Ecology and conservation biology of ground beetles (Coleoptera: Carabidae) in an age of increasing human dominance

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Introduction

One of the famous sayings of modern entomology is provided by the evolutionary biologist, B.S. Haldane. At a debate with his theologist colleague, he was asked what he had discovered about the Lord during his lifetime of studying His creation. "That He has an inordinate fondness for beetles" replied Haldane with aplomb (Evans & Bellamy 1996).

The basis of Haldane's statement is that the order of beetles, Coleoptera is the most species-rich on Earth. Within beetles, one can argue, the ground beetles, Carabidae must be one of His favourites, because among beetles, this family is one of the most speciose ones. It should be no surprise then, that the study of the family of ground beetles is also very popular. A search made on the Web of Science database resulted in >3000 publications, published between 1996 and 2005, that were dealing with ground beetles.

This field of study therefore cannot be considered esoteric, the domain of a few specialists. I started my research on carabids in 1978, one year after the premature death of the eminent German carabidologist, Hans-Ulrich Thiele, and the publication of his influential treatise on ground beetles (Thiele 1977) in which he summarised, in an almost encyclopaedic manner, our knowledge about the ecology of ground beetles. According to the then-current ecological paradigm, this book was mostly descriptive, with an emphasis on environmental physiology, cultivated by Thiele himself at a high level. The following 30 years brought new ideas and rapid progress, especially in ecology, and especially in Europe. Several researchers (e.g. Piet den Boer and his co-workers in the Netherlands) started their detailed, long-term studies that unearthed several important, so far unknown aspects of the ecology of ground beetles: the pattern and causes of long-term fluctuations of species, dispersal, population survival. These were laying the foundation for several new areas, including metapopulation theory, ecological restoration, and conservation biology. Others extended the methodological toolkit, making it possible to study phenomena, even quantitatively, that were unavailable due to methodological limitations. These included the use of the harmonic radar in habitat use studies (Mascanzoni & Wallin 1986), the adoption of biochemical (isoenzyme activity, Lövei 1986) and immunological (ELISA, Crook & Sunderland 1984) methods to study feeding, the combination of laboratory and field methods in population biology (Baars & van Dijk 1984).

My overall aim was to study the population and assemblage patterns of ground beetles living in human-influenced habitats. In our age, sometimes called "homogeocene", this meant more and more of our globe. Human influence is ever increasing, causing a homogenisation of the global flora and fauna ("Macdonaldisation", Lövei 1997), raising the global extinction rate by at least two orders of magnitude (Lövei 2007), and appropriating an ever-increasing share of globally available resources. These developments had a unifying influence on the study (also, but not only) of carabids.

This Thesis summarises my studies on ground beetles in five sub-areas. For any field of science, it is important to have periodical reviews, syntheses of known information. The first part is based on such a review (Lövei & Sunderland 1996), and briefly describes the main features of the ecology and behaviour of ground beetles. The second part presents a few methodological innovations that may offer potential for the further development of the field. Among them there are field as well as data evaluation methods.

The third part concerns life history studies. Knowledge of the biology of the study organisms in ecology is essential. Superficial knowledge in this regard can easily derail ecological studies (on such example is discussed in Lövei & Magura 2006), Therefore it is not only natural, but an obligation for an ecologists to contribute to our still-fragmentary knowledge on life histories. This may be a near-endless task because we can hardly declare that we know "everything there is worth knowing" about a species. The current situation is, however, very differernt: a large part of the known arthropods are represented in collections by a single specimen (singletons), about which we know nothing except the location of its single occurrence and species name (Allison & al. 1997.). With my colleagues, I have been involved in studying life history traits of ground beetles in Hungary, New Zealand an Denmark. Part III is based on this work.

Part IV is devoted to studies on ground beetles, both at species and assemblage level, in habitats under anthropogenic influence. First results of studies with hedgerows are presented that show that forest faunal elements can be maintained in an agricultural landscape in Denmark. Second, the impact of an urbanisation gradient (forest- suburban forest – forest fragment in urban park) on ground beetles is explored. In order to analyse the impact of urbanisation on arthropod (ground beetle) diversity, species richness trends are not instructive – in our Danish study site, the most species rich site was the urban forest fragment. This, however, maksed several important effects of urbanisation on ground beetles.

Included are studies linked to the environmental impact of genetically manipulated plants. The reason is that ground beetles are important in biological control, nutrient cycling, and linking above-and belowground ecological systems, and the genetically manipulated plants can influence these (positively or negatively). Consequently, it is important to include beneficial arthropods (including ground beetles) into environmental impact evaluations. Currently, there are few studies (of mostly short duration) concerning the impact of transgenic plants on biological control agents (Lövei & Arpaia 2005).

The study of a single, well defined group is interesting in itself, but it is also important to link such results to theoretical knowledge. Results emerging from the study of ground beetles have been important to develop ecological theory (for example the long-term studies by den Boer (1987) that lead to the concept of metapopulations) albeit not to the extent that their abundance, wide occurrence and the amount of knowledge would justify. Results related to theoretical aspects are summarised in the fifth part, which contains results from Europe as well as New Zealand.

Part I: The ecology and behaviour of ground beetles

The family Carabidae, the ground beetles, contains more than 40,000 described species classified into some 86 tribes (Erwin 1985). 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 (Lawrence & Britton 1991). They are well-proportioned cursorial beetles with prominent mandibles and palps, long slender legs, striate 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 (Crowson 1981). Different authors divide the family into different subfamilies; except for the tiger beetles (see Pearson 1988), our ecological knowledge is scant concerning subfamilies outside the Carabinae [sensu Lawrence & Britton 1991]. The abundance, species richness, and attractive coloration of many species have made carabids popular objects of study for both professional and amateur entomologists.

Carabids are present worldwide, with species richness highest in the tropical regions (Erwin 1985). However, our knowledge mainly stems from research done in the temperate regions of the Northern Hemisphere. The resulting bias is inevitable. The examples below 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 are one of the dominant predatory invertebrate groups (Erwin & Adis 1982). Through a series of taxon pulses, they have radiated to drier environments as well as higher latitudes and a1titudes (Erwin 1979a). By the late Permian- early Triassic, several lineages developed a cosmopolitan distribution pattern, as demonstrated by the fossil record (Ponomarenko 1977). 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 (Evans 1977, 1986). 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.) (Erwin 1985). Several other structural, physiological, and behavioural 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 (Erwin 1985). This distribution pattern suggests that humidity is a general limiting factor. The main structural pat-

terns in carabid evolution are flightlessness and arboreal, fossorial, and troglobitic adaptations (Erwin 1985). Flightlessness has repeatedly evolved in many groups (Darlington 1943). In the tropics, >30% of species are arboreal, exhibiting special morphological and behavioural adaptations (Stork 1987).

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 (Sunderland et al 1995a); labor-intensive dissections or sophisticated immunological methods to study feeding (Symondson & Liddell 1995); the use of video equipment to record walking (Halsall & Wratten 1988), searching, and feeding (Chiverton 1988) behaviour; and the use of harmonic radar to study within-habitat movements (Mascanzoni & Wallin 1986). The most popular method is pitfall trapping.

A pitfall trap or Barber-trap (Barber 1931) 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 behaviour.

Pitfall trapping is the most frequently used field method for studying carabids. Although this method is surrounded by controversy and several critical papers (Sunderland et al 1995a 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 behavioural 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 (Luff 1987, Thiele 1977). The female carefully chooses the ovipositing site, sometimes excavating a chamber for the eggs. Some Pterostichini prepare a cocoon for a batch of eggs (Brandmayr & Zetto-Brandmayr 1979). Parental care, at its most developed, consists of no more

than egg guarding or caching seeds in the egg chamber for the emerging larvae (Brandmayr & Zetto-Brandmayr 1979, Horne 1990).

The typical carabid larva is free moving and campodeiform (Crowson 1981) 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 (Erwin 1979b), total 24% of all carabid tribes [in Erwin's classification (Erwin 1979a)]. 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 sclerotised and whitish pupa lays on its back, supported by dorsal setae. Sclerotisation 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 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 (Houston 1981) and in Norway (Refseth 1984). In northern England, *Carabus problematicus* has an annual life cycle below 800m and a biennial one above that altitude (Butterfield 1986). 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 (Weber & Klenner 1987).

Adult longevity can also exceed one season. Individuals from several species have keen kept in the laboratory for up to four years. Individuals from field populations of several species from different parts of the world, for example, Europe (Gergely & Lövei 1987, Houston 1981, Luff 1982), Japan (Sota 1984), and the sub-Antarctic (Davies 1987), can live up to four years and reproduce more than once. Generally, long adult life span is more common in large species and species with winter larvae [also called autumn breeders (den Boer & den Boer-Daanje 1990)] than in ones with summer larvae (spring breeders).

Several species show plasticity of individual development, whereas others seem to have a stable life cycle. 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 (Nelemans et al. 1989). 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 favourable 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 (Colombini et al. 1994), and orientation either toward or away from silhouettes (Colombini et al. 1994, Rijnsdorp 1980). Some riparian ground beetles find their habitat by sensing volatile chemicals emitted by blue algae living in the same habitat (Evans 1988). *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 (Burakowski 1986). Carabids continuously sample their surroundings. For example, *Carabus nemoralis* walks around in different habitats before settling in seminatural habitats in preference to set-aside to arable areas (Kennedy 1994).

Habitat and microhabitat distribution can be influenced by several factors:

1. Temperature or humidity extremes (several examples in Thiele 1977). Favourite wintering sites are well aerated, and winter minimum temperatures are relatively high (Desender et al. 1981, Thomas et al.1991).

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 (Zetto-Brandmayr 1990). 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 in the reverse direction (Lys 1994).

3. Presence and distribution of competitors. For example, forest carabids in Finland were influenced by the distribution of *Formica* ant species (Niemela 1990).

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 (van Huizen 1977).

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 Thiele 1977), 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 m^{-2} (at suitable overwintering sites, *see* Table 1.1).

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 (Roff 1994). Once the benefits of flight do not match its costs, as on, for example, islands and mountain tops, it is quickly lost (Darlington 1943). 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% flight-less, a condition reached through nine or more independent evolutionary transitions (Roff 1994).

Environmental conditions may influence expression of the dimorphism (Aukema 1991). Flight ability varies little between the sexes (Roff 1994). The proportion of flightless individuals in dimorphic species increases with increasing habitat persistency and time since colonization (den Boer et al. 1980). The proportion of macropterous *P. melanarius* can be as low as 2% in stable habitats (e.g. old forest patches) (den Boer 1970) or as high as 24-45% in less stable ones (e.g, newly reclaimed polders of The Netherlands) (Haeck 1971).

Flight is greatly influenced by temperature, rain, and wind (van Huizen 1979). In some species (such as the Palaearctic *Amara 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 (van Huizen 1990). Females of more species from ephemeral habitats than from persistent ones carried ripe eggs (van Huizen 1990), which increases the probability of (re)colonizing empty habitat patches.

Table 1.1 *Maximum densities (individuals m^{-2}) of ground beetle adults and larvae in different habitats.*

Species category	Arable field crops		Field boundary	Forest, heath
	Annual	**Biennial & perennial**		
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
Larvae, individual species	5.46 (0.07- 33; 10)	6	14.5 (4-42; 6)	7.8
Larvae, total	29.4, 49, 77	-	49, 87	

Data are given as mean (minimum-maximurn; N). Only data giving true density vaIues (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. For <5 observations; individual values are given.

Many carabids have been transported intercontinentally, e.g. from Europe to North America (Lindroth 1969, Spence & Spence 1988). Studies in Canada of the effects of invasion by *P. melanarius* showed them to be negligible (Niemela & Spence 1991).

ACTIVITY: DAILY AND SEASONAL

Daily Activity Cycles

More carabids are nocturnal than diurnal. For example, in the United Kingdom, 60% of species are nocturnal and 20% diurnal (Luff 1978). 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 (Dennison & Hodkinson 1984). Overall, nocturnal species are larger than diurnal ones. Night-active species are also dark and dull;, diurnal species display iridescent colors. Diel periodicity can vary with habitat (forest species tend to be nocturnal whereas grassland species are diurnal) (Greenslade 1963) and time of year *(P. melanarius* is nocturnal until August and is mainly diurnal later, Desender et al. 1985). Changes in temperature (Jones 1979), light intensity, and humidity (Thiele 1977) also influence activity. In hot countries, nocturnalism becomes more common; conversely, species that are nocturnal in central Europe become diurnal in the arctic (Thiele 1977). Specialist feeders may synchronize their activity with that of their prey (Alderweireldt & Desender 1990). Desert carabids exhibit peak activity at temperature minima (Erbeling 1987). 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 (Thiele 1977). In some species, larvae and adults undergo different cycles (Kegel 1990).

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 (Makarov 1994*).* Such rhythms are inseparable from individual, especially larval, development.

Facultative diapause of summer larvae can synchronize the life cycle (Luff 1987). 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 (den Boer & den Boer-Daanje 1990) or species with vs. without diapausing larvae (Hurka 1986). In extratropical regions, the cues regulating these cycles involve temperature and photoperiod (Thiele 1977). Seasonal activity and reproductive rhythms in tropical species are regulated by seasonal changes in soil moisture and flooding (Paarmann 1986).

FEEDING

Searching Behaviour

Whereas many carabids presumably find their food via random search, several diurnal species hunt by sight (Paarmann 1986). Other species use chemical cues from aphids (Chiverton 1988), springtails (de Ruiter et al.1989), or snails (Wheater 1989) 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 (New 1991). After the beetle encounters a prey item in a patch, its search behaviour characteristically intensifies for a specified "giving-up" time period. The general walking pattern often alternates between frequently turning and rarely turning walking phases (Mols 1979, Wallin 1991), but this pattern is not necessarily nor always connected to feeding behaviour.

Once prey is located, species typically switch to a well-defined prey-catching behaviour. Many morphological and behavioural 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, behaviour, and morphology in both adults and larvae (Bauer 1979, 1986, Bauer & Kredler 1993).

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 (Pakarinen 1994), thus preventing the mucus production that is the slugs' defence 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 extra-orally di-

gested food (Cohen 1995). The alimentary canal is tripartite. The foregut, including the crop, is the main site of digestion (Paarmann 1986); enzymes synthesized in the midgut are passed forward to the foregut. The enzyme set contains proteases, carboxylases, amylases (Metzenauer 1981), and oligo- and polysaccharidases; this composition is thought to be a primitive character (Jaspar-Versali 1987). Absorption takes place in the hindgut. The speed of digestion depends on temperature and the size of a food item (Sopp & Sunderland 1989) as well as on subsequent feeding (Lövei et al. 1991). Traces of a meal could be detected for up to 14 days (Lövei et al. 1991, Sopp & Sunderland 1989).

Food Choice

Early data on several species indicated varying extents of polyphagy (Davies 1987, Forbes 1883, Skuhravy 1959a). Carabids are mostly polyphagous feeders that consume animal (live prey and carrion) and plant material; several species are phytophagous (Luff 1987, Thiele 1977). A worldwide survey of the literature (Larochelle 1990) 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 (Lindroth 1949). 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 (New 1991, Sunderland 1987). 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-labelled prey techniques, gut dissection, various serological techniques, electrophoresis, and DNA techniques. (Sunderland 1987, Symondson & Liddell 1995).

Dissection of several thousand individuals of 24 European species (Hengeveld 1980b) revealed the remains of aphids, spiders, lepidopteran larvae and adults, fly larvae, mites, heteropterans, opilionids, beetles, and springtails. All species in Hengeveld's study (1980b) were polyphagous and consumed plant material in addition to the other food items. A multivariate analysis (Hengeveld 1980a) 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* (Hengeveld 1980a). 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 (Pollet & Desender 1987).

Food Consumption

Carabids are voracious feeders, consuming close to their own body mass of food daily (Thiele 1977). Food is used to build fat reserves, especially before reproduction and hibernation (Thiele 1977). Feeding conditions during larval development determine adult size, which is a major determinant of potential fecundity (Nelemans 1987a). 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 (Sota 1985), 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 (Nelemans et al. 1989, van Dijk 1994) and North America (Weseloh 1993).

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 (Bernays et al. 1994, Simpson & Simpson 1990). In carabids, females often have more prey types than males (Pollet & Desender 1987). Moreover, Wallin et al. (1992) found that egg number and size were influenced by food composition. Signs of optimal digestion were found in two carabid species (Lövei et al. 1991). 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 behaviour to several hundred per female in species that do not guard eggs (Zetto-Brandmayr 1983). Eggs can be laid in one batch, several batches in one season, or over several seasons. As many as 30-40% of individuals in a population can reproduce in more than one year (Sota 1987, van Dijk 1972, Vlijm et al. 1968, Cartellieri & Lövei 2003). 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. van Dijk 1972), whereas the reverse is true in other species (Burgess 1911, Davies 1987, Gergely & Lövei 1987, Sota 1984).

Increased mortality during reproduction may result from ecological rather than physiological factors (Calow 1979), 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. Under conditions of limited food supply, this survive-but-not-reproduce option enables predators to survive until better food conditions allow reproduction (Mols 1988, Wiedenmann & O'Neill 1990), Data from Europe (van Dijk 1983, van Dijk 1994), Japan (Sota 1984), and North America (Lenski 1984) 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 (1984) 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 (Grüm 1984). These results, along with observations of low egg numbers in cave-inhabiting species (Deleurance & Deleurance 1964) and of species demonstrating parental care in Europe and New Zealand (Brandmayr & Zetto-Brandmayr 1979), 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 (Grüm 1984). 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 (Grime 1977) is promising (Eyre 1994).

MORTALITY AND POPULATION DYNAMICS

Although abiotic influences on survivorship are inevitable, constituting the principal mortality factors for all life-cycle stages of ground beetles (den Boer 1977), 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 (Thiele 1977) is probably not correct. Eggs of *Pterostichus oblongopunctatus* suffered 83% mortality in fresh litter but only 7% in sterilized soil (Heessen 1981). 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 mouldy (Brandmayr & Zetto-Brandmayr 1979).

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 (Nelemans 1987b, Nelemans et al. 1989). 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% (Brunsting et al. 1986). 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 (Freeland 1983, Price 1980). Although predators, parasites, and pathogens affect a1 1 ground beetle developmental stages (Luff 1987, Thiele 1977), quantitative data remain scarce.

ADULT MORTALITY Up to 4 1 % parasitism by nematodes and ectoparasitic fungi was found an 14 species of *Bembidion* in Norway (Andersen & Skorping 1991). Nematode infection in insects may cause sterility (Poinar 1975), 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 (Andersen & Skorping 1991).

Most observational evidence indicates that predation is an important mortality factor for adults. Hundreds of vertebrate species prey on carabids (Larochelle 1975a, 1975b, 1980). The ecological significance of predation pressure by small mammals was demonstrated in exclosure experiments in North America (Parmenter & MacMahon 1988) and England (Churchfield et al. 1991), where excluding small mammals resulted in an increase in both species richness and density of carabids.

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 (den Boer 1977, Luff 1982), and this comparison is generally accepted as a valid method for estimating density fluctuations and effective rates of reproduction.

Population variability in carabids (Luff 1982) seems to be at the lower end of values for insects (Williamson 1972). Although environmental fluctuations in caves are smaller than in other terrestrial habitats, population fluctuations of the cave-inhabiting *Neophaenops tellkampfi* in Mammoth Caves, Kentucky, were between those of *Calathus melanocephalus* and *Pterostichus versicolor,* two common species living on heath in Drenthe, The Netherlands (Kane & Ryan 1983). Different intrinsic and extrinsic factors -life span, fecundity, reproductive patterns, and rate of development- contribute to this relative stability (Luff 1982).

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 (den Boer 1977). Den Boer (1987) synthesized the regional population fluctuation patterns of carabids collected over 23 years in the Dutch province of Drenthe. Using a distribution of population sizes (den Boer 1977), 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 recolonise 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 (1990) 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 m between habitat fragments and showed an average survival time of 744 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 (1988) and Turin & Peters (1986) have examined the effects of these changes in The Netherlands since 1850. Poorly dispersing species (for example *Abax parallelepipedus, Calathus erratus,* and *P. oblongopunctatus)* generally decreased; well dispersing species *(Amara lunicollis, Dicheirotrichus gustavi, Stenolophus*

rufus) 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 (Luff 1987, Thiele 1977, van Dijk 1987). 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.

The mean body size of carabid assemblages in woodlands, moors, and grasslands in north-eastern England was related to several environmental factors (Blake et al. 1994). 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 (Sustek 1987, Elek & Lövei 2007).

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, non-comparable habitats, the methods used (examples in Niemela 1993), and a general lack of experimental tests (Niemela 1993). Significant interspecific competition exists between adults of the North American *Carabus limbatus* and *Carabus sylvanus* (Lenski 1984). However, another study showed that most species do not compete in a western European beech forest (Loreau 1990). Similar conclusions emerge from evaluations of resource-partitioning descriptions; competition cannot be proven except in a few cases.

Such studies focused on the adult stage, but larvae have more restricted tolerance limits because of more restricted food range, mobility, and weaker chitinisation, and are less adapted to evade resource shortages. Consequently, the importance of competition among larvae can be greater than that among adults (Brunsting et al. 1986).

At the assemblage level, resource-partitioning patterns have been described in several studies (reviewed in Niemela 1993), 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. 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 (Niemela & Spence 1991) 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 (Wilson 1990), 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 (Forbes 1883), they have generally been considered beneficial natural enemies of agricultural pests, although a few species are pests themselves (Luff 1987, Thiele 1977).

The carabid fauna of agricultural fields originates in riparian (Thiele 1977) or steppe (Lövei & Sárospataki 1990) habitats. Data are few outside those obtained in Europe and North America. In Canada, many species in cultivated land are either introduced European species (Allen 1979, Spence & Spence 1988) 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 (Luff 1987), although species of *Chlaenius* and *Carabus* can be abundant (Yano et al.1989). In arid areas, Tenebrionidae are more prevalent than Carabidae (Faragalla & Adam 1985). In New Zealand, carabids can be significant predators (Barker 1991), but they are not as prevalent there as they are in northern cultivated fields (Lövei 1991).

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 (Luff 1987, Thiele 1977).

The Effectiveness of Carabids as Natural Enemies

Predator-prey studies have traditionally focused on interactions between specialist predators and their prey (Hassell 1978). Although *Calosoma sycophantha,* one of the first insects introduced for biological control (Burgess 1911), 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 (De Angelis et al. 1975, Murdoch et al. 1985). The ground beetles meet these criteria; they are self-damping during their larval stage (Brunsting & Heessen 1984), are polyphagous feeders (Heliovaara & Vaisanen 1993), 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-cal1ed natural enemy ravine (Southwood & Comins 1976). To increase carabids' effectiveness, biological control practitioners should consider the general habitat favourability 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 recolonisation foci (Lys 1994, Thomas et al.1991).

The effectiveness of a natural enemy can be established through several sequential steps (Luck et al. 1988, Sunderland 1987, Wratten 1987): 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 (Potts & Vickerman 1974) 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 (Heliovaara & Vaisanen 1993), habitat classification for nature protection (Luff et al. 1992, Pizzolotto 1994), or characterization of soil-nutrient status in forestry (Szyszko 1983). They might also serve as biodiversity indicators (Niemela et al. 2000). However, most of the groups that are candidates for these purposes have not been subjected to a critical assessment using set criteria (Pearson & Cassola 1992). Once we develop these criteria, we can realistically assess the suitability of ground beetles as indicator organisms.

Part II. Methodological innovations

This chapter deals with efforts to further develop the methodology of studying ground beetles. Proven, reliable and well-known methods, continuously used by a large number of practicioners, are essential for cultivating a branch of science. At the same time, the development, adaptation and testing of new methods provides the possibility of further advance in a field. Aptly put by Csikszentmihalyi (1997, p.340): "whenever new methods are discovered, new avenues of knowledge are opened". The results in this part concern such methods: the use of the harmonic radar, a new device to study habitat use via tracking individual behaviour, two aspects of trapping methodology, and a new mathematical method to evaluate changes in ground beetle assemblages (in this instance changes generated by increasing degrees of urbanisation). This part is based on two published papers (Lövei & al. 1997, Sapia & al. 2006), and a manuscript (Lovei, unpublished).

Examining the relationship between components of trapping effort (the relationship between trap number and the length of the trapping period), as well as among different sampling regimes in time gave interesting possibilities to improve the design of monitoring programs.

Ground beetles are often nocturnal, which often makes their study in the field difficult. Tracking individuals during activity gives important cues about their habitat use – but this is often complicated for carabid beetles. One of the first tracking method used in ground beetle research was radioactive isotope labelling (Baars 1980). Normal radiotracking is complicated because of the cost and size of radiotransmitters (at least as of today). They are active for a limited time only, still too heavy for ground beetles, and are easily lost. These factors practically prevent them from being used in invertebrate studies. The harmonic radar (Mascanzoni & Wallin 1986) solves several of these difficulties. However, their use has been restricted to a few countries – and mostly for their original purpose, rescuing avalanche victims. Our studies were among the first ones where the introduction of this device to a country (New Zealand) was with the purpose of using them for ecological research. As the detection range critically depends on the type of diodes used and the aerial shape and size, we calibrated the transponders for New Zealand conditions (Lovei & al. 1997). Initial testing indicated that the method is useful, especially for studying invertebrates without destroying their habitat.

Methodological innovations, 1. The non-equivalence of the two components of trapping effort: sampling duration and the number of traps

Pitfall trapping (Barber 1931) is a frequently used field collecting method in the study of organisms active on the soil surface. A pitfall trap is a container dug into the soil so that its rim is usually flush with the surface, and captures organisms walking on this surface, usually soil (but a trap can be set to catch from the top of, or within litter, soil, grass, etc.). Pitfall trapping is a “passive” sampling method where the activity of the target organism is necessary for capture. The variation of pitfall trap design is vast, using different materials, shapes, and sizes (Southwood & Henderson 2003). The trap can contain an attractant, a killing/preserving liquid, or nothing – each of these has its own modifying effect on the catch (Southwood & Henderson 2003). The use of pitfall traps and their biases have been hotly debated without bringing about many generally accepted ways of standardisation (Lövei & Sunderland 1996, but see Niemela & al. 1990, Digweed & al. 1995, Koivula & al. 2003). One of the few accepted standards is the reporting of the sampling effort. Sampling effort depends on two components: pitfall trap numbers and the time the traps were open. The widely used ‘sampling/trapping effort unit’ is the product of these two components, and usually takes the form of “trap-nights” (or its multiples) and is seen as a universal currency for comparisons of different pitfall trapping projects.

This characterisation of the trapping effort, however, contains an important assumption. It is generally assumed that two catching sessions are equivalent if they result from an effort of the same number of trap-days (more correctly: trap-nights), irrespective whether this is derived as "*n* traps x *z* nights" or "*n*/2 traps x 2*z* nights". This assumption remains untested, although it could critically influence our sampling of the assemblage under study, as well as the comparisons we make among different locations, assemblages and habitats. However, while different aspects of this technique, the distance, design, or material of the traps, the influence of habitat and the preservative fluid have been studied and discussed (for a recent review see Woodcock 2005), there is no similar evaluation of the equivalence of the two components of this trapping effort unit.

Material and Methods

The "trapping currency" project

The study site was an experimental apple orchard at the field station of the Plant Protection Institute field at Julianna-major, near Budapest, central Hungary. This area is hilly, with various broad-acre crops on the valley bottom, orchards on the lower slopes of hills, and a modified oak-hornbeam forest at higher elevations. The study was done in an apple orchard, divided into two parts. Half of the orchard received pesticide treatments, usually three—four times during the first half of the season, while the other half had no such treatments. A more complete description of the study site, management and the surroundings see in Lövei (1981) and Mészáros (1984a).

During a 10-year long biodiversity study of the apple orchard (Mészáros 1984a), one of the methods used to describe and monitor the fauna was pitfall trapping. Pitfall traps were 500 ml glass jars, with 70% ethylene glycol as killing agent and preservative, placed under the south-eastern corner of an apple tree, about 2 m from the trunk. All traps were covered with a galvanised iron square mounted on pegs, to prevent bycatch and to protect the catch from scavengers. Traps were checked weekly, when the catch was removed, and kept in 70% ethyl alcohol until identification. Identification was made by using keys by Freude & al. (1976) and voucher specimens kept in the PPI Department of Zoology arthropod collection.

The first data set was collected using 20 pitfall traps, set up in two groups of 10 in the pesticide-free vs. pesticide-treated parts of the orchard. This trapping was run for several years from early April until late October. For the comparison, material collected during the 1981 season was used. The placement of traps in 1981 was randomised, with the minimum distance between traps being the between-tree distance, 10 m. This trapping session was run for 28 weeks, i.e. 560 trap-weeks, and was called the "time sampling". The second set of data was collected during the autumn of 1981 (18 September – 21 October), when a grid of 100 pitfall traps was set up (half of it in the unsprayed, half in the sprayed block) and run for 4 weeks (400 trap-weeks), called the "spatial sampling". Traps were checked weekly, and the catch was handled the same way as in the time sample.

Results

The "time sampling" series

The catch by the 20 traps over the season was 1823 individuals of 45 identified species (35 individuals, 1.9% of the catch was not identified to species; 28 of these were individuals belonging to the genus *Amara,* and 7 to the genus *Harpalus*). The most common species (Table 2.1) in the catch were *Platynus dorsalis, Poecilus cupreus, Harpalus rufipes, Brachinus explodens* and *H. tardus*. The five most common species constituted 75.0% of the total catch. The Berger-Parker dominance index was d = 0.25. There were 8 singletons in this sample (*Asaphidion flavipes, Calathus melanocephalus, Badister meridionalis, Pterostichus oblongopunctatus, Trechus quadristriatus,* and 3 unidentified but different *Harpalus* spp.*),* as well as 4 more species with 2 individuals each. Thus 26.7 % of the species found can be considered rare.

The "spatial sampling" series

This trapping session, over four weeks in autumn, collected 757 individual beetles of 52 species. The most common species were: *P. cupreus, Metabletus truncatulus, Bembidion lampros, Amara familiaris,* and *H. tardus*. These five species constituted 65.4% of the total catch. The Berger-Parker dominance index was d=0.29, less diverse than the time series. There were 18 singletons (*Acupalpus muncipalis, Abax ater, Amara intricata, A. apricaria, A. similata, Badister lacertosus, B. meridionalis, Bradycellus harpalinus, Carabus hortensis, Dolichus halensis, Harpalus signaticornis, H. picipennis, Leistus rufomarginatus, Panageus crux-major, Parophonus com-*

planatus, *Pterostichus striatus* and *Stomis pumicatus*). From a further 6 species, 2 individuals each were captured. A higher share (46.2%) of the species were rare than in the time sample.

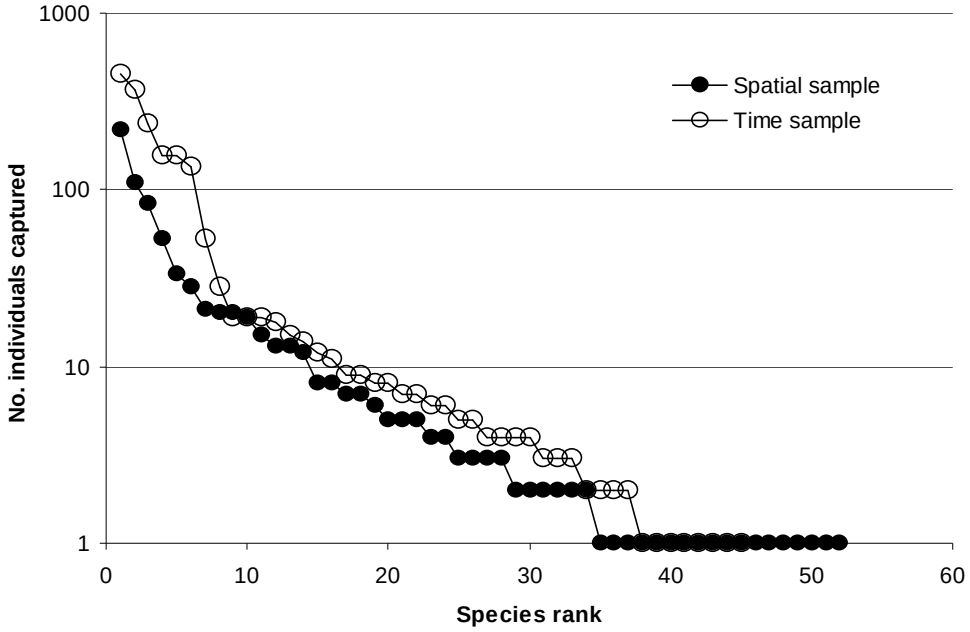

Figure 2.1. *Rank-abundance curves of the carabid assemblage in an apple orchard near Budapest, central Hungary, sampled by two different trapping arrangements: 20 traps for 28 weeks (Time sample) and 100 traps for 4 weeks (Spatial sample).*

Comparing the two trapping series

The "time series" trapping had a higher trapping effort, collected more individuals and the assemblage showed a higher activity density (Table 2.1) – yet it yielded fewer species than the "spatial sampling" series. The rank-abundance curves (Figure 2.1) indicate that the time sample had a less diverse assemblage than the spatial sampling series. There are several differences in the species lists, too (Table 2.1). Thirty-one species were shared, which made up 97.7% of the total number of individuals captured in the time series; and 81% of the total in the spatial series. Consequently, the time series can loosely be considered a sub-sample of the spatial series, because an overwhelming majority of the individuals belonged to species that were also captured by the spatial sampling series – but not the opposite. Nevertheless, the time sample had 14 unique species, while the spatial sample had 21 such species. This latter only included 3 species of *Amara* and thus the difference cannot fully be attributed to the unidentified *Amara* species in the time series sample.

