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# Emergence of Carabidae (Coleoptera) from pupation: a technique for studying the 'productivity' of carabid habitats

Gordon Purvis & Abdoulla Fadl

*Purvis, G. & Fadl, A., Department of Environmental Resource Management, University College, Belfield, Dublin 4, Ireland*

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An emergence arena method for estimation of within-field carabid recruitment from pupation is described. Use of the method is illustrated in a field plot experiment to assess the effect of time of soil cultivation on carabid survival in arable land. The population 'productivity' of *Pterostichus melanarius* (Illig.), a larval overwinterer in arable fields, was found to be reduced by 80% following spring tillage operations. In contrast, *Bembidion lampros* (Herbst.), an adult overwinterer in field margins, showed decreased emergence density on winter-sown plots. The value of the method in quantitative investigation of populations in fragmented habitats is discussed.

## 1. Introduction

Whatever their aim, many studies of carabid ecology rely exclusively on pitfall trapping as a simple, cheap and relatively non-labour-intensive method of collecting large quantities of data (Southwood 1978). However, the technique has many shortcomings (Adis 1979). Trap catches reflect not only absolute population density, but also to a large degree, population activity — a combination referred to as 'activity-density' by Thiele (1977). It is the activity part of this combination which causes problems of interpretation since carabid catches in pitfalls are known to depend on many, often unquantifiable, factors: e.g. climate, habitat structure, food availability and seasonally changing behaviour — which may differ between the sexes. The relative abundance of different species in catches is also strongly influenced by interspecific differences in trappability associated with differences in size, agility and hunting/foraging behaviour (Mommertz *et al.* 1996). Additionally, the type of trap and collecting fluid used can strongy influence catches (Luff 1975). All of these effects mean that pitfall data can be used as a means of comparing relative carabid incidence, only when great care is taken in data interpretation (Ericson 1979, Luff 1982).

To overcome some of the difficulties inherent in interpreting pitfall data, it has been suggested that pooled trap catches made over the course of an entire season give a more reliable measure of actual abundance of some species in different sites (Baars 1979). However, adult carabids are often highly mobile and population redistribution during the adult instar is often an integral part of carabid lifecycles and greatly assists population survival in patchy highly disturbed environments (Den Boer 1977, 1981). In such circumstances, pooling seasonal trap catches may mask much useful information regarding population processes (Fadl *et al*. 1996).

A number of studies have utilised pitfalls enclosed within arenas of defined area in order to estimate absolute population densities at specific points in time (Sunderland *et al*. 1995). We suggest that in studies concerned with carabids in environments strongly influenced by human activities, the parameter of greatest interest is actually the 'productivity' of different sites in terms of the total numbers $m^{-2}$ emerging from pupation. Estimation of emergence densities can potentially define the relative contribution that any particular type of habitat makes to the next, highly mobile adult generation and may be of great value in the identification of management features which are of prime importance to carabid survival. To-date very few attempts have been made to estimate carabid densities in this way. Scheller (1984) made possibly the first partially successful attempt to estimate the within-site recruitment of carabid populations in a cereal crop. Desender *et al.* (1985), estimated 'instantaneous' carabid population density over a two-week trapping interval using enclosed pitfalls in grazed pasture. More recently, Ulber and Wolf-Schwerin (1995) produced estimates of partial carabid emergence densities for successive intervals within the total emergence period of several species. Helenius (1995) has described a method of estimating the total new generation emergence by integration of successive short-term catches made in trapping arenas which, as in Ulber and Wolf-Schwerin's (1995) study, were regularly moved to new positions throughout the season.

In this paper, we describe a similar, but simpler technique for the estimation of total carabid emergence without the neccessity of moving arenas and integrating catches. We illustrate its interpretive value when used in a replicated plot experiment designed to quantify the effect of autumn versus spring soil cultivation on carabid populations in arable fields. The hypothesis being tested in this work is that species which overwinter in fields as larvae, such as *Pterostichus melanarius* (Illig.), are especially vulnerable to soil cultivation in the spring when late larval and pupal instars are likely to be injured. A survey of the incidence of *P. melanarius* in fields of different cultivation history hinted that this may well be true (Fadl *et al*. 1996) but suggested that rapid post-emergence dispersal from fields generating the majority of adults made it difficult to demonstrate any cultivation effect on this species using conventional pitfall trapping. Here we present emergence data for *P. melanarius* and a contrasting summer-breeding species, *Bembidion lampros* (Herbst.) which, because it overwinters as an adult at the margins of cultivated fields (Mitchell 1963, Wallin 1989), we would not expect to be influenced directly by soil cultivation.

