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ECOLOGY AND BEHAVIOR OF GROUND BEETLES (COLEOPTERA: CARABIDAE)

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ABSTRACT

The ground beetles form the speciose beetle family Carabidae and, since their emergence in the Tertiary, have populated all habitats except deserts. Our knowledge about carabids is biased toward species living in north-temperate regions. Most carabids are predatory, consume a wide range of food types, and experience food shortages in the field. Feeding on both plant and animal material and scavenging are probably more significant than currently acknowledged. The most important mortality sources are abiotic factors and predators; pathogens and parasites can be important for some developmental stages. Although competition among larvae and adults does occur, the importance of competition as a community organization is not proven. Carabids are abundant in agricultural fields all over the world and may be important natural enemies of agricultural pests.

INTRODUCTION

The family Carabidae, the ground beetles, contains more than 40,000 described species classified into some 86 tribes (66). It is the largest adephagan family and one of the most speciose of beetle families. The suborder Adephaga is a relatively large group of specialized beetles that is morphologically defined by the presence of six abdominal ventrites, pygidial defense glands in the adult, and liquid-feeding mouthparts in the larvae (112). They are well-proportioned cursorial beetles with prominent mandibles and palps, long slender legs, striate

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elytra, and sets of punctures with tactile setae. Most have an antenna-cleaning organ and largely pubescent antennae. The adults are dark colored, shiny or matte. Some have bright or metallic colors, and some are pubescent. The larvae are campodeiform, have well-developed legs, antennae, and mandibles, and bear fixed urogomphi (34, 112). Major taxonomic problems remain to be solved (8), despite cladograms with new phylogenetic hypotheses that have emerged from significant comparative anatomical studies on the adult feeding apparatus (71), antenna cleaner (96), thorax and locomotory adaptations (69, 70), hind-wing structure (89, 197), pygidial glands (77), ovipositor (15, 25), and the chemistry of defensive secretions (134). Different authors divide the family into different subfamilies; except for the tiger beetles (see 149), our ecological knowledge is scant concerning subfamilies outside the Carabinae [sensu Lawrence & Britton (112)].

The abundance, species richness, and attractive coloration of many species have made carabids popular objects of study for both professional and amateur entomologists. The last attempted synthesis on carabid biology was the descriptive monograph by Thiele (182); only certain aspects of the field have been reviewed since (2, 111, 126, 142). Proceedings of triennial meetings, started in 1969 by Dutch and German carabidologists, provide a series of useful snapshots of the state of the art in this field (19, 48, 50–53, 57, 68, 173). A quarterly journal, *Carabologia,* serves as a forum for both amateur and professional carabidologists.

In this review, we intend to summarize some of the significant achievements in carabid ecology and behavior since Thiele's (182) book was published. Carabids are present worldwide, with species richness highest in the tropical regions (66). However, our knowledge mainly stems from research done in the temperate regions of the Northern Hemisphere. The resulting bias in this review is inevitable. Our examples are illustrative, not exhaustive, and are intended to support generalizations that can serve as guidelines or hypotheses for the study of carabids in other regions.

CARABID EVOLUTION AND ADAPTATIONS

Carabids emerged in the early Tertiary as wet-biotope generalists in tropical habitats, where they remain the dominant predatory invertebrate group (67). Through a series of taxon pulses, they have radiated to drier environments as well as higher latitudes and altitudes (64). By the late Permian/early Triassic, several lineages developed a cosmopolitan distribution pattern, as demonstrated by the fossil record (155). Although this group has retained an easy-to-recognize generalist body plan, their body shape and leg morphology are characteristically modified for running, digging, burrowing, climbing, and swimming (69, 70). Different parts of the morphological apparatus and physiological mechanisms can evolve at different rates. Thus, a species can remain a generalist structurally and still become a specialist physiologically in order to, for example, live at glacier edges (*Nebria* spp.) (66). Several other structural, physiological, and behavioral adaptations enabled carabids to invade all major habitats, where at least some lineages have attained dominance; the only exception is deserts, where carabids are limited to streams and oases (66). This distribution pattern suggests that humidity is a general limiting factor. The main structural patterns in carabid evolution are flightlessness and arboreal, fossorial, and troglobitic adaptations (66). Flightlessness has repeatedly evolved in many groups (35). In the tropics, >30% of species are arboreal, exhibiting special morphological and behavioral adaptations (172). A few groups are adapted to life in self-made tunnels (mainly in sand or finely textured soil in the tropics), and even fewer groups, of cosmopolitan distribution, reside in caves (66).

CARABID STUDY METHODS

The combination of cryptic lifestyles and polyphagous feeding habits means that many aspects of carabid natural history and ecology are not easy to study. Techniques used include different trapping and marking methods for collecting beetles and estimating density (176); labor-intensive dissections or sophisticated immunological methods to study feeding (180); the use of video equipment to record walking (88), searching, and feeding (30) behavior; and the use of harmonic radar to study within-habitat movements (130). The most popular method is pitfall trapping.

A pitfall trap [or Barber-trap (9)] is a container—any one of many different designs—sunk into the ground so that its opening is at surface level. Many surface-dwelling arthropods fall in and cannot escape. The trap is a passive catching device; capture results from the activity of the target organism. The quantity and composition of the catch will vary depending on the size, shape, construction material, and distribution in space and time of the trap, as well as the preservative used and all the factors governing activity and behavior.

Pitfall trapping is the most frequently used field method for studying carabids. Although this method is surrounded by controversy and several critical papers (176 and references therein) have been published, general practice has changed little because no similarly convenient method has been recommended. Pitfall trapping remains suitable for studying several population parameters and certain community measurements such as species presence. Pitfall traps should probably not be used to study community patterns such as relative species composition or diversity. After detailed methodological and behavioral studies have been completed and validation techniques developed, pitfall trapping might be reinstated as an efficient method of studying carabid adults. However, this method cannot be expected to fill the profound gap in our knowledge of larval ecology.

ONTOGENY AND LONGEVITY

Carabids are holometabolous insects that usually lay their eggs singly. Some species lay eggs in small or larger batches in crevices or in the soil after a varying degree of preparatory work by the female (126, 182). The female carefully chooses the ovipositing site, sometimes excavating a chamber for the eggs. Some Pterostichini prepare a cocoon for a batch of eggs (20). Parental care, at its most developed, consists of no more than egg guarding or caching seeds in the egg chamber for the emerging larvae (20, 97).

The typical carabid larva is free moving and campodeiform (34) and usually undergoes three stages before pupating in a specially constructed pupal chamber in the soil. Some species (for example, *Harpalus* and *Amara* spp.) have only two larval stages. Seven tribes, plus a hypothesized ten more, have specialized larvae with more larval stages that, in at least the later stages, exhibit reduced mobility. These species, which are ant or termite symbionts or specialized ectoparasites or predators (65), total 24% of all carabid tribes [in Erwin's classification (64)]. However, as not all members of these tribes exhibit these traits, these specialized larval bionomics characterize only a small minority of all species.

The larvae (second or third stage) of many species undergo diapause, either hibernation or aestivation. The weakly sclerotized and whitish pupa lays on its back, supported by dorsal setae. Sclerotization and coloration of the adult takes place after eclosion; teneral beetles can be recognized for various lengths of time, usually weeks.

In general, ground beetles develop from egg to adult in less than one year, reproduce once, and then perish. However, individual development can last up to four years under harsh climates or adverse food conditions. *Carabus glabratus,* a species with larval hibernation and autumn reproduction in central and western Europe, has a biennial life cycle with spring breeding in upland areas of northern England (99) and in Norway (158). In northern England, *Carabus problematicus* has an annual life cycle at altitudes below 800 m and a biennial one above that (26). The European *Carabus auronitens* has a flexible life-history strategy (opportunistic oviposition, asynchronous development, partial survival of the old generation, fat body reserves, and long-term dormancy), which reduces the risk of the whole population being affected by bad weather during the postecdysial ripening (200).

Adult longevity can also exceed one season. Individuals from several species have been kept in the laboratory for up to four years. Many species (from the tribes Agonini, Harpalini, Pterostichini, Carabini) have life spans over one year

(182). Individuals from field populations of several species from different parts of the world, for example, Europe (83, 99, 125, 186, 194), Japan (166), and the sub-Antarctic (36), can live up to four years and reproduce more than once. Cave-inhabiting species often live long lives; *Laemostenus schreibersi* can live for up to 6.5 years (161). Generally, long adult life span is more common in large species and species with winter larvae [also called autumn breeders (see 49)] than in ones with summer larvae (spring breeders).

Several species show plasticity of individual development, whereas others seem to have a stable life cycle. The originally botanical term *polyvariance* was suggested to describe the former (129). Obligatory univoltism is apparently rare and occurs mainly in species of short longevity. Bi- and multiannual cycles are usually found in species living in harsh environments (sub-Arctic, highland, or xeroterm habitats), and dynamic polyvariance is common.

HABITATS, HABITAT FINDING, AND MICROHABITATS

Persistence in a habitat should depend mostly on the life stage that is most vulnerable, as determined by the longest duration, narrowest tolerance limits, and most limited escape repertoire. All these factors point to the larval stage as the key to understanding occupation of a habitat by a given carabid species. The egg is superficially the most vulnerable of the life stages, but ovipositing females can deliver eggs into microhabitats where their survival can be maximized. Moreover, the egg stage is usually short, and the egg sacs contain the resources necessary for the completion of this life stage. The pupal stage is similarly sensitive. It lacks mobility and often lasts for long periods, but it is often better defended than the egg or larva. The larva has limited mobility, weak chitinization, and therefore feeble tolerance of extremes, and it must also find sufficient food to develop. Larval feeding conditions often determine adult fertility as well (139). For reasons mentioned above, larvae are notoriously difficult to study. However, because larvae usually cannot migrate long distances, they have to survive in the environment where the egg-laying female left them. Therefore, the following discussion on adult habitat choice is justified. Habitat choice is so specific that carabids are often used to characterize habitats (see below).