Table 2.1. *List of species captured by the two sampling regimes, the time sampling and the spatial sampling in an apple orchard, central Hungary. Only species with >5 individuals in at least one of the samples were included.*

Species	**Time-sample**	**Spatial sample**
Platynus dorsalis	450	28
Poecilus cupreus	367	216
Harpalus rufipes	239	13
Brachinus explodens	157	5
Harpalus tardus	156	33
Harpalus distinguendus	135	20
Microlestes maurus	53	13
Amara consularis	19	7
Calathus erratus	19	5
Pterostichus melanarius	19	2
Amara anthobia	18	19
Broscus cephalotes	15	3
Amara similata	14	1
Amara ingenua	12	8
Amara aenea	11	6
Amara bifrons	9	15
Amara familiaris	9	53
Acupalpus meridionalis	8	7
Metabletus truncatulus	8	109
Carabus violaceus	7	-
Anisodactylus signatus	6	4
Bembidion properans	6	21
Bembidion sp 1	5	-
Panageus crux-major	5	1
Bembidion lampros	4	84
Calathus fuscipes	3	5
Poecilus versicolor	2	8
Calathus melanocephalus	1	12
Trechus quadristriatus	1	20
Trapping effort, trap-weeks	560	400
Total no. of individuals captured	1823	757
Overall activity density, no. of individuals/trap-week	3.26	1.89
Total no. of species captured	45	52
Berger-Parker dominance index	0.25	0.29
No. of unique species	14	21
No. of singletons	8	18

Methodological innovations, 2. Effects of varying sampling regimes on the observed diversity of carabid assemblages

To further examine the relationship between trapping effort and the characterisation of ground beetle assemblages, we analysed different time sampling arrangements from a seasonal capture session within the Danglobe Project. Danglobe is a component of Globenet, an international research project, which aims at assessing changes in biodiversity caused by anthropogenic modification of landscapes in different countries, using a common sampling method (pitfall trapping) and reference group (carabid beetles, Coleoptera: Carabidae) (Niemelä & al. 2000). The original set-up of the Globenet Project calls for season-long, continuous sampling (Niemela & al. 2000). However, in any monitoring scheme, there is a continuous drive (often by the end users) to simplify the methods and evaluation. This is a legitimate requirement, given the frequent lack of logistical support and trained personnel.

In this respect, the standard literature on ground beetles has little to offer. Published studies have examined the impact of the trap material and size (Work & al. 2002), trap arrangement (Ward & al. 2001, Hansen & New 2005) and preservative (Thiele 1977) on the catch, but the standard recommendation is still the use of season-long sampling (Woodcock 2005). A comparison between continuous pitfall trapping and combinations of early and late season sampling periods (Niemelä & al. 1990) established that the latter can be an adequate sampling method to address several types of ecological problems, especially those that focus on individual species or groups of locally abundant species. There is no general assessment or recommendation whether traping can be reduced in time and still yield usable results, for example, in biodiversity assessments.

To fill this knowledge gap, we have examined the effect of reduced or altered sampling effort on the diversity relationships among three stages of the urbanisation process: rural, suburban, and urban areas.

Material and Methods

To assess the impact of different sampling arrangements on diversity, we used the material collected in the Danglobe Project, in and around the town of Sorø, Denmark, in 2004 (more details on methods see in Part IV and Elek & Lövei 2005).

We compared the diversity extracted from continuous trapping material from 2004 with three other “imaginary sampling regimes” as follows: (1) considering only every second fortnightly sample (= pulsating sampling), (2) considering the catch for three, equally spaced fortnightly intervals during the sampling period (at the beginning, middle and end of the growing season), and (3) evaluating only material trapped during two fortnights, during the peak of the carabid activity period. These data were thus subsets of the data from continuous trapping.

We analysed the diversity of the ground beetle assemblages using the Renyi diversity profiles. The Renyi diversity index provides a non-point description of diversity, overcoming the problems with single index descriptions (Magurran 2003). The samples were analysed by using DivOrd 1.70, a computer program for diversity ordering (Tóthmérész 1993a) which calculates and displays the Rényi diversity profiles of communities and several other diversity measures. DivOrd is based on parametric families of diversity indices, superior to simple diversity indices [for details, see Tóthmérész & Magura (2005)]. For data analysis, two index families were used, the Rényi diversity and the Right Tail Sum (RST) diversity (Patil & Taillie 1979).

Results

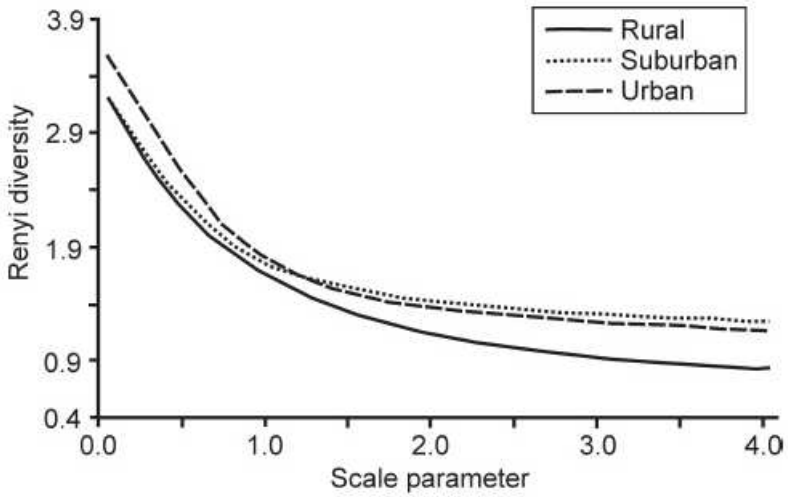

Fig 2.2. *The Rényi diversity profiles for carabid assemblages in rural, suburban and urban areas at Sorø, Denmark, in 2004.*

The diversity relations of whole-season samples

The comparison of the Rényi diversity profiles (Fig. 2.2) of the three carabid assemblages (rural, suburban and urban) indicated that the rural areas were less diverse than either the urban or the suburban areas. The urban and suburban diversity profiles intersected, which means that the diversity relationship between the suburban and urban area was not unequivocal. The urban area was more diverse considering the dominant species, while the suburban area was more diverse considering the rare species. Using the RTS-diversity profiles (Fig.2.3), this change in the diversity ordering between urban and suburban areas can be located (Tóthmérész 1995). The urban and suburban profiles crossed each other between the 4th and 5th most frequent species. The RTS diversity curves showed that the suburban areas could be considered more diverse than the urban areas only if the four most abundant species were included in the evaluation.

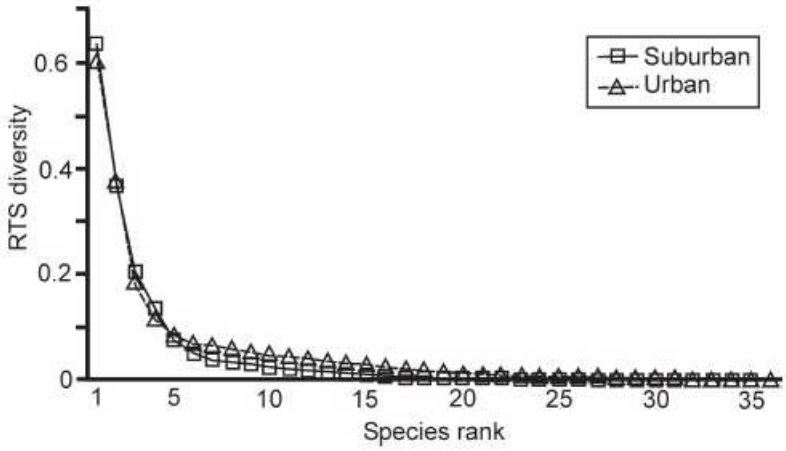

***Fig 2.3**. Right Tail Sum (RTS) diversity profiles of the carabid assemblages at the suburban and urban areas at Sorø, Denmark, in 2004.*

Diversity relations of reduced sampling methods

The pulsating sampling method, i.e. sampling for 2 weeks every month, gave the same diversity ordering results as continuous sampling. The Rényi diversity profiles of rural, suburban and urban areas (Fig. 2.4), when applying the pulsating sampling method (weeks 1, 3, 5, 7, 9 and 11), coincided with the diversity profiles of the continuous sampling method. There were only minor differences between the two procedures, usually at the beginning of the profile, indicating that some rare species were present only in the data from continuous trapping. This is a direct consequence of reduced trapping effort, and does not greatly change the diversity of the assemblage.

A further reduction in the time of sampling, i.e. three 2-week periods over the growing season, had clearer impact on the diversity profiles in the three habitat types, compared the above two methods. In all three urbanisation stages, it detected fewer species (Fig. 2.4a-c). In the rural area, the profile indicated a more diverse assemblage over most of the scale parameter than the first two sampling regimes (Fig. 2.4a). At the suburban areas, the difference was less pronounced, and the profile ran very close to those of the continuous sampling above $\alpha > 1.3$ (Fig. 2.4b). A similar course was seen in the urban area (Fig 2.4c), but here the two curves ran close to each other at only $\alpha > 1.5$.

The three fortnightly periods of sampling indicated a different relationship among the three urbanisation stages, too (Fig. 2.5). The forest area was ordered in-between the urban and suburban at low values of the scale parameter, and its low diversity became apparent only at $\alpha > 1.5$. The suburban assemblage seemed to be more diverse than the urban one at the interval $0.7 < \alpha < 4.0$ (Fig. 2.5). Both of these indications were different from the results obtained from the full as well as the pulsating sampling regimes.

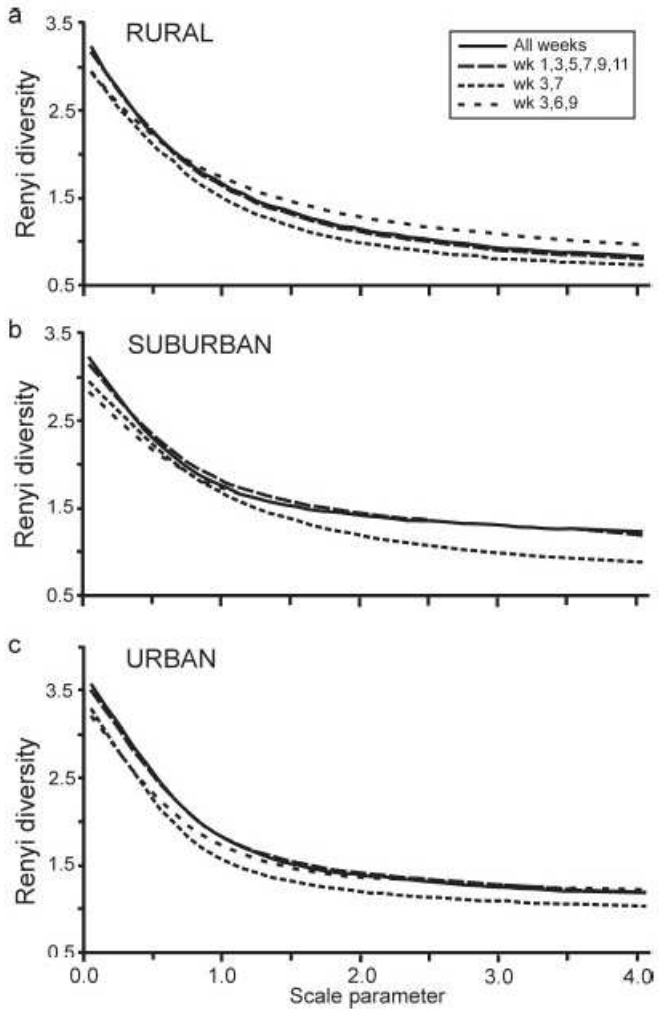

Fig. 2.4. *Rényi diversity profiles of the carabid assemblages sampled using various sampling regimes in rural (a), suburban (b) and urban (c) areas at Sorø, Denmark, in 2004.*

Restricting the trapping further to two fortnights during the peak carabid activity substantially altered the diversity profiles, and all three profiles ran consistently below the other curves, thus underestimating the diversity of the assemblage virtually throughout the whole range of the scale parameter alpha (Figs. 2.4a-c).

Comparing the diversity trends among the urbanisation stages, sampling only during the two peak activity periods also distorts the relationships: the suburban area seemed to support the most diverse carabid assemblage for most of the profile (Fig. 2.6), except when $\alpha < 0.4$, i.e. when the rare species had high influence on the diversity measure. This sampling method correctly indicated the urban area as being the most diverse one, but not between α values of 0.5 and 2.1 (Fig. 2.6). The relationship between the rural and suburban areas was correctly represented, except for very small values of the scale parameter, α.

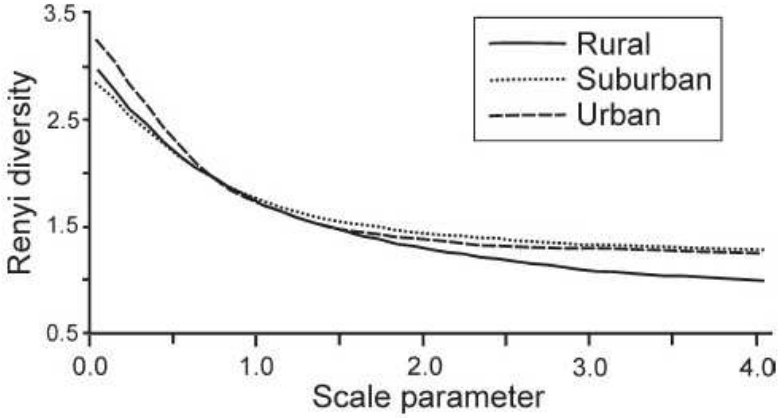

Fig. 2.5. *Rényi diversity profiles of carabid assemblages of rural, suburban and urban areas, sampled over three fortnightly intervals during the growing season at Sorø, Denmark in 2004.*

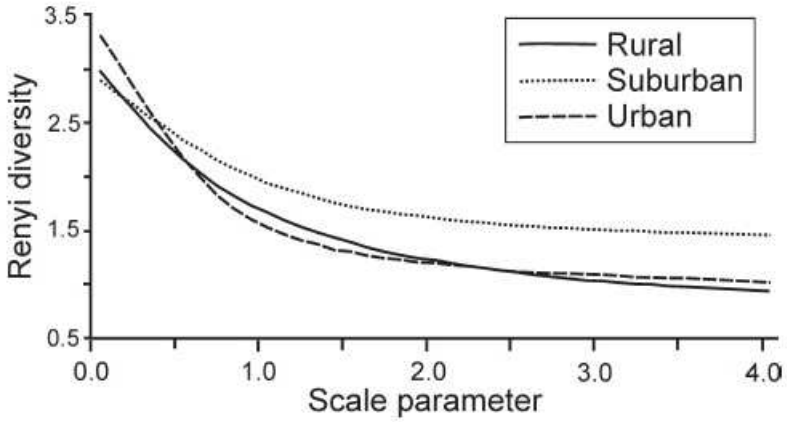

Fig. 2.6. *Rényi diversity profiles of carabid assemblages of rural, suburban and urban areas, sampled over two fortnightly intervals at peak carabid activity during the growing season at Sorø, Denmark, in 2004.*

Methdological innovations, 3. Harmonic radar - a method using inexpensive tags to study invertebrate movement on land

Spatial behaviour of individuals is a key component to understanding the population dynamics of organisms (Turchin 1991). Many animals do not easily lend themselves to such studies and observing them without disturbing their natural behaviour and habitat is difficult. Many organisms are cryptic, sensitive, or too rare to study directly. Capture-recapture methods are suitable for many organisms (Southwood & Henderson 2003) but their resolution levels in space and time are often not fine enough. Tracking and remote sensing methods can overcome this limitation (Riley 1989; Pride & Swift 1992).

These methods usually requires locating an individual carrying a small radio transmitter, and for small organisms, this is problematic. Two important technical limitations are the size of the transmitter/battery, and the limited lifetime of the energy source. Miniature, lightweight transmitters are now available, and have been used for tracking invertebrates (Riecken & Raths 1996). Their cost, however, puts them beyond many research budgets. Moreover, even a miniature transmitter needs an energy source, and this limits its useful life. Technical failures can also be frequent (Riecken & Raths 1996).

An alternative is to use a passive reflector that does not depend on an attached energy source. If a conductor with nonlinear characteristics, a diode, is illuminated by radar waves, it can re-radiate an harmonic of the original radar signal. This harmonic signal can be detected and used to locate the reflector together with anything attached to it. The energy to operate the reflector is delivered by the illuminating radar. The harmonic radar is such a device. It is a hand-held emitter which generates a continuous, unmodulated wave. Diodes are available that reflect the signal at double the original wavelength. The harmonic radar unit also detects the reflected signal and transforms it into an audible signal. The reflected signal is not specific, so individual markings have to be applied to the animals if they are to be identified once they are found. The harmonic radar was originally developed to locate avalanche victims and it was first used for tracking invertebrate movements around 1985 (Mascanzoni & Wallin 1986; Hockmann et al. 1989; Wallin 1991).

Methods

We used a portable transmitter-receiver designed by Recco (Recco Rescue Systems, Lidingö, Sweden), which weighs about 8 kg. It consists of a battery, a hand-held Yagi aerial which is both the transmitter and the receiver, and earphones. The transmitter emits a 1.7 W continuous microwave frequency of 917 MHz.

The tag on the target organism reflects this energy at double the frequency (1,834 MHz). The detection range depends on the type of diode used to construct the tag, and the shape and size of the aerial connected to the diode.

We tested the following Schottkey type diodes: Recco^{-}, S2 (provided by Recco, Lidingö, Sweden), HI 48, Hewlett-Packard HP 280C 3C1 (5082-2800), HP 2835, Z 3040 (Dick Smith Electronics, equivalent to 1N 60 specifications), Z 3232 (Dick Smith Electronics), 1N 34 and 1N 60 (which are equivalents), and BAT 85.

Transponders were made by soldering an aerial of copper wire (0.5 mm diameter) to a diode to form a closed loop. Each transponder was tested ten times with the wire loop in two configurations, a circle and an elongated oval and with the long axis either parallel or perpendicular to the microwave beam. The maximum detection distance was measured with the harmonic radar. Following testing with closed-loops, each diode was connected to the rectangular Recco^{-}, aerial and the maximum detection range measured with the aerial parallel and perpendicular to the microwave beam.

The three diodes which performed best were tested again with a single length of wire attached to the cathode end of each diode as by Mascanzoni & Wallin (1986). The length of the copper wire varied between 0 - 20 cm. Parallel and perpendicular readings were made.

Tests were conducted in an open field. Each transponder was placed on a plastic plate to isolate it from damp grass that alter detectable range. Readings were taken with the radar held 1.2 m above the ground. Care was taken to keep the polarity of the diodes the same in relation to the direction of the beam. The diode that proved most effective in the first part of the experiment was then used to test different aerial shapes on the maximum detection range.

Transponders were attached to five ground beetles (*Plocamosthetus planiusculus* White, Coleoptera: Carabidae), and 37 snails (*Paryphanta busbyi watti* (Powell), Pulmonata: Rhytididae), to study their spatial behaviour and habitat preference. Tagged organisms were relocated at periodic intervals by systematic searching. In this section, only the results concerning ground beetles will be detailed.

Results

The effects of diode type and aerial design on detection distances

The maximum detection distances varied from less than 2 m to 13 m, depending upon diode type, position, aerial length and shape (Tables 2.2, 2.3). Transponders were always detected from further away when parallel to the radar beam rather than perpendicular to it. The aerial length allowing maximum detection distance was 12cm for both linear or oval aerials, orientations and all types of diodes tested (Fig. 2.7; data for oval aerials not shown).

The Recco aerial was superior to the simple wire loop aerials (Table 2.2), possibly because of its larger surface area. Diodes with copper sheet aerials were always superior to the wire loop aerials of similar size and were sometimes better than wire loop aerials regardless of loop size (Devine 1997).

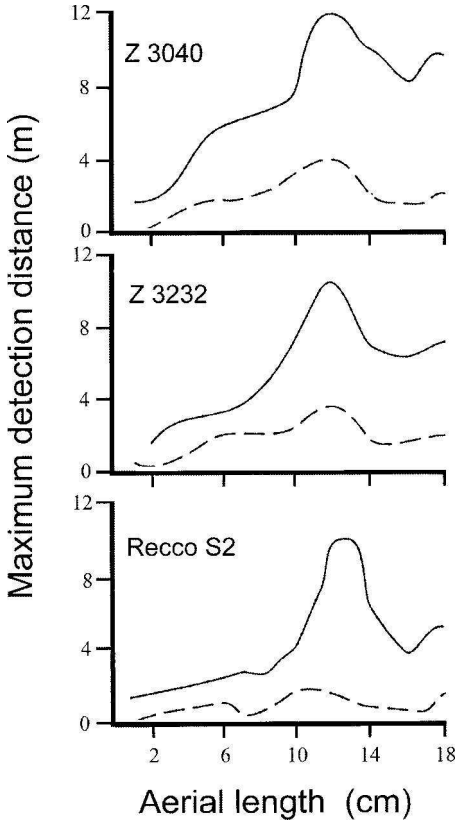

Figure 2.7. *Maximum detection range of the diodes Z 3040, Z 3232, and Recco S2 with different aerial lengths in parallel (solid line) and perpendicular (broken line) orientation to the radar beam. The aerial was always attached to the cathode end of the diode.*

Table 2.2. *Maximum detectable distance for different diodes, orientations and aerial shapes tested. The aerial length was 12 cm in all cases.*

	Maximum detectable distance (m)							
Aerial shape/orientation	**Recco S2**	**HI4 8**	**HP280C 3C1**	**Z304 0**	**Z323 2**	**1N34 1N 60**	**HP 2835**	**BAT 85**[1]
Elongated parallel	9.82	4.00	4.90	12.00	10.12	10.36	8.00	no test
Elongat. perpendicular	2.40	0.65	1.81	4.00	3.85	3.61	1.90	no test
Circular	2.20	0.60	1.40	2.60	1.90	2.80	2.10	no test
Recco parallel	13.20	7.70	3.80	8.00	8.00	7.00	10.30	1.20
Recco perpendicular	3.60	3.00	1.40	3.40	3.40	2.90	6.00	0.00

[1] The BAT 85 diode responded poorly in initial tests so was not tested in all combinations.

Table 2.3*. Maximum detectable distance (m) for transponders manufactured from Z 3040 diode - copper sheet combinations with different aerial shapes.*

Orientation/ location	**Rectangular**		**Continuous circular/diode across**	**Circular**	
	Narrow	**Wide**		**Large**	**Small**
Parallel	5.50	10.70	1.50	7.60	6.10
Perpendicular	5.50	10.60	1.50	7.40	6.20
Behind tree	1.70	3.80	0.00	3.10	1.90
Under dry litter	5.50	10.90	1.50	7.50	4.60

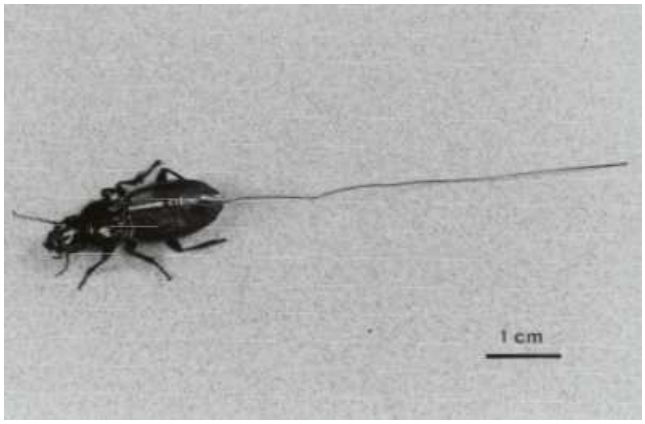

Figure 2.8. *A female carabid beetle,* Plocamosthetus planiusculus *fitted with a Schottkey-type diode and appropriate aerial for harmonic radar studies.*

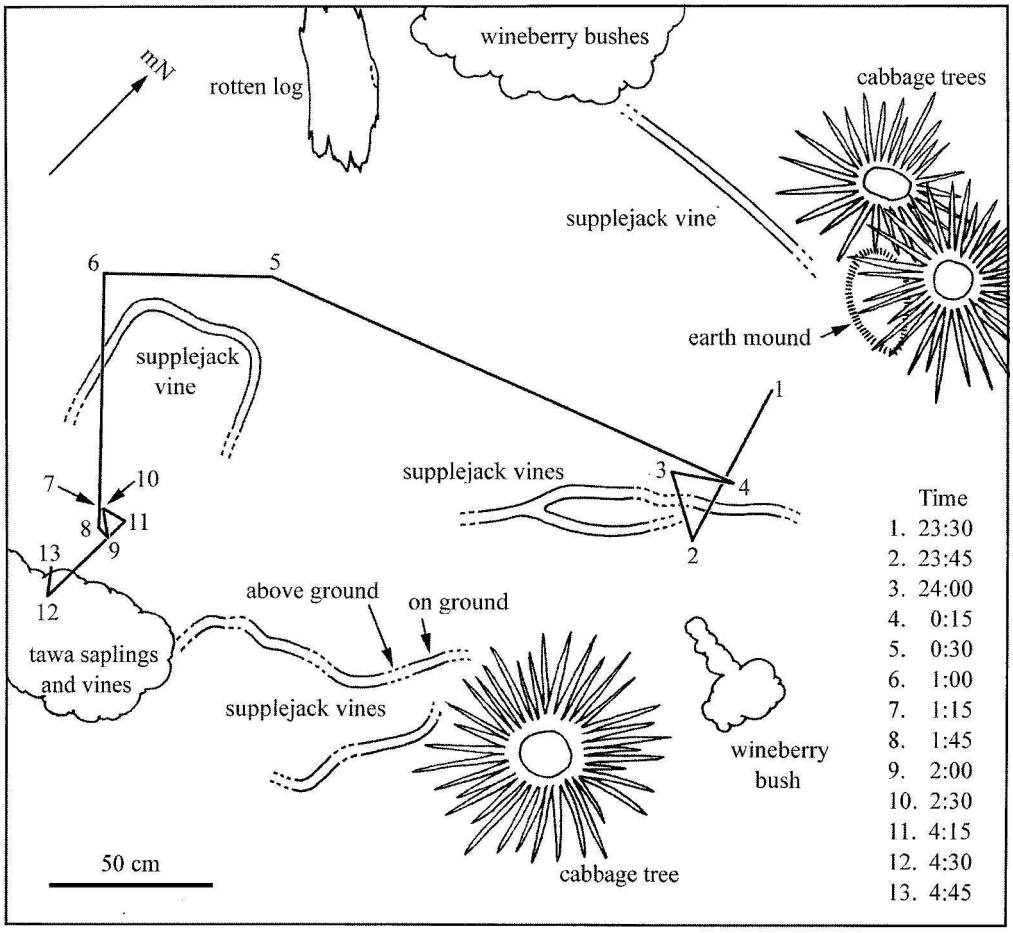

Figure 2.9. *Movements of a male carabid beetle,* Plocamostethus planiusculus, *in Keeble's Bush, Manawatu, North Island, New Zealand, during the night of 23-24 February 1997. The beetle was relocated every 15 min.*

Diode attachment and movements of tagged animals

Each tag, consisting of a diode with an appropriately shaped aerial, was glued to the elytra of the ground beetle or to the shell of the snail (Fig. 2.8). We found that quick-drying adhesive (Ados1 or Uhu brand) was suitable for ground beetles.

We were able to relocate ground beetles over several one-night sessions. Typically, movement was only a few metres per night. We relocated the beetles every 15 or 30 min. No long term directional movement was detected (Fig. 2.9) but the beetles showed signs of ‘typical’ invertebrate searching behaviour. This included movement within a small area with frequent turns, followed by longer walks in straight lines.

Discussion

The non-equivalence of trap number and trapping period

The results of comparing two different combinations of trap numbers x trapping duration from the same habitat and the same year indicated that the often used "common unit" for pitfall trapping, trap-days /trap-nights or trap-weeks, that express the trapping effort as the product of the number of traps x length of trapping time may not universally be used for comparisons of pitfall trapping sessions with different ratios of the component efforts.

The 20 traps may not have been representative of the variety of microhabitats in the orchard (which the 100 traps covered much better). This, however, is usually not seen as a problem, and even some current recommendations (e.g. Woodcock 2005) suggest fewer traps, while a shorter–than-full-season trapping arrangement is often condemned (e.g. den Boer 2002). From the results both seem unwarranted recommendations, at least when the aim is to sample the diversity of ground beetles present in a habitat.

Another possible limitation could be an inter-trap distance that does not allow the traps to be independent of each other. Such interference effect would be larger during a short trapping session when immigration and the appearance of a new generation of adults is less probable or significant. Consequently, a depletion effect resulting from too close trap locations could be stronger during our 100-traps short session, and the differences indicated would tend to be less than in reality. The 10 m inter-trap distance may be too small in a forest (Digweed & al. 1995), although the assemblage structure was not distorted in Digweed & al.'s (1995) study. In our case, the distance did not have a depletion effect on the catch. Edge traps of our 100-trap trapping grid, where the inter-trap distance was 10 m, captured neither more individuals, nor more species than the central ones (data not shown).

All of the above biases would favour the time series sampling. In spite of this, we found that the spatial sampling series collected more species than the time sampling series.

The two components of the measurement unit, trap number and time, are usually considered equivalent. From this it would follow that a shorter trapping period can be counteracted by increasing the number of traps. Viceversa, if the number of traps are limited, the length of time can compensate for this. In fact, Niemela & al. (1990) conclude: "shorter sampling periods may depict the fauna as accurately as a spatially limited sample", i.e. the two components are of equal influence.

Our comparisons showed that this is not strictly nor necessarily so, and that trap number may have more influence on the final result than the length of the trapping period. This is a counterintuitive but important result. Recommendations often emphasise the length of the trapping period. Short pitfall trapping sessions are often criticised due to the lack of covering the whole period of activity of ground beetles, and thus missing species that do not appear during the period of trapping (den Boer 2002, Woodcock 2005, but see Niemela & al. 1990, Sapia & al. 2006).

Based on the above (limited) comparisons, this aspect of the trapping error may have been over-emphasised.

In conclusion, if a compromise has to be made under a fixed total sampling effort in a bio-diversity study, it is wise policy to operate the maximum possible number of traps, and reduce the length of the trapping session rather than the opposite.

The effect of sampling regimes on diversity in carabid assemblages

In comparative diversity studies, the frequent question is "which assemblage is more diverse?" (Tóthmérész 1995). The answer often depends on the choice of the diversity index, which lead some ecologists to declare the quest for an answer futile and the methods nearly useless (Hurlbert 1971). The use of one-parametric index families can resolve this paradox (Tóthmérész 1995, Southwood & Henderson 2003). This method has first been suggested by A. Rényi (1961) and is more used in physics and information theory. From time to time, ecologists announce its "redis-covery" which is unwarranted (Lövei 2005).

Analysing the diversity along an urbanisation gradient using Rényi scalable diversity in-dex, we verified that in Denmark the diversity between a rural, forested area and urban forest patches increased along the urbanisation gradient. This trend contrasts with findings in several other countries, for example Finland (Alaruikka & al. 2002), but is similar to the trends found in Central Europe (Magura & al. 2004) and merits further study.

Our results also showed that it is not necessary to follow the season-long, continuous pitfall trapping recommended by several authors, at least for the evaluation of diversity. With respect to diversity, the data resulting from the pulsating method produced the same results as continuous trapping did, suggesting that the number of the sampling occasions can be somewhat reduced.

These results are encouraging for the development of more benign and less arduous monitoring methods for carabids. Reducing the sampling effort without significantly distorting the detected diversity relationships may be desirable not only for logistic reasons, but also for biomonitoring of areas where e.g. endangered species occur. However, compared to the pulsating method, the other sampling regimes with even shorter duration did not give the same results as the continuous sampling. These regimes should therefore be used with caution if they would be considered a basis for comparative diversity studies.

Our method of generating sub-samples in time was simple, and assumed that the catch in fortnight *x* did not influence the catch in the subsequent intervals. This is not necessarily true, and thus the results obtained should be viewed with caution. The overlap in diversity between the continuous and the pulsating sampling regimes, however, indicates that our assumption may not be grossly incorrect.

We note that the use of pitfall trapping may generate relative abundance patterns that are biased. Large species can be more mobile and less able to escape once fallen into the trap, so may be more "catchable". This is a perennial problem of any trapping method that relies on the activ-

ity of the study subject to generate samples. For comparative purposes and for species inventory, these methods are useful. The above limitations should be kept in mind when drawing conclusions on general diversity trends, comparing, for example, forested vs. other types of habitats.

Finally, we wish to stress that our experiment only addressed the question of sampling period, an important element in monitoring, but not other, equally important aspects of sampling such as the number of traps, their distance, material, or way of operating. These questions should be addressed in a more complex experiment, because the need for monitoring will gain importance in conservation biology as well as in monitoring the impact of different agricultural and forestry operations in an increasingly human-dominated world.

The usefulness of the harmonic radar as a tool to study invertebrate movement

Harmonic radar is suitable for detailed studies of spatial behaviour over both short and long intervals in New Zealand providing the animals have localised ranges. Cryptic invertebrates can be relocated with minimal disturbance to the habitat.

The normal movement speed of the study organism should be considered when deciding on the time intervals between relocations. Ground beetles can move fast and far enough (up to 30m within 1h, Wallin 1991) to make relocation very difficult in dense forest habitats common in New Zealand. For such organisms, relocation every 10-15 min is recommended, at least during the initial phase of the study.

Mascanzoni & Wallin (1986) found no spurious signals. In contrast, we experienced a variable amount of background noise, caused by incidental metal objects such as fences or rubbish tins. Operator experience helped to distinguish background noise from the transponder signal at extreme range. Water (and humidity) attenuated the signal, and other, unexplained interference sometimes reduced the detection range to a few m. The clarity of the signal improved but maximum detection distance did not change when the target was on vegetation.

The orientation of a transponder with respect to the microwave beam had a marked effect on the maximum detectable distance: when the long axis of the transponder was perpendicular to the beam, the detectable distance was much smaller. Mascanzoni & Wallin (1986), using an older version of the apparatus and a different antenna, did not mention orientation, but probably made their measurements with the transponder in the parallel position. The only diode common to both studies (the HP 2835) gave similar readings to theirs in this position only.

Some organisms may spontaneously generate false signals. When tracking ground beetles, we were misled several times by a false signal, whose origin was always a tree weta (*Hemideina crassidens* (Blanchard), Orthoptera: Stenopelmatidae). The cause of this is not known.

While the weight of the aerial was not significant for the carabid, the necessary length of the aerial could hamper normal movement. To minimize this, a very fine and flexible wire is preferred that can freely trail behind the beetle.