## 2. Materials and methods

### 2.1. Plot experiment

A randomised block experiment was established on a field cultivated and sown in the autumn with winter wheat. Initially, the entire field was ploughed on 20 October, 1993 and four replicate plots of two treatments — autumn-sown winter wheat and spring-sown barley — were established (Fig. 1). Plots were unbarriered and measured $30 \times 28$ m. Winter wheat plots were tilled with a power harrow along with the rest of the field and sown with winter-wheat on 28 October, 1993. Spring-sown plots were left fallow after ploughing until 28 April, 1994 when they were cultivated with a power harrow and sown with spring barley. No insecticide or molluscicide applications were made to either treatment. Applications of herbicide, fungicide and fertiliser to each treatment followed standard farm practice (Table 1). Carabid activity on the open plots was monitored using 10 glass jar pitfalls (5 cm diam.) arranged in two lines of 5 down the length of each plot. These were filled with 2–3 cm of water to which a little detergent was added and were operated for trapping periods of 1 week duration at regular intervals (usually every other week) from October, 1993 until September, 1994, inclusive. Trapped beetles were sexed and up to a maximum of 50 females of each species per plot were dissected and classified into one of four ovary development stages on each sampling date (see Fadl *et al*. 1996):

Stage I – ovaries not discernible – cuticle, especially the ovipositor, not fully pigmented
Stage II – ovaries discernible, only pale immature eggs present
Stage III – ovaries with mature pigmented eggs
Stage IV – all eggs laid and fat body spent

Additionally, the number of mature eggs in all gravid, stage III females was counted.

For treatment comparison, trap catches on each plot were pooled and transformed to natural logarithms ($\ln(x + 1)$) before analysis of variance using a randomised block model.

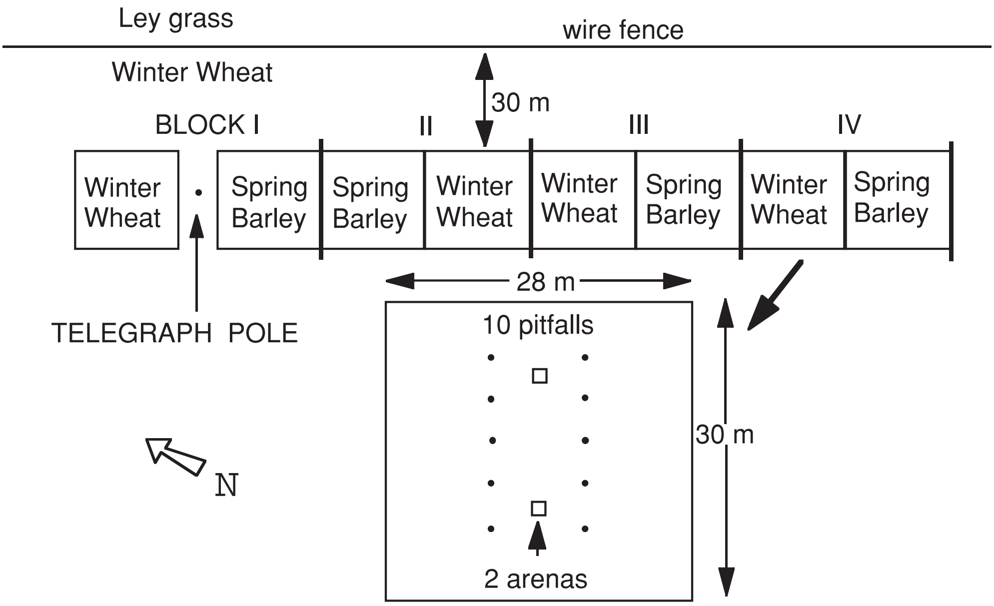


Fig. 1. Plot layout and position of open-plot pitfalls and emergence arenas.

