inodorum</i> , <i>Papaver rhoeas</i> , <i>Taraxacum</i> , <i>Trifolium repens</i> , <i>P. annua</i> , <i>Brassica napus</i> , <i>Cerastium triviale</i> , <i>Chenopodium album</i> , <i>C. arvense</i> , a seed mixture	<i>S. media</i> , flowers of <i>Barbarea vulgaris</i> , fruits of <i>Deschampsia flexuosa</i> , <i>Taraxacum</i> , <i>Trifolium repens</i> , <i>P. annua</i> , <i>Brassica napus</i> , <i>Cerastium triviale</i> , <i>Chenopodium album</i> , <i>Triticum</i> , <i>Nasturtium</i> , <i>Reseda luteola</i> , <i>Cynosurus cristatus</i> , <i>C. arvense</i>		Burmeister, 1939 Lindroth, 1945 Larochelle, 1990 Jorgensen & Toft, 1997a Saska & Jarošik, 2001 Honek et al., 2003, 2005 Saska, 2008 Klimes & Saska, 2010
		<i>A. familiaris</i>	<i>Stellaria media</i>	<i>C. bursa-pastoris</i> , <i>S. media</i> , <i>C. arvense</i> , <i>C. tomentosum</i> , <i>Z. mays</i> , <i>P. annua</i> , <i>P. pratensis</i> , seed mixture		Lindroth, 1945; Saska & Jarošik, 2001; Honek et al., 2003, 2005; Saska et al., 2008; Lundgren, 2009; Klimes & Saska, 2010
		<i>A. littorea</i>		<i>C. arvense</i> , <i>C. bursa-pastoris</i> seed mixture		Honek et al., 2003, 2005; Lundgren, 2009
		<i>A. nitida</i>	<i>C. bursa-pastoris</i>	Principally granivory	vegetable remains (d)	Brandmayr, 1972; Saska & Jarošik, 2001; Honek et al., 2005; Lundgren, 2009
		<i>A. ovata</i>		Flowers and pods of <i>Alliaria</i> , pods of <i>Barbarea vulgaris</i> and <i>Brassica</i> ; seeds of <i>Reseda luteola</i> , fruits of <i>Cynosurus</i> ; seeds of cereals and crucifers, <i>R. luteola</i> , <i>C. bursa-pastoris</i> , <i>C. arvense</i> , seed mixture		Lindroth, 1945 Honek & Martinkova, 2001 Honek et al., 2003, 2005 Lundgren, 2009
		<i>A. montivaga</i>		<i>T. officinale</i> preferred "Dandelion specialist"		Honek et al., 2005
	subg. <i>Celia</i>	<i>C. praetermissa</i>		Fruits of <i>Solidago virgaurea</i>		Lindroth, 1945
		<i>C. bifrons</i>		<i>Gutierrezia serotinae</i> , cereals, a seed mixture		Lindroth, 1945; Honek et al., 2005
		<i>C. ingenua</i>		<i>Polygonum aviculare</i> and another 9 seed species, seed mixture		Lindroth, 1945, 1985–1986; Honek et al., 2005
		<i>C. fusca</i>		<i>Artemisia campestris</i>		Lindroth, 1986; Mark Telfer's website
		<i>C. quenseli</i>		<i>Wahlbergella affinis</i> , <i>Polygonum aviculare</i> , <i>Trisetum spicatum</i> , <i>Luzula multiflora</i> , <i>Galium verum</i> , <i>Thymus serpyllum</i>		Burmeister, 1939 Lindroth, 1945, 1985–1986 Larochelle, 1990
	<i>Zabrus</i>	<i>Z. tenebrioides</i>		Accepts fresh meat if offered with lettuce seeds, <i>Triticum</i> , <i>Avena</i> , <i>Hordeum</i> , <i>Secale</i> a seed mixture		Gersdorf, 1937 in Thiele, 1977; Zavoronkova, 1969; Honek et al., 2005, 2007; Pierce, 1971; Bassett, 1978 in Lundgren, 2009