We believe that the harmonic radar can be used for tracking a wide range of invertebrates

and vertebrates that are expected to undertake small-scale movements. Many such animals are in need of protection and management, but our lack of knowledge of their spatial behaviour and habitat preferences often limits the effectiveness of our actions. We suggest that harmonic radar can be fruitfully used to describe habitat use of such animals as geckoes, tuatara, weta, as well as large flightless beetles. The inability to identify the target individual is not necessarily an obstacle because we are often interested in microhabitat use, and/or direct measurements (size, body mass), so the organism has to be handled anyway. Even lighter tag designs now exist for smaller organisms that are active above ground level, so bees (Riley *& al.* 1996), caterpillars, butterflies and parasitic flies (Roland *& al.* 1996) can now be tagged and relocated. This extends the applicability of the method to an even wider range of organisms.

CONCLUSIONS

In summary, work under this part documented that

1) The often used “common currency” for trapping effort needs to be re-examined because its two components, number of traps and length of operation do not contribute to the catch in the same way. This has an important consequence for the design of biodiversity monitoring: trapping effort allocation for monitoring is better when the number of traps is at the possible maximum and the length of time shortened rather than the other way around.

2) A comparative analysis of different sampling methods in time showed that, at least for species inventories and diversity evaluation, a “pulsated” sampling gives similar results to the continuous one. This may ease the effect of sampling on arthropod assemblages with threatened species.

3) We introduced the technique of the harmonic radar to study arthropod movement in New Zealand. Several diodes were tested and compared, and an optimal aerial configuration was determined. The usefulness of the technique was demonstrated on a ground beetle. This technique is suitable to study cryptic animals and important data can be collected using a non-invasive method. This is especially significant where such studies were only possible by severe habitat disturbance only (done while searching for the animals).

Part III. Life history studies

Life history studies of ground beetles accompanied my whole career. From these studies, however, only selected, recent examples are included, emphasising the attempt to standardise the description of yearly activity in these beetles.

In Hungary, we studied and described the seasonal activity of three species: *Anisodactylus signatus* (Fazekas et al. 1997), *Platynus dorsalis,* and *Brachinus explodens* (Fazekas et al. 1999). During this work, we developed a new method to describe, in a standardised way, seasonal activity. This method relies on the combination of calculating sliding averages, and the division of the total activity period according to the quantile method. In order to discount the impact of *ad hoc* activity variations, first the seasonal activity curve is reconstructed, by calculating a weighted sliding average of the individual data points. Following this, the species' activity is divided into four parts, based on the cumulative (smoothed) activity curve, and the cardinal points of the activity curve (main activity period, activity peak) are unambiguously identified. The activity peak falls where this smoothed curve reaches 50% of the individuals captured. This is more unequivocal and less variable than the traditional way of presenting seasonal activity curves that considers the time of the highest per-period catch as the activity peak. This can (and does) vary from year to year. Our method similarly identifies the main activity period, which starts when 25% of the total numer of individuals is captured, and ends when the cumulative total catch reached 75%.

New Zealand is rich in carabids, but our knowledge about their biology and ecology is very fragmentary (Larochelle & Lariviere 2001). We were the first to quantitatively describe the life history of six common, endemic species of ground beetles (Cartellieri & Lövei 2003). We have shown that the activity and reproduction of these species shows distinct seasonality (previously, several arguments have been published that claimed a lack of seasonality in surface-active arthropods, because of the mild, relatively aseasonal climate in New Zealand, (e.g. Moeed & Meads 1986), the individuals can live longer than one year, and –at least some species – are iteroparous. During these studies, we have also used the method developed during life history studies done in Hungary.

Life history studies, 1. Seasonal activity and reproduction of *Anisodactylus signatus*, *Platynus dorsalis* and *Brachinus explodens* in Hungary

Anisodactylus signatus

The ground beetle species Anisodactylus signatus (Panzer) is present in most of western and central Europe, reaches as far north as Denmark (Turin et al, 1977), and extends eastward through Russia and China. The species is scarce in Western and Central Europe (Freude et al. 1976), but is frequent in cultivated fields in Eastern Europe (Lövei & Sárospataki 1990). A. signatus is one of the most common carabids in agricultural fields in Hungary (Horvatovich & Szarukán 1986), and occurs widely in European Russia (Berim & Novikov 1983; Matalin 1992), Central Asia (Saipulaeva, 1986), and Heilongjiang Province, China (Deng & Li 1981).

Species in the genus *Anisodactylus* demonstrate different degrees of mixed feeding. However, both larvae and adults of this species consume plant material, mainly germinating seeds (Ponomarenko 1969; Horvatovich & Szarukán 1981; Berim & Novikov 1983), and there are indications that A. *signatus* may be a reluctant predator, preferring plant material to animal prey (Berim & Novikov 1983). Seasonal activity is unevenly documented within this species' wide distribution range (e.g. Kasandrova & Sharova 1971; Berim & Novikov 1983); other aspects of its population biology, such as age structure and egg production remain little studied.

Platynus dorsalis and *Brachinus explodens*

Both species are widespread in central Europe, *P. dorsalis* is generally common (Lövei & Sárospataki 1990), *B. explodens* demonstrates locally high densities. Data on the life history of these species (Skuhravy 1959b; Wautier & Viala 1969; Wautier 1971) indicate that both are spring breeders with summer larvae. *P. dorsalis* is considered an important aphid predator (Skuhravy 1959a; Sunderland 1975; Scheller 1984) and affect the establishment and early population growth of aphids (Sunderland & Vickerman 1980; Griffiths et al 1985). Data are limited on *B. explodens* but Kromp (1989) found it common in an organically managed agricultural field in Austria while it was rare in conventional fields. Below we present information on seasonal activity and age structure, and estimate total reproductive output of these two species in central Hungary.

Material and Methods

Material was collected as part of a research project in two agroecosystem in Hungary: maize (Mészáros 1984b) and apple (Mészáros 1984a) – see the description of collection sites, periods and methods detailed in those publications. Beetles collected by pitfall traps were identified,

separated, aged, sexed and dissected. Ageing was done based on coloration, chitinisation, and the extent of bristle and mandible wear. Three categories were distinguished:

(a) 'teneral': newly emerged beetles, recognized from sclerite coloration and softness

(b) 'young': in *A. signatus,* such individuals were adults that had not yet overwintered and were easily distinguished until the end of their first season. In both *P. dorsalis* and *B. explodens,* such individuals were overwintered adults entering their first reproductive season, recognised from hardened sclerite but little wear on bristles or mandibles.

(c) 'Old': adults past their first reproductive season/overwintering, recognised by wear on both mandibula and bristles. We could not distinguish between second-year and older beetles.

Following this, the males and females were dissected to determine the developmental stage of their testes and ovaries and the number of eggs, following the method of van Dijk (1972, 1979a) and Wallin (1989). A total of 789 *A. signatus,* 674 *P. dorsalis* and 458 of *B. explodens* individuals were dissected. The length and width of eggs was measured under microscope, and the volume was calculated using the formula for a rotating ellipsoid (Juliano 1985).

Seasonal activity

Seasonal activity was described using the quantile method. Standardised, smoothed seasonal activity curves were constructed, plotting the weighted sliding average (over three catching periods, with the middle period given double weighting) of the cumulative, total catch against time (expressed in weeks). Based on this curve, three “cardinal dates” were established, corresponding to the dates when 25, 50, and 75% of the cumulative total catch had been captured. The total activity period was divided into early, main, and late stages. The main activity period was delimited by the dates on which 25 and 75% of the cumulative total catch was reached, and the activity maximum was defined as the date when 50% of the total catch was reached. For a more detailed description, see Fazekas & al. (1997).

Estimating reproductive output

The reproductive output of the population was estimated by Grüm's method (Grüm 1984). This method requires calculation of the mean number of ripe eggs in the ovaries, at weekly intervals, followed by the observed rate of egg deposition:

$$\mu = \frac{(\ln N_{k-1} - \ln N_k)}{dt}$$

where d*t*=number of days between the estimation of N_{k-1} and N_k (the last two values of N_i). Then the mean number of eggs laid by a female in the population during the entire breeding period becomes:

$$\nu = \sum_{i=0}^{k} N_i \hat{\mu}_i T_i$$

where T_i is the number of days in the *i*th period, and μ is the previously estimated rate of egg deposition.

Differences in the mean numbers of eggs per female were tested with the GT2 method for multiple comparisons of means (Sokal & Rohlf 1995).

Results

Anisodactylus signatus

In Central Hungary, Tukrospuszta (Site 1), adults were captured throughout the 8 May to 31 October trapping period. The mean activity period occurred during the last three weeks of July, with the peak in mid-July (Table 3.1). The seasonal activity curve was skewed to the right (Fig.3.1).

Table 3.1. *Main activity periods and peak activity dates of the different age classes of* Anisodactylus signatus *at two localities in Hungary.*

Age class	***Tukrospuszta***		***Ujfeherto***	
	Main activity period	**Activity peak**	**Main activity period**	**Activity peak**
	All beetles			
Old	6 Jun–9Jul	23 Jun	10-29Jun	17 Jun
Teneral	8-18 Jul	13 Jul	20 Jul–18 Aug	1 Aug
Young	7-28 Jul	13 Jul	31 Jul–8 sep	19 Aug
Total	7-29 Jul	14 Jul	11 Jul–22 Aug	1 Aug
	Females			
Old	9 Jun-15 Jul	25 Jun	11-27 Jun	19 Jun
Teneral	6-16 Jul	10 Jul	20 Jul-17 Aug	5 Aug
Young	10 Jul-3 Aug	16 Jul	2 Aug-2 Sep	24 Aug
Total	6-24 Jul	12 Jul	1 Jul-24 Aug	1 Aug
	Males			
Old	9 Jun-10 Jul	25 Jun	1-29 Jun	15 Jun
Teneral	9 Jul–2 Aug	15 Jul	20 Jul-17 Aug	30Jul
Young	8-25 Jul	14 Jul	29 Jul–1 Sep	16 Aug
Total	2-21 Jul	10 Jul	15 Jul-21 Aug	31 Jul

In eastern Hungary, at Ilonatanya (Site 2), trapping did not occur throughout the entire activity period. Beetles were first caught during the week preceding May 28th, and a steady increase was observed until trapping was discontinued at the end of July. At the other eastern site, Ujfeherto (Site 3), beetles were caught and remained active from the first week of trapping until trapping was discontinued in late September. The main activity period took place between mid-July and late August, and was almost three weeks longer than at Tukrospuszta (Table 3.1). The peak of activity occurred on August 1st (Table 3.1), also later than in central Hungary. The seasonal dynamics curve was less skewed than that of the population at Tukrospuszta.

Seasonal activity of the age classes

Central Hungary, Tukrospuszta. Old beetles were captured on all sampling occasions (Fig. 3.1). The main activity period was about one month long, starting in June (Table 3.1). Tenerals first appeared on 27 June and peaked on 13 July. Small numbers of tenerals were trapped almost every week until early October. This resulted in an activity curve that was extremely skewed to the right (Fig. 3.1). Young beetles appeared about two weeks after the first tenerals; the peak occurred on the same day (Table 3.1). Activity continued until harvest in late September (Fig. 3.1).

Eastern Hungary, Ilonatanya (Site 2). Only old beetles were captured from the beginning of the trapping on 7 May until early July (Fig. 3.1). Increasing numbers of tenerals and young beetles were caught from early July until trapping was discontinued at the end of July.

Eastern Hungary, Ujfeherto (Site 3). Old beetles were captured from the first week of trapping, 14-21 April, until late July; one was captured in late August. The mean activity period was shorter than at Tukrospuszta, but peaked one week earlier (Table 1). Tenerals appeared during the week of 7-14 July and were captured until late September (Fig. 2). The main activity period took place one month later than the main activity of the same age class at Tukrospuszta (Table 3.1). The activity of young beetles peaked later and lasted longer than that of the tenerals (Table 3.1). The cardinal dates of activity of the tenerals and young beetles completely overlapped at Tukrospuszta but not at Ujfeherto (Table 3.1).

Inter-site comparisons

The mean activity period of all females combined was less than three weeks at Tukrospuszta vs. almost two months at Ujfeherto. Males showed a similar but less pronounced trend (5 weeks vs. 8 weeks, Table 3.1). A number of further differences were also observed when the age classes were considered separately: (1) a short mean activity period for old Ujfeherto females (16 days) vs. a long one at Tukrospuszta (36 days) but no such difference for old males; (2) a very short mean activity period for teneral Tukrospuszta females, 20 days longer for Ujfeherto females (Table 3.1); (3) similar mean activity periods for young females at the two sites, but twice as long for young males at Ujfeherto (34 days) vs. Tukrospuszta (17 days). In general, activity curves were more tightly synchronized at Tukrospuszta (shorter mean activity periods) except for old beetles (Table 3.1). The span of the peak activity dates indicates the same; they all occur within three weeks at Tukrospuszta while they span two months at Ujfeherto (Table 3.1).

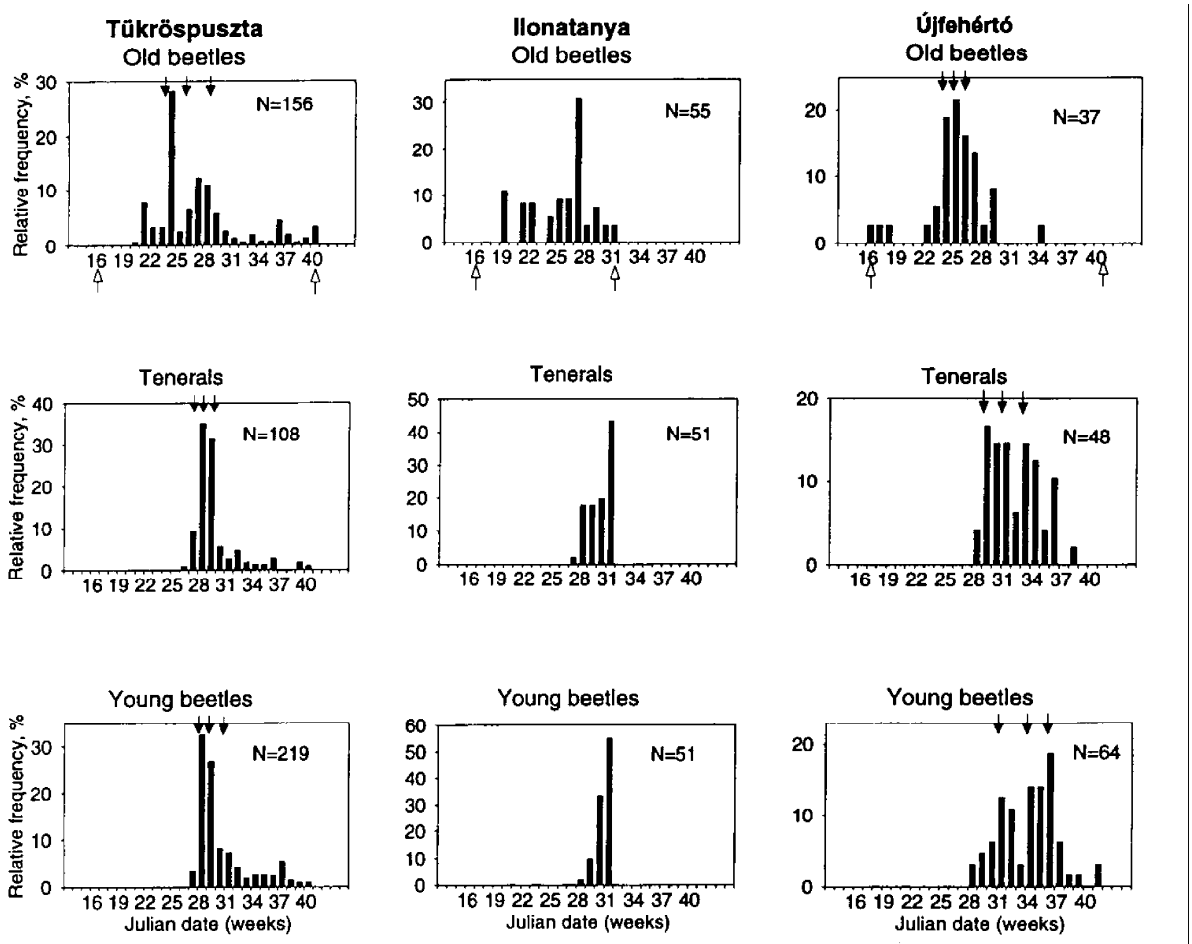

Fig. 3.1. *Seasonal dynamics of three age classes of* A. signatus *at three locations in Hungary. Arrrows denote trapping and the main activity period and the activity peak.*

"Old" adults occurred as 32%, 35% and 25% of individuals collected at the three sites, respectively. At Tukrospuszta , 69% of all beetles captured were males. In the apple orchards in eastern Hungary (sites 2 and 3), females outnumbered males (62% of all beetles at Ujfeherto and 65% at Ilonatanya were females). The sex ratio of "young" adults was more even, with 69% females at both Tukrospuszta and Ujfeherto, 46% at Ilonatanya (but note the shorter trapping period there).

Egg production

None of the young females had eggs in their ovaries.Gravid females had a maximum of 6 eggs at Tukrospuszta , 10 eggs at Ilonatanya, and 5 eggs at Ujfeherto. At Tukrospuszta, Ilonatanya, and Ujfeherto, respectively, 44%,82% and 21% of the old females were gravid. At Tukrospuszta, the earliest collection of gravid female occurred on 23 May (with 3 eggs) and the last one was collected on 18 July (2 eggs); females with the maximum number of eggs were collected in early June. Similar dates cannot be reliably established for the two other locations due to the short trapping period at Ilonatanya, and the low number of gravid females (5 only) captured at Ujfeherto. The mean number of eggs per gravid female was 2.67 (*s.d* = 1.68,

n = 18) at Tukrospuszta and 4.0 (*s.d.* = 2.36, *n* = 28) at Ilonatanya. This difference is significant (Student's two-sample t-test, *t* = 2.08, d.f. = 44, p = 0.043). The difference in the populations' mean egg number was even greater (Tukrospuszta : mean = 1.17, *s.d.* = 1.73, *n* = 41; Ilonatanya: mean = 3.29, *s.d.* = 2.63, *n* = 34, Student's *t* = 4.19 d.f. = 73, p = 0.001).

The estimated seasonal egg production at Tukrospuszta, according to Grum's method, was between 20.9 and 10.3 eggs/female (Table 3.2). The most realistic estimate, based on the longest period for the estimation of egg deposition rate was 15.6 eggs/ female.

Table 3.2. *Estimates of mean total seasonal fecundity, according to Grum's method, for* Anisodactylus signatus *females in the population at Tukrospuszta, Hungary, 1978. Three periods were used to determine egg laying rate.*

Period	N_{k-1}	N_k	**Egg laying rate**	**Total fecundity**
3-10 July	2.6	1.00	0.14	10.3
11-18 July	1.0	0.14	0.28	20.9
3-18 July	2.6	0.14	0.21	15.6

Platynus dorsalis

Seasonal activity

Adult activity started in mid-April to early May, and lasted until August. The activity peaks were in May-June (Fig 3.2). Males were caught earlier than females in two of the three study years. Males remained active later in the season than females, usually by one-two weeks but this difference was a full month in 1990 (last female 27 August; last male 25 September). The sex ratios were about equal (Tab. 3.3). Tenerals were present in July but few were caught (4.1% of the total catch). Tenerals were recognisable until early August. Adult *P.dorsalis* have a soft chitinisation which may have contributed to a relatively short period during which the tenerals could be recognised.

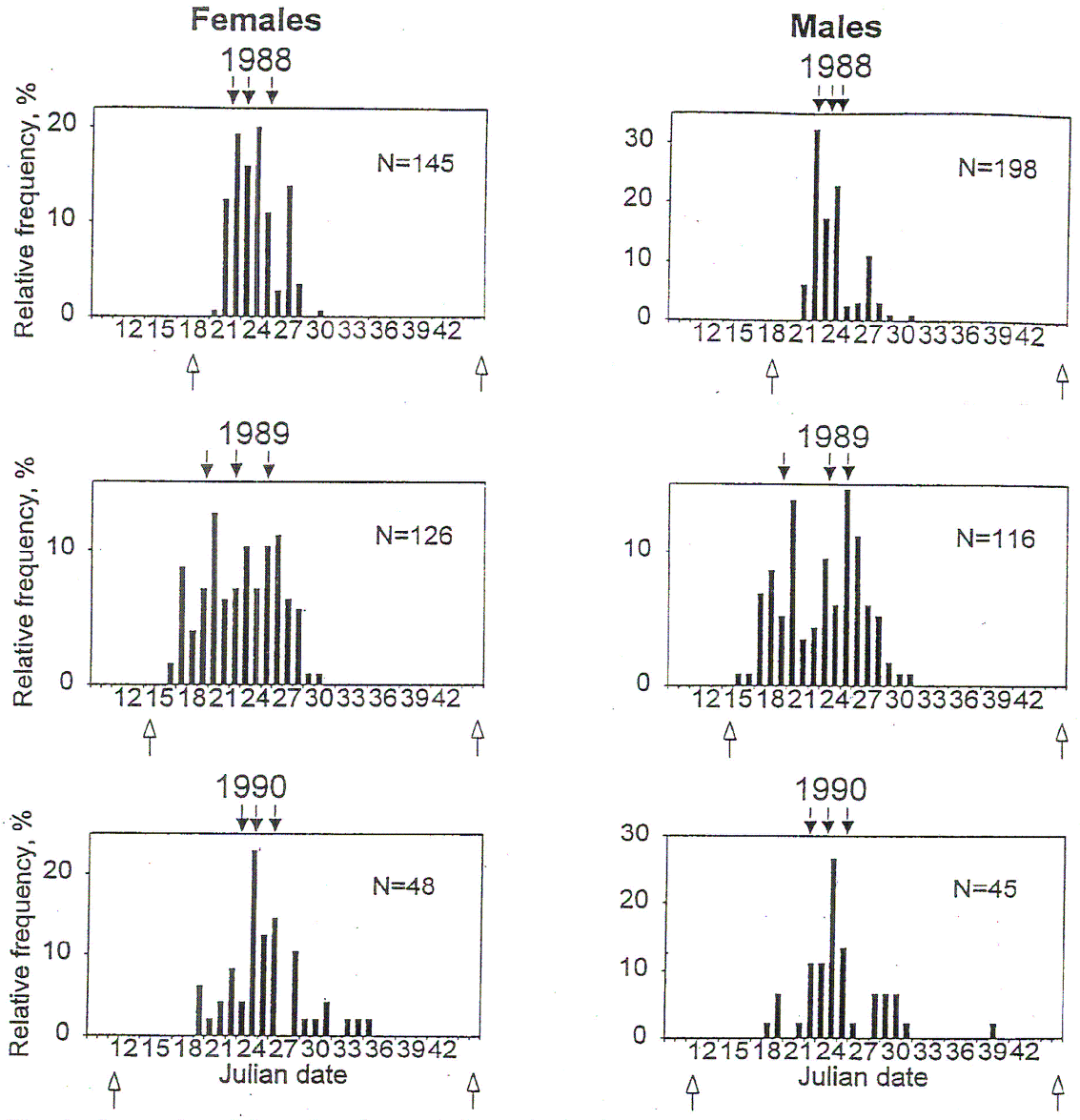

Fig 3.2 *Seasonal activity of male and female* Platynus dorsalis *between 1988-1990 at Julianna-major, Budapest, Hungary. Arrows under the panels denote the start and finish of the trapping period. The central arrow on top marks the median date of activity, the left and right ones indicate the main activity period.*

Reproduction

The reproductive period lasted ten weeks. Ripe eggs in the ovaries were found between April and the end of July. The earliest gravid female was captured during the week preceding 18 April (in 1989); while the latest was 27 August (one specimen in 1990). From the end of June some females had distinct *corpora lutea* in their ovaries, which means that the beetles had produced eggs ("spent"). All the non-teneral females in the sample either contained eggs in the ovaries or were spent. Peak egg numbers and the highest mean number of eggs occurred between the second half of May and first half of June. The maximum number of eggs found in one female varied two-fold over the study period: the maximum was 16 in 1989 but only 8 in 1990. The period between the median date of presence of gravid females and that of teneral beetles was about six weeks. This could be considered as the average duration of individual development.

The mean number of eggs in the ovaries over the three years was 5.4 eggs/female (*s.d.*=3.9, *n*= 277). The mean egg number in 1988 was significantly higher than in 1989 or 1990 (GT2 (1988-89) = 5.04, GT2 (1988-90) = 5.34, both $p<0.001$; GT2 (1989-1990) = 0.975, N.S., *d.f.* = 3, 274). The estimated seasonal egg production according to Grüm's method, was 49.8 eggs/female in 1988, and 26.9 eggs/female in 1990 (Tab 3.4).

The egg laying rate could not be calculated for 1989, and in the two other years, the difference was considerable (Table 3.4). The total fecundity, estimated by Grüm's method, varied almost two-fold, also causing a similar difference in clutch volume (Table 3.4). The total number of eggs was correlated with the number of mature males caught each week (linear regression: r=0.87 for 1988, r=0.78 for 1989, r=0.80 for 1990, all $p<0.01$). All the males except the tenerals had mature testes.

Brachinus explodens

Seasonal activity

The first adults were caught in late March, and the last in late August. In some years, seasonal activity was longer. The last male in 1988 was caught during the last week of September, and the last female in 1990 was found in the trap on 16 October. The onset of activity of both sexes was identical in two of the three years of study. The end of activity period was almost a month apart, longer for males in 1988 while longer for females in 1990. They were of equal length in 1989. The activity peaks were in May-June (Fig 3.3). The sex ratios were about equal in 1988 and 1990, but in 1989 three times more females than males were caught (Tab 3.3). Tenerals were caught for a short period comparable to that of *A.dorsale*, generally from mid-July to early August. *B. explodens* has a weak chitinization similar to *A.dorsale*, which may have been responsible for the short period during which tenerals were recognizable.

Table 3.3. *Sex ratio, age structure, activity and reproductive periods of* Platynus dorsalis *and* Brachinus explodens *caught in an abandoned apple orchard, Juliannamajor, Budapest, Hungary, 1988-90.*

	Platynus dorsalis			***Brachinus explodens***		
Characteristics	**1988**	**1989**	**1990**	**1988**	**1989**	**1990**
No. of beetles caught	341	240	98	103	223	132
Sex ratio	44:56	52:48	52:48	53:47	77:23	51:49
% of old beetles	6.9	10.3	10.4	7.6	3.6	3.0
Activity period	Apr-Aug			Apr-Sep		
Activity peak	early June			late May - early June		
Reproductive period	May-July			May-July		
Reproductive peak	early June			late May		
Tenerals appear	July			late July-Aug		

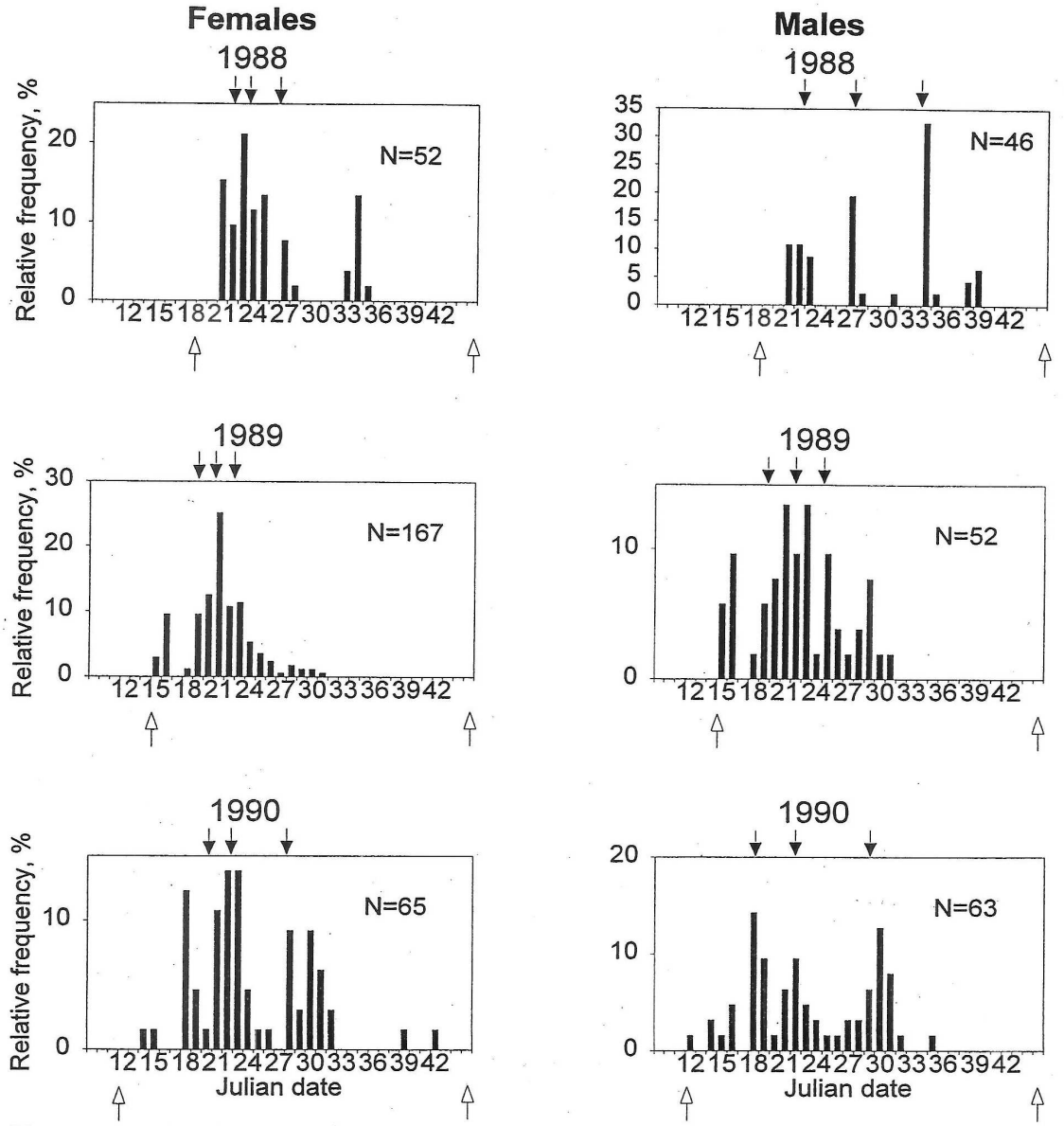

Fig 3.3. *Seasonal activity of male and female* Brachinus explodens *between 1988-1990 at Juliannamajor, Budapest, Hungary. Symbols as on Fig. 3.2.*

Tab 3.4. *Reproductive characteristics, estimates of mean seasonal fecundity, egg and clutch volume of* Platynus dorsalis *and* Brachinus explodens *at Juliannamajor, Budapest, Hungary, 1988-90.*

	Platynus dorsalis			***Brachinus explodens***		
Characteristics	**1988**	**1989**	**1990**	**1988**	**1989**	**1990**
No. of gravid females	128	115	34	42	117	34
No. of eggs/female	6.2±3.1	4.5±2.2	4.0±1.9	13.2±7.2	13.0±7.6	15.7±11.8
Egg laying rate	0.19	*	0.11	0.03	0.02	0.03
Total fecundity	49.8	*	26.9	21.3	15.5	28.7
Egg length x width (mm)	0.98±0.06 x 0.40±0.02 (n=185)			0.61±0.05 x 0.26±0.0 (n=61)		
Egg volume, mm^3	0.082			0.022		
Mean clutch volume, mm^3	4.08	n.c.	2.21	0.468	0.341	0.631
Female body length, mm	7.02±0.35			6.04±0.42		

Reproduction

The reproductive period was eight weeks long. "Spent" females occurred from July, and tenerals were found during the second half of July and in August (6.3% of the total catch). Ripe eggs in the ovaries were found from May (mid-April in 1989) to July. The last gravid females were collected 10-18 July. Peak egg numbers and the highest mean number of eggs occurred during the second half of May and the first week of June. The duration of development lasted about 6 weeks. The mean number of eggs was 13.5 (*s.d.*= 8.4, *n* = 193). The yearly means did not differ significantly from each other (GT2 = 0.132, 1.289 and 1.649, all N.S., *d.f.* = 3, 190). The greatest number of eggs in one female was 51, found on 5 June 1990. The yearly maxima were 32 in 1988, 46 in 1989 and 51 in 1990.

The egg laying rate was low and varied little. Total fecundity, according to the Grüm method, varied almost two-fold (Tab 3.4). The eggs of *B. explodens* were only about 1/4 the size of the *P. dorsalis* eggs, so the total estimated clutch volume was 11 - 13% of that of *P. dorsalis* (Tab 3.4).

There was no significant correlation between the weekly number of males caught and the total number of eggs found. All the males except the tenerals had matured testes.

Life hisotry studies, 2. Seasonal dynamics and reproductive phenology of ground beetles in fragments of native forest in the Manawatu, North Island, New Zealand

There are 424 known and an estimated 600 species of ground beetles in New Zealand (Larochelle & Lariviere 2001). A high proportion of these are believed to be endemic, as noted for other invertebrate groups in New Zealand (Watt 1982). Existing knowledge of the population status and life history of New Zealand ground beetles is very scarce. The few published studies on this group mostly deal with ground beetles in agricultural fields (Barker 1991; Sunderland et al. 1995b; but see Butcher & Emberson 1981); until 2000, there was no published life history study on native ground beetles. Such information would be valuable to guide conservation efforts, such as relocations, or to time vertebrate pest poisoning operations to minimise risk to non-target carabids.

We studied and described the seasonal activity and reproductive phenology of six native carabid species present in native forest fragments near Palmerston North, Manawatu region, North Island. Our findings indicated that several of these species have distinctly seasonal activity, long lifespans and low reproductive rate.

Study area and Methods

Study area

Beetles were collected in pitfall traps in three native forest fragments near Palmerston North. The habitat and collections details see in Part IV. Species were identified to species using a reference collection, and keys in Britton (1940); *Ctenognathus adamsi* Broun and *Z. cf. femoralis* Broun were kindly identified by J. I. Townsend. Subsequently, individuals were aged and dissected.