The directed random walk, followed by a frequently turning walk in the presence of favorable conditions, would eventually lead carabids to their preferred habitats, but several different mechanisms help beetles find or remain in suitable habitats. These mechanisms include internal clocks, sun-compass orientation (33, 182), and orientation either toward or away from silhouettes (33, 159, 182). Some riparian ground beetles find their habitat by sensing volatile chemicals emitted by blue algae living in the same habitat (72). *Agonum quadripunctatum,* a forest species in Europe and North America associated with burnt areas, is a good flyer and is probably attracted to the smell of smoke (23). Carabids continuously sample their surroundings. For example, *Carabus nemoralis* walked around in different habitats before settling in seminatural habitats in preference to set-aside to arable areas (107).

Habitat and microhabitat distribution can be influenced by several factors:

1. Temperature or humidity extremes (several examples in 182). Favorite wintering sites are well aerated, and winter minimum temperatures are relatively high (58, 183).
2. Food conditions. For example, exclusively spermophagous *Ophonus* spp. are present in open habitats where seeds of Umbelliferae are available, whereas polyphagous *Harpalus* spp. aggregate in crops (209). Marked *Poecilus cupreus* and *Pterostichus melanarius* moved from winter wheat to a weed strip within the wheat field (where feeding conditions were better) much more frequently than they moved the reverse direction (128).
3. Presence and distribution of competitors. For example, forest carabids in Finland were influenced by the distribution of *Formica* ant species (141).
4. Life history and season. *Amara plebeja,* for instance, has different hibernation (woodland) and reproduction (grassland) habitats. The beetles fly between habitats in spring and autumn. Flight muscles are temporarily autolysed between flights, then completely reconstructed for the return flight. In the autumn, they fly toward woodland silhouette shapes (190).

DENSITY AND DISPERSAL

Carabids are often numerically dominant in collections of soil-active arthropods. However, for reasons mentioned above, this result cannot equate with high density. Data, especially in the older literature (including 182), are confusing because of the frequent acceptance of pitfall trap catches as density data. Data obtained by true density measurement methods indicate that densities fluctuate in space and time from <1 (in many habitats) to >1000 individuals per square meter (at suitable overwintering sites, see Table 1).

As a group, carabids originally used fully functional wings as the primary dispersal mode. However, flight is very costly and is subject to intense selection (160). Once the benefits of flight do not match its costs, as on, for example, islands and mountain tops, it is quickly lost (35, but see 145). Flightlessness and flight dimorphism (some individuals in a given species possess wings, others do not) has repeatedly evolved in carabids. For example, of the carabid fauna of Newfoundland (157 species), 12.7% are dimorphic and 21.0% flightless, a condition reached through nine or more independent evolutionary transitions (160). Wing dimorphism seems to be inherited in a simple Mendelian fashion through a dominant gene for short-wingedness (5, 117); in some

Table 1 Maximal densities (individuals per square meter) of ground beetle adults and larvae in different habitats^a

	Arable fields			
Species category	Annual crops	Biennial/ perennial crops	Field boundary	Forest, heath
Species size <5 mm	5.96 (0.2–77; 72)	3.61 (0.3–2.4; 7)	66.62 (0.6–923; 23)	—
Species size >5 mm	1.83 (0.02–33; 47)	4.82 (0.7–22; 7)	14.32 (0.03–87; 18)	2.54 (0.04–22.5; 19)
Adult total	31.73 (1.2–96.1; 12)	—	233.27 (14.5–1113; 9)	2^b
Larvae, individual species	5.46 (0.07–33; 10)	6^b	14.5 (4–42; 6)	7.8^b
Larvae, total	29.4, 49, 77^b	—	49, 87^b	—

[a] Data are given as mean (minimum–maximum; *N*). Only data giving true density values (obtained by soil samples, soil flooding, mark-recapture, fenced pitfalls, quadrat sampling, and vaccuum sampling) were considered and include data on 71 adult plus 13 larval taxa, obtained between 1970–1994 in 14 countries in Europe and North America. From KD Sunderland & GL Lövei, unpublished manuscript. A full list of references obtainable by request.

[b] Fewer than five observations; individual values given.

species, the trait is polymorphic (56). Environmental conditions may influence expression of the dimorphism (6). Flight ability varies little between the sexes (160).

The proportion of flightless individuals in dimorphic species increases with increasing habitat persistency and time since colonization (54). The proportion of macropterous *P. melanarius* can be as low as 2% in stable habitats (e.g. old forest patches) (42) or as high as 24–45% in less stable ones (e.g. newly reclaimed polders of The Netherlands) (87). In Edmonton, Canada, this species was first reported in 1959. Currently, 60–70% of the frontier population, ~70 km from the city, has wings; in the source population in the city, only 20% of the beetles are now macropterous (143).

Flight is greatly influenced by temperature, rain, and wind (191). In some species (such as the Palearctic *A. plebeja*), the flight muscles are broken down during egg production and then resynthesized; in others, flight capability during reproduction is not impaired, and up to 80% of dispersing females carry fertilized eggs (192). This percentage characterized species from both persistent and ephemeral habitats. However, females of more species from ephemeral habitats than from persistent ones carried ripe eggs (192), which increased the probability of (re)colonizing empty habitat patches.

Many carabids have been transported intercontinentally, e.g. from Europe to North America (115, 171). Studies in Canada of the effects of invasion by *P. melanarius* showed them to be negligible (143).

ACTIVITY: DIEL AND SEASONAL

Diel Activity Cycles

More carabids are nocturnal than diurnal. For example, in the United Kingdom, 60% of species are nocturnal and 20% diurnal (124). The diurnal activity dendrogram for carabids in UK woodlands revealed groupings for diurnal, nocturnal, and crepuscular species, plus species that overlapped some of these categories (55). Overall, nocturnal species are larger than diurnal ones. Also, their coloration often differs: Night-active species are dark and dull, and diurnal species display iridescent colors. Diel periodicity can vary with habitat (forest species tend to be nocturnal whereas grassland species are diurnal) (84) and time of year (*P. melanarius* is nocturnal until August and is mainly diurnal later) (59). Changes in temperature (102), light intensity, and humidity (182) also influence activity. In hot countries, nocturnalism becomes more common; conversely, species that are nocturnal in central Europe become diurnal in the arctic (182). Specialist feeders may synchronize their activity with that of their prey (1). Desert carabids exhibit peak activity at temperature minima (62). Cave-dwelling species often are active in short bursts between periods of inactivity (182); they sometimes exhibit diel activity cycles despite constant, very low illumination and air humidity. Such circadian clocks may serve to synchronize the activity of males and females (199). Individuals within a population can undergo different activity cycles; for example, some individuals of *Carabus auratus* are diurnal, some nocturnal, and others indifferent to diel periods (182). In some species, larvae and adults undergo different cycles (106).

Sublethal dosages of insecticides can cause marked increases in carabid activity (135) and may also indirectly cause activity increases by reducing food supplies (29).

Seasonal Rhythms

Seasonal rhythms involving dormant periods during winter and/or summer (aestivation) are an integral part of the life history of temperate-region ground beetles. The activity of the two most typical groups peaks in either spring or autumn. This peak usually coincides with the reproductive period, although the connection between activity and reproductive rhythms is flexible in many species (129). Such rhythms are inseparable from individual, especially larval, development.

Facultative diapause of summer larvae can synchronize the life cycle (126). Because of the variability in activity and reproductive seasons and the growing body of evidence on adult longevity, some authors have suggested rejecting the traditional concepts of spring-reproducing vs autumn-reproducing species and adult overwinterers vs larval overwinterers in favor of categories containing species with summer larvae vs winter larvae (49) or species with vs without diapausing larvae (100). In extratropical regions, the cues regulating these cycles involve temperature and photoperiod (182). Seasonal activity and reproductive rhythms in tropical species are regulated by seasonal changes in soil moisture and flooding (146).

FEEDING

Searching Behavior

Whereas many carabids presumably find their food via random search, several diurnal species hunt by sight (80). Other species use chemical cues from aphids (30), springtails (55a), or snails (202) to find prey. The use of chemical information is probably more common than the few reported cases would suggest.

Carabids exhibit the search pattern common to invertebrate predators (140). After the beetle encounters a prey item in a patch, its search behavior characteristically intensifies for a specified "give-up" time period. In some species that search two-dimensionally, finding a prey triggers a three-dimensional search behavior [e.g. *Pterostichus cupreus* climbs the plant when it senses an aphid at the base (30)]. The general walking pattern often alternates between frequently turning and rarely turning walking phases (132, 195), but this pattern is not necessarily nor always connected to feeding behavior.

Once prey is located, species typically switch to a well-defined prey-catching behavior. Many morphological and behavioral adaptations are at work in this stage of feeding, mostly in specialized species. Prey catching, studied in fine detail for several European species that hunt springtails, has revealed a fascinating array of adaptations involving sight, behavior, and morphology in both adults and larvae (11–13).