Table 1. Summary of cultivation practice and farm inputs on winter-sown and spring-sown treatment plots.

| Cultivation/Input | Winter-sown wheat | Spring-sown barley |
|---|---|---|
| Ploughing date | 20.10.93 | 20.10.93 |
| Soil cultivation/crop sowing | 28.10.93 | 28.04.94 |
| Fertiliser: | | |
| — N | 140 kg/ha | 100 kg/ha |
| — P | – | 50 kg/ha |
| — K | – | 100 kg/ha |
| Herbicide: | | |
| — Advance (Bromoxynil + Ioxynil + Fluroxypyr, (2.01 l/ha) | 13.04.94 | – |
| — Starane (Fluroxypyr, 1.01 l/ha) | – | 27.05.94 |
| Fungicide: | | |
| — Folicur (Tebuconazole, 1.0 l/ha) | 20.05.94 | – |
| — Radar (Propiconazole, 0.3 l/ha) | – | 13.06.94 |
| — Impact Excel (Flutriafol + Chlorothalonil, 2.0 l/ha) | 26.06.94 | – |
| — Legend (Propiconazole + Fenpropidin, 0.8 l/ha) | – | 05.07.94 |
| Growth regulator: | | |
| — Cycocel, 1.5 l/ha | 27.04.94 | – |

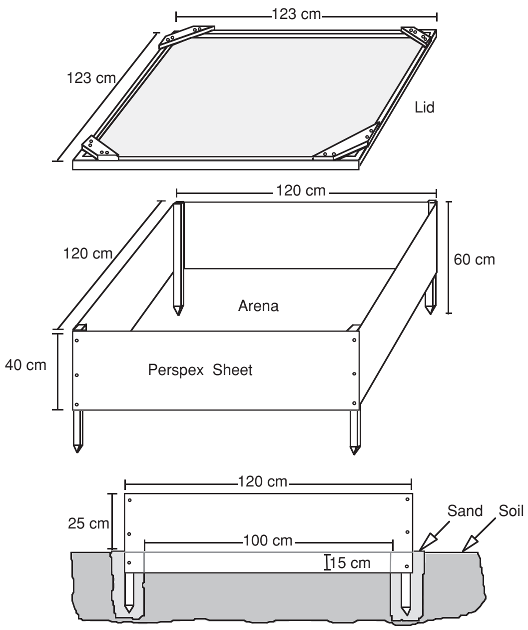


Fig. 2. Emergence arena construction.

## 2.2. Assessment of carabid emergence

Carabid emergence from defined areas measuring 1 $m^2$ was assessed on the plots using enclosed arenas illustrated in Fig. 2. Arenas were inserted in the plots by first digging a trench approximately 30 cm deep around an undisturbed block of soil measuring $1 \times 1$m. Around this block, an enclosure was assembled in the trench using four, 6mm thick sheets of opaque grey perspex ($1.2 \times 0.4$ m) screwed to wooden corner stakes ($4.5 \times 4.5$ mm). A mixture of soil and course builders sand was used to backfill the trench inside and outside the arena walls and was trodden tightly down to ensure that the perspex sheet was buried to a minimum depth of 15 cm. Sand was used in this installation procedure to ensure that the field soil (a silty clay loam, 30–34% clay content) did not crack or shrink from the arena walls during dry weather. Four glass jar pitfalls (5 cm diam.) containing 2–3 cm of water to which a little detergent was added were inserted in the centre of each arena using a 5 cm soil corer. The top of each arena was covered with a tightly fitting, removable lid comprising a light wooden frame to which 475 μ nylon monofilament mesh was glued and stapled. Two arenas were installed on each plot (= 8 per treatment — see Fig. 1) and were left in place from their installation at the end of April until the end of August, 1994. During this time, arena pitfalls were emptied weekly.

In the laboratory, newly emerged tenerals were distinguished from any old generation adults that were initially caught and all females were dissected to confirm their newly-emerged (ovary development stage I) status. Weekly catches of each species were summed to provide a total seasonal emergence count from each arena. For the purpose of treatment comparison, catches from arenas within plots were pooled to provide single mean estimates of numbers emerging per $m^2$ which, after transformation to natural logarithms ($\ln(x + 1)$) to normalise typically skewed counts data, were submitted to analysis of variance using a randomised block model. Results are presented as back-transformed mean numbers per $m^2$ with least significant ratios ($P < 0.05$).