Ageing was based on the extent of bristle and mandible wear, elytral hardness, and colour as for European species detailed in the previous section. Due to the lack of calibration or any comparative studies on New Zealand beetles, only three age categories were distinguished in this study: tenerals, young adults, and old adults. “Teneral” adults were recently-hatched beetles with weak chitinisation and brownish elytra. “Young” adults had hardened, black elytra, sharp mandibles and long, intact bristles. “Old” adults, believed to be at least in their second year of life, had hard and black elytra, blunt-tipped mandibles and several broken or worn bristles. No distinction was made between second-year and older beetles.

Females were dissected to assess reproductive status, and divided into three groups based on the developmental state of their ovaries: females with resorbed ovaries (not in reproductive state), females with developed ovaries (reproductively active), and gravid females (with eggs). The eggs found in gravid females were counted.

Seasonal activity was described using the quantile method described earlier. This method could not be applied to *Z. cf. femoralis*, *M. capito*, and *H. mucronata* because they showed continuous activity or two maxima. Julian dates, that number weeks consecutively from Week 1 in

January to Week 52 in December, are used here. On Fig. 1–5, mid year was selected as the starting point so that the activity peak during the southern summer did not appear cut into two at the two ends of the *x*-axis.

Results

General carabid activity

Woodville Recreational Reserve The ground beetle fauna was much more diverse here (nine species, Lövei & Cartellieri 2000) and individuals were more active (416 adults caught in total) than at the two other study sites (Fig. 3.4A–C). Activity commenced in August, and ceased in May, following a unimodal curve (Fig. 3.4A). The activity level was, at maximum, about 5 times higher than at Keeble's Bush.

Keeble's Bush At Keeble's Bush, *M. capito* and *H. mucronata* represented the majority of carabids caught (totals of 74 individuals in 1990–91, and 29 individuals in 1999–2000). In addition, three *Plocamostethus planiusculus* males were caught in December 1999. The two common species showed some activity all year round, but there were seasonal differences. Activity during the winter months was low (0.1 individuals trap^{-1} fortnight^{-1}) but increased to >3 times this level during spring (October) and late summer (January, see Fig. 3.4B).

Atawhai Road Here, only two species, *M. capito* and *H. mucronata*, and 24 individuals were caught. The catches in the pitfall traps indicated very low activity (max. 0.25 individuals trap^{-1} fortnight^{-1}, Fig. 3.4C). Some beetle activity was detected year-round but there were no obvious maxima. However, due to the low numbers captured, we could not define seasonality with confidence.

Individual species accounts

Zolus cf. femoralis

Zolus cf. femoralis (Zolini) occurred only at the Woodville Reserve site, and 75% of all specimens were caught near a stream. The sex ratio varied, but overall, 3 times more females than males were collected (Table 3.5).

Both sexes were active during a 6-week period in the austral spring (August/September) and for a longer period in the summer/autumn (Fig. 3.5A). Almost no activity was recorded between late September and early October and for a longer period between early May and mid July. Spring activity was simultaneous and equal for males and females, whereas in autumn, females remained active for more than 2 months longer than males. The late summer activity for males lasted from late December to the end of January, whereas females were active until May. Teneral beetles of both genders were found only in January and early February.

All but one of the females dissected had fully developed reproductive organs. The single non-reproducing female was a teneral beetle caught in early February (Weeks 4/5). Females with eggs were found in late January, early May, mid August, and September. Gravid females had an average of 8.8 eggs/female (Table 3.5). The greatest number of eggs was found in late April/early May.

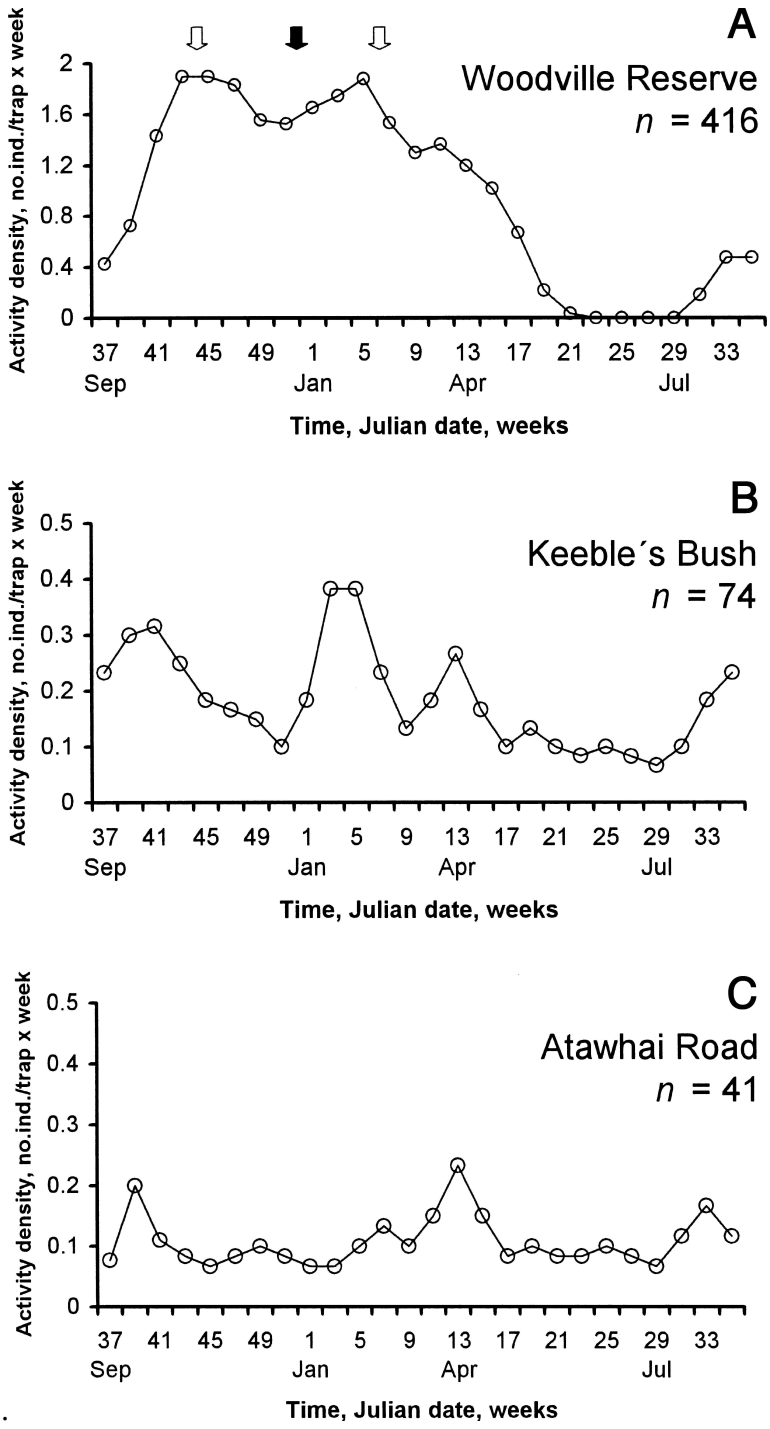

Fig. 3.4. *Seasonal dynamics of ground beetles at the three study sites in the Manawatu, North Island, New Zealand. Data are combined from 1990–92 and 1999–2000 where appropriate (see text). The seasonal curves start at Week 37 (early September), the start of the pitfall trapping, to place the main activity period near the middle of the graph. White arrows indicate the start and end of the main activity period; black arrow denotes the time of the peak activity, as calculated by the quartile method.*

Holcaspis mucronata

Holcaspis mucronata (Pterostichini) was captured at all three sites, and showed sporadic continuous activity throughout the year (Fig. 3.5B). The activity curve seemed to have two maxima, one in the spring (November) and a more pronounced one in the autumn (late March–April). Only part of the total catch was identified to gender, so differences in seasonality between the genders are difficult to detect. However, the male autumn activity period seemed to be shorter and more restricted to March, whereas females had a broader activity period extending to April/May. Two teneral beetles were caught: one at Atawhai Road in late December, and one at Woodville Reserve during January. The sex ratio (Table 3.5) showed a slight predominance of females.

Reproductive females were found in spring (October) and again during the maximum activity period in autumn (late March–April). Nearly all gravid females were captured at the small, suburban site at Atawhai Road. The reproductive season lasted from March to May (Weeks 12/13 and 18/19). Too few individuals were caught to distinguish between reproductive periods of old and young females. Six gravid females had an average of 3.9 eggs in their ovaries (range 1–7, Table 3.6).

Megadromus capito

Megadromus capito (Pterostichini) was captured at all three study sites. The highest numbers were caught in Keeble's Bush, and only mature males were caught at Atawhai Road. The majority of beetles in the Woodville Reserve were females, and included two tenerals. Overall, beetles were captured in all months but were very rare between late autumn and mid winter (from early April, Weeks 14/15 to late July, Weeks 30/31, Fig. 3.6). Male adults showed two activity maxima, a smaller one in late August/ early September and a larger one in January/ February (Fig. 3.6). The female activity curve differed slightly from that of the male, and showed a broad maximum from November to the end of January (Fig. 3.6). Ageing suggested that two age cohorts, young and old adults were present.

Teneral beetles were collected in January– February, plus a single teneral female in March. Reproductive females were found over the entire main activity period from late October until May with highest numbers in December. However, the numbers were too small to determine any differences in reproductive activity between young and old females. Gravid females were caught between October and March, with an average of eight eggs (Table 3.6).

Table 3.5. *Sex ratio and seasonal activity characteristics of six species of ground beetles living in forest fragments of the Manawatu region, North Island, New Zealand.*

Characteristics	***Zolus cf.femoralis***	***Holcaspis mucronata***	***Megadromus capito***	***Megadromus turgidiceps***	***Plocamosthetus planiusculus***	***Ctenognathus adamsi***
No. individuals caught	43	88	74	24	121	200
Sex ratio, male:female	1:3	1:1.3	1:0.6	1:0.38	1:0.7	1:0.9
Activity period	Aug/Dec–Feb	Whole year	Whole year	Jan–Mar	Nov–Apr	Dec–Feb
Activity peak	Sep/Jan	Nov/May	Aug–Sep/ Dec–Jan	Feb–Mar	Feb–Mar	Jan
Reproductive period	Aug–May	Oct/Mar–May	Oct–May	Dec–May	Aug–May	Aug/Dec–Apr
Tenerals appear	Jan	Dec	Sep–Oct/Jan	Mar	Jan–May	Oct/Dec–Apr

Table 3.6. *Reproductive parameters of the six ground beetle species in forest fragments of the Manawatu, New Zealand. (s.d.= standard deviation.)*

Species	**Beetle size (mean ± *s.d.*, mm)**	**Number of females**			**No. of eggs/ gravid female***	
		Dissected	**With developed ovaries**	**With eggs**	**Mean**	**Min.–max.**
Zolus cf. femoralis	7.6±0.6	14	4	7	8.8	3–18
Holcaspis mucronata	14.9±0.8	8	1	6	3.9	1–7
Megadromus capito	21.8±1.2	24	9	9	7.9	2–19
Megadromus turgidiceps	19.7±1.4	8	1	6	5.0	2–8
Plocamosthetus planiusculus	27.5±2.0	32	15	3	1, 5, 12	
Ctenognathus adamsi	12.4 ± 0.6	44	13	12	4.3	1–8

*In samples with $n < 5$, individual data are given.

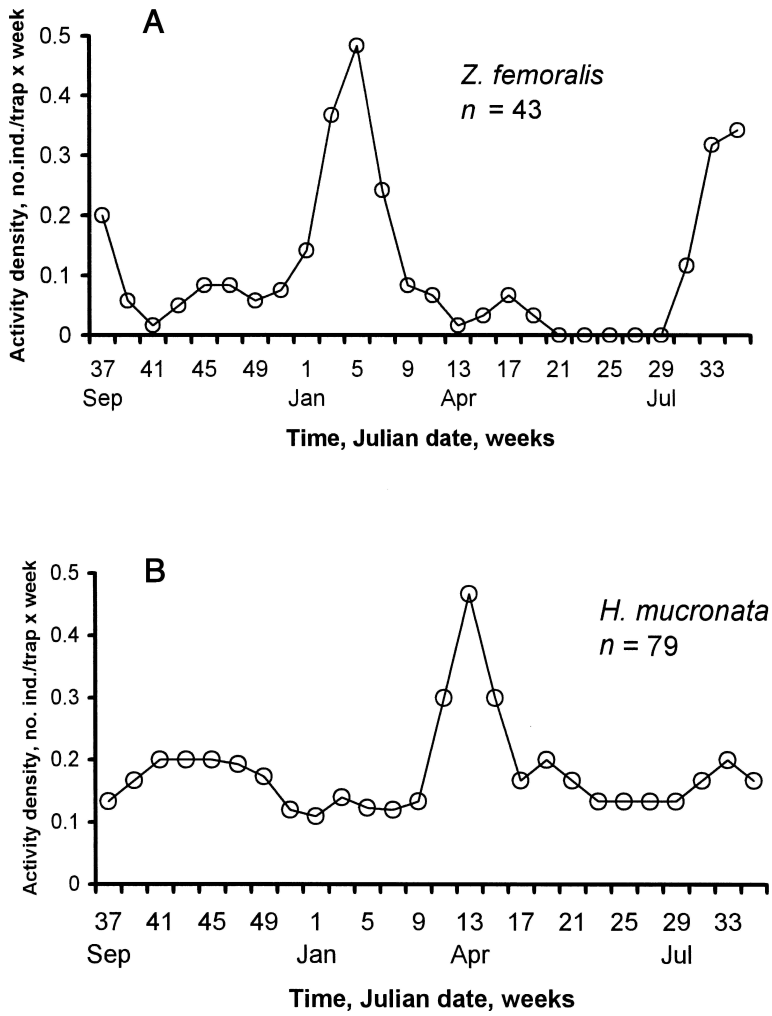

Fig. 3.5. *Seasonal dynamics of* ***A****,* Zolus cf. femoralis *and* ***B****,* Holcaspis mucronata *in the Manawatu, North Island, New Zealand. The seasonal curves start at Week 37, the start of the pitfall trapping, to place the main activity period near the middle of the graph.*

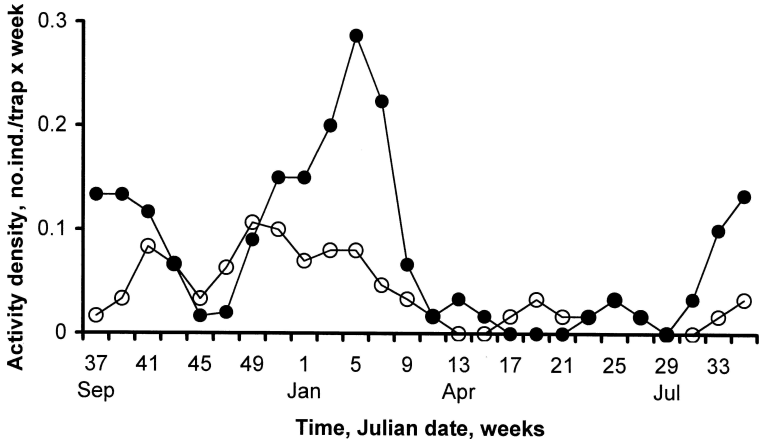

Fig. 3.6. *Seasonal dynamics of females (open circles, n = 20) and males (filled circles, n = 42) of* Megadromus capito *in the Manawatu, North Island, New Zealand.*

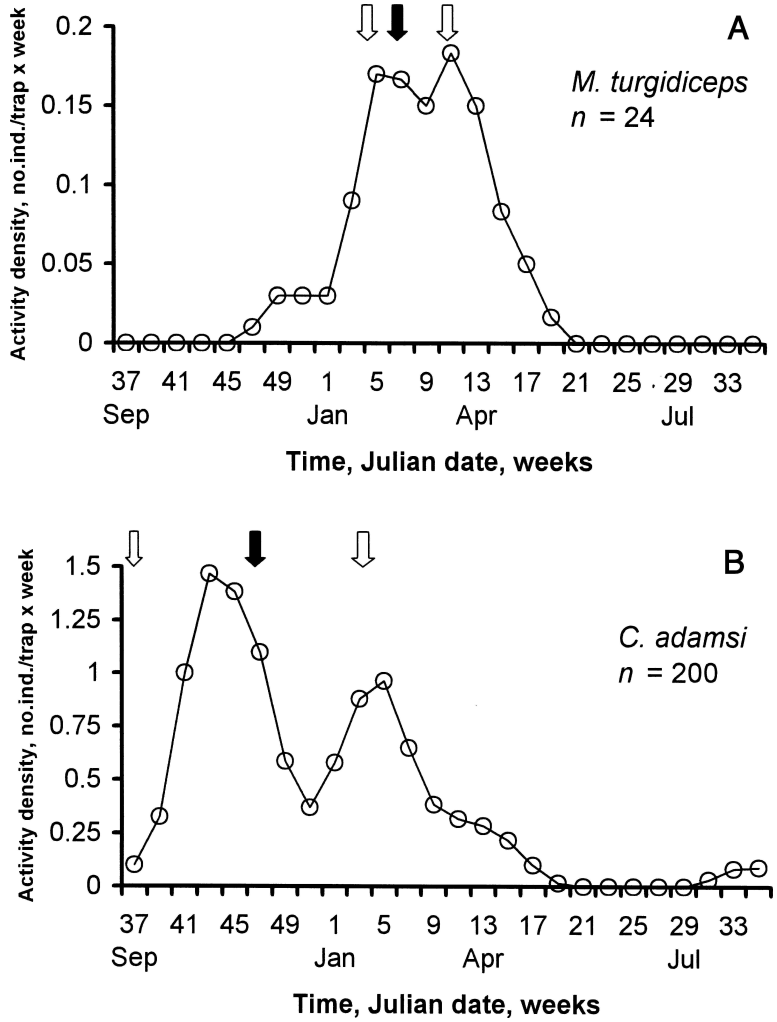

Fig. 3.7. *Seasonal dynamics of* ***A***, Megadromus turgidiceps *and* ***B***, Ctenognathus adamsii *in the Manawatu, North Island, New Zealand. White arrows indicate the start and end of the main activity period; black arrows denote the time of the peak activity.*

Megadromus turgidiceps

Megadromus turgidiceps (Pterostichini) was collected only at Woodville Reserve, and not commonly (24 individuals caught). They were active from late November (Weeks 48/49) to late April (Weeks 16/17), with the main activity period in summer and autumn, from late January to the end of March (Weeks 4/5–12/13, Fig. 3.7A). Over twice as many males than females were captured (Table 3.5).

We could not reliably distinguish old from young adults because of the low sample size. Non-teneral males were caught only in the first half of the activity period, from December to February (Weeks 48/49– Weeks 6/7). Females were found from late December onwards until the end of the autumn season in April. Teneral beetles, all males, were found over a 6-week period from mid February until April (Weeks 6/7–14/15).

Eight females were dissected. Six of them were gravid, with an average of five eggs (Table 2). One female in February contained corpora lutea, indicating that it had completed egg laying; another, caught in April, had developed ovaries but no eggs nor corpora lutea. The reproductive season could be long, as the first gravid female was captured in mid December, and the last one in early May.

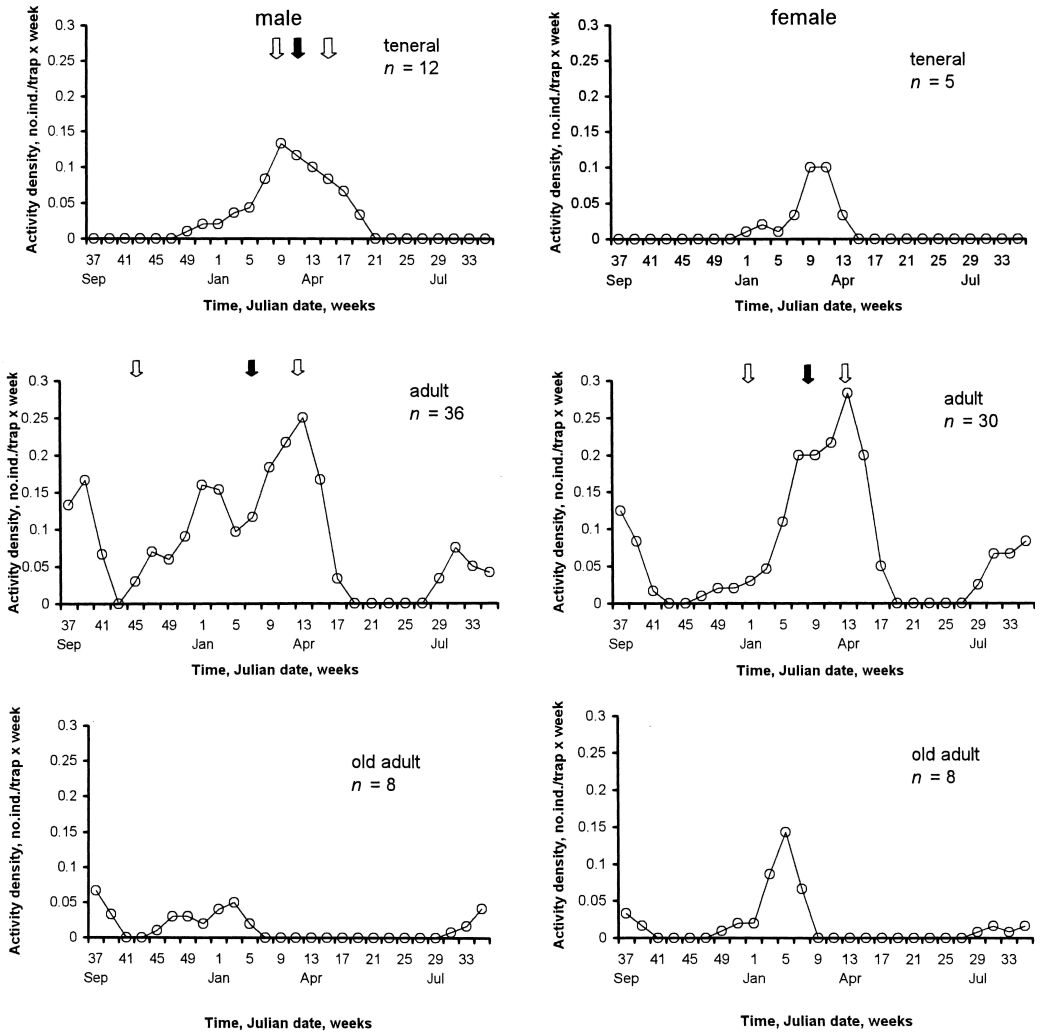

Fig. 3.8. *Seasonal dynamics of* Plocamostethus planiusculus *in the Manawatu Gorge, North Island, New Zealand, during the 1991–92 and 1999–2000 seasons. Age classes and genders are separate. The seasonal curves start at Week 37, the start of the pitfall trapping, to place the main activity period near the middle of the graph. Arrows indicate (only in categories with n > 10) the start and end of the main activity period (white arrows) and the time of the peak activity (black arrows).*

Ctenognathus adamsi

This is a soft-cuticled, medium-sized species in the tribe Agonini that was caught only at the Woodville Recreational Reserve. This species may be gregarious, because most of the individuals were caught in one trap group near a stream. The sex ratio was even (Table 3.4).

The activity patterns of the genders was difficult to judge because a large proportion of beetles caught during the spring activity period was identified only to species. Gender was not established, and this material was later lost. However, for all other periods where male and female beetles were

identified, gender activity was synchronised. Activity lasted from August until April (Weeks 32/33–16/17, Fig. 3.7B). The spring activity maximum was larger than the autumn one, but there was only a small decrease in activity between the two periods. As the material was collected in different years, we cannot exclude the possibility that the activity was unimodal. The main activity period, calculated by the quartile method, fell in spring, between September (Weeks 36/37) and January (Weeks 2/3), with a peak during November (Weeks 46/47). Teneral beetles of both genders were caught in October and again, in larger numbers, in December/January. A few teneral males were also caught in April.

Females with developed ovaries were found in August, and again from December to April. Gravid females with an average of 4.3 eggs were caught during the same periods (Table 3.6). Thus, reproduction in this species seemed to extend over the whole active period.

Plocamostethus planiusculus

The activity of this pterostichine species was low in the spring, but beetles were caught in high numbers during autumn (Fig. 5). The first male and first female were captured in August (Weeks 32/33). The last male was found in May (Weeks 18/19), and the last female a fortnight earlier. Old adults appeared at the beginning of the activity period, but no old males were captured after late January (Weeks 4/5) or old females after mid February (Weeks 6/7).

Teneral beetles showed little overlap with the activity of old individuals, and most appeared during summer/autumn (December–May, Weeks 52/1–18/ 19, Fig. 3.7).

Females with developed ovaries or eggs were found over the whole activity period, i.e., from August until the start of May (Fig. 3.7). Young and old females appeared to have separate reproductive periods. Old females reproduced during their activity period in February, whereas most reproductively active young females were not found before March (Week 9). The latest reproductive young female was also the latest active female, caught during the second half of April (Weeks 16/17). Three gravid females were caught, and they had 1, 5, and 12 developed eggs in their ovaries.

DISCUSSION

European species

Anisodactylus signatus

At all sites, the "old" beetles were already active at the start of the trapping. These individuals evidently overwintered as adults. Adult overwintering is also suggested by the appearance of tenerals during autumn (late September–early October). These overwintered adults probably represented the first, smaller peak of the seasonal activity curves in mid-June, which coincided with the peak of egg production. The second, larger activity peak signalled the emergence of "young" individuals; teneral beetles continued to emerge until early October. The time period between the start of reproductive activity in May and the appearance of teneral beetles in June is too short for these to have been the offspring of adults reproducing within the same season; the emerging teneral adults overwintered in larval or pupal stage. If the thermal developmental threshold of pupae were similar to the thermal threshold of the adult activity in spring, overwintered pupae would moult into teneral adults earlier. The fact that this did not happen suggests that at least some individuals overwintered as larvae.

The survival pattern of the old beetles varied across regions. The sudden and complete disappearance of old beetles at Ujfeherto and the continued presence of this age class at Tukrospuszta until October suggests that eastern adults may die after one year, while those in central Hungary may live longer. The extent of overlap between "old" and "young" beetles was also different, with less overlap in the east. Although our material was collected in different years, a similar phenomenon was noted by Kasandrova & Sharova (1971) in Russia. Near Ohrenburg, Russia, Lapshin (1971) found old adults from the middle of May to the middle of July; young beetles did not occur during this time.

This long activity period with the presence of more generations is similar to the seasonal activity of autumn-breeding carabid species like *Harpalus rufipes* (Luff 1980), as opposed to the activity of other spring breeders, e.g. *Platynus dorsalis* (Fazekas et al. 1997) or *Clivina fossor* (Desender 1983), which have no surface-active adults after early August.

Platynus dorsalis and *Brachinus explodens*

Both *P. dorsalis* (Hokkanen & Holopainen 1986) and *B. explodens* (Kromp 1989) are abundant in biologically managed fields, but rare in conventionally managed ones in Europe. Both species were present but few were captured in the insecticide-treated part of the same apple orchard (Mészáros 1984a). Our pitfalls contained formalin as killing agent and thus the sex ratio of the catch should be treated with caution. It should be noted, however, that sex ratio of the same species studied by live pitfall traps in earlier years were similar (Lövei, unpublished data).

P. dorsalis prefers weedy plots in arable land (Powell et al. 1985) especially in spring (Jensen et al. 1989) and the density of this species was positively correlated with weed cover in England (Coombes & Sotherton 1986). The high abundance of *P. dorsalis* in our study area is probably also

associated with the dense weedy undergrowth which developed after the abandonment of the orchard. This species in central Hungary demonstrated similar activity and reproductive patterns similar to those in cereal fields in Germany (Kreckwitz 1980).

Skuhravy (1959b) found more eggs (mean = 7.34 eggs/female) in the ovaries of *P. dorsalis* in arable land in Czechoslovakia than we did in Hungary. Skuhravy's data, however, were collected over a single year, so they do not necessarily indicate a consistent regional difference. In England, Chiverton & Sotherton (1991) found an average of 9.7 eggs per female in unsprayed plots, vs. 5.9 eggs in sprayed plots. In laboratory experiments, Bilde & Toft (1995) found that females laid a mean of 5.6 eggs over 5 weeks but this is probably less than the reproductive effort under field conditions. Bilde (in litt.) found an average of 11.88 eggs per female (n = 111) under field conditions in Denmark..

These data may indicate that *P. dorsalis* females develop one batch of eggs per season but the size of this batch varies considerably, according to local food availability. Grüm's method of calculating total egg output assumes that eggs are laid continuously over the reproduction period, and thus may overestimate the reproductive output for *P. dorsalis*. The estimation of total fecundity depends crucially on the egg laying rate. In our estimates, this is one of the factors (the other one is egg size difference) that produce the observed large difference between the total reproductive output of the two species (Table 2). This difference means that while the number of eggs found in individual females was higher in *B. explodens*, the total fecundity was similar for the two species or possibly even greater for *P. dorsalis*.

Several authors have used egg numbers in ovaries as a measure of reproductive output. Grüm (1973) estimated the fecundity by assuming a constant oviposition rate throughout the period of female maturity. This method, however, may not be not appropriate for all carabid species. Females of *Harpalus aeneus* and *Pterostichus madidus* did not lay more eggs in the laboratory than the peak number observed in the ovaries during the reproductive season. These species lay a single batch of eggs (Luff 1982). Several species like *Pterostichus versicolor* , *Calathus melanocephalus* (van Dijk 1979 a,b), or *Pterostichus oblongopunctatus* (Heessen 1980) lay eggs countinuously so the total number of eggs laid in a season and the number found in the ovaries is not equal. Grüm's method is more suitable for these species, but its application to species that lay a single batch of eggs remains problematic.

Reproductive output in ground beetles typically varies among years. It is influenced by food supply and perhaps adult density. Baars & van Dijk (1984) showed a negative correlation between the density of *C. melanocephalus* and the number of eggs in their ovaries. In years with low population density, the mean number of eggs laid was 3-4 times higher than the mean number of ripe eggs in the ovaries, whereas in high density years they did not differ (van Dijk 1986). A similar phenomenon was found for *Anisodactylus signatus* in Hungary (Fazekas et al. 1997).

The apparent codominance of *P. dorsalis* and *Brachinus* spp. has also been found in Sweden (Lindroth 1985) and Spain (Zaballos 1985). We found not only that the occurrence of the two species was associated, but some of their life history features were also similar. The activity and reproductive periods coincided and peak egg numbers were also found on the same dates. One difference between the two species was that more *P. dorsalis* adults entered a second reproductive season than those of *B. explodens*. There seems to be an even larger difference between the reproductive output between the two species. They key to the understanding of this difference may lie in the ecology of the larval stages.

Carabid seasonality in New Zealand

Carabids are generally most active during spring and summer (Butcher & Emberson 1981; Moeed & Meads 1986). However, little is known about the life history patterns of New Zealand carabids, especially species inhabiting native forests (Larochelle & Lariviere 2001). The work done in New Zealand represents the first quantitative life history study, giving details of some of the common forest species of the lower North Island. All species studied showed clear seasonality**.** The seasonal patterns detected seemed not only to differ between species, but also between the study locations in the Manawatu Plain (Keeble's Bush and Atawhai Road) and in the Manawatu Gorge (Woodville Recreational Reserve).

The two species commonly found in the Manawatu Plain, *H. mucronata* and *M. capito*, were active throughout the year. *H. mucronata* was caught evenly throughout the year, but *M. capito* appeared irregularly during winter. In this species, reproductively active females were found only from October to March. The sample of dissected *H. mucronata* females was small, but none was reproductively active during the winter. Thus, it is very likely that these two species have a reproductive season restricted to the warmer part of the year, as did the other four species found in the Woodville Recreational Reserve.

Teneral beetles were caught only occasionally, always during summer. Thus, like reproductive activity, hatching of tenerals may also be restricted to summer in these species.

The species common in the Manawatu Gorge (*P. planiusculus*, *Z. cf. femoralis*, and *C. adamsi*) were active between August and May. Three additional species, caught in small numbers at the Manawatu Gorge area, exhibited a similar activity pattern (Lövei & Cartellieri unpubl. data). The activity season of *M. turgidiceps* seemed to be shorter, and was restricted to summer and autumn. All four species were most active between January and March. Those species that started their season in spring had a second, smaller activity period in August/September. No activity took place between May and August during the austral winter.

In all species common in the Manawatu Gorge, reproductively active females, and in some species, gravid females, were found over the whole activity period from spring to autumn. This suggests a prolonged egg-laying period that is longer than for species in the Northern Hemisphere, and

is inconsistent with the classical division of carabids into groups of spring and autumn breeders (Thiele 1977). Perhaps the mild winter climate of this part of New Zealand allows larvae to remain active and develop with no need to overwinter.

Egg production in all studied New Zealand species was low. The long egg-laying period, during which females may develop several small clutches, may compensate for the low number of eggs per female recorded in this study. Teneral beetles of *Z. cf. femoralis* and *C. adamsi* were found throughout their activity period. This result confirms a long egg-laying period with continuous development of eggs, larvae, and pupae leading to an unsynchronised hatching of tenerals during the summer. In *P. planiusculus* and *M. turgidiceps*, however, teneral beetles were not found before January or March, respectively. This may indicate some synchronised development of eggs and larvae in these species.

In general, the high percentage of adults in the old age class suggested that the larger species of the tribe Pterostichini (*P. planiusculus*, *M. capito,* and probably, *H. mucronata*) could live longer than 1 year, and that females could have two or more reproductive periods. This has been shown for several other carabid species (Schjøtz-Christensen 1965; van Dijk 1972; Gergely & Lövei 1987; Sota 1987; Lövei & McCambridge 2002), and is probably much more common in ground beetles than has been previously thought (Lövei & Sunderland 1996).

All species studied demonstrated seasonality. Egg production in most species was low, which is consistent with the suspected long lifespan of several species. Long-lived species often have low densities and low reproductive capacity, which dampens year-to-year population fluctuations (Lövei & Sunderland 1996), but also makes these species vulnerable to predation. In New Zealand, introduced mammals have brought several native species to the brink of extinction (Atkinson & Cameron 1993). A similar picture is emerging concerning predator effects on invertebrates, and this could explain the species-poor carabid assemblages in several forest fragments in the Manawatu (Lövei & Cartellieri 2000). Active management might be necessary, and for this, similar work on other species, on the flexibility of seasonal activity, and on food habits would be needed.