Most carabid adults use their well-developed mandibles to kill and fragment prey into pieces. Specialist species attacking snails seem to paralyze their prey by biting (147), thus preventing the mucus production that is the slugs' defense reaction. Many large species eject a fluid rich in digestive enzymes; subsequently, they consume the liquid portion of their partially digested prey, sometimes with undigested prey fragments. Larvae only consume extraorally digested food (for a more detailed discussion of preoral digestion, see 32). The alimentary canal is tripartite. The foregut, including the crop, is the main site of digestion (80); enzymes synthesized in the midgut are passed forward to the foregut. The enzyme set contains proteases, carboxylases, amylases (131), and oligo- and polysaccharidases; this composition is thought to be a primitive character (101). Absorption takes place in the hindgut. The speed of digestion depends on temperature and the size of a food item (164) as well as on subsequent feeding (122). Traces of a meal could be detected for up to 14 days (122, 164).

Food Choice

Early data on several species indicated varying extents of polyphagy (37, 76, 163). The accumulated results have been extensively reviewed by Thiele (182) and, for agricultural species, by Allen (2) and Luff (126).

Carabids are mostly polyphagous feeders that consume animal (live prey and carrion) and plant material; several species are phytophagous (126, 182). A worldwide survey of the literature (111) reporting on 1054 species of carabids and cicindelids showed that 775 species (73.5%) were exclusively carnivorous, 85 species (8.1%) phytophagous, and 206 species (19.5%) omnivorous. These data, although they may indicate the general feeding habit of the family, are often based on laboratory data and are heavily biased toward northern hemisphere species. On a smaller scale, another survey showed that 27% of the 362 species in Fennoscandia were predators, 13% omnivores, and 24% herbivores; at the time of study, the food of 36% of the species was not known (114). More detailed analysis of the restricted range of species (see below) also indicates that the degree of predatory habit in the family has generally been overestimated, especially as the degree of plant and carrion feeding is not well known. In general, larvae are more carnivorous and restricted in food range while adults exhibit very catholic feeding habits, with some groups (Cychrini, Notiophilini, Loricerini, Nebriini) demonstrating varying degrees of specialization. The following paragraphs summarize the feeding of adult beetles.

Catholic feeding habits, frequent nocturnal activity, and extraintestinal digestion, among other factors, present problems for the study of feeding (140, 175). Methods applied to investigate feeding in carabids include casual or regular direct observation, exclusion techniques, forced feeding in the laboratory, density manipulation of prey and predator, the use of radioactive tracers, isotope-labeled prey techniques, gut dissection, various serological techniques, and electrophoresis. These methods and their limitations have been repeatedly reviewed (e.g. 175, 180).

Dissection of several thousand individuals of 24 European species (95) revealed the remains of aphids, spiders, lepidopteran larvae and adults, fly larvae, mites, heteropterans, opilionids, beetles, and springtails. Similar studies, conducted in Belgium (154) and New Zealand (177), also found enchytraeid worms, lumbricid worms, nematodes, hymenopterans, beetle larvae, eggs, centipedes, millipedes, mollusks, spores, fungal hyphae, seeds, and pollen. Cannibalism has also been reported.

All species in Hengeveld's study (95) were polyphagous and consumed plant material in addition to the other food items. A multivariate analysis (94) identified one group with a diet containing a high proportion of springtails and a restricted variety of other arthropods (some *Notiophilus, Leistus,* and *Agonum* species). Members of another group in the study, which eat what they can swallow, were species of *Amara, Harpalus,* and *Pterostichus* (94).

While the results mentioned above show the wide range of prey taken by ground beetles, most of these studies did not consider prey availability. Where it has been considered, opportunistic feeding habits are found. For example, ten abundant grassland species in Belgium fed mainly on springtails, the most abundant prey group (154).

Food Consumption

Carabids are voracious feeders, consuming close to their own body mass of food daily (182). Food is used to build fat reserves, especially before reproduction and hibernation (182). Feeding conditions during larval development determine adult size, which is a major determinant of potential fecundity (138). Realized fecundity depends on adult feeding conditions (see below).

Although potential food consumption can be assessed straightforwardly in the laboratory, quantification of feeding rates in the field is difficult for reasons mentioned earlier. One possible solution is to monitor egg production and/or body-mass changes by regularly sampling field populations and compare these data to calibration measurements taken on beetles kept in the laboratory under known conditions. Such measurements, performed on *Carabus yaconinus* in Japan (167), indicated that field prey consumption by females allowed them to realize 59% of their possible maximum egg production in May and 45% in June. Field consumption was similarly below the potential maximum in other species in The Netherlands (139, 189) and North America (201).

Carabids, like other animals, forage for nutrients and energy, which are packaged in food items. Feeding in the context of optimality of food composition has been little studied in carabids. Nutritional requirements for carabids have not been specifically identified nor has the observation that certain species are more specific than others been addressed from a nutritional point of view. The dietary advantages of mixed food over a single food type are well known for polyphagous invertebrate herbivores (14, 162). In carabids, females often have more prey types than males (154). Moreover, Wallin et al (196) found that egg number and size were influenced by food composition. Signs of optimal digestion were found in two carabid species (122). These data suggest that food composition is not irrelevant for foraging ground beetles, and beetles may have the ability to select a diet that matches their particular needs.

The feeding studies to date have left us with some notable gaps: (*a*) Although the range of methods applied is very wide, the degree of distortion obtained is not possible to assess. (*b*) Adult feeding is generally overemphasized, and detailed information on larval feeding is lacking. (*c*) Most studies have a narrow focus; they were done in agricultural fields and/or considered a single prey group (aphids, slugs, etc). (*d*) The degree of true carnivory vs carrion feeding is not adequately determined. (*e*) The degree of mixed feeding (plant and animal material) is probably underestimated. (*f*) The literature has a heavy geographical bias toward the Northern Hemisphere. (*g*) Physiological studies are scarce, and consequently, food-choice criteria are poorly understood in terms of diet composition.

REPRODUCTION

Fecundity can range from five to ten eggs per female in species with egg-guarding behavior to several hundred per female in species that do not guard eggs (208). Eggs can be laid in one batch, several batches in one season, or over several seasons. As many as 30–60% of individuals in a population can reproduce in more than one year (168, 186, 193). The dependence of fecundity on age is not well understood. For several species, young females have a higher reproductive output than old ones (e.g. 186), whereas the reverse is true in other species (24, 36, 83, 166).

Many carabids are apparently iteroparous rather than semelparous reproducers; such behavior results in less fluctuation in numbers over the years (125). Murdoch (136) hypothesized that the stabilizing mechanism worked so that female survival was inversely related to the amount of reproduction during the previous season, reporting that observations of *Agonum* species in England confirmed this assertion. His suggestion generally did not find support (7, 113, 166, 189, 198, but see 63). Increased mortality during reproduction may result from ecological rather than physiological factors (27), such as exposure of reproducing individuals to higher levels of external hazards such as predators or disease.

In all carabid species examined, as well as in several other predators, the variable egg production is related to the amount of food. The first priority of the adults is to meet energy demands for survival and use the surplus for reproduction. This makes sense in that under conditions of limited food supply, the survive-but-not-reproduce option enables predators to survive until better food conditions allow reproduction (133, 203). Data from Europe (187, 189), Japan (166), and North America (113) indicate that carabids in the field regularly experience food shortage and rarely realize their full reproductive potential.

In searching for an explanation of carabid fecundity, Grüm (86) found that egg numbers tended to decrease as body mass increased. Autumn breeders had higher egg numbers than spring breeders, and egg-laying rates were inversely correlated with female mobility (86). These results, along with observations of low egg numbers in cave-inhabiting species (41) and of species demonstrating parental care in Europe and New Zealand (20; GL Lövei, unpublished data), conform to some predictions of the *r*- and *K*-strategies theory. Also, ground beetle species living in unstable habitats have higher egg numbers than relatives living under less variable conditions. Similar differences are observed in adult life spans and egg numbers among the Polish and Dutch populations of several species (86). However, the *r-K* theory is only one of the hypotheses suggested to explain life-history features. The application of alternative theories such as Grime's C-S-R model (85) is promising (73).

MORTALITY AND POPULATION DYNAMICS

Although abiotic influences on survivorship are inevitable, constituting the principal mortality factors for all life-cycle stages of ground beetles (45), other factors play an important role in carabid population dynamics.

Mortality of the Different Stages

EGG MORTALITY The traditional assumption that egg mortality is not significant (182) is probably not correct. Eggs of *Pterostichus oblongopunctatus* suffered 83% mortality in fresh litter but only 7% in sterilized soil (91). One potential advantage of brood watching could be protection from pathogens, although females have not been observed cleaning, surface sterilizing, or even doing anything with their eggs in the egg chamber. However, when abandoned by females, eggs quickly become moldy (20).

LARVAL MORTALITY Larval mortality is probably a key factor in overall mortality of ground beetles, but because of the lack of appropriate methodology to study larvae, evidence for the importance of larval mortality is scant. Because larvae have weak chitinization and limited mobility, they are sensitive to desiccation, starvation, parasites, and diseases. Larvae are also cannibalistic. In laboratory and field experiments with surface-active larvae of *Nebria brevicollis,* mortality varied between 25 and 97%, depending on food conditions; parasitism caused up to 25% mortality (138, 139). The results of similar experiments with larvae of *P. oblongopunctatus,* combined with computer simulations, indicated a cumulative mortality rate for larvae and pupae of 96% (22, 92). These authors concluded that events during larval life are the most important for population regulation.

Parasitism is recognized as a very important factor in host population biology, both on ecological and evolutionary time scales (81, 157). Although predators, parasites, and pathogens affect all ground beetle developmental stages (126, 182), quantitative data remain scarce.

ADULT MORTALITY Up to 41% parasitism by nematodes and ectoparasitic fungi was found on 14 species of *Bembidion* in Norway (3). Nematode infection in insects may cause sterility (153), resulting in obvious fitness effects. The benefit of living in exposed habitats could be freedom from parasites; the cost would be higher risks of predation and/or more frequent catastrophic events, such as flooding (3).