Tribe	Genus/ subgenus	Species	Diet larvae/ references	Diet adults/references	Diet adults/ unpubl. data	References
		<i>Zabrus costai</i>			<i>P. bulbosa</i> , (fo)	
Harpalinae, Anisodactylini	<i>Scybalicus</i>	<i>S. oblongiusculus</i>			Fresh meat, seeds of various species, <i>Daucus</i> , <i>Foeniculum</i> (lpe)	
	<i>Anisodactylus</i>	<i>A. binotatus</i>		<i>Fragaria</i>	Vegetable remains (d)	Kirchner, 1939; Larochelle, 1977 in Lundgren, 1990
		<i>A. signatus</i>		<i>C. arvensis</i> , seed mixture	<i>Daucus</i> , <i>Foeniculum</i> , <i>Tenebrio</i> , fresh meat (lpe)	Honek et al., 2003, 2005, 2007
		<i>A. nemorivagus</i>			Vegetable remains (d)	
Harpalinae, Stenolophini	<i>Bradycellus</i>	<i>B. (Tetraplatypus)</i> <i>ganglbaueri</i>		<i>Satureja montana</i> , <i>S. subspicata</i> , <i>S. vulgaris</i> , <i>S. juliana</i> , <i>S. hortensis</i>	Meat, <i>S. montana</i> , <i>S. subspicata</i> , <i>S. vulgaris</i> , <i>S. juliana</i> , <i>S. hortensis</i> Refuses other seeds (lpe), animal remains in gut (d), <i>S. montana</i> (fo)	Zetto Brandmayr & Brandmayr, 1978a
		<i>B. (Tetraplatypus)</i> <i>ruficollis</i>		<i>Calluna</i> seeds (67,2%) in the ingested food		Melber, 1983
		<i>B. (T.) verbasci</i>			<i>Daucus</i> , <i>Ligusticum</i> ; meat (lpe)	
		<i>B. (T.) harpalinus</i>		Seed heads of Gramineae		Larochelle, 1990
	<i>Acupalpus</i>	<i>A. flavicollis</i>			Vegetable remains (d)	
		<i>A. meridianus</i>		Seed mixture		Honek et al., 2005
Harpalinae, -ni, Harpalina	<i>Ophonus</i> subg. <i>Ophonus</i>		Primarily granivorous	Primarily granivorous		Brandmayr et al., 1980, 1990; Brandmayr & Zetto Brandmayr, 1982; Zetto Brandmayr, 1990; Toft & Bilde, 2002; Giglio et al., 2008
		<i>O. stictus</i>		"granivorous tendencies" on <i>Daucus</i> heads		Brandmayr, 1972 Larochelle, 1990
		<i>O. ardosiacus</i> (<i>rotundicollis</i>)	<i>Daucus</i> <i>carota</i> , <i>Seseli</i> , <i>Foeniculum</i> , <i>Bupleurum</i> <i>junceum</i> , <i>Sium</i> <i>sisarum</i>	<i>D. carota</i> , <i>Pastinaca</i>	<i>Daucus</i> (lpe + fo), <i>Peucedanum</i> , <i>Seseli elatior</i> <i>Foeniculum</i> , <i>Angelica</i> , <i>Bupleurum junceum</i> , <i>Sium sisarum</i> , <i>Tenebrio</i> , refuses meat (lpe), vegetable remains (d)	Brandmayr et al., 1980 Zetto Brandmayr, 1976, 1978, 1980, 1983 Larochelle, 1990 Zetto Brandmayr, 1990
		<i>O. diffinis</i>	<i>D. carota</i> , <i>Foeniculum</i>	<i>D. carota</i> , <i>Foeniculum</i>	<i>Daucus</i> , vegetable remains (d), <i>Daucus</i> (fo), refuses meat (lpe)	Zetto Brandmayr, 1976, 1978 Larochelle, 1990
		<i>O. sabulicola</i>	Seed of Umbrelliferae	Seed of Umbrelliferae	<i>Daucus</i> , <i>F. vulgare</i> (lpe)	Larochelle, 1990; Alessi, 1995