CONCLUSION

In conclusion, during our work on life histories of ground beetles:

a) a standardised method was developed to describe the seasonal activity of ground beetles, based on the combination of sliding averages and the quartiles of the cumulative activity.

b) the seasonal dynamics and reproduction in Hungary was described for three species: *A. signatus*, *P. dorsalis* and *B. explodens.* In all three species, “old” individuals were found, indicating a life span longer than 1 year, and possible iteroparity.

c) the seasonality and reproductive actitvity of several New Zealand endemic ground beetle species were described. All of the demonstrated distinct seasonality, long life span, iteroparity and low egg numbers in their ovaries.

Part IV Carabids in human-managed habitats in a human-dominated era

This part presents results linked to studies on ground beetles either in relation to cultivated land as their habitats, or their role as tools to monitor the impacts of agricultural technologies.

Much of Europe has been cultivated for thousands of years, so that by today, very few "pristine" areas remain. For example, 70% of the area of Britain is classified as agricultural (DEFRA 2001). A significant part of European biodiversity finds necessary resources, in part or in whole, on cultivated land. However, we still do not know what part and how significant a part of invertebrate biodiversity lives in such habitats. The first part of this section presents results from Denmark that deal with the question: what level of ground beetle diversity occurs in hedgerows of different botanical composition in a cultivated countryside?

Habitats are not stable and human impact is increasing even in Europe where human population levels are stable. One of the most obvious threats to diversity is increasing urbanisation. The attention of ecologists has only recently turned to the study of the impacts of urbanisation on biodiversity (Niemelä 1999). The reasons are multiple but one important factor is that biodiversity provides essential ecosystem services to people even in cities and thus influences the inhabitants' quality of life (Niemelä 1999). The effects of urbanisation on ground beetles, studied in Denmark as part of an international project, appear in the second section of this part. The findings indicate an interesting parallel with results obtained in Hungary: the largest number of species was found in urban forest fragments in both countries – but this was due to the presence of non-forest species in such fragments.

Agriculture is now recognised as a major factor in determining environmental quality (Kareiva *et al.* 2007) and any new agricultural innovation will face an increasingly strict "environmental audit" (Hails 2002). A significant, controversial and recent agricultural innovation is the growing of genetically modified crop plants. Such plants are required to undergo a pre-release risk assessment to avoid negative environmental impacts. The overall reason to do this is to avoid damaging beneficial ecological interactions (termed "ecosystem services") (Lövei 2001a). Our research group was the first that included ground beetles in such biosafety studies, and the final section of this part presents results of laboratory experiments on two species of ground beetles. These indicate that ground beetles can react to food quality through changes in the composition of their prey, and they are amenable to be used as pre-release test organisms in GM biosafety studies.

Carabids in human-managed habitats in a human-dominated era, 1. Ground beetle assemblages in narrow hedgerows in a Danish agricultural landscape

Although the species richness found on cultivated land can be high (see, for example, Mészáros 1984a,b), non-cultivated areas in an agricultural landscape generally significantly contribute to biodiversity (Maudsley 2000). With the increasing human pressure on land, an increasing proportion of non-cultivated habitats will be enclosed in a cultivated habitat matrix, and their significance as biodiversity refuges would increase (Tscharntke *et al.* 2005). However, the level of biodiversity that cultivated land can support is not well characterised nor understood although an improved understanding would help to achieve a more efficient management of biodiversity as well as of the ecosystem services they provide (Daily 1999).

Hedgerows can support biodiversity in agricultural landscapes in several ways. For species inhabiting cultivated land, they can provide shelter, refuge and possible source (recolonisation) habitats during and after agricultural operations, serve as overwintering or oversummering sites (Maudsley 2000), or provide alternative food sources. Hedges support shrub and tree-living species as well as edge-preferring ones. Hedges also add to the fauna through supporting grassland or forest species (Petit & Usher 1998, Sustek 1992, Toft & Lövei 2002) and link fragmented habitats, thus enabling the dispersal and survival of metapopulations.

Material and Methods

Sites & sampling procedure

Our study area was near Bjerringbro, central Jutland, Denmark. Nine old, well established hedges of the single-row type were selected for study, three each of hawthorn (*Crataegus monogyna*), rowan (*Sorbus intermedia*), or spruce (two of white spruce *Picea glauca*, and one of sitka spruce, *Picea sitchensis*). Although there was some variation regionally in the composition of hedgerows (Ravn & Sigsgaard 1999), the selected hedgerows were mainly monospecific, except some presence of elderberry (*Sambucus nigra*) in the hawthorn hedges. The total width of the hedgerows was variable. The range of means at the three locations were as follows: hawthorn, 2.4 - 4.0 m; rowan, 2.6 - 5.0 m; spruce, 3.0 - 3.3 m. The sitka hedge was planted alternately in two rows, creating a centre with strong shade, where there was little vegetation. The nine sample locations were at a distance of 200m – 10km from each other, all enclosed within a 4km x 10km area.

Due to serious constraints on the total sampling effort it was decided that instead of continuous sampling between May and September, which allows operating a limited number of traps, the number of samples was to be doubled while the sampling period reduced. Such a sampling regime in Jutland detected the presence of 85% of the ground-active spider species that were found with whole-year sampling with the same number of traps (S. Toft, University Århus, Denmark, pers. comm. 2003). This was therefore judged an acceptable compromise.

Individual hedgerows were sampled twice yearly, during the early (June 1999) and late (early September 1999) carabid activity peak, using 20 pitfalls per habitat patch. Ten of the traps were set at the edge, and ten in the centre of the hedgerow, at a distance of 10 m between individual traps. Neighbouring traps alternated with respect to position to have a minimum distance of 20 m between two traps. Traps (500 ml plastic cups of 10 cm diameter, filled with about 200 ml of 70% ethylene glycol and a drop of detergent) were set for one week at a time. For further details of handling and identification, see Lövei *et al.* (2002).

Vegetation structure. The structure of ground cover was described using a pin frame. The frame holds 10 pins at a distance of 10cm from each other along a horizontal support rail. Individual pins were 1m long steel pins marked every 1cm between 0-5cm from the ground, and every 5cm between 5-50cm. The number of plants touching any interval was counted. Touches >50cm were summarised into one category. Four frames (total of 40 pins) were taken from each shelterbelt during late August 1999.

Evaluation. For evaluation, the early and late summer catches of 10 traps in identical position (edge or centre) were summarised, giving 18 sites. These were tested by ANOVA, Tukey's a posteriori test for differences in species number and number of individuals caught. Edge and centre traps were not significantly different within one location, and the catches from 20 traps per site were combined during further evaluation. The number of individuals and the species richness of the trapped carabids were examined by repeated measure analysis of variance (ANOVA) after log(x+1) transformation. The composition of the assemblages was evaluated by ordination, using Non-metric Multidimensional Scaling (NMDS), using the Rogers-Tanimoto Index (Legendre & Legendre 1998).

Diversity. Diversity profiles (diversity ordering) were used for scale-dependent diversity characterisation. Diversity profiles were calculated by the DivOrd package (Tóthmérész 1993a).

Commonness & rarity was evaluated using a semi-quantitative scoring system. We defined the commonness/rarity categories as follows: local scale: rare - occurring, on average, in 1-4 pitfall traps; moderately abundant: in 5-14 traps; common: caught in 15 - 20 pitfalls. Values are the averages obtained from 3 locations for each habitat type. At the regional scale, rare: present in 1 hedgerow only; moderate: present in 2 hedgerows; widespread: present in all 3 hedgerows.

Habitat affinity. The characteristic species of the habitats was explored by the IndVal (Indicator Value) procedure (Dufrêne & Legendre, 1997). The IndVal method is robust to differences in the numbers of sites between site groups, to differences in abundance between sites within a particular group, and to differences in the absolute abundances of different species or taxa (McGeoch & Chown, 1998). The IndVal method is a quantitative characterisation of the idea of indicator species of the classical plant sociology, based on a computerised randomisation procedure.

Effect of vegetation characteristics on ground beetle assemblages. The relationship between species richness and the number of individuals captured and habitat structure characteristics (total number of touches by herbs, grasses and all plants; touches of same below 5 cm, and above 50 cm,

average vegetation height for the same categories, thickness of litter layer, and the width of shelter-belt) were examined by forward stepwise multiple regression analysis. All vegetation characteristics were calculated as per-pin averages.

Ground beetle species were classified according to broad habitat preferences, based on Freude *et al.* (1976) as forest species, species of agricultural fields, grasslands, xerophilous species and plant debris-preferring species.

Results

Assemblage composition

A total of 71 carabid species were identified among the 2865 individuals captured: 52 species (1450 individuals) were found in hawthorn hedges, 55 species (919 individuals) in rowan, and 41 species (496 individuals) in spruce. Overall, the most common species were *Platynus dorsalis*, *Pterostichus melanarius*, *Calathus fuscipes*, *Calathus melanocephalus* and *Carabus nemoralis* (Table 4.1). These species were common in all three hedgerow types studied but there were variations in rank (Table 4.1). In rowan, *Bembidion tetracolum*, *Trechus quadristriatus* and *Pterostichus versicolor* were third, fourth and fifth in the capture rank. In spruce, *Bembidion lampros* was the fifth most common species. In hawthorn, *Nebria brevicollis* (third most common species) and *Calathus rotundicollis* (fifth most common) were in the first five common species (Table 4.1).

Assemblage differences by habitat type

There were significant differences in the mean number of species caught in individual traps as well as in the numbers captured. The most species-rich habitat, on this basis, was the hawthorn hedgerow, followed by rowan and spruce (Figures 4.1, 4.2).

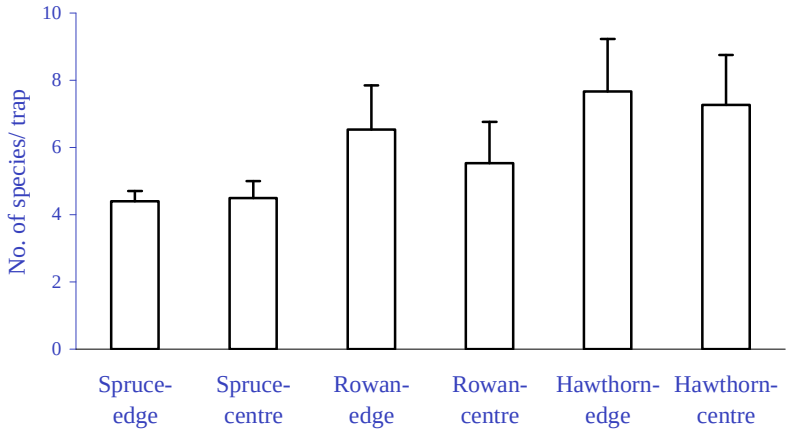

Figure 4.1. *The average number of carabid species captured in pitfall traps in hawthorn, rowan and spruce hedgerows in Bjerringbro area, central Jutland, Denmark. The vertical lines indicate one standard deviation.*

Table 4.1. *The list of the ground beetle species commonly captured (>10 individuals) in pitfall traps in different hedgerows in the Bjerringbro area, central Jutland, Denmark, in 1999. Sequence is by rank, considering the overall total numbers captured.*

Species	**Spruce**	**Rowan**	**Hawthorn**	**Total**
Platynus dorsalis	70	169	351	590
Pterostichus melanarius	57	101	301	459
Calathus fuscipes	51	57	102	210
Calathus melanocephalus	61	72	71	204
Carabus nemoralis	33	58	90	181
Trechus quadristriatus	25	82	34	141
Nebria brevicollis	13	3	118	134
Pterostichus versicolor	18	76	29	123
Bembidion lampros	38	50	27	115
Calathus rotundicollis	2	4	99	105
Bembidion tetracolum	2	93	4	99
Harpalus quadristriatus	0	0	32	32
Harpalus rufipes	6	10	16	32
Amara familiaris	19	4	5	28
Leistus ferrugineus	6	4	15	25
Harpalus tardus	15	8	1	24
Pterostichus cupreus	12	9	3	24
Pterostichus oblongopunctatus	1	16	7	24
Syntomus truncatellus	12	12	0	24
Carabus coriaceus	3	10	8	21
Calathus erratus	1	4	12	17
Notiophilus palustris	4	3	9	16
Bembidion obsutum	1	2	12	15
Harpalus rufibarbis	0	3	12	15
Syntomus foveatus	4	11	0	15
Notiophilus biguttatus	0	1	11	12
Calathus micropterus	4	2	5	11
Carabus violaceus	7	3	1	11
Pterostichus nigrita	2	1	8	11

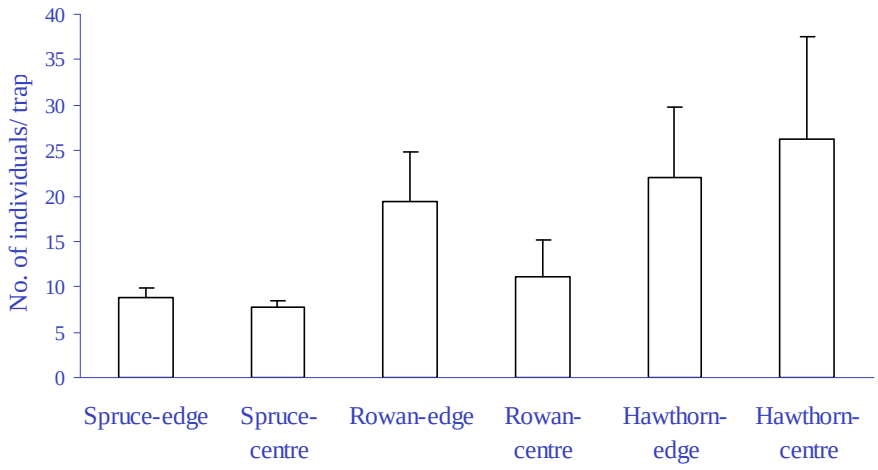

Figure 4.2. *The average number of carabid individuals captured in pitfall traps in hawthorn, rowan and spruce hedgerows in Bjerringbro area, central Jutland, Denmark. The vertical lines indicate one standard deviation.*

Assemblage ordination & diversity

The three hedge types were clearly separated by ordination (Figure 4.3). There was overlap along the first axis, but the second axis separated the three hedgerow types.

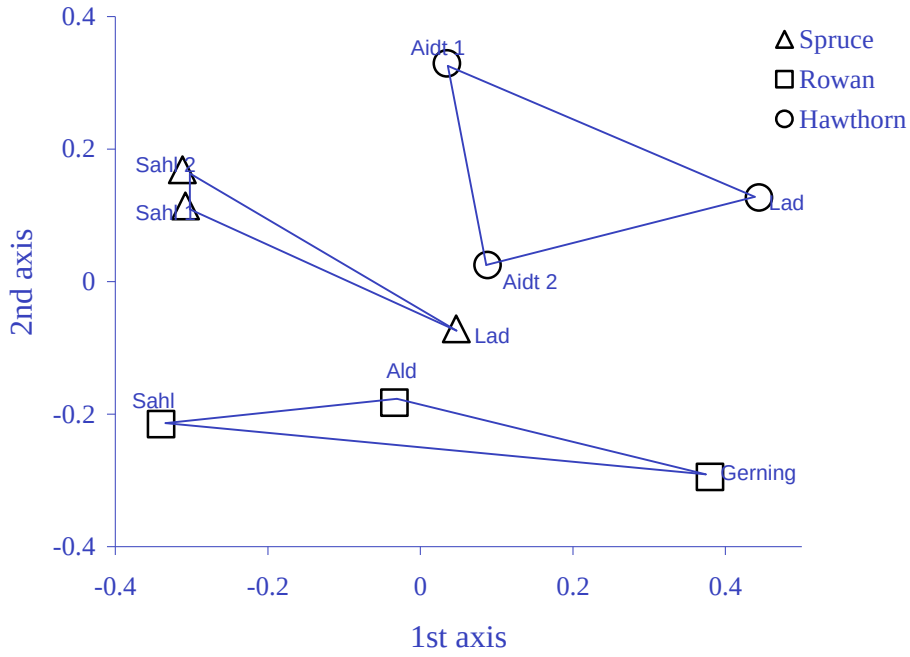

Figure 4.3. *Ordering of the carabid assemblages captured at nine sampling locations in three types of hedges in the Bjerringbro area, central Jutland, Denmark. The non-metric multidimensional scaling, Rogers-Tanimoto Index is used.*

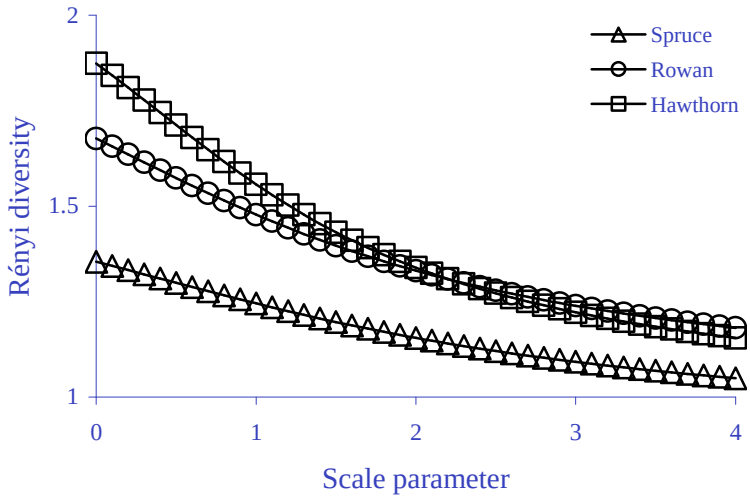

Figure 4.4*. Scale-dependent diversity ordering of the carabid assemblages caught in three hedgerow types in Bjerringbro area, central Jutland, Denmark, by the Rényi diversity function.*

The diversity of the carabid assemblage in the spruce hedges was unequivocally less than the other two hedge types (Fig. 4.4). However, the diversity in hawthorn and rowan hedges cannot be unequivocally ordered. This means that in some respects, the carabid assemblage in hawthorn hedges was more diverse than that in rowan (the 'hawthorn' curve run above the 'rowan' curve), but in other respects, the two assemblages did not differ.

Vegetation - ground beetle relationships

Only a few of the measured ground level habitat strcuture variables indicated a significant regression between the two response variables and the tested habitat structure variables (Table 4.2). Litter depth negatively influenced both the number of individuals and the number of species overall. This can be influenced by beetles entering the hedges from the neighbouring agricultural habitats – they are not adapted to thick deciduous litter. There is probably an added factor of physcial complexity that slows down movement speed by walking beetles.

Hedge width had a positive influence on both assemblage caracteristics – activity density and species richness. The wider hedge can generate less variable and more favourable humidity and temperature conditions, more variable microsites, more available habitat, or prey. The significant (p=0.04572) negative relationship between the number of species/trap and total grass density (Table 4.2) may indicate that beetle movement is hampered by dense vegetation, as generalist species are not well adapted to move in such habitats.

Table 4.2. *The results of the forward stepwise multiple linear regression (all variables were normally distributed, Kolmogorov-Smirnov test, KS>0.1330, p>0.10 in all cases).*

Characteristic	**N/habitat**	**S/habitat**	**N/Trap**	**S/Trap**
Overall regression	F=7.9164 d.f.=3, 5 r=0.9089 p=0.0240	F=3.8110 d.f.=5, 3 r=0.9295 p=0.1500	F=7.9164 d.f.=3, 5 r=0.9089 p=0.0240	F=6.6916 d.f.=3, 5 r=0.8948 p=0.0335
Hedge width, cm	+**	+*	+**	+*
Litter depth, cm	–**	n.s.	–**	–**
Grass density, <5cm	Not entered	Not entered	Not entered	Not entered
Grass density >5cm	Not entered	Not entered	Not entered	Not entered
Grass density, total	Not entered	Not entered	Not entered	–*
Herbs <5cm >	Not entered	Not entered	Not entered	Not entered
Herbs >5cm <	Not entered	Not entered	Not entered	Not entered
Herbs Total	Not entered	n.s.	Not entered	Not entered
Grass+Herbs <5cm	Not entered	n.s.	Not entered	Not entered
Grass+Herbs >5cm	Not entered	n.s.	Not entered	Not entered
Grass+Herbs Total	n.s.	Not entered	n.s.	Not entered

Commonness and rarity patterns

Spruce had the largest number of species (29) that were absent from the regional species pool (Table 4.3). Locally rare species were mostly restricted (20 species but only three of these were specific to this hedge type) but some of them widespread at the regional scale (Table 4.3). Species moderately abundant locally were mostly widespread; no species was locally common (Table 4.3).

Rowan had the highest number of species not occurring in other hedges: 57% of the species were in the restricted/rare category, and 30% of them specific to this hedge type. Three rare species were widespread, but none of these was specific to rowan hedges. There were no common species and moderately common species were all widespread (Table 4.3).

Rare species in hawthorn, however, were more widespread than in other hedges: 80.8% of the specie spool was locally rare, but more than half of these species wer either moderately distributed at a regional scale or were widespread (Table 4.3). Species with moderate activity density at local scale were mostly widespread. Of the widespread species, hawthorn had one species that was also common; none of the other hedges had such a species (Table 4.3).

Among rare and restricted species, rowan had the largest share (17.8% of species occuring in that hedge type), followed by hawthorn (9.6%) and spruce (6.9%). However, 5.7% of the moderately widespread species were hedge-specific in hawthorn, while the same was only 2.4% and 1.8% for rowan and spruce, respectively.

Table 4.3. *The number of ground beetle species according to local and regional commonness/rarity, based on pitfall trapping at nine localities in Bjerringbro, Jutland, Denmark. Categories: local scale: rare - occurring, on average, in 1-4 pitfall traps; moderately abundant: in 5-14 traps; common: caught in 15 - 20 pitfalls. Regional scale: restricted: present in 1 hedgerow only; moderate: present in 2 hedgerows; widespread: present in all 3 hedgerows. The second number indicates the number of species that were hedge-specific.*

Local scale	**Regional scale**			
	Absent	**Restricted**	**Moderate**	**Widespread**
Spruce (S=42)				
Absent	29			
Rare		20 / 3	12 / 1	3 / 0
Moderate		0	1 / 0	6 / 0
Common		0	0	0
Rowan (S=56)				
Absent	15			
Rare		32 / 10	12 / 1	3 / 0
Moderate		0	0	9 / 0
Common		0	0	0
Hawthorn (S=52)				
Absent	19			
Rare		20 / 5	13 / 3	9 / 0
Moderate		0	1 / 0	8 / 0
Common		0	0	1 / 0

Habitat affinity of individual species

Twenty-nine of the 71 species captured were amenable to a quantitative analysis of habitat affinity. According to the IndVal analysis (Table 4.4), 13 species did not show affinity to any of the three hedge types studied. These species can be considered generalists, at least in the studied landscape. *P. oblongopunctatus* was the oly species avoiding spruce hedges but not discriminaating between the two different deciduous hedge types. Eleven more species were identified as preferring hawthorn or rowan (Table 4.4). this preference,however, was not always accompanied by an avoidance of spruce. For example, *Leistus ferrugineus,* while identified as linked to hawthorn hedges, was captured more in spruce than rowan hedges (Table 4.4). Four species preferred spruce – all of these occurred also in rowan hedges, and only one of them was not captured atl all in hawthorn hedges.

Table 4.4. *The IndVal values of selected species and their numbers captured in pitfall traps during June and September 1999 at nine locations in the Bjerringbro area, Jutland, Denmark.*

Species	**IndVal**	***p***	**Number of individuals captured in June/September**		
			Spruce	**Rowan**	**Hawthorn**
All habitats					
Pterostichus melanarius	58.33	ns	57 / 18	101 / 34	301 / 53
Platyderus dorsalis	52.78	ns	70 / 22	169 / 32	351 / 41
Calathus melanocephalus	50.56	ns	61 / 25	72 / 30	71 / 36
Calathus fuscipes	42.78	ns	51 / 21	57 / 20	102 / 36
Carabus nemoralis	41.11	ns	33 / 20	58 / 29	90 / 25
Trechus quadristriatus	39.44	ns	25 / 19	82 / 32	34 / 20
Bembidion lampros	37.78	ns	38 / 22	50 / 28	27 / 18
Pterostichus versicolor	23.33	ns	18 / 11	76 / 15	29 / 16
Harpalus rufipes	14.44	ns	6 / 6	10 / 8	16 / 12
Carabus coriaceus	10.00	ns	3 / 3	10 / 9	8 / 6
Notiophilus palustris	7.78	ns	4 / 4	3 / 3	9 / 7
Pterostichus cupreus	7.22	ns	12 / 5	9 / 6	3 / 2
Calathus micropterus	5.56	ns	4 / 3	2 / 2	5 / 5
Deciduous hedge					
Pterostichus oblongopunctatus	11.50	*	1 / 1	16 / 9	7 / 6
Spruce					
Amara familiaris	16.17	*	19 / 12	4 / 3	5 / 4
Harpalus tardus	15.38	*	15 / 12	8 / 5	1 / 1
Syntomus truncatellus	10.00	*	12 / 9	12 / 7	0 / 0
Carabus violaceus	6.48	*	7 / 5	3 / 3	1 / 1
Rowan					
Bembidion tetracolum	36.01	*	2 / 2	93 / 23	4 / 3
Syntomus foveatus	4.89	*	4 / 3	11 / 4	0 / 0
Hawthorn					
Calathus rotundicollis	37.71	*	2 / 2	4 / 3	99 / 24
Nebria brevicollis	29.35	*	13 / 8	3 / 3	118 / 20
Harpalus quadripunctatus	20.00	*	0 / 0	0 / 0	32 / 12
Notiophilus biguttatus	16.81	*	0 / 0	1 / 1	11 / 11
Leistus ferrugineus	10.00	*	6 / 5	4 / 2	15 / 10
Harpalus rufibarbis	9.33	*	0 / 0	3 / 3	12 / 7
Pterostichus niger	8.48	*	2 / 2	1 / 1	8 / 7
Calathus erratus	7.06	*	1 / 1	4 / 3	12 / 6
Bembidion obtusum	6.67	*	1 / 1	2 / 2	12 / 5

Carabids in human-managed habitats in a human-dominated era, 2. Ground beetle assemblages along an urbanisation gradient

There are more than 6 billions humans on Earth, and they have large influence on virtually all other living beings. The ever- increasing human impact and its possible consequences are at the forefront of much research and thought, realising that the future of life may be at stake (Wilson 2002). Most concern is on "wild nature", whether protected or not (Balmford & Bond, 2005), even though significant parts of biodiversity are in non-protected environments under varying degree of human manipulation (Tscharntke et al. 2005). One of the most intensively managed and modified of human environments is the urbanised area. Urbanisation involves the profound modification of the original habitat (McIntyre et al. 2001), with the loss of most of its original plant and animal species (Marzluff et al. 2001), often accompanied by the replacement of native species by non-native ones (Blair 2004). Urbanised areas are on the increase world-wide, leading to the prediction that more than 60% of humanity will live in cities by 2025 (Anthrop 2000). Biodiversity provides important environmental services in cities, including the removal of dust, mitigation of microclimatic extremes, modulation of humidity (Bolund & Hunhammar 1999) but probably the most significant are the psychological benefits resulting from human biophilia (Wilson 1984).

Recently, Globenet, an international research project was initiated to conduct comparable studies in different countries to assess the influence of urbanisation on biodiversity (Niemelä *et al.* 2000). This project applies the forest-suburban-urban gradient approach (Pickett *et al.* 2001) using a common methodology (pitfall trapping) and evaluating the responses of a common invertebrate taxon (ground beetles, Carabidae) to urbanisation. Ground beetles were selected since they are sufficiently varied both taxonomically and ecologically, abundant and sensitive to human disturbance (Lövei & Sunderland 1996). In the Globenet project, three kinds of forested habitats (natural forest, suburban forested area and urban parks) are compared which represent different levels of disturbance.

Results from the Globenet Project have so far been published from Finland (Alaruikka *et al.* 2002; Venn *et al.* 2003), Canada (Niemelä *et al.* 2002), Bulgaria (Niemelä *et al.* 2002), Japan (Ishitani *et al.* 2003), Belgium (Gaublomme *et al.* 2005), and Hungary (Magura *et al.* 2004). These studies mostly found that the highest diversity is present in the least disturbed habitat, the original forest, and species richness gradually decreases towards the most disturbed habitat, the urban park (Niemelä *et al.* 2002; Ishitani *et al.* 2003). In 2003, we started Danglobe, the Danish component of this international project. After presenting patterns of ground beetles assemblages in these urbanisaiont stages in Denmark, we proceed to test several hypotheses that claim to explain the consequences of disturbance.

The first and widely known hypothesis concerning the effect of disturbance is the *Intermediate Disturbance Hypothesis* (IDH, Connell 1978). This hypothesis predicts the highest level of diver-

sity at intermediate levels of disturbance. An alternative, the "*Increasing Disturbance Hypothesis*" (IncDH, Gray 1987 1989) suggests that species richness should monotonously decrease with increasing levels of disturbance. An increasing disturbance is predicted to cause the forest specialists of the original (forest) habitat to decrease in both abundance and species richness along the urbanisation gradient. (*Habitat Specialist Hypothesis*, HSH, Magura *et al.* 2004). Gray (1989) hypothesized that in habitats influenced by disturbance, overall diversity should decrease, opportunistic (generalist) species should gain dominance (*opportunistic species hypothesis,* OSH). Gray (1989) also suggested that in habitats affected by (increased) disturbance the mean size of the species present should decrease (*decreasing mean body size hypothesis,* DBSH).

The *Food-access Hypothesis* (FAH) argues that the availability of food can be the most variable in the urban park due to its high environmental heterogeneity. This creates the most favourable feeding conditions for omnivorous species. Consequently, we hypothesise that the number of omnivorous species will be highest in the park.

Material and Methods

Our s*tudy area* was in and around the town of Sorø (ca. 7000 inhabitants in 2003), a regional centre about 80 km west of Copenhagen, on the island of Zealand. Three habitat types were selected, that represented forest, suburban and urban areas, according to the Globenet protocol (Niemelä *et al.* 2000). The (natural) *forest area* was a large, near-continuous forest, ca. 3km west from the town centre, bordered by Lake Sorø and the outskirts of the town. The *suburban area* was northeast of the town centre, bordered by the old cemetery on one side, and by an overgrown, old ditch, a dirt road and a wet forest area under intensive forestry management on the other. The *urban area* was in the park complex of the Sorø Akademi. For further details on habitats, see Elek & Lövei (2005, 2007).

Sampling design. Carabid beetles were collected at each of the four sites of the three sampling areas using pitfall traps as prescribed by the Globenet procotol (Niemela *et al.* 2000). Traps were checked fortnightly between late April and mid –October, 2004. The total trapping effort was 2640 trap-weeks (120 traps × 22 weeks); only very few (<10) trap catches were lost.

Beetles were identified to species, using keys by Lindroth (1985, 1986) and Hurka (1996). Voucher specimens are deposited at the Zoological Museum, University of Copenhagen, Denmark. For analyses, we pooled samples from the whole season.

Data analysis. For numerical analyses, beetles were classified according to their habitat preference, feeding type and body size. Habitat preference classes were forest specialists, open habitat species and generalists, based on information in Lindroth (1985, 1986). Feeding preferences, based on literature information (Larochelle 1990) included the classes of predators, omnivores and herbivores. To classify body size, data from Lindroth (1985, 1986) were used to calculate geometric means, and three classes (small. 3.5-9.5 mm, medium: 9.6 – 15.2 mm and large: >15.2 mm) were established using a size distribution graph. To test for differences in the overall carabid abundance

and species richness among three sampling areas (forest, suburban and urban) and among the 12 sites, nested analyses of variance (ANOVA) were performed using data from the individual traps (sites nested within the sampling areas). The abundance and species richness of the three habitat preference groups were also tested by nested ANOVA. Normality was tested by the Kolmogorov-Smirnov tests (Sokal & Rohlf 1995). During the analysis of data, we did not find significant difference from the normal distribution. When ANOVA revealed a significant difference among the means, a least-significant-difference test (LSD) for multiple comparisons was performed.

In order to determine the contribution of different ecological groups (habitat preference, feeding type, body size classes) to the total species richness among the three habitats (forest, suburban and ubran), the relative frequency of the species richness was calculated for each group. The relative species frequency was defined as species richness of a certain group divided by the total number of species per trap. The relative species frequencies of the three groups were also tested by nested ANOVA and, where necessary, a subsequent least-significant-difference test (LSD).

The calculations were performed using the Statistica software package (Statsoft 2000). The multidimensional scaling was applied to display similarities in the abundance of carabids among the sites using the Sørensen index of similarity. This analysis was performed by the NuCoSa software package (Tóthmérész 1993b).

Results

Overall, 10314 individuals belonging to 43 species were collected. The most species-rich habitat was the park, with 4389 individuals of 37 species, followed by the forest habitat, where the same trapping effort resulted in 4255 beetles of 25 species. The suburban area had the fewest beetles (1670 individuals) and species (24 species). About one-third of the species occurred in all three habitats (16 species, 35 %). A further 18 species (39%) were restricted to a single habitat, and 11 species (24%) were captured in two habitats.

The common species were, in the order of decreasing abundance: *Pterostichus melanarius, Nebria brevicollis, Platynus assimilis, Carabus coriaceus, Carabus nemoralis, Carabus hortensis, Pterostichus niger, C. rotundicollis, Leistus rufomarginatus, Pterostichus oblongopunctatus, Badister bullatus, Pterostichus strenuus, Notiophilus biguttatus, Notiophilus rufipes, Harpalus latus,* and *Synuchus vivalis*. The species captured in all three habitats made up 42% of the fauna of the urban site, 64% of the suburban site, and 61% of the forest site.

The number of unique species was highest at the urban site (12 species, 34% of the species captured in that habitat), and included *Patrobus atrorufus, Calathus rotundicollis, Agonum albipes, Agonum muelleri, Bembidion tetracolum, Agonum piceum, Bembidion biguttatum, Clivina fossor, Elaphrus cupreus, Badister sodalis, Harpalus rufipes,* and *Leistus ferrugineus* (Table 4.5). The forest site contained 4 unique species (19% of the fauna): *Carabus violaceus, Carabus convexus, Pterostichus lepidus,* and *Stomis pumicatus*. The suburban habitat had no unique species.