# 3. Results

## 3.1. *Pterostichus melanarius*

Mean catches of *P. melanarius* in open traps and inside arenas on each treatment are shown in Fig. 3 along with the proportion of dissected females in each ovary development stage on all plots combined (there was no subtantial difference in these proportions between treatments). Relatively small catches of overwintering adults were made, largely on winter-sown plots, up to early June, the few females dissected during this period all being at stage II with only immature eggs present in the ovaries. From June onwards, open-plot trap catches increased rapidly on both treatments as newly emerged stage I females emerged. No old generation *P. melanarius* were caught inside the arenas but catches of the newly emerging generation arising from overwintered larvae were made from early June to early August coinciding with the appearence of the new generation in open traps (Fig. 3).

Table 2. Backtransformed mean open plot trap catches of *P. melanarius* for the periods March–May (overwintered beetles) and June–August (new generation beetles) and mean emergence arena density estimates on winter-sown and spring-sown plots (*LSR* = least significant ratio, $p < 0.05$).

| | Winter-sown | Spring-sown | *LSR* |
|---|---|---|---|
| Open plot catch (March–May) | 3.6 | 0.2 | 1.93 |
| Open plot catch (June–August) | 719.5 | 1 022.5 | 1.28 |
| Emergence density (nos. $m^{-2}$) | 13.8 | 2.5 | 3.29 |

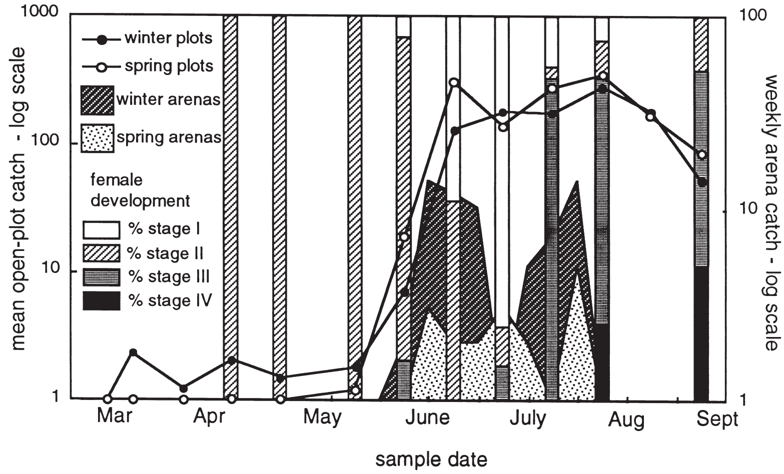


Fig. 3. Mean open-plot pitfall trap catches and mean arena emergence catches of *P. melanarius* on winter-sown and spring-sown plots. Columns indicate the overall relative incidence of ovary development classes (%) on each sampling date.

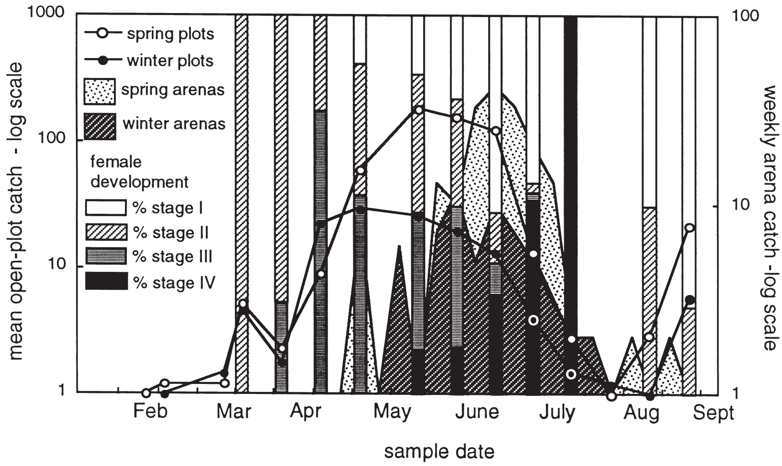


Fig. 4. Mean open-plot pitfall trap catches and mean arena emergence catches of *B. lampros* on winter-sown and spring-sown plots. Columns indicate the overall relative incidence of ovary development classes (%) on each sampling date.