Most observational evidence indicates that predation is an important mortality factor for adults. Hundreds of vertebrate species prey on carabids (108–110). The ecological significance of predation pressure by small mammals was demonstrated in exclosure experiments in North America (148) and England (31), where excluding small mammals resulted in an increase in both species richness and density of carabids.

Antipredator Defenses

The evolution of terrestrial faunal groups that prey on carabids, such as amphibians, reptiles, birds, and mammals, has probably constituted a major driving force of carabid evolution (66). The large suite of antipredator defenses includes morphological, biochemical, and behavioral components. For example, morphological traits in arboreal carabids include cryptic or warning coloration, mimicry, narrow body shape, dorso-ventral flattening, large eyes, and long legs (172). Inactive beetles rest at safe sites, under stones, in crevices, in the soil, or on undersides of leaves; night activity is also thought to be an antipredator defense. Attacked beetles run to safety and hide (172), take to water (4, 174), demonstrate catalepsy (17), regurgitate crop contents and/or digestive fluid (79), and bite their attacker (61). Stridulation is also a widespread and effective deterrent (78, 82). Conspicuous elytral spots, which are present in many carabid species, may deflect attack from the vital anterior body parts (103). Batesian mimicry has been reported in carabids (116), and Müllerian mimicry was reported in tiger beetles (149). The hardened cuticle and fused elytra of large species (75) also provide structural protection from predators. The most effective defense is the excretion of compounds from pygidial glands that are universally present in carabids. The anatomy, chemistry, and effectiveness of these glands and their products has been extensively studied and reviewed (18, 105, 134).

Population Dynamics

Most of the available field data on carabids come from results of pitfall-trap catches. Catches of the same species in the same habitat from different years correlate well with changes in density (43, 125), and this comparison is generally accepted as a valid method for estimating density fluctuations and effective rates of reproduction.

Population variability in carabids (125) seems to be at the lower end of values for insects (204). Although environmental fluctuations in caves are smaller than in other terrestrial habitats, population fluctuations of the cave-inhabiting *Neaphaenops tellkampfi* in Mammoth Caves, Kentucky, were between those of *Calathus melanocephalus* and *Pterostichus versicolor,* two common species living on heath in Drenthe, The Netherlands (104). Different intrinsic and extrinsic factors—life span, fecundity, reproductive patterns, and rate of development—are thought to contribute to this relative stability (125).

Population Survival and Metapopulation Dynamics

The study of carabids has contributed significantly to the appreciation of landscape-scale dynamics. Particularly important are studies started in the late 1950s in The Netherlands (43). den Boer (46) synthesized the regional population fluctuation patterns of carabids collected over 23 years in the Dutch province of Drenthe. Using a distribution of population sizes (43), he distinguished several population fluctuation types. Species with high dispersal power (e.g. *Pterostichus niger*) exhibit population fluctuation patterns different from those of species with limited dispersal ability (e.g. *Pterostichus lepidus*). Species in Drenthe show a continuum between these two extremes. Based on this pattern, the frequency of extinction and the mean survival times of populations of the different species were simulated. This technique indicated that local populations of poorly dispersing species survive, on average, for 40–50 years. If changes in the locations of suitable habitat patches are faster, the species cannot recolonize new habitat patches fast enough and become regionally extinct. For most of Europe, these changes occur faster than required by the poorly dispersing species.

de Vries & den Boer (59a) compared the regional distribution of *Agonum ericeti,* a species found in moist heath, in 1959–1962 with its distribution in 1988–1989. This species cannot travel more than 200 meters between habitat fragments and showed an average survival time of 7–44 years in different-sized, small habitat fragments. In larger fragments, population fluctuation is asynchronous and the multipartite population can survive longer. These authors concluded that *A. ericeti* needs a habitat fragment of 50–70 ha for continuous population survival.

With the intensification of agriculture, fragmentation of natural habitats has occurred worldwide during the twentieth century. Turin & den Boer (184) and Turin & Peters (185) have examined the effects of these changes in The Netherlands since 1850. Poorly dispersing species (for example *Abax paral-*

lelepipedus, Calathus erratus, and *P. oblongopunctatus*) generally decreased; well-dispersing species (*Amara lunicollis, Dicheirotrichus gustavi, Stenolophus mixtus*) were stable or increasing; and species tolerating agricultural habitats (*C. melanocephalus, Dyschirius globosus, P. melanarius*) increased during this period. Whether these changes were caused by habitat fragmentation or habitat destruction was not clear.

ASSEMBLAGES AND COMMUNITIES

Patterns in Carabid Assemblages

Carabid assemblages are moderately species rich. Usually, no more than 10–40 species are active in a habitat in the same season; regional assemblages are correspondingly richer (98, 126, 182, 188). Generalizations are difficult as the extension of an assemblage in space or time is usually not defined; the number also depends on the method and intensity of the sampling. With the advent of more accessible and more powerful data handling, the regional and continental distribution patterns can be described and evaluated (144, 151). Future evaluations of the nestedness of ground beetle faunas is another promising endeavor.

Southwood (169) described the species packing of ground beetles at Silwood Park in southern England, a site containing 28 species. The report made no mention of the presence, abundance, or species richness of potential competitor groups (ants, spiders). More than 50 pair-wise interactions were considered significant. During the growing season, from March to November, the activity periods of the most common species filled the available time; for large species, this species packing was tighter during the summer than in spring or autumn. Species body sizes were regularly arranged between 5 and 25 mm, with an obvious gap between 12 and 14 mm, bordered by the two most common species. Habitat specialization occurred but complete lack of spatial overlap was found in only 8 of the potential 57 species-pair interactions.

The mean body size of carabid assemblages in woodlands, moors, and grasslands in northeastern England was related to several environmental factors (16). The outstanding factor was the level of disturbance that eliminated large species from the assemblage. Species body-size distribution within carabid assemblages was similarly displaced toward smaller values as disturbance from urbanization increased (179).

Coexistence and Competition

The occurrence and importance of competition among carabid beetles has been long debated. Generally, the evidence for interspecific competition as a regulatory force in populations is inconclusive, because of methodological limitations, unrealistic densities, noncomparable habitats, the methods used (examples in 142), and a general lack of experimental tests (142). Significant interspecific competition exists between adults of the North American *Carabus limbatus* and *Carabus sylvosus* (113). However, another study showed that most species do not compete in a western European beech forest (119). Similar conclusions emerge from evaluations of resource-partitioning descriptions; competition cannot be proven except in a few cases (44). In the sub-Antarctic, *Amblystogenium pacificum* and *Amblystogenium minimum* showed character displacement expected to result from competition (36).

These studies focused on the adult stage, but larvae have more restricted tolerance limits because of more restricted food range, mobility, and weaker chitinization, and are less adapted to evade resource shortages. Consequently, the importance of competition among larvae can be greater than that among adults (22, 92).

At the assemblage level, resource-partitioning patterns have been described in several studies (reviewed in 142), which have often invoked competition, present or past, as an explanation for the observed patterns of size distribution, food range, and seasonal or daily activity. These conclusions have generated lively but inconclusive debate (e.g. 44, 47 vs 118). Currently, there is no convincing evidence that competition has an important role in causing the observed patterns in carabid assemblages. A recent study on the invasion of a European carabid beetle into a Canadian forest (143) also showed a lack of competitive effects on the resident carabids.

The very concept of carabid communities is fallacious. This concept is based on a taxonomic affiliation, and carabids cannot even be considered to constitute an ecological guild. Although many carabid species can be classified as generalist predators, others that coexist with them clearly belong to different guilds. Carabids share the generalist, surface-active predator guild with at least some spiders and ants. For example, significant competition seems to take place between ants and ground beetles (205), so neglecting ants in "carabid community studies" leads to misleading conclusions.

ECONOMIC IMPORTANCE OF GROUND BEETLES

Occurrence in Agricultural Fields

Carabids are common in agricultural fields in the Northern Hemisphere. Since an early publication by Forbes (76), they have generally been considered beneficial natural enemies of agricultural pests, although a few species are pests themselves (126, 182). Thiele has synthesized the information on their biology, with special reference to their role as natural enemies (182); Allen (2) and Luff (126) have provided limited updates.

The carabid fauna of agricultural fields originates in riparian (182) or steppe

(121) habitats. Data are few outside those obtained in Europe and North America. In Canada, many species in cultivated land are either introduced European species (2, 171) or North American representatives of genera common in European agricultural fields, such as *Pterostichus, Harpalus,* or *Agonum.* In Japan, the fauna is similar to that of the European cultivated habitats at the generic level (126), although species of *Chlaenius* and *Carabus* can be abundant (207). In arid areas, Tenebrionidae are more prevalent than Carabidae (74). In New Zealand, carabids can be significant predators (10), but they are not as prevalent there as they are in northern cultivated fields (120).

Agriculture profoundly influences the composition, abundance, and spatial distribution of ground beetles through the use of agrochemicals, changes in habitat structure from cultivation methods and crop type, etc (57, 173; see reviews in 126, 182).

The Effectiveness of Carabids as Natural Enemies

Predator-prey studies have traditionally focused on interactions between specialist predators and their prey (90). Although *Calosoma sycophantha,* one of the first insects introduced for biological control (24), is such a specialist, most carabids do not fall into this category. The exploration of conditions under which generalist predators can limit prey has revealed that such predators are self-damping and highly polyphagous and that their life cycles are not in synchrony with their prey (38, 137). The ground beetles fit these criteria; they are self-damping during their larval stage (21), are polyphagous feeders (95), and having a long life cycle, are not normally tightly coupled to their prey. They can suppress pest outbreaks, but in general, their major beneficial role is to prolong the period between pest outbreaks, i.e. when the pest abundance is in the so-called natural enemy ravine (170). To increase carabids' effectiveness, biological control practitioners should consider the general habitat favorability that will keep carabids near their required site of action. A successful application of this technique could use habitat islands to serve as refuges and recolonization foci (128, 183).