The highest number of species (see Table 4.5) was shared by the urban and suburban habitats, including 6 species: *Agonum duftschmidi, Anchomenus dorsalis, Pterostichus nigrita, Loricera pilicornis, Carabus granulatus,* and *Harpalus affinis*. Shared species between the urban and forest site were *Trechus quadristriatus, Pterostichus vernalis* and *Leistus terminatus*. Only two species were shared between the suburban and forest areas: *Abax parallelepipedus,* and *Cychrus caraboides*.

Table 4.5. *The number of species shared among the different habitats along the urbanisation gradient near Sorø, W Zealand, Denmark, during May-October 2004.*

Urbanisation gradient stages & their combinations	**No. of species shared**
Urban-suburban-forest	16
Urban-suburban	6
Urban-forest	3
Urban only	12
Suburban-forest	2
Forest only	4
Total	43

Patterns of activity density and species richness

The total number of individuals was significantly higher in the park and forest areas than the suburban one (Table 4.6). The number of individuals belonging to predatory (carnivorous) species was also significantly higher at the park (urban) and forest areas than the suburban ones while the abundance of generalists in the urban area was significantly higher than at the other ones.

The number of forest species was high in the forest area, but the suburban and park (urban) areas did not differ significantly (Table 4.6). The number of open-habitat species in the urban area was significantly higher than at either the suburban or the forest areas - but the latter two did not differ significantly.

The species richness of predatory (carnivorous) carabids was significantly higher in the forest areas than in the other two. In contrast, the number of omnivorous species was significantly higher in the park (urban) area than at the suburban or forest areas, the last two not differing significantly from each other. There were more generalist species in both the urban and forest areas than in the suburban one, but the first two did not differ significantly (Table 4.6).

Table 4.6. *Nested ANOVA indicating differences in carabid activity density and species richness of overall catches, feeding type and habitat affinity along the forest (F) -suburban (S) -urban (U) gradient in and around the city of Sorø, Denmark, in 2004. The last column shows the differences based on the LSD (least significant difference) test (p< 0.05).*

Characteristics	**Source of variation**	**d.f.**	**MS**	**F**	***p***	**LSD test**
Number of individuals						
All species	Gradient	2	58721.43	14.66	<0.001	U=F>S
	Sites	9	4004.38	0.94	0.48	
	Error	108	4217.66			
Predators	Gradient	2	57364.31	15.05	<0.05	U=F>S
	Sites	9	3810.76	0.91	0.51	
	Error	108	4171.93			
Omnivores	Gradient	2	14.35	2.21	<0.25	
	Sites	9	6.48	7.15	0.00	
	Error	108	0.90			
Forest species	Gradient	2	24411.73	7.72	<0.25	
	Sites	9	3161.33	2.10	0.03	
	Error	108	1499.48			
Open-habitat species	Gradient	2	677.27	1.51	<0.25	
	Sites	9	447.69	6.93	0.00	
	Error	108	64.58			
Generalists	Gradient	2	20893.96	12.73	<0.005	U>F>S
	Sites	9	1640.95	1.59	0.12	
	Error	108	1029.15			
Number of species						
Total no. of species	Gradient	2	114.43	3.85	ns	
	Sites	9	29.64	6.10	0.00	
	Error	108	4.86			
Predators	Gradient	2	96.63	5.45	<0.025	F>U>S
	Sites	9	17.70	5.00	0.00	
	Error	108	3.53			
Omnivores	Gradient	2	5.85	4.33	<0.05	U>S=F
	Sites	9	1.358	4.06	0.00	
	Error	108	0.33			
Forest species	Gradient	2	70.05	11.99	<0.001	F>U=S
	Sites	9	5.83	4.26	0.00	
	Error	108	1.37			
Open-habitat species	Gradient	2	35.30	3.94	<0.05	U>S=F
	Sites	9	8.94	8.77	0.00	
	Error	108	1.01			
Generalist species	Gradient	2	23.63	6.79	<0.01	U=F>S
	Sites	9	3.47	4.00	0.00	
	Error	108	0.86			

Size trends along the gradient

The activity density of small species did not differ significantly among the areas (Table 4.7) while that of medium-sized species was significantly higher in the urban than the suburban or forest areas. The activity density of large beetles was significantly higher in the suburban and forest than at the urban areas (Table 4.7).

The species richness of small species was higher in the urban area, and showed significant difference in comparison to both other urbanisation stages, while the suburban and forest areas did not differ from each other (Fig 4.5). The number of medium-sized species was highest in urban site, the forest had an intermediate position, and the lowest value was found in the suburban area. The number of large ground beetles has the opposite pattern, the number of these species was highest in the forest area, the suburban had an intermediate position, and the urban areas had the lowest value (Fig. 4.5).

Table 4.7*. Nested ANOVA indicating differences in carabid activity density and species richness of body size trends along the forest (F) -suburban (S) -urban (U) gradient in and around the city of Sorø, Denmark, in 2004. The last column shows the differences based on the LSD (least significant difference) test (p< 0.05).*

Body size classes	**Source of variation**	**d.f.**	**MS**	**F**	***p***	**LSD test**
Activity density						
Small (3.5mm-9.5mm)	Gradient	2	1116.52	1.89	n.s.	
	Sites	9	588.45	8.04	0.00	
	Error	108	588.45			
Medium (9.5mm-5.2mm)	Gradient	2	23215.06	15.72	<0.01	U>S=F
	Sites	9	1476.66	1.41	0.19	
	Error	108	1045.62			
Large (>15.2mm)	Gradient	2	42133.11	22.91	<0.001	U<S=F
	Sites	9	1838.76	1.26	0.26	
	Error	108	1458.24			
Species richness						
Small (3.5mm-9.5mm)	Gradient	2	69.77	6.00	<0.01	U>S=F
	Sites	9	11.61	7.14	0.00	
	Error	108	1.62			
Medium (9.5mm-5.2mm)	Gradient	2	26.27	5.26	<0.025	U>F>S
	Sites	9	4.98	6.52	0.00	
	Error	108	0.76			
Large (>15.2mm)	Gradient	2	42133.11	22.91	<0.001	U<S<F
	Sites	9	1838.76	1.26	0.04	
	Error	108	1458.28			

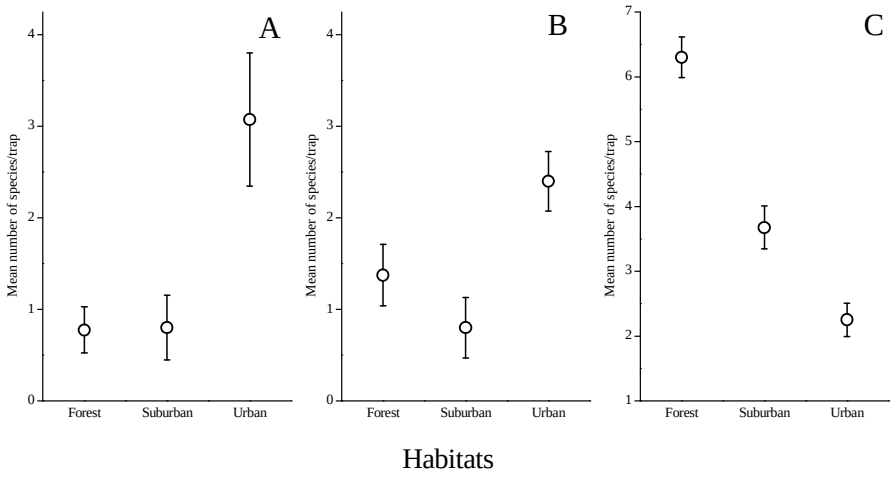

Figure 4.5. *Species richness of small (body length 3.5-9.5 mm) (A), medium-sized (9.5-15.2 mm) (B) and large (>15.2 mm) (C) carabid species along the forest-suburban-urban gradient in Sorø, Denmark, in 2004. Data are means, intervals indicate ± one s.e.*

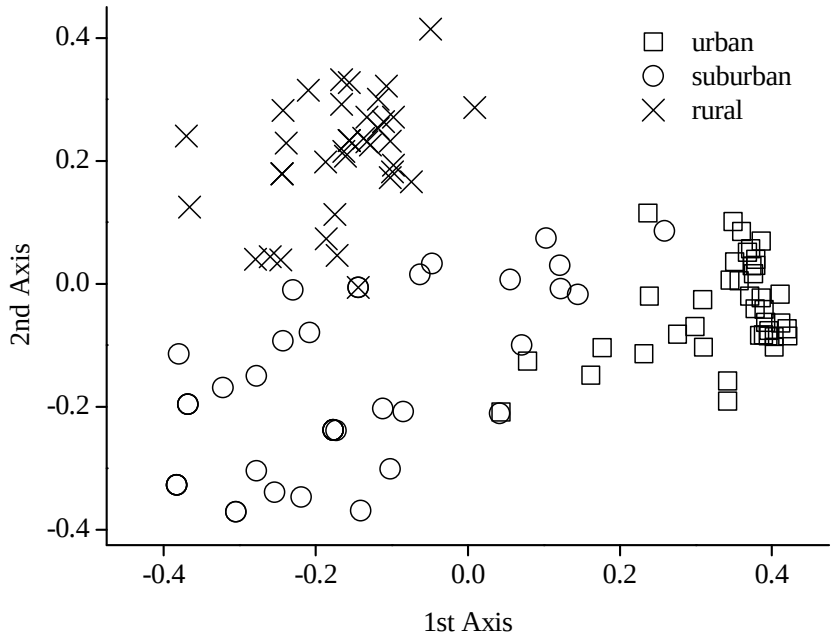

Figure 4.6. *Non-metric multidimensional scale ordination of the total seasonal abundance of carabids captured, along a forest-suburban-urban gradient in Sorø, Denmark, in 2004, using a Sørensen similarity index . The stress of the two dimensional configuration was 0.423.*

Table 4.8*. Nested ANOVA indicating differences in relative species richness of body size classes along the forest-(F), suburban-(S) and urban-(U) gradient in and around the city of Sorø, Denmark, in 2004. The last column shows the differences based on the LSD (least significant difference) test (p< 0.05).*

Characteristics	Source of variation	d.f.	MS	F	*p*	LSD test
Body size classes						
Small	Gradient	2	0.92	10.40	>0.01	U>S=F
(3.5mm-9.5mm)	Sites	9	0.08	5.54	0.00	
	Error	107	0.01			
Medium	Gradient	2	0.47	6.11	>0.025	U>S=F
(9.5mm-15.2mm)	Sites	9	0.07	9.12	0.00	
	Error	107	0.008			
Large (>15.2mm)	Gradient	2	2.73	18.36	<0.001	F=S>U
	Sites	9	0.14	9.38	0.00	
	Error	107	0.015			
Habitat affinity						
Open-habitat species	Gradient	2	0.35	9.10	<0.01	U>S=F
	Sites	9	0.03	4.52	0.00	
	Error	107	0.008			
Generalist	Gradient	2	0.15	15.31	>0.001	U>F>S
	Sites	9	0.01	1.50	0.15	
	Error	107	0.006			
Forest species	Gradient	2	0.97	15.44	>0.001	S>F>U
	Sites	9	0.062	4.99	0.00	
	Error	107	0.01			
Feeding type						
Omnivorous	Gradient	2	0.006	0.56	>0.1	n.s
	Sites	9	0.01	2.47	0.01	
	Error	107	0.004			
Herbivorous	Gradient	2	0.003	1.35	>0.1	n.s.
	Sites	9	0.002	2.02	0.04	
	Error	107	0.001			
Predators	Gradient	2	0.02	1.26	>0.1	n.s.
	Sites	9	0.02	3.30	0.001	
	Error	107	0.006			

Relative species frequency analysis

The relative frequency of small-sized species was higher in the urban area, and showed significant difference in comparison to both other urbanisation stages, while the suburban and forest areas did not differ from each other (Table 4.8). The relative number of medium-sized species increased from the forest toward the urban area while the suburban and forest areas did not differ from each other. The relative number of large species was highest in the forest and suburban areas, with the urban area having the lowest value (Table 4.8).

The relative number of open-habitat species in the urban area was significantly higher than at the suburban or forest areas, which did not differ significantly (Table 4.8). The contribution of generalist species was higher in both the urban and forest areas than in the suburban, but the first two did not differ significantly. The relative frequency of forest species was significantly higher in the suburban areas than at the forest and park (urban) area. The relative frequency of the species based on feeding type was not significantly different by urbanisation stage (see Table 4.8).

Comparison of different stages of urbanisation gradient

The results of non-metric multidimensional scaling with Sorensen similarity plot showed a marked separation of areas along the forest-suburban-urban gradient. The points representing the forest and urban traps separated well along the first axis while the points representing the suburban and forest areas separated along the the second axis (Fig. 4.6).

Carabids in human-managed habitats in a human-dominated era, 3. The potential effect of transgenic plants on generalist natural enemies of pests: Tri-trophic interactions between two carabids and their prey fed on GM-product-containing diet

Agriculture has long been recognised as an important factor in environmental management. With the increasing human population, the environmental impact of agriculture is expected to increase (Tilman et al. 2001). In spite of significant advances in agricultural technology, a substantial amount of agricultural produce is lost to pests, weeds and diseases (Conway & Toenniessen 1999). During the breeding of our major crop plants for high yield and edibility, several desirable traits, including resistance to pest insects, have been lost (Gatehouse et al. 1991). The use of genetic engineering to produce pest-resistant transgenic plants represents one of many current approaches aiming to increase agricultural production.

However, as the experience with pesticides indicates very well, it is short-sighted to look at the pest damage problem in isolation. Agricultural fields, even if often impoverished with respect to 'natural' habitats, contain many species participating in ecological interactions that are vital for the productive functioning of these systems (Thomas & Waage 1996, Gould 1998). Pest control provided by naturally occurring predatory arthropods is one of those important functions.

Our current knowledge on the impact of GM plants on natural enemies is limited. A recent review (Lövei & Arpaia 2005) found 26 published papers, reporting on 35 experiments on 18 predatory species in three insect orders. Most of these (17 studies) were on Heteroptera (involving 11 species), seven on Neuroptera (all on *C. carnea*), and 11 on beetles (eight on Coccinellidae, three on Carabidae, involving three species each in two families). *Chrysoperla carnea* (of which only the larvae are predatory) is the most often studied predator species. Apart from this, more than a single study was done on only a handful of species: two coccinellids (*Adalia bipunctata*, and *Coleomegilla maculata*, three and four studies, respectively) and a few heteropterans (*Perillus bioculatus* - three studies, *Geocoris puncticeps*, *Orius tristicolor*, *O. insidiosus* - two each). Typically, a laboratory test on predators was of short duration, performed at a constant temperature, with unlimited access to a single type of prey, under a no-choice feeding regime. The majority of studies (18) involved Bt-toxin, either in the artificial diet, or in GM plants. Six of the Bt-related studies involved plant- or (mostly) pollen-feeding species.

A total of 126 parameters were quantified in these laboratory tests. Most of these were connected to development, general biology, or fitness, which we classified into nine major groups (Table 4.9). Most commonly, survival/mortality (37), development time (22), and body mass/size (20) were measured. Surprisingly, prey consumption was measured in only 13 cases. Reproduction-related measurements were taken in 12 cases.

Employing a "bean-counting algorithm" for the available data, 135 assessments could be categorised (Table 4.9), with the majority (47.4%) showing no significant response (neutral). How-

ever, a positive effect was found in 16 cases (12% of total tests, half of them significant), whereas a negative impact was registered for 55 (41%) cases (30% of all tests were significantly, 11% non-significantly negative). The relative distribution of the five classes per parameter was typically highest in the 'neutral' class, and was skewed towards the negative (Table 4.9). The characters with the lowest frequency in the "non-responsive" class that can be considered the most sensitive, were longevity, reproduction, and egg/progeny viability. Enzyme activity, while always sensitive, was an equivocal character: the activity of certain enzymes decreased, while that of others increased, both significantly (Table 4.9).

Table 4.9. *The relative distribution of reaction classes, from significantly* negative to significantly positive, of the different parameters quantified in laboratory tests of GM plant impacts on predatory insects.*

Parameter	**Relative no. of cases (%)****					**Total no. of tests**
	Negative significant	**Negative non-significant**	**Neutral**	**Positive non-significant**	**Positive significant**	
Survival/mortality	15.5	18	56	10	-	39
Development time	28	12	56	-	4	25
Body mass/size	22	17	48	9	4	23
Prey consumption	33	-	58	-	8	12
Reproduction	42	8	42	8	-	12
Enzyme activity	44	-	-	-	66	9
Longevity	60	-	40	-	-	5
Egg viability	80	-	-	20	-	5
Behaviour	50	-	50	-	-	4
Total	30	11	47.5	6	6	135

*Significance level was set at $P<0.05$.
**The lines are % of cases of the no. of tests that quantified the given parameter. Overall total refers to all the parameters in all tests.

The conclusion of the review is that that we are much in need of a larger body of empirical data on the impact of GM plants on natural enemies. These data should be systematically collected, including species in taxa not studied so far. They should be tested under ecologically more realistic laboratory "worst case" scenarios, choosing sensitive and reliably measurable response parameters over realistic time scales. We should consider that multiple stresses are the norm under field conditions, not the exception, that organisms often react in non-linear ways to combined stresses (Stamp et al., 1997), and we should at least attempt to mimic these conditions in laboratory tests. These altered practices, several of which are easily achievable, would hopefully improve our powers of prediction regarding the potential ecological impacts of growing GM crops.

We contributed to this goal by studying, in the laboratory, ground beetles and their interaction with prey fed proteinase inhibitor-containing food. Proteinase inhibitors reduce or block the ability of arthropods to digest their food and are used to make crop plants resistant to herbivores (Schuler et al. 1998).

The inhibitor may reduce the growth of the pest keeping it in the "window of vulnerability" for longer, which could increase the biological control exerted by the natural enemies. However, arthropod natural enemies are sensitive to both quantity and quality of their prey. Indirect, tri- or multitrophic effects where plant traits indirectly influence higher trophic levels are well documented (reviewed in Price *et al.* 1980, Van der Putten et al. 2001). Effects through changes in prey quality have been less demonstrated, but it occurs in spiders (Mayntz & Toft, 2001), parasitoids (Murugan et al. 2000a) and ladybirds (Murugan et al. 2000b), for example.

PIs and PI-expressing transgenic plants can have tri-trophic impacts on natural enemies. Tomato moth (*Lacanobia oleracea*) larvae fed with artificial diet containing cowpea trypsin inhibitor (CpTI) or with transgenic potato plants expressing CpTI were less successfully parasitised by the wasp *Eulophus pennicornis* than control larvae (Bell *et al.* 2001). When predatory stinkbugs (*Perillus bioculatus*) were fed solely on Colorado potato beetles (*Leptinotarsa decemlineata*) injected with oryzacystatin (OC-I), they had negligible mortality but their reproductive success was significantly impaired (Overney et al. 1998; Ashouri et al. 1998).

In a series of experiments, we sought to examine whether proteinase-inhibitor-fed prey can influence feeding and other biological parameters in generalist predators. As model generalists, we selected two species of ground beetles (Coleoptera: Carabidae), and examined their reactions under laboratory conditions. As a first step, we examined whether a specific proteinase inhibitor in the food of a herbivore can affect the consumption of this herbivore by a polyphagous predator, *Harpalus affinis* (Jørgensen & Lövei 1999). We also studied if this effect lasts longer in the predator than the actual exposure to the proteinase inhibitor fed prey. This was followed by long-term exposure of the same prey to the same predator (Lövei et al. 2000, Lövei *et al.* manuscript), followed by experiments with a second, more strictly predatory species, *Nebria brevicollis* (Burgess et al. 2002), and extending the methodology to use physiological parameters (enzyme activity) as a potential response parameter of the GM impact.

Here only a summary of the methods and findings are given. Further details can be found in the above-mentioned publications.

Materials and Methods

Prey organism

We used larvae of the cosmopolitan, polyphagous noctuid moth *Helicoverpa armigera* as prey. *H. armigera* eggs were obtained from a culture at the HortResearch, Mt. Albert Research Centre, Auckland, New Zealand (in the short-term experiment, done in New Zealand) or from the NERC Institute of Virology, Oxford, U.K. (for the long-term feeding experiment with *H.affinis* and the *N.brevicollis* experiments, done in Denmark). Once hatched, they were reared on a modified Teakle & Jensen (1985) diet. The treated diet also contained 1% bovine pancreatic trypsin inhibitor (BPTI) (Sigma,

St. Louis, U.S.A.) (of total protein content), a level previously shown to delay larval development and achieved in several plant species by genetic engineering (Felton & Gatehouse 1996). The total protein content was equal in all diets.

After about 5-6 days for the control fed and about 6-8 days for the BPTI fed caterpillars, when the caterpillars were almost ready to moult into 3rd instar, they were freeze killed and kept in the freezer (−18° C) until experiments started. BPTI-fed fourth instar *H. armigera* larvae had a mean BPTI content of 22.62 μg/g insect (*s.e.* = 2.32 μg, details see in Burgess et al. 2002).

Predators

Adults of the ground beetles *H. affinis* and *Nebria brevicollis* were chosen as predators in experimental tri-trophic systems. *H.affinis* is a highly heliophilous species, and attains the highest population numbers on dry grassy and meadow soil with moderately dense and tall vegetation. It is a spring breeder, hibernates as an adult, and tenerals appear in the autumn (Sunderland et al. 1995b). *H. affinis* is an omnivorous carabid, feeding mostly on seed, but a smaller amount of animal food is also ingested (Cornic 1973, Sunderland et al. 1995b). Reproducing adults are less phytophagous than tenerals (Cornic 1973).

N. brevicollis is common in agricultural fields in Europe (Lövei & Sárospataki 1990) and is a voracious predator with a wide prey range (Nelemans 1987a). Teneral adults emerge in the spring, feed intensively over a few weeks to accumulate fat reserves, and then aestivate. They emerge from aestivation to reproduce in the autumn and their larval progeny overwinter (Lindroth 1985; Nelemans 1987b).

Predator rearing conditions

For *short-term experiments*, adult *H. affinis* were caught in dry pitfall traps placed in crop fields at Flock House Research Farm near Palmerston North, New Zealand, during the southern spring (29 November - 13 December 1996) and late summer (5-21 February 1997). Females and males were kept separately in well-aired plastic containers in the laboratory at natural daylength and temperatures ranging from 20°C to 28°C. The beetles were fed dry cat food biscuits and water (wet cotton wool) *ad libitum*. Spring-collected and autumn-collected beetles were distinguished throughout the experiments.

Long-term and N.brevicollis *experiments*: Beetles were collected by pitfall trapping in barley fields at the research farm at Flakkebjerg, Denmark, over a two-week period at the start of their spring activity (early May in 2001). Sexes were separately kept in large Petri dishes (19cm in diameter) with a layer of sand until the experiments started. The beetles were kept at day length 16:8 L:D, at 21°C: 15 °C. The substrate was watered and beetles fed one high-protein larva per beetle once (*H.affinis*) or three times (*N.brevicollis*) weekly.

H. affinis, s*hort-term feeding experiments*

Beetles, previously starved for 72 h, were weighed and placed in individual Petri dishes. They were randomly assigned to one of the two diet treatments, either an *ad libitum*, pre-weighed, food of BPTI-fed caterpillars or of the control caterpillars. The beetles were allowed to feed for 24h, under natural photoperiod and laboratory ambient temperature (same range as before). Subsequently the food remains were collected, dried for 72h in a vacuum oven at 40°C and weighed.

After the first 24h, the beetles were weighed again and transferred to clean Petri dishes. Both groups were supplied with control prey, and allowed to feed for another 24h. All the food remains were collected, dried and measured as after day 1. The results were analysed as mass specific consumption rate (mg dry mass consumed/mg beetle mass) to account for the size differences of the beetles. The total sample size as 109 (n = 55 beetles; 43 spring caught, 12 autumn caught; offered BPTI-fed caterpillars and n = 54 beetles; 42 spring caught, 12 autumn caught; offered control-fed caterpillars).

H. affinis, l*ong-term feeding experiments*

Beetles kept individually in Petri dishes (9cm) lined with moist filter paper were starved for 5 days prior to the start of the experiment. The beetles were divided into four groups, which were as similar as possible regarding sex, initial mass and date of capture, and exposed to the following treatments:

1. Control: prey raised on diet without protease inhibitor (non-BPTI-prey) during the entire experiment. n= 38
2. Control/BPTI: During the first 6 weeks of the experiment, the predator was fed non- BPTI-prey, followed by 6 weeks of feeding on BPTI-prey only. This treatment was designed to reveal if the possible effect of the protease inhibitor was age- or season- dependent. n=38
3. BPTI/Control: 6 weeks on BPTI-containing diet (BPTI-prey), followed by non- BPTI prey. This tested whether the possible effect was reversible or not. n=38.
4. BPTI, long-term. The predator had access only to BPTI-prey during the entire experiment. n=37

Beetles were fed once a week with freshly weighed, frozen caterpillars. The prey was weighed (to ±0.ımg) to ensure an equal amount of prey (about 50mg) for individual beetles, the prey remains were weighed to determine food consumption. The beetles were weighed once a week immediately before each feeding (±0.1mg). The filter papers in the Petri dishes were watered twice a week, but never before weighing the beetles. Mortality was observed and noted once a week.

Experiments with N.brevicollis

Rearing and experimental conditions wer similar to the *H.affinis* long-term experiments, except that there were only two treatments: BPTI-containing prey and control. After the final weighing, all surviving beetles were dissected and their digestive tracts excised and freeze-dried for determination of gut proteolytic enzyme activity. Nine further *N. brevicollis* adults were collected from the field at this time (early July) and their guts were also excised and freeze-dried. Details of the enzyme activity measurements see in Burgess et al. (2002).

Analysis. Experimental data were evaluated by appropriate ANOVAs with repeated measures. The independent factor was the diet (BPTI-treated caterpillars or control caterpillars). The sex of the beetles (female, male) and catching period (spring, late summer) were treated as independent variables in the ANOVA, but are looked at as co-variables. Proportional data (food consumption as a proportion of food supplied and food conversion to beetle body mass) were log-transformed before analysis. ANOVA was also used to compare serine protease activity levels (log-transformed) and percent inhibition due to cysteine protease activity (angular transformed).

Beetle survival was compared using log-rank test modified for censored data (Pyke & Thompson, 1986) because someof the beetles were still alive at the end of the experiment. Peto and Peto's logrank test are used to compare all four treatments simultaneously.

Results

Short-term feeding experiments with H.affinis

There was a significant difference within treatment (F= 9.8703; $F_{1, 105}$= 3.9315; P= 0.002) as well as within catching period (F= 6.1287; $F_{1, 105}$= 3.9315; P= 0.015). Overall, the beetles eating BPTI-treated caterpillars ate less than those only offered the control caterpillars (Fig. 4.7). Younger (late summer) beetles always ate less than the older (spring) ones. There was a significant interaction between treatment and catching period (F= 5.2373; $F_{1, 105}$= 3.9315; P= 0.024).

The within subject analysis takes the time, as repeated factor, into account. There was a significant difference in the overall interaction (F= 3.8342; $F_{3, 105}$= 2.6911; P= 0.012). The effect of time itself was highly significant (F= 40.5338; $F_{1, 105}$= 3.9315; P< 0.0001); indicating that the beetles ate more during day 1 than during day 2. There was no significant interaction between time and treatment (F= 0.9779; $F_{1, 105}$= 3.9315; P= 0.325), but there was a significant interaction between time and catching period (F= 4.1549; $F_{1, 105}$ = 3.9315; P= 0.044). Overall, the beetles reacted the same way to the treatments but the spring and late summer beetles reacted differently over time. A significant interaction was found between time, treatment and catching period (F= 7.0307; $F_{1, 105}$= 3.9315; P= 0.009). Within the BPTI-treated group, the late summer beetles ate less both during day 1 and day 2 whereas for the control beetles this was only true for day 1.

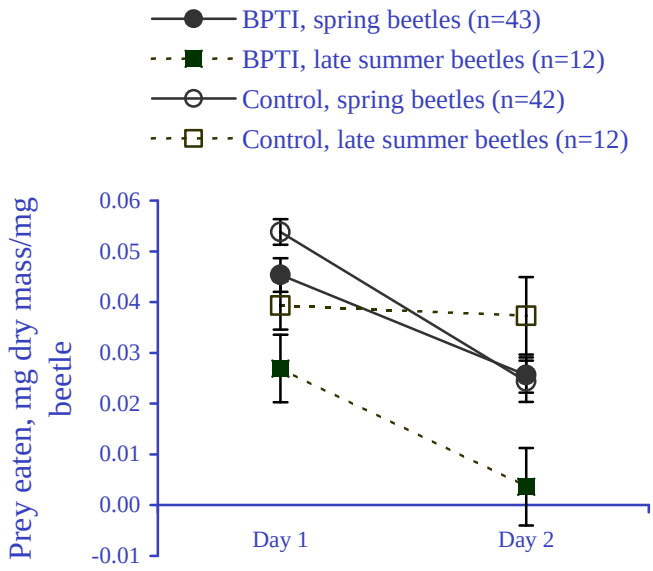

Figure 4.7*. Consumption by old (spring beetles) and young (autumn beetles) adults of the ground beetle* Harpalus affinis *eating* Helicoverpa armigera *caterpillars fed either proteinase inhibitor-containing (BPTI) or control diet. Data are means ± one s.e.*

Long-term feeding experiments with H. affinis

During the first 5 weeks, no beetles were experiencing a remarkable change in body mass irrespective of treatment. After the 5th week a small decrease and then an increase was noticed except for the beetles of the BPTI treatment that only lost body mass. After week 8, the beetles of the control treatment were almost constant. The body mass of the beetles in the ControlBPTI treatment was decreasing from 51.13 mg to 43.17 mg in week 11 followed by an increase to 48.30 mg in week 12. The BPTIControl and BPTI treatments were experiencing small decrease and increase and the BPTIControl was decreasing from 45.6 mg to 38.72 mg in week 12.

No difference in beetle mass was found at the beginning of the experiment, (GLM, *d.f.* = 3, P>0.4 –0.71), at week 6 when two groups were changing prey type nor at the end of the experiment. Hence, there was no evidence that differences in prey quality had an effect on predator body mass.

Survival

In the control treatment, the mortality increased rapidly and about 25% of the beetles died during from week 9 to week 11. The average life span when 50 % had died was reached by week 9. Only 10% were alive by the end of the experiment. In the ControlBPTI treatment the mortality increased rapidly during the first few weeks, and only 7 % of the beetles were alive by week10. The average life span was 7 weeks. In the BPTIControl treatment the survival with almost the same number each week until week 10 when 14% of the beetles were alive and stayed alive for the rest of the experiment. The average life span was also 7 weeks. In the BPTI treatment the number of surviving beetles steadily decreased until week 10 when 10 % of the beetles were alive and stayed alive for the re-

maining weeks of the experiment. The average life span was 7 weeks. The four different treatments had no influence on the beetle mortality (Peto and Petos log rank, log rank= 7.81, d.f. = 3, P >0.05).

The effect of initial body mass on mortality

Among the beetles included in the feeding experiments there was a remarkable difference in body mass: the smallest weighed 29.5mg and the largest 70mg. The possible relationship between size (initial body mass) and survival was examined by regression (fig. 4.8). There was no significant of initial body mass on survival in the control treatment (r^2=0.0043, p>0.71), but in all other treatments, where beetles consumed BPTI-containing prey, larger beetles lived longer, i.e. ther was a higher mortality of smaller beetles (p<0.0001-0.005).

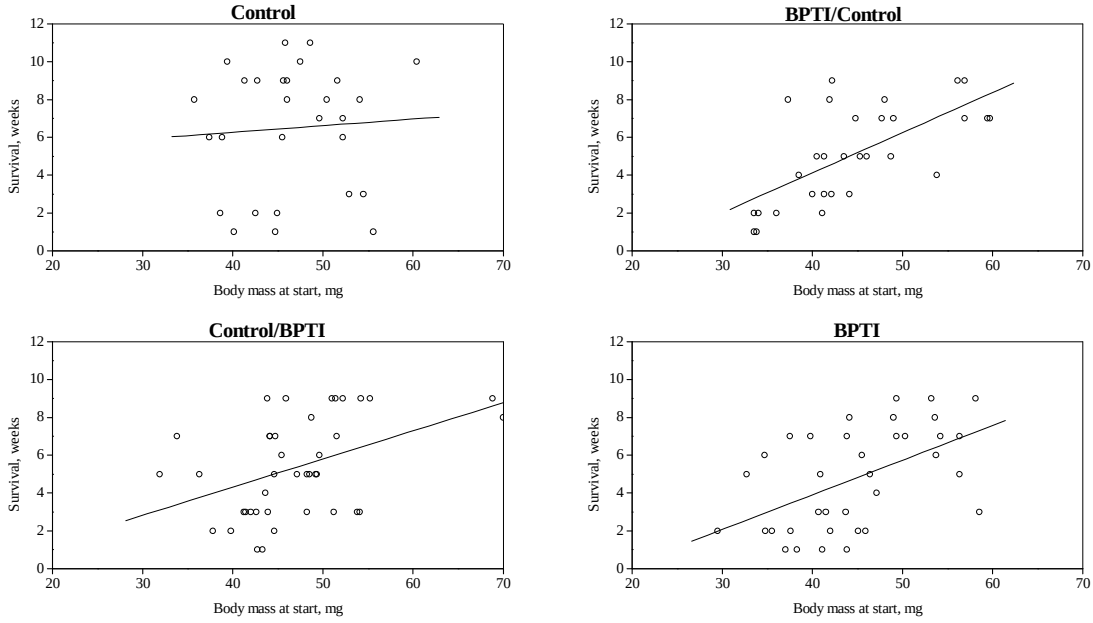

Fig. 4.8. *Survival in relation to initial body mass in adults of H. affinis under four different feeding regimes under laboratory conditions. BPTI denotes the proteinase inhibitor (bovine pancreatic trypsin inhibitor).*

Effects of BPTI-fed H. armigera *on* N. brevicollis

Prey type had no effect on beetle survival. Both groups declined in number over the 24 days of the experiment, with 78% of control and 72% of BPTI-fed prey-fed (AF prey-fed) beetles remaining alive on the final day.