	subg. <i>Hespero-</i> <i>phonus</i>	<i>H. azureus</i>	Specialists on seed-heads of <i>D. carota</i> and umbellifers, <i>Foeniculum</i> , <i>C. bursa-pastoris</i> Meat sometimes preferred	Specialists on seed-heads of <i>D. carota</i> and umbellifers, <i>Foeniculum</i> , <i>C. bursa-pastoris</i> Meat sometimes preferred	<i>Daucus</i> , meat, sometimes accepts meat (lpe), vegetable remains (d)	Zetto Brandmayr, 1976, 1978 Honek et al., 2003, 2007 Brandmayr et al., 1980
	subg. <i>Metophonus</i>	<i>M. cordatus</i>		<i>D. carota</i> , <i>Foeniculum</i>	<i>Daucus</i> , <i>Foeniculum</i> (lpe), vegetable remains (d)	Brandmayr, 1972; Larochelle, 1990
		<i>M. melleti</i>		<i>Daucus</i>	<i>Daucus</i> , <i>Foeniculum</i> (lpe)	Larochelle, 1990
		<i>M. puncticeps</i>	<i>D. carota</i> , <i>Foeniculum</i>	<i>D. carota</i> , <i>Foeniculum</i>	<i>Daucus</i> (lpe + fo), <i>Peucedanum</i> , <i>Laserpitium</i> <i>siler</i> , <i>Sesleria autumnalis</i> , <i>Foeniculum</i> , <i>Artemisia</i> spp., <i>Ligusticum</i> , <i>Anthriscus</i> <i>cerefolius</i> , <i>Sium sisarum</i> , refuses meat (lpe), vegetable remains (d)	Brandmayr Zetto & Brandmayr, 1975 Zetto Brandmayr, 1976, 1978 Lundgren, 2009
		<i>M. puncticollis</i>	<i>D. carota</i> , <i>Foeniculum</i>	<i>D. carota</i> , <i>Foeniculum</i>	<i>Daucus</i> , <i>Peucedanum</i> , <i>Laserpitium</i> , <i>Sesleria aut.</i> , <i>Plantago</i> spp., refuses meat (lpe), vegetable remains (d)	Zetto Brandmayr, 1976, 1978
		<i>M. rupicola</i>		Specialists on seed-heads of <i>Daucus</i>	<i>Daucus</i>	Larochelle, 1990
	subg. <i>Incisophonus</i>	<i>I. incisus</i>			<i>Daucus</i> , <i>Foeniculum</i> , <i>Bupleurum junceum</i> , <i>Silene</i> <i>vulgaris</i> , <i>Angelica silv.</i> , <i>Sium</i> <i>lancif.</i> , <i>Anthriscus silvestris</i> , refuses meat (lpe)	
	<i>Cryptophonus</i>	<i>Cryptophonus</i> <i>tenebrosus</i>	<i>D. carota</i> , <i>Foeniculum</i>		<i>Daucus</i> , <i>Foeniculum</i> , refuses meat (lpe) vegetable remains (d)	Brandmayr & Zetto Brandmayr, 1980, 1982
	<i>Pseudo-</i> <i>-ophonus</i> subg. <i>Pseudo-</i> <i>-ophonus</i>	<i>Pseudoophonus</i> <i>rufipes</i> (<i>pubescens</i> <i>auctorum</i>)	<i>T. officinale</i> , <i>Chenopodium</i> <i>album</i> , <i>Sinapis</i> <i>arvensis</i> , <i>S.</i> <i>media</i> , <i>Polygonum</i> <i>aviculare</i> , a seed mixture "seed consumers"	<i>T. officinale</i> , <i>Chenopodium</i> <i>album</i> , <i>Sinapis arvensis</i> , <i>S. media</i> , <i>Polygonum aviculare</i> , a seed mixture "seed consumers"	Vegetable and animal remains (d)	Briggs, 1965; Larochelle, 1990; Jørgensen & Toft, 1997b; Honek et al., 2003, 2005; Martinkova et al., 2006; Saska et al., 2008, 2010; for a complete list of seeds and authors see Lundgren, 2009
		<i>P. griseus</i>		<i>Fragaria</i>		Larochelle, 1990