The effectiveness of a natural enemy can be established through several sequential steps (123, 175, 206): 1. evaluating dynamics and correlating predator and pest density, 2. obtaining direct evidence of a trophic link between the prey and the predator, 3. experimentally manipulating predator density and its effect on pest numbers, 4. integrating the above information to quantify the effect of predator on prey.

Most studies of carabids and their prey are of the first and second type; fewer authors have considered steps 3 and 4. Well-founded evidence (gathered by means of all four steps above) for the significance of carabids as natural enemies comes from studies of polyphagous predators (carabids, spiders, staphylinids) in cereals in England (28, 60, 156, 164, 165, 178) showing that they can significantly decrease the peak density of aphids. Early-season predation, when aphid density is low, is the most significant. The relative importance of these predators varies among years and sites; often the effect cannot be attributed to one particular predator group. In some years, carabids are the most significant predators.

Carabids as Environmental Indicators

Carabids can and have been used as indicator organisms for assessments of environmental pollution (93), habitat classification for nature protection (127, 152), or characterization of soil-nutrient status in forestry (181). They might also serve as biodiversity indicators (N Stork, personal communication). However, most of the groups that are candidates for these purposes have not been subjected to a critical assessment using set criteria (150). Once we develop these criteria, we can realistically assess the suitability of ground beetles as indicator organisms.

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Literature Cited

1. Alderweireldt M, Desender K. 1990. Variation of carabid diel activity patterns in pastures and cultivated fields. See Ref. 173, pp. 335–38
2. Allen RT. 1979. The occurrence and importance of ground beetles in agricultural and surrounding habitats. See Ref. 68, pp. 485–507
3. Andersen J, Skorping A. 1991. Parasites of carabid beetles: prevalance depends on habitat selection of the host. *Can. J. Zool.* 69:1216–20
4. Arens W, Bauer T. 1987. Diving behaviour and respiration in *Blethisa multipunctata* in comparison with two other ground beetles. *Physiol. Entomol.* 12: 255–61
5. Aukema B. 1990. Wing-length determination in two wing-dimorphic *Calathus* species (Coleoptera: Carabidae). *Hereditas* 113:189–202
6. Aukema B. 1991. Fecundity in relation to wing-morph of three closely related species of the *melanocephalus* group of the genus *Calathus* (Coleoptera: Carabidae). *Oecologia* 87:118–26
7. Baars MA, van Dijk TS. 1984. Population dynamics of two carabid species in a Dutch heathland. II. Egg production and survival in relation to density. *J. Anim. Ecol.* 53:389–400
8. Ball GE. 1979. Conspectus of carabid classification: history, holomorphology and higher taxa. See Ref. 68, pp. 63–111
9. Barber H. 1931. Traps for cave-inhabiting insects. *J. Elisa Mitchell Sci. Soc.* 46:259–66
10. Barker GM. 1991. Biology of slugs

(Agrolimacidae and Arionidae: Mollusca) in New Zealand hill country pastures. *Oecologia* 85:581–95
11. Bauer T. 1979. The behavioural strategy used by imago and larva of *Notiophilus biguttatus* F. (Coleoptera, Carabidae) in hunting Collembola. See Ref. 53, pp. 133–42
12. Bauer T. 1986. How to capture springtails on the soil surface. The method of *Loricera pilicornis* F. See Ref. 50, pp. 43–48
13. Bauer T, Kredler M. 1993. Morphology of the compound eyes as an indicator of life-style in carabid beetles. *Can. J. Zool.* 71:799–810
14. Bernays EA, Bright KL, Gonzalez N, Angel J. 1994. Dietary mixing in a generalist herbivore: tests of two hypotheses. *Ecology* 75:1997–2006
15. Bils W. 1976. Das Abdomenende weiblicher, terrestrisch lebender Adephaga (Coleoptera) und seine Bedeutung fuer die Phylogenie. *Zoomorphologie* 84: 113–93
16. Blake S, Foster GN, Eyre MD, Luff ML. 1994. Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. *Pedobiologia* 38:502–12
17. Bleich OE. 1928. Thanatose und Hypnose bei Coleopteren. *Z. Wiss. Biol. Abt. A* 10:1–61
18. Blum MS. 1996. Semiochemical parsimony in the Arthropoda. *Annu. Rev. Entomol.* 41:291–312
19. Brandmayr P, den Boer PJ, Weber F, eds. 1983. *Ecology of Carabids: The Synthesis of Field Study and Laboratory Experiment.* Wageningen: Centre Agric. Publ. Doc. 196 pp.
20. Brandmayr P, Zetto-Brandmayr T. 1979. The evolution of parental care phenomena in Pterostichine ground beetles with special reference to the genera *Abax* and *Molops* (Col. Carabidae). See Ref. 53, pp. 35–49
21. Brunsting A, Heessen HJL. 1984. Density regulation in the carabid beetle *Pterostichus oblongopunctatus. J. Anim. Ecol.* 53:751–60
22. Brunsting A, Siepel H, van Schaik Zillesen PG. 1986. The role of larvae in the population ecology of Carabidae. See Ref. 52, pp. 399–411
23. Burakowski B. 1986. The life cycle and food preference of *Agonum quadripunctatum* (De Geer). See Ref. 50, pp. 35–39
24. Burgess AF. 1911. *Calosoma sycophanta:* its life history, behavior and successful colonization in New England. *US Dep. Agric. Bur. Entomol. Bull. 101*
25. Burmeister E-G. 1980. Funktsionsmorphologie und Evolution des Ovipositor der Adephaga (Coleoptera). *Verh. Naturwiss. Ver. Hamburg* 24:89–184
26. Butterfield JEL. 1986. Changes in lifecycle strategies of *Carabus problematicus* over a range of altitudes in Northern England. *Ecol. Entomol.* 11: 17–26
27. Calow P. 1979. The cost of reproduction—a physiological approach. *Biol. Rev.* 54:23–40
28. Chambers RJ, Sunderland KD, Wyatt IJ, Vickerman GP. 1983. The effects of predator exclusion and caging on cereal aphids in winter wheat. *J. Appl. Ecol.* 20:209–24
29. Chiverton PA. 1984. Pitfall-trap catches of the carabid beetle *Pterostichus melanarius,* in relation to gut contents and prey densities, in insecticide treated and untreated spring barley. *Entomol. Exp. Appl.* 36:23–30
30. Chiverton PA. 1988. Searching behaviour and cereal aphid consumption by *Bembidion lampros* and *Pterostichus cupreus,* in relation to temperature and prey density. *Entomol. Exp. Appl.* 47: 173–82
31. Churchfield JS, Hollier J, Brown VK. 1991. The effects of small mammal predators on grassland invertebrates, investigated by field exclosure experiment. *Oikos* 60:283–90
32. Cohen AC. 1995. Extraoral digestion in predaceous terrestrial Arthropoda. *Annu. Rev. Entomol.* 40:85–103
33. Colombini I, Chelazzi L, Scapini F. 1994. Solar and landscape cues as orientation mechanisms in the beachdwelling beetle *Eurynebria complanata* (Coleoptera, Carabidae). *Mar. Biol.* 118: 425–32
34. Crowson RA. 1981. *The Biology of the Coleoptera.* London: Academic. 802 pp.
35. Darlington PJ. 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas, and atrophy of wings. *Ecol. Monogr.* 13:37–61
36. Davies L. 1987. Long adult life, low reproduction and competition in two sub-Antarctic carabid beetles. *Ecol. Entomol.* 12:149–62
37. Davies MJ. 1953. The contents of the crops of some British carabid beetles. *Entomol. Mon. Mag.* 89:18–23
38. De Angelis DL, Goldstein Ra, O'Neill RV. 1975. A model for trophic interaction. *Ecology* 56:881–92
39. Deleted in proof
40. Deleted in proof
41. Deleurance S, Deleurance EP. 1964. Reproduction et cycle evolutif larvaire des *Aphenops* (*A. cerberus* Dieck, *A.*