The body mass values of control and AF prey-fed beetles did not differ significantly from each other at any weighing occasion. However, there were significant differences in the changes in beetle mass observed from one weighing occasion to the next that could be attributed to prey type (Fig. 4.9). On average, all beetles gained mass during each interval, except for the intervals between Days 10 and 14 and Days 17 and 21, when both groups lost mass. During those two intervals, the AF

prey-fed beetles lost significantly more mass than the control beetles ($P < 0.05$, ANOVA). Conversely, between Days 21 and 24 the AF prey-fed beetles gained significantly more mass than the control beetles ($P < 0.05$, ANOVA). Covariate analysis of the effect of prey type on body mass change using beetle mass at the beginning of each interval as a covariate showed that beetle size had no influence on the magnitude of mass changes observed.

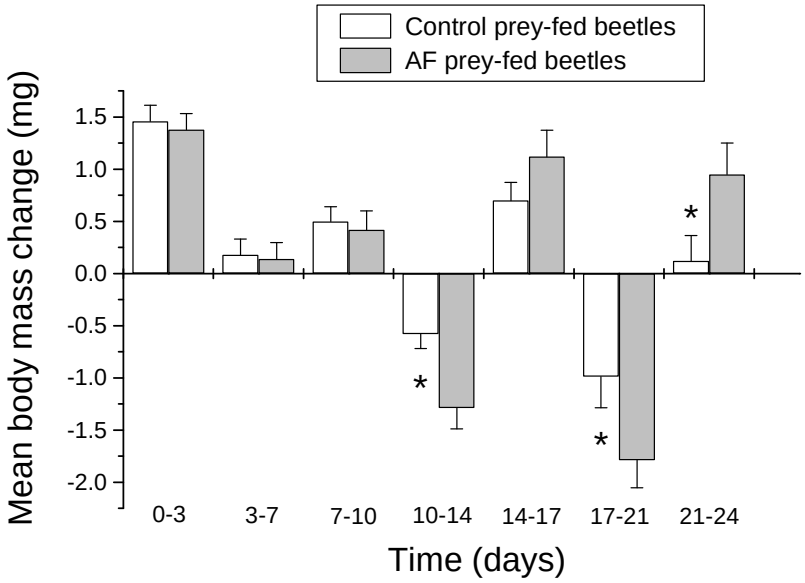

Figure 4.9. *Mean changes, from one weighing occasion to the next, in the body mass of* N. brevicollis *adults supplied with prey (larvae of* H. armigera*) fed with control diet or diet with 0.5% (w:w, fresh mass) BPTI added. Error bars denote the standard error of the mean. Asterisks indicate significant differences between control and BPTI treatments (ANOVA, P<0.05) for each weighing occasion. N = 97 for both treatments.*

The final mass of beetles in the experiment (55.69 mg, *s.e.* = 0.82 mg, $n = 76$ for controls; 55.48 mg, *s.e* = 0.90 mg, $n = 69$ for BPTI prey-fed) did not differ significantly from those of beetles collected from the field at the same time for enzyme analysis (55.66 mg, *s.e.* = 3.31 mg, $n = 13$) ($P < 0.05$, ANOVA).

Prey consumption and body mass changes

Equal amounts of control and BPTI-fed prey were supplied to beetles on each weighing day, except for Day 7, when the BPTI prey-fed beetles received significantly more prey than the controls. Between Days 7 and 10, these beetles also consumed significantly more prey than their control counterparts ($P < 0.05$, ANOVA). BPTI prey-fed beetles also ate significantly more than the controls between Days 21 and 24 ($P < 0.05$, ANOVA), even though their food supplies were equal. Beetles in both groups were given more prey from Day 14 onwards than they had received earlier in the

experiment. This was in response to the body mass losses first observed on Day 14 and also because there were more *H. armigera* larvae available by then. Prey type had no effect on the proportions of food consumed to food supplied (food consumed between Days x and y/food supplied on Day x).

Prey type had a significant effect on the abilities of beetles to convert the food they consumed into body mass change (interval mass change/food consumed) between Days 3 and 7 and Days 17 and 21 ($P < 0.05$, ANOVA). During both intervals, beetles converted control prey into body mass with greater efficiency than BPTI-fed prey.

Influence of sex on N. brevicollis *body mass change*

Female beetles were significantly heavier than male beetles on every weighing occasion ($P < 0.05$, ANOVA). Male and female beetles underwent similar changes in body mass during each interval, except between Days 14 and 17 when female beetles gained significantly more mass than male beetles ($P < 0.05$). There were no gender–based differences in prey supplied or consumed. However, between Days 14 and 17, females beetles converted their prey into body mass with greater efficiency than the males ($P < 0.05$). Furthermore, on Days 3 to 7, 14 to 17, 17 to 21 and 21 to 24, there were significant interactions between gender and prey-type effects on food conversion ($P < 0.05$), but these showed no consistent trends.

Table 4.10. *Mean digestive protease activity levels (pmol/min/mg insect) in adult* N. brevicollis. *Values without a letter in common differ significantly from others for the same enzyme type, $P < 0.05$, ANOVA of all beetles. Asterisks indicate significantly higher values in pairwise comparisons of experimental beetles only ($P < 0.05$, ANOVA).*

Protease	**Beetles consuming control prey**			**Beetles consuming BPTI-fed prey**			**Field-collected beetles**		
	Mean	*s.e.*	´*n*	Mean	*s.e.*	*n*	Mean	*s.e.*	*n*
Chymotrypsin	18.5[a]	1.99	76	38.1[a]*	4.34	69	105.7[b]	26.5	12
Elastase	96[a]	11.2	76	216[ab]*	25.3	69	302[b]	74.7	12
Trypsin	176[a]*	20.4	76	71[a]	8.7	69	632[b]	145	12
LAP	310	19.7	76	331	24.6	69	311	50.8	12
Cysteine proteases	18.2[a]	1.65	51	15.8[a]	1.65	40	128[b]	34.0	12

N. brevicollis *digestive protease activities*

Field-collected beetles had significantly higher levels of cysteine protease, chymotrypsin and trypsin activity than the beetles used in the experiment (Table 4.10) ($P < 0.05$, ANOVA). They also had higher levels of elastase than the control beetles, but not the BPTI prey-fed beetles in the experiment. There were no differences in leucine aminopeptidase (LAP) levels among the three groups of beetles. BPTI prey-fed beetles had significantly higher levels of chymotrypsin and elastase, and lower levels of trypsin, than control beetles (Table 4.10) ($P < 0.05$, ANOVA). LAP and cysteine protease activity levels were similar in both groups of experimental beetles.

Discussion

Biodiversity in narrow hedges in Denmark

This study applied the "space not time" –type compromise recommended in Part II. A small number of traps run over a longer time would be an inferior allocation of resources than extending the spatial dimension (i.e. increase the number of traps) in crucial activity periods. This decision was also supported by the spider data from the surrouding area (cited in Toft & Lövei 2002). We are aware that this would not be an acceptable compromise when biology or reproduction is the focus of the studies. In biodiversity studies, however, we would urge to think about these questions in the planning stage. Exploring the spatial vs. temporal dimensions could result in different results (Gruttke & Kornacker 1995, see also Part II).

Narrow hedgerows did not differ with respect to trap position (edge vs. centre). However, the narrow hedges supported several forest species, in contrast to the claim that the minimum width should be 4m before the habitat is suitable for forest species (Spreier 1982). The presence of field-living species, such as *P. dorsalis*, *P. melanarius*, and *T. quadristriatus* (Kromp 1999), indicated the influence of the surrounding matrix. Field-living carabid species use hedges and field edges as overwintering sites (review in Kromp 1999). Overall, it seems that narrow hedges provide habitat for both field-living and forest-living species. The surrounding matrix influenced hedgerow carabids more than hedgerow spiders (Toft & Lövei 2002).

Hedge species composition also had a profound influence on carabid assemblages, and native plants harboured more species than non-native ones. This was also found in Moravia, central Europe (Sustek 1992). Overall, hawthorn can be considered the best habitat type. This can be explained because this species is native, and for ground beetles, this hadge could provide the best combinations of conditions (vegetation structure, microclimate, soil, available food, protection from predators, etc.) within their tolerance limits. Rowan also had high number of individuals and species. Rowan is not a native species to the study area, although present in Europe (Lövei 2001b). The thick deciduous litter produced by rowan trees seemed to be advantageous for ground beetles. Deciduous litter can provide favourable microclimate, and creates a complex spatial structure through generating stratification that can allow the coexistence of some ground beetle species (Loreau 1987). However, from the patchiness of occurrences at regional scale, rowan seems to provide a more coarse-grained habitat, i.e. there are more areas where conditions are not favourable for ground beetles than in hawthorn.

Similar factors can explain why spruce hedges had a relatively poor ground beetle assemblage. The soil underneath is acidic, due to the breakdown of pine leaves. This could decrease the density of other arthropods and thus the food supply for ground beetles.

The causes of individual species habitat preferences are not always known. *P. oblognopunctatus* has a preference for habitats covered with deciduous litter (Magura & al. 2000). This species is

active not on the surface but inside the litter layer (Loreau 1987) and thus in a microhabitat that is not used by other, larger species.

From the results we obtained it seems that to conserve and maintain arthropod (ground beetle) biodiversity, hedges composed of deciduous species are superior to non-native, and especially to needle-leaved species.

Effect of urbanisation on ground beetles in Denmark

Our results indicate considerable effects of urbanisation on Danish forest carabids. Most of the species we found (40 of the 46 species) are common in Denmark (Bangsholt 1983). Five species are moderately frequent or rare.

Opposite to the trend in Finland (Niemelä et al. 2002; Alaruikka et al. 2002), Japan (Ishitani et al. 2003) and Belgium (Gaublomme et al. 2005), the urban area had the highest species richness in Denmark (similar to Hungary: Magura et al. 2004). This trend in Denmark was caused mostly by species attracted to humidity, probably caused by the vicinity of the Sorø Lake. The nature-friendly management of the park may also have contributed to this: there are numerous patches of wood and grassland, creating habitat heterogeneity. The cut vegetation is returned to the understory of the forested patches. This may allow natural nutrient cycling, supporting more soil-living arthropods that may provide food for carabid larvae and adults. Further, lack of disturbance may allow carabid larvae to develop. The rural (forest) site was more homogenous than the park and here we found only forest species. There were more forest species here than in other areas; nevertheless, the overall species richness was lower, due to the absence of species that colonised the more modified suburban and park habitats.

We suggest that differences in landscape structure are also important. The landscape in the study area of W Zealand is highly patchy, possibly providing “green corridors” for dispersal. A significant fraction of the fauna can survive in urbanised areas, but about 20% of the species did not occur outside the forest. This underlines that even relatively benign forest and park management cannot create conditions that are suitable for forest specialist species. The special conditions in the human-influenced urban areas are also reflected in the high share of unique species in the park. These species did not colonise the suburban or forest habitats, in spite of their relative closeness, as well as some shared botanical features.

Evaluation of the research hypotheses

Intermediate disturbance and opportunistic species dominance hypotheses. Our findings concur with results by Niemelä et al. (2002) and Magura et al. (2004) in not supporting the IDH: species richness was not the highest in the moderately disturbed suburban areas. This may be because basal species in food webs probably conform to this hypothesis but top consumers do not (Wootton 1998), and carabids are considered higher-level consumers (Lövei & Sunderland 1996).

Our results supported the OSH prediction, as the ratio of individuals of the opportunistic carabid species to the total number of individuals was significantly higher in the urban area than in the other ones. Niemelä et al. (2002) reported similar findings from urban areas in Canada and Finland.

Habitat specialist hypothesis. As predicted, both the number of forest species and their relative frequency significantly decreased from the natural forest habitats to the urban ones. Also, the number of open-habitat species was significantly higher in the urban area than in the suburban or rural areas. A possible cause of this is the impact of the "habitat matrix", in our case the presence of open habitats (lawns) in the urban area. The matrix species influence the species richness patterns in forest fragments (Lövei et al. 2006). Other impacts of masking habitat fragmentation and disturbance effects include microclimatic changes at edges, short-term crowding effects, and time lags (Ewers & Didham, 2006).

Mean body size hypothesis. In our study, smaller species were more abundant in urban remnants of the original forest. The larger, less mobile species were more abundant in the forest area. However, the smaller forest species were also more abundant in urban forest fragments while the small and medium-sized species were numerous in the urban habitat. Disturbance caused by urbanisation produced smaller average carabid body size also in Slovakia (Šustek 1987). Carabid body size changed from small in urban to larger in both suburban and forest areas in Bulgaria and Finland (Niemelä *et al.* 2002). This phenomenon, however, could be better understood by studying the possible size trends of species that occur in more than one habitat because conditions experienced during larval development period often constraint adult body size. A more detailed analysis of body size trends (Magura *et al.* 2006) could also be instructive.

The *food-access hypothesis* was supported because the species richness of omnivorous species was highest in the urban area. The predatory species were not absent from the park, indicating that park management was important to retain species from the original habitat, but as more predatory species were present in the forest habitats, conditions were obviously better there than in the park.

Implications for management

Forested urban habitat fragments can retain several species from the original forest fauna but the abundance and species richness of the stenotopic specialist species will decrease with the increasing level of anthropogenic disturbance. The fragmentation of the original forest and increasing level of human impact can lead to loss of several forest specialists as well as to the successful colonization by generalist and open-habitat species, leading to increased diverstiy in urban habitats. Urban green areas, including forest patches improve the quality of urban life and should be conserved. Apart from their recreational value, such green urban spaces provide seemingly adequate habitat for numerous species of ground beetles whose original habitat is in forest areas away from the city. Be-

nign management of urban parks (gravel paths instead of asphalt, retaining as much plant material as possible within the habitat, and providing decaying wood in the understory) improve habitat quality for invertebrates, contributing to their continued survival. However, increasing human transport over the globe carries the added impact of homogenising the world's flora and fauna and over a longer term may decrease overall global diversity (Lövei 1997). Consequently, species richness as a sole indicator of the effectiveness of species preservation in cultivated or urban areas is not an entirely suitable parameter: species identity should also be considered.

The impact of GM-laced prey on polyphagous predators

In the short-term experiments, adult *H.affinis* consumed less of the BPTI-treated prey than control prey. It is not clear what had caused this difference. One obvious possibility is that prey caterpillars carried some food in their guts and the BPTI present in the diet inhibited the predator's feeding. Alternatively, prey caterpillars, due to their diet, could have had a nutritional composition that made them less suitable for the predators.

The prolonged effect of the BPTI also seems counter-intuitive. Lövei et al.'s (1991) experiments indicate that in several beetle species, a subsequent feeding opportunity hastens the emptying of the earlier meal. Similarly, a fast defecation of the BPTI-treated prey in favour of the later, non-treated one would seem advantageous. This would result in increased feeding of the subsequent, more favourable prey. However, we did not observe this in our experiments. The cause of this could be due to behaviour (gustatory effect) or a subtle physiological effect.

The BPTI-treated caterpillars affected consumption in *H. affinis* negatively compared with the control caterpillars both in the spring beetles and in late summer beetles. The difference was most pronounced with the late summer (freshly emerged) beetles. These beetles also responded very different from the spring caught beetles with respect to the amount eaten on day 2. Such different food sensitivities by age or sex are not unknown in predatory beetles. Two generations of beetles that overlap, may have different food preferences (Lövei & Sunderland 1996), and can have different metabolism. This is plausible as the two generations feed for different purposes. Young, autumn-hatched beetles have to feed to build up fat storage so they can survive the hibernation (Wallin 1989) whereas the old generation feed to be able to breed.

Our first experiment gave a clear indication that seasonality/age of the predators has to be taken into account when considering sensitivity to prey quality. In addition, our results indicate that genetic manipulation of plants can influence interactions at higher trophic levels. It would be wise to consider these aspects when deciding about the deployment of genetically engineered plants in order to maximize their intended positive effects on agricultural production.

Our *long-term experiments* were conducted over 12 weeks. It is not likely that a predator only encounters "transgenic" prey throughout a lifetime like the long-term treatment of the current experiments. However, if transgenic plants get more widespread, the possibility that predators meet

prey exposed to GMPs of different traits would increase. Under such conditions, the exposure time increases and long-term experiments such as the current get increasingly realistic.

Carabids are sensitive to the quality of their diet. Fecundity in *Calathus melanocephalus* decreased when the beetles were fed aphids (a low-quality food) vs. fruit flies (Bilde & Toft 1999). Not many experiments have been conducted on the effects of diet quality on the change in body mass in carabids. Experiments with *N. brevicollis* show a tendency towards an increasing weight loss in short periods of time when fed prey fed PIs but generally no effect of PIs on body mass was found (see earlier). Jørgensen & Lövei (1999) found a significant difference in changes in body mass when feeding *H. affinis* over 48 h. In long-term experiments, no difference was found in mortality and body mass changes. The difference could emerge because adults can adapt to PIs and would only be sensitive during the first few days of exposure. *H. affinis* has a mixed diet, eating also seeds and plant material (Sunderland et al. 1995b), and it is plausible that *H. affinis* has means to overcome an initial PI effect. An omnivorous insect is exposed to the protease inhibitors just as herbivorous insects and it may be the reason why only insects that to some extend are herbivorous (omni- and herbivorous) are able to develop tolerance towards the PI.

Many animals are more vulnerable to toxins when they are young than when they are older. It is possible that the beetles are more susceptible when they are newly emerged from hibernation (Jørgensen & Lövei 1999). In the long-term experiments, this possibility was tested by feeding *H.affinis* on control prey first and BPTI-prey later in the experiment. No effect of this treatment was found, so *H. affinis* did not seem more susceptible to nutritional stress when younger. However, size-dependence of life span in the experiments indicates differential sensitivity to nutritional stress.

Some predators prefer mobile prey to non-moving ones (Eubanks & Denno 2000). If the prey weakens because of the effect of the PIs, they may become less mobile. The predators may ignore them, eating prey that is more active. This is, however, not the case for *H. affinis*. Preference tests were made in other experiments and no preference to live over dead prey was shown (Jørgensen & Lövei 1999).

Many carabids are semelparous and die after one reproductive season (Lövei & Sunderland 1996). Towards the end of the experiments, mortality of *H. affinis* increased rapidly, probably because of the approaching autumn when many post-reproductive individuals die. However, life span in laboratory experiments was a median of >250 days (Lövei & McCambridge 2002), although on a different diet. It is possible that the forced predatory habit caused a different mortality pattern in *H.affinis.* Fecundity in omnivorous carabids can decrease if it is only fed animal food (Jørgensen & Toft 1997).

The potential tri-trophic effects of a PI-plant will depend not only on the concentration of PI to which the predator is exposed but also on its sensitivity to the PI in question. In this study, beetles consuming prey with a mean BPTI content of 0.0023% (w:w fresh mass) had digestive protease profiles that differed significantly from their control counterparts, suggesting that, even at this low

concentration, the PI may have had an effect on the beetle's digestive ability. Reduced trypsin activity in the *N. brevicollis* beetles that consumed BPTI-fed prey suggests that the PI in the prey had a direct impact on this protease, since BPTI is a trypsin inhibitor. Interestingly, the levels of two other serine proteases, chymotrypsin and elastase, were raised in these insects suggesting some kind of compensatory mechanism.

This study has revealed the potential for slight and/or transient tri-trophic impacts from PIs on two species of ground beetles. However, beetle survival was not affected by ingestion of BPTI-fed prey and beetle body mass at the end of the experiment was similar to that of field beetles or controls. Mass-related tolerance to nutritional stress were found in both species. More research is required before the implications for field release of transgenic PI-plants can be ascertained. In particular, further studies in which ground beetles are offered realistic mixtures of prey insect species, including some that have fed on PI-expressing transgenic plants, would be valuable.

CONCLUSION

In summary, work presented in this part documented that

a) even narrow tree hedges can maintain elements of forest (ground beetle) fauna in a cultivated countryside in Denmark. The composition of hedges has an impact on ground beetles, native hedges being the most effective in keeping such species in an otherwise cultivated landscape.

b) urbanisation substantially influences ground beetle fauna. The overall impact in our studies was an increase in biodiversity in terms of species richness. The overall impacts, however, emerge as an interplay of detrimental changes in conditions for forest specialist species (larger, mainly predatory species decrease), and the creation of new habitats for non-forest ones (small and omnivorous species increase) as the degree of urbanisation increases.

c) generalist predators can react to GM agents via the food chain, in tri-trophic or indirect interactions. In the case of the omnivorours ground beetles, *H. affinis*, exposure to a proteinase inhibitor via its prey resulted, in the short run, a decrease in prey consumption that lasted longer than the actual short term exposure of the GM agent. On the longer term, adult ground beetles were able to compensate for this effect and they did not consume less or more of the modified food, nor did they show different body mass change pattern. The nutritional stress, however, was revealed by the differential mortality pattern: smaller adults of *H.affinis* kept on GM-containing prey lived shorter. Adults of *N. brevicollis* showed reduced digestive enzyme activites.

These experiments, beyond the actual results, have

f) proven that genetically modified plants can have indirect effects via the food chain on beneficial organisms

g) draw the generalist natural enemies into the circle of beneficial organisms inot GM risk assessment

h) developed and tested methods by which such risk assessment can be done.

Part V – Theoretical studies

The study of a well defined taxocoene is interesting enough in itself, but good science seeks generalities. From this it follows that the results obtained through the study of such a group should be confronted with, and linked to, more general theories. The study of ground beetles played an important role in the development of several ecological theories, (see, for example, the long-term studies by den Boer and co-workers (e.g. den Boer 1987) that lead to the concept of metapopulations). However, this link has perhaps not been so well cultivated as the general amount of knowledge about ground beetles, and the intensity of studies of this group would justify. The last section summarises some of my own contributions to this area, concerning the theory of island biogeography, and the impact of isolation on assemblage structure. Results presented in Part II about the relationship between trap number and trapping duration can also be considered a theoreticla contribution to the shape of the time-space-species number relationship. However, the consequences of those findings to sampling design were judged potentially more important and these results were therefore put into the "methodological innovations" section.

Life history cannot be ignored and those who consider organisms as mere examples to illustrate an ecological theory will often go wrong. The closing part of this section, based on a published paper (Lövei & Magura 2006) wants to reinforce the warning that biology cannot be ignored in ecological theory.

Theoretical studies, 1. The influence of matrix and edges on species richness patterns of ground beetles in habitat islands

One of the most influential of ecological concepts is MacArthur and Wilson's Island Biogeography Theory (MacArthur & Wilson 1967). The original theory considered real islands, but the concept was soon applied to habitat islands, and became an important study topic with strong links to conservation biology (Harris 1984). The major difference between real and habitat islands is the nature of the surrounding matrix. In real islands, the surrounding matrix is usually hostile to organisms occurring on islands (although whether this is a significant barrier depends on the dispersal ability of the organisms concerned, see Báldi & Kisbenedek 1999). In the case of terrestrial habitat islands, the matrix is usually less hostile (Gascon & Lovejoy 1998; Ås 1999; Hobbs 2001) and can contain their set of species ("matrix species"). Such matrix species can also occur in the habitat islands themselves. Larger habitat islands or ones closer to a colonist source area do not always have more species (Holt et al. 1995) but this could arise because of the indiscriminate inclusion of such "matrix species" (Cook et al. 2002). Such results lead to a call for "further refinements of the paradigm …to adapt and broaden the theory. For island biogeography theory to be applied to terrestrial habitat 'islands' which are heterogeneous and subject to edge effects, methodological allowances need to be made for the likelihood that species can colonize the 'islands' from the sea..." (Cook et al. 2002).

Habitat fragments are not uniform, but have well-defined edges. Edges are transition zones between adjacent habitats and form ecotones (Holland et al. 1991). Forest edges, for example, have distinct microclimates, abrupt changes in light regimen, substrate, and water conditions, and are generally rich in microhabitats (Murcia 1995; Didham & Lawton 1999). This gives rise to "edge-preferring species", species that are characteristic of edge habitats (Odum 1971). With the fragmentation of habitats, edges are becoming proportionately greater relative to interiors (Saunders et al. 1991). We hypothesise that the existence of edge-preferring species can also have important implications for the species richness-area relationship.

Material and Methods

Study area and sampling

We used data collected over five years (1995-1999) from 19 forest patches (Table 4.1), with their size ranging from 41ha to 3995 ha, located on the Bereg Plain in NE Hungary and in SW Ukraine. This is a relatively undisturbed, forested marginal area of the Great Hungarian Plain. The "matrix" is composed by a mosaic of grasslands and non-intensively cultivated fields. All the patches sampled were natural, although their degree of isolation has probably changed during the gradual transformation of the landscape. Beetles were collected using unbaited pitfall traps, consisting of plastic cups with 70% ethylene glycol as a killing and preserving solution. There were 9-18 traps/patch (depend-

ing on the area), scattered randomly within individual patches, and were checked monthly from April to October.

Data analyses

The area of the forest islands was measured using the ArcView GIS program package on a digitized 1:25000 map. The area of the forest edge was calculated as the product of the perimeter of the forest patches and the width of the forest edge, taken as 5 m.

Linear regression analysis was used to examine the relationships between the studied variables (area of the forest fragment, proportion of the edge area to the total fragment area, shape index) and the total number of carabid species in the fragment, the number of forest specialist species, the number of generalist (matrix) species, and the number of edge preferring species.
For further details on methods, see Lövei et al. 2006.

Results

The species richness in all patches combined was 56 species, dominated by the 41 generalist (matrix) species (Table 5.1). Seven species were identified as edge-preferring species, comparable to the number of forest specialists (8 species). The following eight species were identified as mountain forest specialists: *Abax parallelus, Carabus arcensis, C. intricatus, Cychrus caraboides, Cymindis cingulata, Leistus piceus, Molops piceus,* and *Pterostichus melas.*

There was a significant negative relationship between the species richness and the area of the forest concerning all captured carabid species (R= – 0.49, $F_{(1,17)}$=5.22, *P*=0.04, Fig. 5.1a). Forest patch size and the number of generalist species showed a marginally significant negative relationship (R= – 0.46, $F_{(1,17)}$=4.45, *P*=0.05, Fig.5.1b). These species did not respond to these forest patches as if they were islands.

The number of edge preferring species vs. the area of the forest patch showed a negative, but not significant relationship (R= – 0.33, $F_{(1,17)}$=2.09, *P*=0.17, Fig. 5.1c). The number of edge specialist species was unrelated to the shape index (R=0.22, $F_{(1,17)}$=0.88, *P*=0.36). However, the number of edge preferring species is expected to be dependent not on the total area of the fragment, but rather on the ratio of the edge area to the total area. The smaller patches had relatively larger edge area, and this was reflected by the significant positive relationship between the number of edge-preferring species and the edge/total area ratio (R=0.51, $F_{(1,17)}$=5.84, *P*=0.03, Fig. 5.2). Furthermore, a significant negative relationship was found between the edge preferring species/ forest specialist species ratio and the patch size (R= –0.50, $F_{(1,17)}$=5.56, *P*=0.03). All these results indicated the increasing importance of edge species with decreasing patch size.

There was a significant positive (R=0.49, $F_{(1,17)}$=5.44, *P*=0.03) relationship between the size of the forest patch and the number of forest specialist species (Fig. 5.1d).

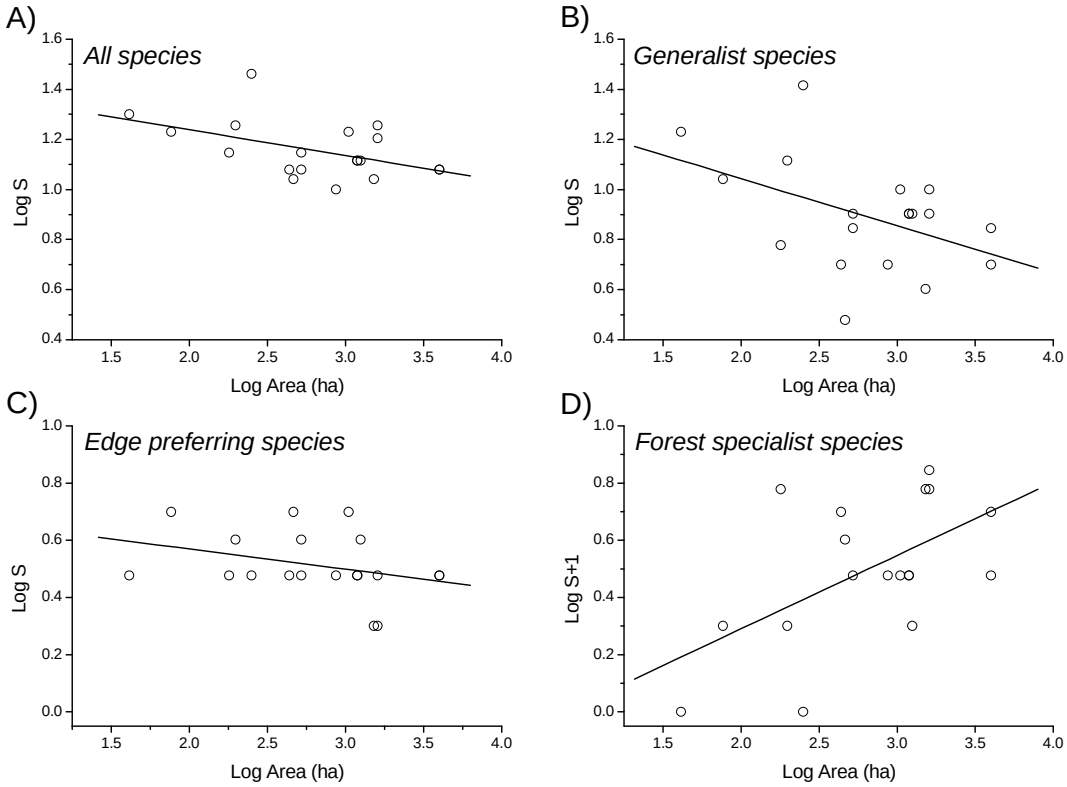

Figure 5.1 *The habitat area:species number relationship in carabids by habitat affinities. A) The relationship for all species was negative (R= – 0.49, $F_{(1,17)}$=5.22, P=0.04), caused mainly by the generalists (panel B, R= – 0.46, $F_{(1,17)}$=4.45, P=0.05). C) Edge – preferring species did not show a significant relationship with area (R= – 0.33, $F_{(1,17)}$=2.09, P=0.17). D) Forest specialists showed a significant positive relationship with area (R= 0.56, $F_{(1,17)}$=7.80, P=0.01).*

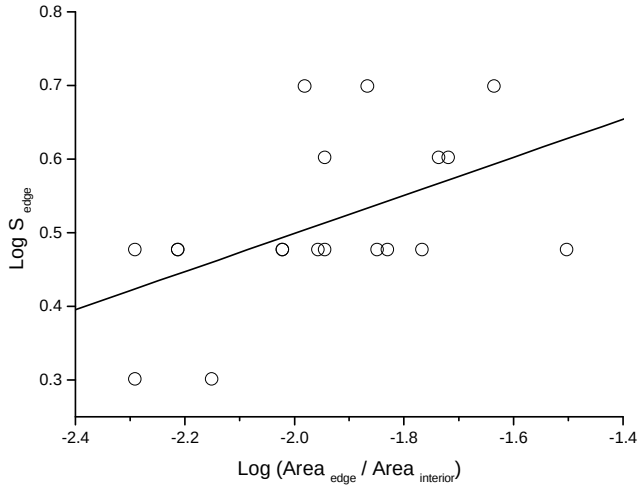

Figure 5.2 *The relationship between the number of edge-preferring species and the area of edge (outer 5 m of the fragment) in relation to patch interior. Smaller patches have relatively larger edge areas than large patches, and the importance of edge species correspondingly increases (R= 0.51, $F_{(1,17)}$=5.84, P=0.03).*

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Table 5.1 *The name, area-related characteristics, the number of pitfall traps, and the number of ground beetle species by habitat affinity category captured in the studied forest fragments on the Bereg Plain, NE Hungary and Ukraine. Fragments are arranged by decreasing number of all carabid species caught.*

Site	Area (ha)	Perimeter (m)	Shape-index	Number of pitfall traps	Number of			
					All species caught	Forest specialist species	Edge preferring species	Generalist species
Peres	249	7077	1.26	12	29	0	3	26
Téglás	41	2588	1.14	12	20	0	3	17
Déda, Hungary	197	7544	1.51	18	18	1	4	13
Rafajna, 1996	1609	16467	1.16	12	18	6	2	10
Déda, Ukraine	76	3555	1.14	12	17	1	5	11
Lónya	1047	21871	1.91	18	17	2	5	10
Rafajna, 1998	1609	16467	1.16	9	16	5	3	8
Puskinó, 1998	523	11883	1.47	9	14	2	4	8
Munkács	180	6145	1.29	9	14	5	3	6
Bockerek	1249	45822	3.66	18	13	1	4	8
Dobrony, 1996	1191	22672	1.85	12	13	2	3	8
Dobrony, 1997	1191	22672	1.85	9	13	2	3	8
Beregújfalu, 1998	3995	48954	2.18	9	12	4	3	5
Puskinó, 1999	523	11883	1.47	9	12	2	3	7
Beregújfalu, 1999	3995	48954	2.18	9	12	2	3	7
Gát	437	12922	1.74	9	12	4	3	5
Alsóremete	463	12594	1.65	9	11	3	5	3
Alsókerepec	1520	21478	1.55	9	11	5	2	4
Gút	871	19233	1.84	9	10	2	3	5

Theoretical studies, 2. The collapse of animal assemblages in isolated forest fragments

Due to its long isolation from the rest of the world, the New Zealand archipelago has biota that are of special value for biodiversity and conservation (Daugherty et al. 1993). They are characterised by a very high level of endemism, reaching, for example, >90% for species of Coleoptera (Watt 1982). Although profound human modification of the original biota started with the arrival of people about 1000 y BP, present conditions have been formed during the more recent, large-scale settlement since last century (Atkinson & Cameron 1993). Modern agriculture, especially on the North Island, has modified large tracts of the original vegetation, eliminated substantial parts of the forest cover and fragmented much of the rest. This profoundly influenced all habitats via introductions of plants and animals that had no evolutionary equivalent in New Zealand during the last 70 million years (Daugherty et al. 1990).

Problems affecting endemic vertebrate organisms have received early attention (Daugherty et al. 1990, 1993). However, many other native organisms face similar problems, and this has spawned special invertebrate conservation programmes relatively recently (Creswell & Weitch 1994; Sherley 1998). A particular difficulty is that conservation biology in New Zealand is too often hampered by lack of knowledge of basic biology, in some cases even of systematics, of the species affected.