	<i>Harpalus</i>					Zetto Brandmayr, 1990; Toft & Bilde, 2002; Lundgren, 2009
		<i>H. honestus</i>	Meat, Orthoptera, <i>Tenebrio molitor</i> , <i>Peucedanum</i> , <i>Daucus</i> , <i>araxacum</i>			Bertrandi & Zetto Brandmayr, 1991 Zetto Brandmayr, 1990

Tribe	Genus/ subgenus	Species	Diet larvae/ references	Diet adults/references	Diet adults/ unpubl. data	References
		<i>H. anxius</i>			Vegetable and animal remains (d)	
		<i>H. dimidiatus</i>	<i>Daucus</i>	"granivorous tendencies"	<i>Daucus</i> , <i>Foeniculum</i> , <i>Tenebrio</i> , fresh meat (lpe) vegetable and animal remains (d)	Brandmayr, 1972 Larochelle, 1990 Bertrandi & Zetto Brandmayr, 1991
		<i>H. affinis</i> (<i>aeneus</i> auctorum)	<i>Daucus</i> , <i>Foeniculum</i>	<i>Picea</i> , <i>Fragaria</i> , <i>S. media</i> , <i>T. officinalis</i> , <i>D. sanguinalis</i> , <i>Trifolium pratense</i> , <i>Cerastium arvense</i> , <i>C. bursa-pastoris</i> , <i>P. annua</i> , <i>Cirsium album</i> , <i>C. arvense</i> , seed mixture, <i>Daucus</i> , <i>Foeniculum</i>		Bertrandi & Zetto Brandmayr, 1991 Honek et al., 2003, 2005, 2006 Martinkova et al., 2006 Saska et al., 2008 Lundgren, 2009
		<i>H. atratus</i>	<i>D. carota</i> , a seed mixture	Shrubby trees, <i>C. arvense</i>		Larochelle, 1990; Bertrandi & Zetto Brandmayr, 1991; Honek et al., 2003, 2005
		<i>H. luteicornis</i>		Seed mixture		Honek et al., 2005
		<i>H. servus</i>		<i>Secale</i> , <i>Hordeum</i> , <i>Camelina sativa</i> , forest trees		Larochelle, 1990
		<i>H. solitarius</i> (<i>fuliginosus</i> auct.)		<i>Carex pitulifera</i>		Kjellsson, 1985 in Lundgren, 2009
		<i>H. tardus</i>	<i>D. carota</i>	<i>C. arvense</i> , <i>C. bursa-pastoris</i>		Bertrandi & Zetto Brandmayr, 1991 Honek & Martinkova, 2001 Honek et al., 2003, 2005
		<i>H. marginellus</i>		"granivorous tendencies"	Vegetable and animal remains (d)	Brandmayr, 1972; Larochelle, 1990
		<i>H. rubripes</i>		<i>Daucus</i> , <i>Foeniculum</i>	Meat (lpe), Vegetable remains (d)	Brandmayr, 1972; Bertrandi & Zetto Brandmayr, 1991; Larochelle, 1990
		<i>H. sulphuripes</i>		<i>Foeniculum</i> , <i>Triticum</i> , meat		Bertrandi & Zetto Brandmayr, 1991
		<i>H. distinguendus</i>		<i>Fragaria</i> , <i>P. annua</i> , <i>Daucus</i> , <i>S. media</i> , <i>C. arvense</i> , <i>C. bursa-pastoris</i> , <i>Foeniculum</i> , <i>Triticum</i> , <i>Taraxacum</i> , <i>Linum</i> , <i>Peucedanum</i> , cereals, a seed mixture	Fresh meat (lpe) <i>Daucus</i> , <i>Foeniculum</i> (fo)	Bertrandi & Zetto Brandmayr, 1991 Larochelle, 1990 Honek & Martinkova, 2001 Honek et al., 2003, 2005, 2006
		<i>H. serripes</i>			vegetable and animal remains (d) <i>Bromus erectus</i> (fo)	