crypticola Lindner), insectes Coleopteres cavernicoles. *C. R. Acad. Sci. Paris* 258:4369–70
42. den Boer PJ. 1970. On the significance of dispersal power for populations of carabid beetles (Coleoptera, Carabidae). *Oecologia* 4:1–28
43. den Boer PJ. 1977. Dispersal power and survival. Carabids in a cultivated countryside (with a mathematical appendix by J. Reddingius). *Misc. Pap. Landbouwhogesch. Wageningen* 14:1–190
44. den Boer PJ. 1980. Exclusion or coexistence and the taxonomic or ecological relationship between species. *Neth. J. Zool.* 30(2):278–306
45. den Boer PJ. 1986. What can carabid beetles tell us about dynamics of populations? See Ref. 52, pp. 315–30
46. den Boer PJ. 1987. On the turnover of carabid populations in changing environments. *Acta Phythopathol. Entomol. Hung.* 22:71–83
47. den Boer PJ. 1989. Comment on the article "On testing temporal niche differentiation in carabid beetles" by M. Loreau. *Oecologia* 81:97–98
48. den Boer PJ, ed. 1971. Dispersal and dispersal power of carabid beetles. *Misc. Pap. Landbouwh. Wageningen* 8:1–151
49. den Boer PJ, den Boer-Daanje W. 1990. On life history tactics in carabid beetles: Are there only spring and autumn breeders? See Ref. 173, pp. 247–58
50. den Boer PJ, Grüm L, Szyszko J, eds. 1986. *Feeding Behaviour and Accessibility of Food for Carabid Beetles.* Warsaw: Warsaw Agric. Univ. Press. 167 pp.
51. den Boer PJ, Lövei GL, Stork NE, Sunderland KD, eds. 1987. Proc. 6th European carabidologist meeting. *Acta Phytopathol. Entomol. Hung.* 22:1–458
52. den Boer PJ, Luff ML, Mossakowski D, Weber F, eds. 1986. *Carabid Beetles. Their Adaptations and Dynamics.* Stuttgart/New York: Fischer Verlag. 551 pp.
53. den Boer PJ, Thiele H-U, Weber F, eds. 1979. On the evolution of behavour in carabid beetles. *Misc. Pap. Agric. Univ. Wageningen* 18:1–222
54. den Boer PJ, van Huizen THP, den Boer–Daanje W, Aukema B, den Bieman CFM. 1980. Wing polymorphism and dimorphism as stages in an evolutionary process (Coleoptera, Carabidae). *Entomol. Gen.* 6:107–34
55. Dennison DF, Hodkinson ID. 1984. Structure of the predatory beetle community in a woodland soil ecosystem. V. Summary and conclusions. *Pedobiologia* 26:171–77
55a. de Ruiter PC, van Stralen MR, van Euwijk FA, Slob W, Bedaux JJM, Ernsting G. 1989. Effects of hunger and prey traces on the search activity of the predatory beetle *Notiophilus biguttatus. Entomol. Exp. Appl.* 51:87–95
56. Desender K. 1987. Heritability estimates for different morphological traits related to wing development and body size in the halobiont and wing polymorphic carabid beetle *Pogonus chalceus* Marsham (Coleoptera, Carabidae). *Acta Phythopathol. Entomol. Hung.* 22:85–101
57. Desender K, Dufrene M, Loreau M, Luff ML, Maelfait J-P, eds. 1994. *Carabid Beetles: Ecology and Evolution.* Ser. Entomol. 51. Dordrecht: Kluwer Academic. 474 pp.
58. Desender K, Maelfait J-P, D'Hulster M, Vanhercke L. 1981. Ecological and faunal studies on Coleoptera in agricultural land. I. Seasonal occurrence of Carabidae in the grassy edge of a pasture. *Pedobiologia* 22:379–84
59. Desender K, van den Broeck D, Maelfait J-P. 1985. Population biology and reproduction in *Pterostichus melanarius* Ill. (Coleoptera, Carabidae) from a heavily grazed pasture ecosystem. *Med. Fac. Landbouwwet. Rijksuniv. Gent* 50:567–75
59a. de Vries HH, den Boer PJ. 1990. Survival of populations of *Agonum ericeti* Panz. (Col., Carabidae) in relation to fragmentation of habitats. *Neth. J. Zool.* 40:484–98
60. Edwards CA, Sunderland KD, George KS. 1979. Studies of polyphagous predators of cereal aphids. *J. Appl. Ecol.* 16:811–23
61. Eisner T, Hurst JJ, Meinwald T. 1963. Defensive mechanisms of arthropods. XI. The structure, function and phenolic secretion of the glands of a chordeumid millipede and a carabid beetle. *Psyche* 70:94–116
62. Erbeling L. 1987. Thermal ecology of the desert carabid beetle *Thermophilum (Anthia) sexmaculatum* F. (Coleoptera, Carabidae). *Acta Phytopathol. Entomol. Hung.* 22:119–33
63. Ernsting G, Isaaks JA. 1991. Accelerated ageing: a cost of reproduction in the carabid beetle *Notiophilus biguttatus. Func. Ecol.* 5:299–303
64. Erwin TL. 1979. Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analysis of lowland forest sites in temperate and tropical regions. See Ref. 68, pp. 539–92
65. Erwin TL. 1979. A review of the natural

history and evolution of ectoparasitoid relationships in carabid beetles. See Ref. 68, pp. 479–84
66. Erwin TL. 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. In *Taxonomy, Phylogeny and Zoogeography of Beetles and Ants,* ed. GE Ball, pp. 437–72. Dordrecht: Junk. 514 pp.
67. Erwin TL, Adis J. 1982. Amazonian inundation forests: their role as short-term refuges and generators of species richness and taxon pulses. In *Biological Diversification in the Tropics,* ed. G Prance, pp. 358–71. New York: Columbia Univ. Press. 714 pp.
68. Erwin TL, Ball GE, Whitehead DL, Halpern AL, eds. 1979. *Carabid Beetles: Their Evolution, Natural History and Classification.* The Hague: Junk. 635 pp.
69. Evans MEG. 1977. Locomotion in the Coleoptera Adephaga, especially Carabidae. *J. Zool.* 181:189–226
70. Evans MEG. 1986. Carabid locomotor habits and adaptations. See Ref. 52, pp. 59–77
71. Evans MEG, Forsythe TG. 1985. Feeding mechanisms, and their variation in form, of some adult ground-beetles (Coleoptera: Caraboidea). *J. Zool.* 206: 113–43
72. Evans WG. 1988. Chemically mediated habitat recognition in shore insects (Coleoptera: Carabidae; Hemiptera: Saldidae). *J. Chem. Ecol.* 14:1441–54
73. Eyre MD. 1994. Strategic explanations of carabid species distributions in northern England. See Ref. 57, pp. 267–75
74. Faragalla AA, Adam EE. 1985. Pitfall trapping of tenebrionid and carabid beetles (Coleoptera) in different habitats of the central region of Saudi Arabia. *Z. Angew. Entomol.* 99:466–71
75. Fiori G. 1974. Contributi alla conoscenza morfologica et etologica dei Coleotteri. X. La "sutura" elitrale. *Boll. Ist. Entomol. Univ. Bologna* 31:129–52
76. Forbes SA. 1883. The food relations of the Carabidae and the Coccinellidae. *Bull. Ill. State Lab. Nat. Hist.* 1:33–64
77. Forsyth DJ. 1972. The structure of the pygidial defence glands of Carabidae (Coleoptera). *Trans. Zool. Soc. London* 32:249–309
78. Forsythe TG. 1980. Sound production in *Amara familiaris* Duft with a review of sound production in British Carabidae. *Entomol. Mon. Mag.* 115:177–79
79. Forsythe TG. 1982. Qualitative analyses of certain enzymes of the oral defence fluids of *P. madidus. Entomol. Mon. Mag.* 118:1–5
80. Forsythe TG. 1987. *Common Ground Beetles. Naturalists' Handbook 8.* Richmond: Richmond Publishing. 74 pp.
81. Freeland WJ. 1983. Parasites and the coexistence of animal host species. *Am. Nat.* 121:223–36
82. Freitag R, Lee SK. 1972. Sound producing structures in adult *Cicindela tranquebarica* (Coleoptera: Cicindelidae) including a list of tiger beetles and ground beetles with flight wing files. *Can. Entomol.* 104:851–57
83. Gergely G, Lövei GL. 1987. Phenology and reproduction of the ground beetle *Dolichus halensis* in maize fields: a preliminary report. *Acta Phytopathol. Entomol. Hung.* 22:357–61
84. Greenslade PJM. 1963. Daily rhythms of locomotory activity in some Carabidae (Coleoptera). *Entomol. Exp. Appl.* 6:171–80
85. Grime JP. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111: 1169–94
86. Grüm L. 1984. Carabid fecundity as affected by extrinsic and intrinsic factors. *Oecologia* 65:114–21
87. Haeck J. 1971. The immigration and settlement of Carabida in the new IJsselmeerpolders. See Ref. 48, pp. 33–52
88. Halsall NB, Wratten SD. 1988. The efficiency of pitfall trapping for polyphagous predatory Carabidae. *Ecol. Entomol.* 13:293–99
89. Hammond PM. 1979. Wing-folding mechanisms of beetles, with special reference to investigations of Adephagan phylogeny. See Ref. 68, pp. 113–80
90. Hassell MP. 1978. *The Dynamics of Arthropod Prey-Predator Systems.* Princeton: Princeton Univ. Press. 237 pp.
91. Heessen HJL. 1981. Egg mortality in *P. oblongopunctatus* (Coleoptera, Carabidae). *Oecologia* 50:233–35
92. Heessen HJL, Brunsting AMH. 1981. Mortality of larvae of *P. oblongopunctatus* (Coleoptera, Carabidae) and *Philonthus decorus* (Coleoptera, Carabidae). *Neth. J. Zool.* 31:729–45
93. Heliovaara K, Vaisanen R. 1993. *Insects and Pollution.* Boca Raton: CRC Press. 393 pp.
94. Hengeveld R. 1980. Food specialization in ground beetles: an ecological or a phylogenetic process? (Coleoptera, Carabidae). *Neth. J. Zool.* 30:585–94
95. Hengeveld R. 1980. Polyphagy, oligophagy and food specialisation in ground beetles (Coleoptera, Carabidae). *Neth. J. Zool.* 30:564–84