Ground beetles (Carabidae) are generally good dispersers, either by flying, or by walking (Lövei & Sunderland 1996). Thus, it is plausible to assume that they are well adapted to cope with a fragmenting landscape. The Manawatu region, a predominantly agricultural landscape, has few fragments left of its former forest. At the time of study, only the largest one of them was protected and subject to ecological restoration efforts. Our initial aim was to study how ground beetles reacted to isolation and botanical diversity as well as to collect data on their biology. Considerable species richness of native invertebrates can be present in a dense network of fragments of native vegetation and restoration of native vegetation is believed to bring about a restoration of native arthropod fauna (Watts & Gibbs 2000). This generality, however, needs further articulation. We wanted to test the reaction of ground beetles to fragmentation in a landscape where the fragments, while botanically diverse, were relatively distant from each other. In this paper we report that we found only collapsed assemblages in isolated but protected forest fragments. While the causes are not known precisely, forest ground beetles in New Zealand seem to have low powers of dispersal and they probably cannot survive in a fragmented landscape without active management.

Study area and Methods

To study the effect of fragmentation on forest carabids in the preliminary lowland agricultural region of the Manawatu, southern North Island, New Zealand, 3 forest areas around the city of Palmerston North (40^{o} 23' S; 175^{o} 38' E) were selected. None of these were grazed by cattle or sheep. One of them (*Woodville Recreational Reserve)* was a large forest tract in the region, a possible source area for ground beetles (and other native invertebrates). The second one, *Keeble's Bush*, is the largest protected remnant of the once- common forest type on the lowland. The third, *Atawhai Road*, is a small, but carefully established and managed, diverse forest patch in the outskirts of Palmerston North.

Sampling was by pitfall traps (10 cm diameter plastic cups, with 250 ml of ethylene glycol as killing agent and preservative). At Woodville, 15 traps were emptied fortnightly between August 1991 and September 1992. The total trapping effort was 765 trap-weeks. In Keeble's Bush, 10 traps were operated between August 1990 and September 1991, giving a total sampling effort of 516 trap-weeks. At Atawhai Road, 5 pitfall traps were emptied fortnightly between August 1990-September 1991. The total sampling effort was 262 trap-weeks.

Evaluation. The diversity of the assemblages was evaluated with their species number (S) and the Berger-Parker dominance index, *d* (Southwood & Henderson, 2003). At minimum diversity (all specimens belong to one species), this index has a maximum value of d=1.00. The lower values indicate a more diverse assemblage.

Further details on the study areas, sampling and identificaiton are in Lövei & Cartellieri (2000).

Results

Large forest patch, Woodville Reserve, Manawatu Gorge

A total of 339 individuals of 9 species was caught (Table 5.2). The most common species were *Ctenognathus adamsi*, *Plocamosthetus planiusculus*, and *Zolus cf. femoralis*. The single individual of *Holcaspis oedicnema* was caught in late February, *Holcaspis mucronata* and *Megadromus capito* were all caught during the spring - summer season (November- March). Four individuals of *Mecodema simplex* were caught in August - September and 3 further individuals between February and April. This assemblage had the highest activity density of the areas studied, 0.44 beetles/trap-week. The Berger-Parker dominance index of this assemblage was the lowest of the three, *d*= 0.46.

Forest fragment, Keeble`s Bush

At Keeble`s Bush, 50 individuals of two species, *M. capito* and *H. mucronata* were captured (Table 5.2). Both of these species had males and females, so the presence of reproducing populations could be assumed. In addition, we captured teneral individuals of *M. capito*. The dominance index was high, *d*= 0.64. The active density was very low, 0.097 beetles/trap-week.

Table 5.2. *Characteristics of the carabid assemblages as reflected in pitfall trap catches in three forests near Palmerston North, Manawatu, North Island, New Zealand, during 1990-1992.*

Species	**Woodville Reserve**	**Keeble's Bush**	**Atawhai Road**
Ctenognathus adamsi	156	-	-
Holcaspis mucronata	8	18	18
Holcaspis oedicnema	1	-	-
Mecodema simplex	7	-	-
Megadromus capito	8	32	5
Megadromus turgidiceps	20	-	-
Plocamosthetus planiusculus	102	-	1
Psydrinae sp.1	1	-	-
Zolus cf. femoralis	36	-	-
Total numbers caught	339	50	24
No. of species	9	2	3
Sampling effort, trap-weeks	765	516	262
Activity density, no./trap-weeks	0.44	0.097	0.092

Suburban forest patch, Atawhai Road, Palmerston North

A total of 24 individuals were caught that belonged to 3 species: *M. capito, H. mucronata* and *P. planiusculus* (Table 5.2). The presence of a locally reproducing population was proven for *H. mucronata* only, as we trapped teneral individuals. Only males of the other two species were captured. The dominance index of this assemblage was *d*= 0.75. Given that the number of traps was smaller, the overall activity-density was nearly equal to that in Keeble's Bush, 0.092 beetles/trap-week.

Theoretical studies, 3. The importance of life history in ecological theory - size trends in a ground beetle assemblage in relation to life history parameters

This last chapter brings together some obvious messages that bear repeating even if made before:
1. that data presentation methods should be true to data
2. that data presentation methods are important to provide appropriate data perception and
3. that ecological theory is empty and meaningless without a proper consideration of the biological features of organisms whose ecological roles it seeks to provide.

This cautionary tale unfolds as the analysis of the size trends in the paper by Braun et al. (2004) is made.

Size has a significant, substantial impact on ecological interactions (Peters 1983). It modulates resource use, the outcome of species interactions (Peters 1983), and more indirectly, the periods of activity, habitat suitability, and numerous other parameters. The study of size relationships and their role in shaping interactions is an active research area in ecology (Peters 1983; Brown 1995). Changes in either the size in individual species, or the size distribution of the species in a habitat are also parameters potentially indicating environmental stress (McGeoch 1998). Recently, Braun et al. (2004) used this approach to analyse species size trends in ground beetles (Carabidae) in the surroundigs of an abandoned fertiliser factory in Germany. Using the mean size (estimated biovolume) of beetles present, they found that the average species size decreased over time (16 years), in parallel with a decrease in habitat contamination caused by the former fertiliser factory. Based on these results, they speculated about the validity of two conflicting hypotheses of resource use distribution within the family of ground beetles (Carabidae). In Braun et al.'s study (2004) ground beetles were used as a taxonomic (and predatory) group; no consideration was made of the various feeding strategies that are found within the group. However, neither all ground beetles, nor even the majority of them can be considered predatory. In the European fauna, there are many species that are herbivores, or mixed feeders (Lövei & Sunderland 1996). Therefore, data presented in Braun et al. (2004) were re-analysed after re-sorting their species list into three adult feeding categories: predatory species, mixed feeders, and herbivores.

Material and Methods

We distinguished carnivores, herbivores and mixed feeders. Feeding categorisation was based on work by Larochelle (1990), Hůrka (1996) and Lindroth (1985, 1986).

Size trends were analysed using ANOVA, followed by Tukey tests if significant differences were found. Calculations were done using the SPSS statistical software (SPSS 2000). Further, we chose a different graphical representation. Because the original analysis reports a time trend, the use of the histogram in Braun et al. (2004) is inappropriate: histogram considers the independent variable as a categorical one, and time is not a categorical variable. We replaced this data presentation method with a dot plot, where time is represented as a true, measurable variable. A second reason why we employed the representation method of dot plots is because they are especially suitable for presenting trends as the eye is good at interpreting dot patterns (Tufte 2003).

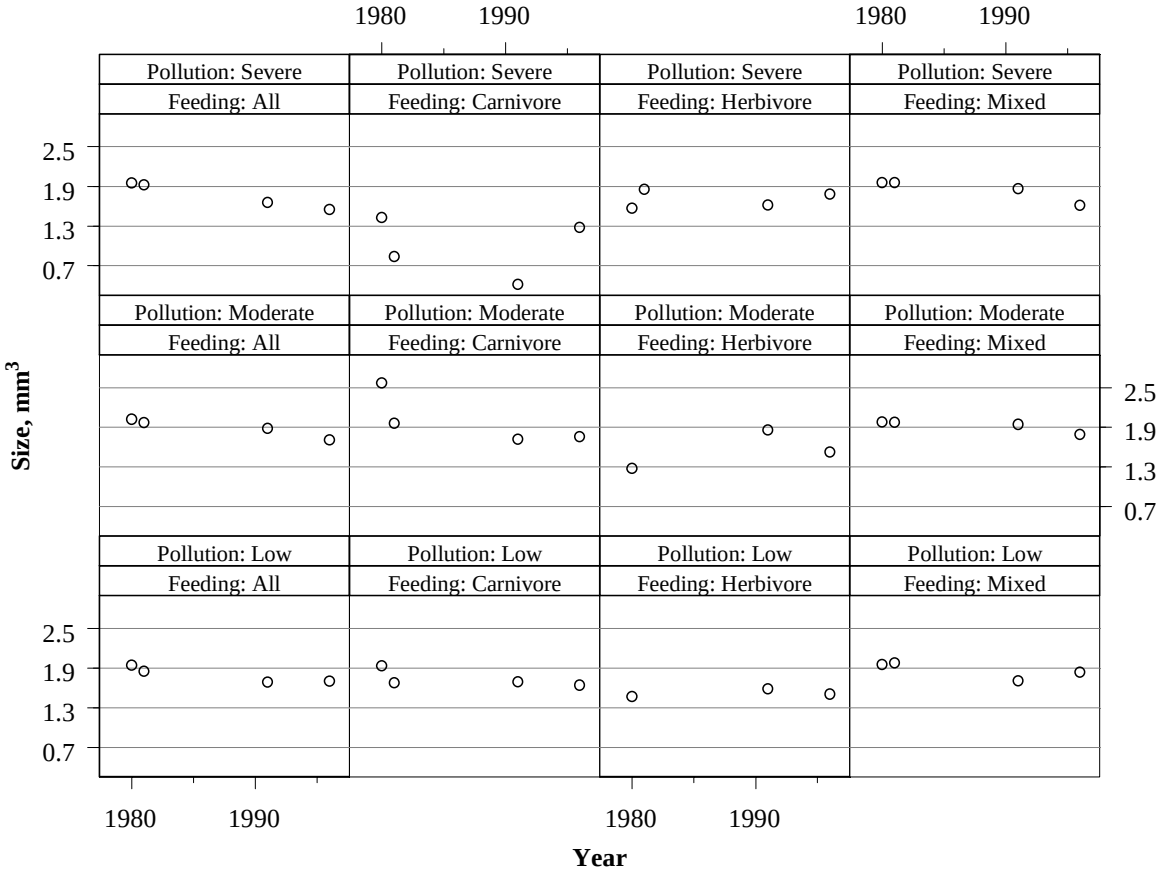

Fig. 5.3. *Size trends (biovolume, mm^3) of ground beetle species captured in three areas under different pollution levels near a fertiliser factory, Germany, in four years between 1980-1996. Data from Braun et al. (2004).*

Results

Size trends of all species

Considering all carabids together (regardless of their feeding categories), the mean size in the 90s was significantly smaller than that in the 80s for all the studied areas (Fig. 5.3. and Table 5.3). This picture changed when the species in the different feeding categories were considered separately.

Analysis by feeding categories

Carnivore species - In the severely polluted area, body size was smallest in 1991, significantly smaller than either in 1980 and 1996 (but not 1990). The other three body size values did not significantly differ from each other, although 1981 was smaller than either 1980 or 1996 (Fig. 5.3. and Table 5.3).

In the moderately polluted area, there is a decreasing trend, but this consists only of a drop from the first year's higher value to a lower level in the following year. Ten years later, this level is somewhat lower, now becoming significantly smaller than the corresponding value for 1980 (but not the more variable 1981). This level shows virtually no difference five years later (Fig. 5.3. and Table 5.3).

In the lightly polluted area, there are no significant time trends. The mean size in 1980 was somewhat larger than in the other three years (Fig. 5.3. and Table 5.3).

Herbivore species - There were few herbivorous species. The size trend in the severely polluted area showed a zigzag pattern, with some significant differences in the middle years. The initial and final years did not differ. The same appeared in the other two areas, at a somewhat lower level (Fig. 5.3. and Table 5.3).

Mixed feeder species - The largest number of species were classified as mixed feeders, and, consequently, this group should contribute considerably to the overall trend. In fact, the trends shown by the mixed feeders were similar to that of ‘all species’. This group shows no significant size difference among the differently polluted areas in 1980 or 1981. Severely and moderately polluted areas seem to support assemblages that became progressively smaller, more in the severely polluted than in the moderately polluted area. There was no decreasing trend in the lightly polluted area, except a smaller assemblage in 1991 (Fig. 5.3. and Table 5.3).

***Table 5.3**. Results of the one-way ANOVA for the ground beetle species collected in the severely, moderately, and lightly polluted areas in 1980, 1981, 1991, 1996, near a fertiliser factory, Germany. Data from Braun et al. (2004).*

Source	SS	d.f.	MS	F	*P*	Tukey-test
All species, severely polluted area						
Year	79.855	3	26.618	93.023	<0.001	1980=1981>1991>1996
Error	1092.223	3817	0.286			
Total	11937.437	3821				
All species, moderately polluted area						
Year	7.279	3	2.426	15.992	<0.001	1980=1981=1991>1996
Error	71.312	470	0.152			
Total	1647.199	474				
All species, lightly polluted area						
Year	4.588	3	1.529	9.386	<0.001	1980>1991; 1980>1996
Error	118.786	729	0.163			
Total	2311.356	733				
Carnivore species, severely polluted area						
Year	68.275	3	22.758	56.302	<0.001	1980>1991; 1996>1991
Error	191.194	473	0.404			
Total	794.861	477				
Carnivore species, moderately polluted area						
Year	4.069	3	1.356	3.976	0.009	1980>1991; 1980>1996
Error	48.440	142	0.341			
Total	521.016	146				
Carnivore species, lightly polluted area						
Year	0.942	3	0.314	1.465	0.224	
Error	66.863	312	0.214			
Total	956.640	316				
Herbivore species, severely polluted area						
Year	4.155	3	1.385	24.174	<0.001	1996>1991
Error	50.995	890	0.057			
Total	2497.278	894				
Herbivore species, moderately polluted area						
Year	4.923	3	1.641	30.136	<0.001	1991>1996
Error	4.847	89	0.054			
Total	249.327	93				
Herbivore species, lightly polluted area						
Year	2.430	3	0.810	12.819	<0.001	not performed*
Error	4.423	70	0.063			
Total	175.991	74				
Mixed feeding species, severely polluted area						
Year	51.720	3	17.240	72.583	<0.001	1980>1991; 1980>1996; 1981>1996; 1991>1996
Error	580.979	2446	0.238			
Total	8645.298	2450				
Mixed feeding species, moderately polluted area						
Year	1.447	3	0.482	9.555	<0.001	1980=1981=1991>1996
Error	11.713	232	0.050			
Total	876.856	236				
Mixed feeding species, lightly polluted area						
Year	3.370	3	1.123	9.220	<0.001	1980=1981=1996>1991
Error	41.419	340	0.122			
Total	1178.725	344				

*too few individuals in 1980 and 1981

Discussion

The influence of matrix and edge species on the species-area relationship in forest fragments

The original Island Biogeography Theory (MacArthur & Wilson 1967) took into account size and isolation, but not the change in habitat quality that, for example, occurs near edges. This would have different consequences, depending on whether species avoid or are attracted to the specific edge type. We evaluated whether considering this aspect would modify or strengthen the expected relationship between area and species richness. Isolation in our setting was not relevant, as all fragments were relatively far from any potential „source" area (in our case, the Carpathian Mountains).

The importance of edges has been recognized (Murcia 1995) but studies of forest fragments are dominated by human-generated fragments (Desender 2005) that are often without a natural edge, and a conceptual basis for edge studies has been lacking until recently (Ries & Sisk 2004). Our study clearly demonstrated the impact of both generalist and edge species on the shape and strength of the species-area relationship in forest fragments.

Comparing our results to those dealing with plants, there were remarkable differences in species composition by class. Among plants in Holt et. al.'s (1995) experiments, the share of generalist species is 23%, while in our material, 73% of the species pool consisted of generalist species. In our study, the number of forest specialists and the number of edge preferring species were nearly equal, indicating that the latter formed a significant component of the fauna.

In spite of these differences, our results corroborated, for an insect group and real habitat islands, that the presence of generalist species can mask the species richness- area relationship as stated by Cook et al. (2002). The distinction between matrix and "island" species is warranted but not entirely new. Several authors studying ground beetles (Bauer 1989; De Vries 1994; Magura et al. 2001) emphasized that during the study of habitat islands, distinction should be made between species that truly perceive the habitat fragments as islands (and are unable to survive in the surrounding matrix), and those that occur in both the fragment and the matrix.

Cook et al. (2002) define "matrix" species as any species occurring outside their experimental islands. This is a significant simplification as the mere occurrence in a habitat, especially in mobile organisms, does not indicate ecological links to that habitat. There can be a significant presence of "tourists" in arthropod assemblages (Novotny & Missa 2000).

The removal of matrix species is expected to increase the strength of the relationship between species richness and patch size (Cook et al. 2002). We demonstrated that after removing not only the

generalist/matrix species, but also the edge preferring species (retaining only the forest species for which the habitat fragments are islands), the strength of the species richness-area relationship increased. Moreover, the negative relationship between the total species richness and the forest area became positive.

Further, we demonstrated that the significance of the edge preferring species within the fauna is related to the proportion of the edge area to the total fragment area. The relationship between the proportion of edge-preferring species and fragment size, logically, is a negative one: the smaller the fragment, the more significant are the edge species in the fauna. Their species richness or their density (Bender et al. 1998) can increase. The area of the edge does not necessarily decrease with the decreasing fragment size, as it depends on the shape of the fragment, its area, and the structure of the edge (Didham & Lawton 1999).

It is probable that the relationship between patch area and edge species is not a simple one. Edge species require the presence of two habitats with different structure and environmental conditions that together form the special "edge" conditions (Ries & Sisk 2004). If the fragment is too small, the presence of one of these habitat types, the "inner" one can be absent. A forest patch needs to be of a minimum size to create conditions characteristic for forest interior, and this is not possible below a certain size. This minimum required size can vary, depending on geographic location, habitat structure, or the age of the fragment. Actual figures for ground beetles can be 0.5 ha (Mader 1984) to tens of hectares (Niemelä 2001). In our study, the smallest fragment was 41 ha (Magura et al. 2001), sufficient for forest interior habitat to exist.

In summary, we verified that not only the generalist species, but also the edge-specialist species can mask the relationship between species richness of carabids and the area of habitat islands.

Collapsed assemblages in New Zealand

When compared to data from the Northern Hemisphere, the activity density values in New Zealand were very low. Typically, pitfall trap studies in northern temperate forests result in catches one-two orders of magnitude larger than ours (Thiele 1977, Niemelä *et al*. 1992). Another study near Wellington, about 170 km south of our site, found 0.02 – 0.195 beetles/trap-week (calculated from data in Crisp et al. 1998). A similar difference between New Zealand and the Northern Hemisphere was found for spider densities (Topping & Lövei 1997). Although pitfall trap catches cannot be directly related to density (Lövei & Sunderland 1996), it is very probable that ground beetle densities are genuinely lower in New Zealand forests than in similar habitats in the Northern Hemisphere.

With respect to the potential source area, both smaller fragments had a ground beetle as-

semblage that can only be described as “collapsed”. Both were complete subsets of the supposed source assemblage: no species was found that was not present in the source area. The species numbers were very low, and the assemblages had low diversity. The smallest fragment had males only of one and a singleton of another species present. Seven out of the nine species forming the ‘source’ assemblage were short-winged or wingless (Cartellieri & Lövei, unpublished data), and thus their power of dispersal was lower than that of flying species. Based on laboratory observations, even large endemic ground beetle species seemed to be more sensitive to desiccation than similar-sized northern temperate species (M. Cartellieri, *pers. obs*.).

On a smaller scale (30 ha), Crisp et al. (1998) also found habitats with collapsed ground beetle assemblages. However, these were on disturbed plots (grazed, burnt, or invaded by non-native plants) where drastic changes in environmental conditions could explain the collapse of the original forest-living ground beetle assemblage. Crisp et al. (1998) concluded that there was a positive trend between the representation (percent of species) of native beetle species and native plant species. This trend does not necessarily hold for ground beetles in forest fragments: all our study sites had predominantly native vegetation, were under protection, suffered no disturbance and were subject to (botanical) restoration efforts. They still had a ‘collapsed’ ground beetle assemblage, so botanical composition may not be the only crucial determinant of species richness of ground-active native invertebrates.

New Zealand forests have been profoundly modified (Dawson 1988) and it may well be impossible to reconstruct the 'original' ground beetle assemblage (or any other animal assamblage). What remains is possibly only a shadow of the former diversity, but the main concern today should be the continued survival of these species.

We believe that forest-living, endemic ground beetles in New Zealand may have very limited dispersal power, probably orders of magnitude smaller than their relatives in the Northern Hemisphere have. Even though Keeble's Bush represented the largest, botanically species-rich remnant of the forest characteristic of the Manawatu area, and it was protected from disturbance, its ground beetle assemblage contained only two species in sharp contrast to the potential species richness, collected in a nearby ‘source’ area. The reasons for this can be manifold, but we suspect that low dispersal power and, at least in Keeble’s Bush, predation risk could be important. . Night-active invertebrate species are at risk from mammal predation, (Parmenter & MacMahon 1988). Predator-naive invertebrates can be driven to extinction by rats and possums (Atkinson & Cameron 1993). Kiore (*Rattus exulans)* and possums (*Trichosurus vulpecula*) are present in Keeble’s Bush (G. Lövei, *pers. obs.*).

The second patch, Atawhai Road, although small, has been carefully assembled to contain a diverse array of trees characteristic of the area, was an established stand with tall trees, and has been kept free of possums and rats. Being in a suburban setting, it was surrounded with less inhospitable habitats than pasture-surrounded Keeble's Bush. Fragment size could be responsible for lack of diversity, but it did not seem to decrease total carabid activity density.

It is very probable that isolated fragments, especially those with introduced mammal populations, will quickly lose their ground- and night-active invertebrates. Ground beetles are at risk because they are relatively large, seem to have low dispersal power, almost all of them are night-active and sensitive to predation by introduced mammals. Relying on natural dispersal power does not seem to be sufficient to keep native ground beetles in the fragmented forest landscape . Without active intervention, even potentially suitable habitat fragments will remain devoid of such species, thus exacerbating conservation problems. Active management should include "dispersal management", where beetles are relocated into uninhabited but suitable fragments. This, paired with predator control and vegetation restoration, two operations that are now standard parts of conservation management in New Zealand, would bring significant invertebrate conservation benefits with little additional effort. However, the phenomenon documented here is relevant for other fragmentation situations in other parts of the world.

The importance of data presentation and target organism biology in ecologial-theoretical interpretations

Most of the support for the role of the increasing specialisation hypothesis in the organisation of ground beetle assemblages claimed by Braun et al. (2004) disappears when the biology (feeding behaviour) of the species is properly taken into account.

Our analysis underlines the notion that taxonomic units rarely correspond to ecological units, and it is rarely justified to consider them as such. Considering the mean size of ground beetles in general may give rise to a statistical artefact. This is due to the oversimplified classification of the family as predators. Considering natural history is essential for the correct ecological interpretation of patterns in nature. Carabids can conveniently be collected by a single method as most of the species, at least in the northern temperate region (but not in the tropics, see Erwin 1979a), have surface-active adults. Traditionally, carabids have been considered predators, but even Thiele (1977) stressed that this can be a misleading simplification. Results published since the early 70s fully support this suggestion (Lövei & Sunderland 1996; Toft & Bilde 2002).

Consequently, the approach followed by Braun et al. (2004) is of limited value, and is in need of further development. The different feeding types of ground beetles should be considered separately and our re-analysis demonstrated that this indeed changed the time-carabid body size relationship. It is ecologically more valid to consider the changes in size and the assumed resource partitioning with at least the different feeding types separately. The assumptions of feeding categories are crucial, and future studies refining these categories (for example, the extent of carrion feeding in carabids, which currently is not well understood, Lövei & Sunderland 1996) might lead to still different results.

A core figure in Braun et al. (2004) was reconstructed, to replace the bar graph with a multi-panel conditioned dot-plot, which is a powerful method to identify the different size trends (Cleveland 1994; Tufte 2003). This also allows presenting the time trends, the relationships of the four sampling years correctly (they are not equally apart from each other), and this representation is preferable to the bar graph which treats the independent variable as a categorical one while time is not a categorical variable (Cleveland 1994). Appropriate data presentation methods are essential to provide a true impression of trends displayed by the data.

When seeking explanations for assemblage organisation, single-group studies can lead to spurious results. In the case of carabids, spiders and ants should be considered, as they have a significant impact on ground beetles (Thiele 1977; Lövei & Sunderland 1996).

A further, modulating influence on assemblage organisation is the permanence of species in a habitat. Species presence is often taken as an indication that the species can find all its needs and survive in the habitat. However, the presence of non-resident species (termed tourists, transient or occasional species) in ecological communities is frequent (Magurran 2003). Such species do not have sufficiently tight links to the habitat where found, and even though their ratio can be high (Novotny & Missa 2000), they are not legitimate members of the local ecological community. Considering all species captured at a location as integral components of that ecosystem is debatable. Species presence is not necessarily permanent, and community organisation could be better understood if permanent and transient species are identified and separated (Magurran & Henderson 2003). The latter may have little explanatory power in the search for assembly and resource distribution patterns (Magurran 2003). Size trends could be different also in this case if we could separate permanent from temporary species in the present case - but this was not possible due to the non-continuous sampling.

CONCLUSION

In this section, analysis of theoretical aspects in experiments with ground beetles showed that:
a) the matrix and edge of habitats (and species preferring such habitats) should be considered when examining island-area relationships as they have large power in shaping the relationship;
b) animal assemblages in isolated habitat fragments are less resilient than plants and are also more difficult to manipulate. Unless specific measures are taken, faunas of isolated fragments (native forest fragments in a pasture "matrix" in New Zealand, with high endemicity) may not recover even if the plant assemblages (on which they indirectly rely) are restored by human intervention;
c) natural history is singificant and should be explicitly considered when invoking ecological theories to explain patterns in arthropod assemblage organisation.

VI. Final thoughts. Ecology in an age of human domination

At the start of my scientific career, humankind numbered less than half of today's. Even then, two outstanding features were evident: that an increasing traffic in goods and people has profound consequences on the Earth's diversity through invasions, and that human dominance set in motion a new extinction wave, perhaps the largest is Earth's history. Here only a personal summary (Lövei 1997, Lövei 2007) of some of the most salient points are presented.

The fossil record indicates that the recent extinction wave, starting at around 40,000 years ago, affecting terrestrial vertebrates was parallel with the arrival of modern humans to areas formerly uninhabited by them. Such "first contact extinctions" are documented from North America, Madagascar or New Zealand. On continents, large mammals were affected, while on islands, the impacts were mainly felt by birds. Hunting, habitat alteration and the introduction of non-native species have certainly contributed to extinctions. In molluscs, birds and mammals, that went extinct since 1600 and have a known cause, 23% was due to hunting, 36% to habitat destruction, and 39% due to the introduction of exotic organisms. Our knowledge about extinctions is very incomplete, due to bias in research by taxonomy (vertebrate groups are better studied), geography (northern areas have received more attention), habitat (terrestrial habitats are better known than marine ones), biological reasons (certain groups do not fossilize) and methodological problems (methods of excavation and identification). Consequently, we can only crudely estimate the current rate of extinction but it is probably at least 100-1000 times higher than background extinction rates. It is evident that we generated a new mass extinction, affecting all species in all habitats, and, by the time it has run its course, it will potentially surpass the previous five mass extinction events in the history of Earth.

Invasions, recognised as one of the drivers of extinction, are already a significant threat to global biodiversity. While a 4% share of exotics in the South African flora already creates problems, many other areas, among them islands (New Zealand: 40%) as well as continents (New York State, North America: 36%) have much higher shares. The massive spread of organisms by humans to other areas of the globe may increase local diversity, but will result in large losses in global biodiversity. In order to understand the danger that pan-mixing of the Earth's fauna and flora signify, let us consider a thought experiment in island biogeography (Fig.6.1). Species richness on an island is largely determined by its area: the larger the area, the more species the island contains. The same applies for continents. For example, mammal species richness is related to the size of the individual continents. The resulting correlation allows to extrapolate the global species richness. A

supercontinent, with an area equal to the total dry land on Earth would support about 2,000 mammal species. Currently, there are about 4,200 mammal species. Therefore geographical isolation allowed evolution to generate nearly twice the biodiversity that could otherwise, on the basis of habitat area alone, be expected. As today human-assisted invasion is becoming a more and more prevalent biogeographic phenomenon, the individual continents are more and more like one supercontinent. It is not surprising that more extinctions are predicted, with possibly catastrophic consequences for biodiversity.

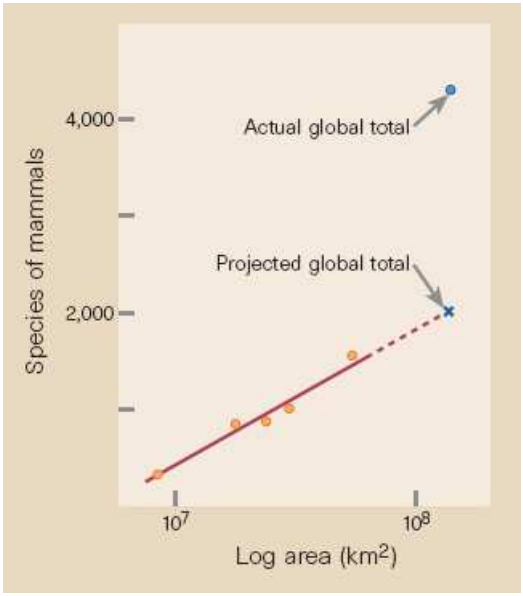

Figure 6.1. *A "species richness vs area" curve for mammals. The number of species on a continent is tightly correlated with the size of the continent, but extrapolating that relation to the land area of Earth yields less than half the total number of species that actually occur on these continents. Much of the global diversity of mammalian species is due to the isolation of separate biotic regions.*

An important paradigm shift in ecology occurred recently: the realisation that human influence is so pervasive that the most urgent task is to find the conditions of sustained functioning of ecological systems, especially those under heavy human influence. The theoretical background to this is provided by the concept of ecosystem services (Daily 1999). To put it simply, I consider the most important scientific problem in ecology to obtain detailed knowledge about the condition, functioning, intensity, and vulnerability of ecosystem services, and what needs to be done to prevent their substantial damage?

The future activities in entomology and ecology will be played out against these large trends. In this final chapter I shall briefly contemplate how could the study of ground beetles contribute to these goals?

The late Pál Juhász-Nagy suggested that the science of "ecology" should be divided to two important sub-disciplines: one he called "synphenobiology", which describes the phenomena and patterns in nature, and the "ecology *sensu stricto*" that seeks the causal explanations creating these phenomena and patterns (Juhász-Nagy 1986). Ecology cannot further develop without cultivating synphenobiology. We need to know how to realise, describe, characterise and interpret patterns and their changes. This is of prime importance from a practical point of view, for example for the already-ubiquitous monitoring. Carabidologists should consider the further cultivation of synphenobiology as an important obligation.

Further, it is urgent to realise that the distinction between "theoretical" and "applied" ecology has no basis whatsoever. This is no great news to colleagues exposed to the thinking behind the agroecology project initiated at the Plant Protection Institute in the late 1970ies. The recently increasing acceptance of this point, alas, is not the result of global ecological enlightening, but the immeasurable (or rather, measurably large) multiplication of the human race, and the resulting large impact on all ecosystems. There is virtually no ecosystem left untouched by humans – there is thus no place where an ecologist could go to find out "the works of nature", and ecosystem in "optimal condition", from which to deduce principles for managing other ecosystems. The study of human-influenced habitats has gained acceptance as part of "ecology true and proper".

Further study of ground beetles lend themselves to the understanding and clarification of several important ecological phenomena:

One is the interaction of different ecological systems, for example the interactions of below-- and above-ground organisms and communities. Ground beetles have soil-dwelling larvae and soil-surface active adults (in the tropics the adults are also in the canopy), and thus could be an important link between these two habitats.

With the increasingly sophisticated data collecting equipments and computer power enables us to collect, organise, and evaluate large amounts of complex data, for example multi-layered digital maps. This triggered the development and current flourishing of landscape ecology. Ground beetles have already played a prominent role in the maturation of this field (see for example Baudry and co-workers' activity in France) because they form a group that can be handled and collected easily. Extending such studies to other parts of the globe would bring exciting results.

Another important research area is connected to ecosystem services. So far the emphasis was on pattern description, assuming that these would correctly represent the importance and intensity of such functions. For example, ground beetle (or predator) density was described in different fields, and a higher beetle density implied higher level of biological control. This is not necessarily so. The development of the ecological methods enables us to examine and measure these functions even under field conditions. It can and should be measured how much do ground beetles contribute to ecological services such as biological control, decomposition, or nutrient cycling.

Important and incompletely answered is the question of the role, possibilities and limitations of ground beetles in ecological indication. According to the general indication principle (Pál Juhász-Nagy 1986), every organism is an indicator. Ground beetles have been popular in such applications for methodological reasons already mentioned earlier. The importance of "bioindication" will not decrease, at least not in the near future, carabidologists could be in the forefront to assist the maturation of the use of arthropods in environmental indication and monitoring.

I have always held the conviction that ecology is THE most important and interesting science in our time. I am also convinced that more and more people realise that this is actually true – against a background that ecological analphabetism is increasingly dangerous for humankind. The future of ecology as a "necessary science" is therefore secure – our future depends on developing an ecologically-based world view and act on it. The science is not lacking in interesting problems – even though it is lacking the means (among which financial is not the least) to tackle them - and this is especially so in Hungary. The future is, however, bright. Until the arrival of the bright future, writer Istvan Orkeny suggests in his short story “Look into the future with optimism”: "…for those few hundred years we just have to hang on”. Or we have to act to shorten that period. I feel we really have to act – time, especially if spent with "business as usual" - is not on our side.

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