	subg. <i>Semiophonus</i>	<i>S. signaticornis</i>		Oat flakes and pieces of <i>T. molitor</i> larvae, <i>C. arvense</i> , <i>C. bursa-pastoris</i> , seed mixture		Hürka, 1992 Honek & Martinkova, 2001 Honek et al., 2003, 2005
	subg. <i>Harpalophonus</i>	<i>H. circumpunctus</i> ssp. <i>italus</i>	Meat, seeds, <i>Tenebrio molitor</i>		<i>Daucus</i> , <i>Foeniculum</i> , <i>Tenebrio</i> , meat (lpe)	Zetto Brandmayr & Brandmayr, 1978b
	<i>Acinopus</i> , subg. <i>Acinopus</i>	<i>A. picipes</i>		seeds	<i>D. carota</i> , <i>F. vulgare</i> , <i>T. aestivum</i> , meat (lpe)	Barbieri, 1998; Larochelle, 1990
	subg. <i>Osimus</i>	<i>O. ammophilus</i>		<i>Medicago minima</i> seeds		Burmeister 1939; Larochelle, 1990; Honek et al., 2005
	<i>Daptus</i>	<i>D. vittatus</i>			Fresh chicken meat (pers. comm. of G. Colombetta)	
	<i>Trichotichnus</i>	<i>T. laevicollis</i>			Fresh meat, <i>Pimpinella</i> sp. (lpe)	
	<i>Parophonus</i>	<i>P. maculicornis</i>		A seed mixture	Fresh meat, seed mixture (lpe)	Lundgren, 2009
		<i>P. mendax</i>			Fresh meat, seed mixture (lpe)	
Harpalinae, -ni, Ditomina	<i>Ditomus</i> (= <i>Sabienus</i>)	<i>Ditomus</i> (= <i>Sabienus</i>) <i>calydonius</i>	<i>D. gingidium polygamus</i> , two nests observed in nature	<i>Daucus</i> , nest observed in nature	Accepts especially <i>D. carota</i> seeds, also unripe, nest observed in laboratory refuses meat (lpe + fo)	Brandmayr & Zetto Brandmayr, 1974, 1987; Brandmayr, 1974; Brandmayr et al., 1994; Zetto Brandmayr, 1990; Zetto Brandmayr et al., 1994
		<i>D. (S.) tricuspoidatus</i>		<i>Ammi majus</i>		Burmeister, 1939 Larochelle, 1990
	<i>Dixus</i>	<i>D. sphaerocephalus</i>		<i>Plantago cornuti</i> , <i>P. crassifolia</i>		Larochelle, 1990 Therond, 1975 in Lundgren, 2009
		<i>Dixus clypeatus</i>	<i>Plantago lanceolata</i> , nest observed in nature, no larvae observed at feeding	<i>Plantago lanceolata</i> , nest observed in nature, grass		Schremmer, 1960 Brandmayr & Zetto Brandmayr, 1987 Larochelle, 1990
	<i>Tschitscherinellus</i>	<i>T. cordatus</i>			Lives in dense stans of <i>Daucus gingidium</i> garigues and feeds on this species (lpe+fo)	
	<i>Carterus</i>	<i>C. fulvipes</i>		Mass swarming from seed cropland in Italy, <i>Daucus</i> , <i>Pimpinella</i> , <i>Apium</i> , <i>Plantago</i> (fo)		Larochelle, 1990 Fabbri & Contarini, 2009
		<i>C. dama</i>		Mass swarming from anise seed cropland, <i>P. anisum</i>	Kept in the lab on <i>Daucus</i> seeds, refuses meat (lpe)	Koçak et al., 2007
Platyninae, Sphodriini, Calathina	<i>Calathus</i> subg. <i>Calathus</i>	<i>C. fuscipes</i>		<i>Picea</i> , <i>Triticum</i> , <i>C. bursa-pastoris</i>		Larochelle, 1990 Goldschmidt & Toft, 1997 Honek & Martinkova, 2001
Platyninae, Platynini	<i>Agonum</i>	<i>A. mülleri</i>		<i>C. bursa-pastoris</i> , <i>P. annua</i>		Saska et al., 2008