96. Hlavac TF. 1971. Differentiation of the carabid antenna cleaner. *Psyche* 78:51–66
97. Horne PA. 1990. Parental care in *Notonomus* Chaudoir (Coleoptera: Carabidae: Pterostichinae). *Aus. Entomol. Mag.* 17:65–69
98. Horvatovich S, Szarukán I. 1986. Faunal investigation of ground beetles (Carabidae), in the arable soils of Hungary. *Acta Agron. Hung.* 35:107–23
99. Houston WWK. 1981. The life cycles and age of *Carabus glabratus* Paykull and *C. problematicus* Herbst. (Col.: Carabidae) on moorland in northern England. *Ecol. Entomol.* 6:263–71
100. Hurka K. 1986. The developmental type of Carabidae in the temperate zones as a taxonomic character. See Ref. 52, pp. 187–93
101. Jaspar-Versali MF, Goffinet G, Jeuniaux C. 1987. The digestive system of adult carabid beetles: an ultrastructural and histoenzymological study. *Acta Phytopathol. Entomol. Hung.* 22:375–82
102. Jones MG. 1979. The abundance and reproductive activity of common carabidae in a winter wheat crop. *Ecol. Entomol.* 4:31–43
103. Kamoun S. 1991. Parasematic coloration: a novel anti-predator mechanism in tiger beetles (Coleoptera: Cicindelidae). *Coleopt. Bull.* 45:15–19
104. Kane TC, Ryan T. 1983. Population ecology of carabid cave beetles. *Oecologia* 60:46–55
105. Kanehisa K, Murase M. 1977. Comparative study of the pygidial defensive systems of carabid beetles. *Appl. Entomol. Zool.* 12:225–35
106. Kegel B. 1990. Diurnal activity of carabid beetles living on arable land. See Ref. 173, pp. 65–76
107. Kennedy P. 1994. The distribution and movement of ground beetles in relation to set-aside arable land. See Ref. 57, pp. 439–44
108. Larochelle A. 1975. A list of mammals as predators of Carabidae. *Carabologia* 3:95–98
109. Larochelle A. 1975. A list of amphibians and reptiles as predators of Carabidae. *Carabologia* 3:99–103
110. Larochelle A. 1980. A list of birds of Europe and Asia as predators of carabid beetles including Cicindelini (Coleoptera: Carabidae). *Cordulia* 6:1–19
111. Larochelle A. 1990. The food of carabid beetles. *Fabreries Suppl.* 5:1–132
112. Lawrence JF, Britton EB. 1991. Coleoptera. In *The Insects of Australia,* 2:543–683. Melbourne: Melbourne Univ. Press. 1137 pp. 2nd ed.
113. Lenski RE. 1984. Food limitation and competition: a field experiment with two Carabus species. *J. Anim. Ecol.* 53:203–16
114. Lindroth CH. 1949. *Die Fennoskandischen Carabiden,* Part 3, *Algemeiner Teil.* Stockholm: Bröderna Lagerström Boktrychare. 911 pp.
115. Lindroth CH. 1969. The ground beetles (Carabidae excl. Cicindelidae), of Canada and Alaska, Part 1. *Opusc. Entomol. Suppl.* 25:1–48
116. Lindroth CH. 1971. Disappearance as a protective factor. A supposed case of Batesian mimicry among beetles (Coleoptera, Carabidae and Chrysomelidae). *Entomol. Scand.* 2:41–48
117. Lindroth CH. 1979. The theory of glacial refugia. See Ref. 68, pp. 385–94
118. Loreau M. 1989. On testing temporal niche differentiation in carabid beetles. *Oecologia* 81:89–96
119. Loreau M. 1990. Competition in a carabid beetle community: field experiment. *Oikos* 58:25–38
120. Lövei GL. 1991. The ground-dwelling predatory arthropod fauna in an organic and abandoned kiwifruit orchard. In *Proc. Symp. Sustainable Agriculture and Organic Food Production, Trentham, New Zealand,* ed. IA Popay, pp. 9–14. Christchurch: NZ Inst. Agric. Sci./NZ Hort. Soc.
121. Lövei GL, Sárospataki M. 1990. Carabids in eastern European agricultural fields: a review. See Ref. 173, pp. 87–93
122. Lövei GL, Sopp PI, Sunderland KD. 1990. Digestion rate in relation to alternative feeding in three species of polyphagous predators. *Ecol. Entomol.* 15:291–300
123. Luck RF, Shepard BM, Kenmore PE. 1988. Experimental methods for evaluating arthropod natural enemies. *Annu. Rev. Entomol.* 33:367–91
124. Luff ML. 1978. Diel activity patterns of some field Carabidae. *Ecol. Entomol.* 3:53–62
125. Luff ML. 1982. Population dynamics of Carabidae. *Ann. Appl. Biol.* 101:164–70
126. Luff ML. 1987. Biology of polyphagous ground beetles in agriculture. *Agric. Zool. Rev.* 2:237–78
127. Luff ML, Eyre MD, Rushton SP. 1992. Classification and prediction of grassland habitats using ground beetles (Coleoptera, Carabidae). *J. Environ. Manage.* 35:301–15
128. Lys J-A. 1994. The positive influence of strip-management on ground beetles

in a cereal field: increase, migration and overwintering. See Ref. 57, pp. 451–55

129. Makarov KV. 1994. Annual reproduction rhythms of ground beetles: a new approach to the old problem. See Ref. 57, pp. 177–82
130. Mascanzoni D, Wallin H. 1986. The harmonic radar: a new method of tracing insects in the field. *Ecol. Entomol.* 11: 387–90
131. Metzenauer P. 1981. Pattern of the intestinal enzymes of the carnivorous ground beetle *Ptereostichus nigrita* (Paykull) (Col. Carabidae). *Zool. Anz.* 207:113–19
132. Mols PJM. 1979. Motivation and walking behaviour of the carabid beetle *Pterostichus coerulescens* L. at different densities and distributions of the prey. See Ref. 53, pp. 185–98
133. Mols PJM. 1988. Simulation of hunger, feeding and egg production in the carabid beetle *Pterostichus coerulescens* L. *Agric. Univ. Wageningen. Pap.* 88–3:1–99
134. Moore BP. 1979. Chemical defense in carabids and its bearing on phylogeny. See Ref. 68, pp. 193–203
135. Moosbeckhofer R. 1983. Laboruntersuchungen ueber den Einfluss von Diazinon, Carbofuran und Chlorfenvinphos auf die Laeufaktivitaet von *Poecilus cupreus* L. (Col., Carabidae). *Z. Angew. Entomol.* 95:15–21
136. Murdoch WW. 1966. Aspects of the population dynamics of some marsh Carabidae. *J. Anim. Ecol.* 35:127–56
137. Murdoch WW, Chesson J, Chesson PL. 1985. Biological control in theory and practice. *Am. Nat.* 125:344–66
138. Nelemans MNE. 1987. Possibilities for flight in the carabid beetle *Nebria brevicollis* (F.). The importance of food during the larval growth. *Oecologia* 72: 502–9
139. Nelemans MNE, den Boer PJ, Spee A. 1989. Recruitment and summer diapause in the dynamics of a population of *Nebria brevicollis* (Coleoptera: Carabidae). *Oikos* 56:157–69
140. New TR. 1991. *Insects as Predators.* Kensington: NSW Univ. Press. 178 pp.
141. Niemela J. 1990. Spatial distribution of carabid beetles in the Southern Finnish taiga: the question of scale. See Ref. 173, pp. 143–55
142. Niemela J. 1993. Interspecific competition in ground-beetle assemblages (Carabidae)—what have we learned. *Oikos* 66:325–35
143. Niemela J, Spence JR. 1991. Distribution and abundance of an exotic ground-beetle (Carabidae)—a test of community impact. *Oikos* 62:351–59
144. Niemela J, Spence JR. 1994. Distribution of forest dwelling carabids (Coleoptera)—spatial scale and the concept of communities. *Ecography* 17:166–75
145. Nilsson AN, Pettersson RB, Lemdahl G. 1993. Macroptery in altitudinal specialists versus brachyptery in generalists—a paradox of alpine Scandinavian carabid beetles (Coleoptera, Carabidae). *J. Biogeogr.* 20:227–34
146. Paarmann W. 1986. Seasonality and its control by environmental factors in tropical ground beetles (Col. Carabidae). See Ref. 52, pp. 157–71
147. Pakarinen E. 1994. The importance of mucus as a defence against carabid beetles by the slugs *Arion fasciatus* and *Deroceras reticulatum*. *J. Mollusc. Stud.* 60:149–55
148. Parmenter RR, MacMahon JA. 1988. Factors influencing species composition and population sizes in a ground beetle community (Carabidae): predation by rodents. *Oikos* 52:350–56
149. Pearson DL. 1988. The biology of tiger beetles. *Annu. Rev. Entomol.* 33:123–47
150. Pearson DL, Cassola F. 1992. World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Cons. Biol.* 6:376–91
151. Penev LD, Turin H. 1994. Patterns of distribution of the genus *Carabus* L. in Europe: approaches and preliminary results. See Ref. 57, pp. 37–43
152. Pizzolotto R. 1994. Ground beetles (Coleoptera, Carabidae) as a tool for environmental management: a geographical information system based on carabids and vegetation for the Karst near Trieste (Italy). See Ref. 57, pp. 343–51
153. Poinar GO. 1975. *Entomogenous Nematodes. A Manual and Host List of Insect-Nematode Associations.* Leiden: Brill
154. Pollet M, Desender K. 1987. Feeding ecology of grassland-inhabiting carabid beetles (Carabidae, Coleoptera) in relation to the availability of some prey groups. *Acta Phytopathol. Entomol. Hung.* 22:223–46
155. Ponomarenko AG. 1977. Mesozoic Coleoptera. *Trans. Paleontol. Inst.* Moscow 161:1–204
156. Potts GR, Vickerman GP. 1974. Studies on the cereal ecosystem. *Adv. Ecol. Res.* 8:107–97
157. Price PW. 1980. *Evolutionary Biology of Parasites.* Princeton: Princeton Univ. Press

158. Refseth D. 1984. The life cycles and growth of *Carabus glabratus* and *C. violaceus* in Budelan, central Norway. *Ecol. Entomol.* 9:449–55
159. Rijnsdorp AD. 1980. Pattern of movement in and dispersal from a Dutch forest of *Carabus problematicus* Hbst (Coleoptera, Carabidae). *Oecologia* 45: 274–81
160. Roff DA. 1994. The evolution of flightlessness: Is history important? *Evol. Ecol.* 8:639–57
161. Rusdea E. 1994. Population dynamics of *Laemostenus schreibersi* (Carabidae) in a cave in Carinthia (Austria). See Ref. 57, pp. 207–12
162. Simpson SJ, Simpson CL. 1990. The mechanisms of nutritional compensation by phytophagous insects. In *Insect-Plant Interactions*, ed. EA Bernays, 2:111–60. Boca Raton, FL: CRC
163. Skuhravy V. 1959. Die Nährung der Feldcarabiden. *Acta Soc. Entomol. Cech.* 56:1–18
164. Sopp PI, Sunderland KD. 1989. Some factors affecting the detection period of aphid remains in predators using ELISA. *Entomol. Exp. Appl.* 51:11–20
165. Sopp PI, Sunderland KD, Fenlon J, Wratten SD. 1992. An improved quantitative method for estimating invertebrate predation in the field using an enzyme-linked immunosorbent assay (ELISA). *J. Appl. Ecol.* 29:295–302
166. Sota T. 1984. Long adult life span and polyphagy of a carabid beetle, *Leptocarabus kumagaii* in relation to reproduction and survival. *Res. Popul. Ecol.* 26:389–400
167. Sota T. 1985. Limitation of reproduction by feeding condition in a carabid beetle, *Carabus yaconinus*. *Res. Popul. Ecol.* 27:171–84
168. Sota T. 1987. Mortality pattern and age structure in two carabid populations with different seasonal life cycles. *Res. Popul. Ecol.* 29:237–54
169. Southwood TRE. 1978. The components of diversity. In *Diversity of Insect Faunas*, ed. LA Mound, N Waloff, pp. 19–40. Oxford: Blackwell. 204 pp.
170. Southwood TRE, Comins HN. 1976. A synoptic population model. *J. Anim. Ecol.* 45:949–65
171. Spence JR, Spence DH. 1988. Of ground beetles and man: introduced species and the synanthropic fauna of western Canada. *Mem. Entomol. Soc. Can.* 144:151–68
172. Stork NE. 1987. Adaptations of arboreal carabids to life in trees. *Acta Phytopathol. Entomol. Hung.* 22:273–91
173. Stork NE, ed. 1990. *The Role of Ground Beetles in Ecological and Environmental Studies*. Andover: Intercept. 424 pp.
174. Sturani M. 1962. Osservazioni e ricerche biologiche sul genere *Carabus* Linnaeus (sensu lato) (Coleoptera: Carabidae). *Mem. Soc. Entomol. Ital.* 41:85–202
175. Sunderland KD. 1987. A review of methods of quantifying invertebrate predation occurring in the field. *Acta Phytopathol. Entomol. Hung.* 22:13–34
176. Sunderland KD, de Snoo GR, Dinter A, Hance T, Helenius J, et al. 1995. Density estimation for invertebrate predators in agroecosystems. *Acta Jutl.* In press
177. Sunderland KD, Lövei GL, Fenlon J. 1995. Diets and reproductive phenologies of the introduced ground beetles *Harpalus affinis* and *Clivina australasiae* (Coloeptera: Carabidae) in New Zealand. *Aust. J. Zool.* 43:39–50
178. Sunderland KD, Vickerman GP. 1980. Aphid feeding by some polyphagous predators in relations to aphid density in cereal fields. *J. Appl. Ecol.* 17:389–96
179. Sustek Z. 1987. Changes in body size structure of carabid communities (Coleoptera, Carabidae) along an urbanisation gradient. *Biologia* 42:145–56
180. Symondson WOC, Liddell JE, eds. 1995. *The Ecology of Agricultural Pests: Biochemical Approaches. Systematics Assoc. Special Vol. Ser. No. 53*. London: Chapman & Hall
181. Szyszko J. 1983. *State of Carabidae (Col.) Fauna in Fresh Pine Forest and Tentative Valorisation of This Environment*. Warsaw: Warsaw Agric. Univ. Press. 80 pp.
182. Thiele H-U. 1977. *Carabid Beetles in Their Environments*. Berlin/Heidelberg: Springer-Verlag. 369 pp.
183. Thomas MB, Wratten SD, Sotherton NW. 1991. Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods: predator densities and emigration. *J. Appl. Ecol.* 28:906–17
184. Turin H, den Boer PJ. 1988. Changes in the distribution of carabid beetles in the Netherlands since 1880. II. Isolation of habitats and long-term time trends in the occurrence of carabid species with different powers of dispersal (Coleoptera, Carabidae). *Biol. Conserv.* 44:179–200
185. Turin H, Peters H. 1986. Changes in the distribution of carabid beetles in the Netherlands since about 1880. I. Introduction. See Ref. 52, pp. 489–95
186. van Dijk TS. 1972. The significance of the diversity in age composition

of *Calathus melanocephalus* L. (Coleoptera, Carabidae) in space and time at Schiermonnikoog. *Oecologia* 10:111–36
187. van Dijk TS. 1983. The influence of food and temperature on the amount of reproduction in carabid beetles. See Ref. 19, pp. 105–23
188. van Dijk TS. 1987. The long-term effects on the carabid fauna of nutrient impoverishment of a previously arable field. *Acta Phytopathol. Entomol. Hung.* 22:103–18
189. van Dijk TS. 1994. On the relationship between food, reproduction and survival of two carabid beetles: *Calathus melanocephalus* and *Pterostichus versicolor. Ecol. Entomol.* 19:263–70
190. van Huizen THP. 1977. The significance of flight activity in the life cycle of *Amara plebeja* Gyllh. (Coleoptera, Carabidae). *Oecologia* 29:27–41
191. van Huizen THP. 1979. Individual and environmental factors determining flight in carabid beetles. See Ref. 53, pp. 199–211
192. van Huizen THP. 1990. 'Gone with the wind': flight activity of carabid beetles in relation to wind direction and to the reproductive state of females in flight. See Ref. 173, pp. 289–93
193. Vlijm L, van Dijk TS, Wijmans YS. 1968. Ecological studies on carabid beetles. III. Winter mortality in adult *Calathus melanocephalus* (Linn.). Egg production and locomotory activity of the population which has hibernated. *Oecologia* 1:304–14
194. Wallin H. 1988. The effects of spatial distribution on the development and reproduction of *Pterostichus cupreus* L., *P. melanarius* Illiger, *P. niger* Schaller and *Harpalus rufipes* De Geer (Coleoptera, Carabidae) on arable land. *J. Appl. Entomol.* 106:483–87
195. Wallin H. 1991. Movement patterns and foraging tactics of a caterpillar hunter inhabiting alfalfa fields. *Funct. Ecol.* 5:740–49
196. Wallin H, Chiverton PA, Ekbom BS, Borg A. 1992. Diet, fecundity and egg size in some polyphagous predatory carabid beetles. *Entomol. Exp. Appl.* 65: 129–40
197. Ward RD. 1979. Metathoracic wing structures as phylogenetic indicators in the Adephaga (Coleoptera). See Ref. 68, pp. 181–91
198. Wasner U. 1977. Zur Oekologie und Biologie sympatrischer *Agonum* (*Europhilus*)—Arten (Carabidae, Coleoptera). I. Individual Entwicklung und Gonadenreifung, Generationsaufbau, Eiproduktion und Fruchtbarkeit. *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere* 106:105–23
199. Weber F, Casale A, Lamprecht G, Rusdea E. 1994. Highly sensitive reactions of microphthalmic carabid beetles to light/dark cycles. See Ref. 57, pp. 219–25
200. Weber F, Klenner M. 1987. Life history phenomena and risk of extinction in a subpopulation of *Carabus auronitens. Acta Phytopathol. Entomol. Hung.* 22: 321–28
201. Weseloh RM. 1993. Adult feeding affects fecundity of the predator, *Calosoma sycophanta* (Col, Carabidae). *Entomophaga* 38:435–39
202. Wheater CP. 1989. Prey detection by some predatory Coleoptera (Carabidae and Staphylinidae). *J. Zool.* 218:171–85
203. Wiedenmann RN, O'Neill RJ. 1990. Effects of low rates of predation on selected life-history characteristics of *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae). *Can. Entomol.* 122: 271–83
204. Williamson M. 1972. *The Analysis of Insect Populations.* London: Arnold. 180 pp.
205. Wilson EO. 1990. *Success and Dominance in Ecosystems: The Case of the Social Insects.* Oldendorf: Ecology Inst. 104 pp.
206. Wratten SD. 1987. The effectiveness of native natural enemies. In *Integrated Pest Management,* ed. AJ Burn, TH Coaker, PC Jepson, pp. 89–112. London: Academic
207. Yano K, Yahiro K, Uwada M, Hirashima T. 1989. Species composition and seasonal abundance of ground beetles (Coleoptera) in a vineyard. *Bull. Fac. Agric. Yamaguchi Univ.* 37:1–14
208. Zetto Brandmayr T. 1983. Life cycle, control of propagation rhythm and fecundity of *Ophonus rotundicollis* Fairm. et. Lab. (Coleoptera, Carabidae, Harpalini) as an adaption to the main feeding plant *Daucus carota* L. (Umbelliferae). See Ref. 19, pp. 93–103
209. Zetto-Brandmayr T. 1990. Spermophagous (seed-eating) ground beetles: first comparison of the diet and ecology of the Harpaline genera *Harpalus* and *Ophonus* (Col. Carabidae). See Ref. 173, pp. 307–16

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