Comparison of open-plot catches made between March and May, revealed significantly ($P < 0.01$) greater activity by overwintering old generation *P. melanarius* on winter-sown plots compared with spring-sown (Fig. 3, Table 2). Following the emergence of new generation beetles, significantly greater trap catches were made on spring-sown plots between June and early August ($P < 0.05$). In contrast, actual numbers of emerging individuals caught within arenas were significantly greater ($P < 0.05$) on the winter-sown compared to the spring cultivated plots (Fig. 3, Table 2). The calculated emergence density of *P. melanarius* was 13.8 per m$^2$ on winter-sown plots compared with only 2.5 individuals per m$^2$ on spring cultivated plots.

Table 3. Backtransformed mean open plot trap catches of *B. lampros* for the period May–July, inclusive, and mean emergence arena density estimates on winter-sown and spring-sown plots (*LSR* = least significant ratio, $p < 0.05$)

| | Winter-sown | Spring-sown | *LSR* |
|---|---|---|---|
| Open plot catch (May–July) | 83.3 | 509.3 | 1.44 |
| Emergence density (nos. m$^{-2}$) | 15.7 | 42.3 | 2.23 |

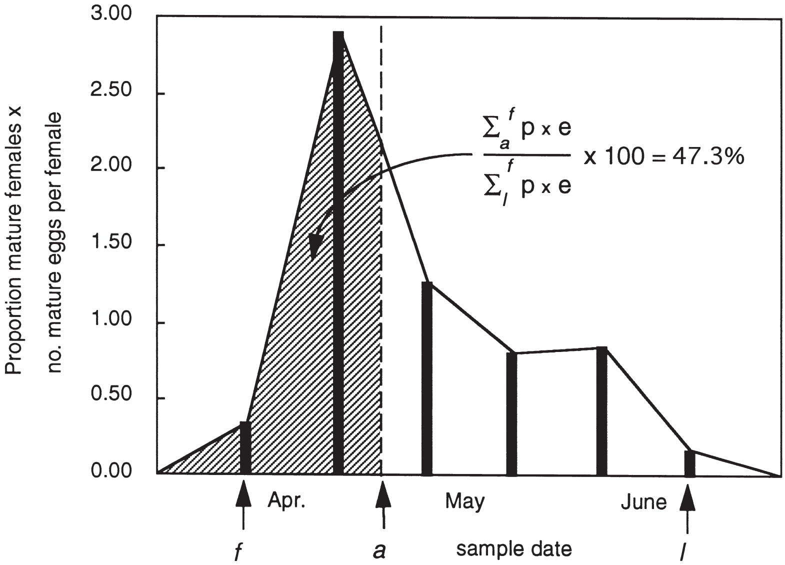


Fig. 5. Estimation of the proportion of total seasonal egg production by *B. lampros* acheived by the time of arena installation (see text for details).

### 3.2. *Bembidion lampros*

A summary of *B. lampros* catches is shown in Fig. 4. The activity of overwintering adults resumed on the field from late February onwards when all dissected females were at ovary development stage II and catches increased rapidly during April to reach a peak in June. Mature stage III females were caught from April onwards when the greatest proportion of mature gravid females were caught. However, the capture of egg-laying females on the open plots continued after the date of arena installation at the end of April with the last few egg-laying females caught in early July. Catches of *B. lampros* in open-plot traps declined during July and very few individuals were caught in August. A marked resumption of open-plot catches occurred in September. New generation stage I female *B. lampros* were first trapped on open plots in May and continued to emerge until the end of July which coincided with the appearence of newly emerged beetles inside arenas (Fig. 4). Arena catches continued until August and throughout this time no old generation beetles (stage II or III) were caught inside arenas.

Catches of *B. lampros* on open plots during the emergence of the new generation from May to July, inclusive, and of total numbers emerging within arenas, were both significantly greater on spring cultivated plots compared to winter-sown plots ($P < 0.001$ and $P < 0.05$, respectively; Fig. 4, Table 3). The mean emergence density obtained on spring cultivated plots was 42.3 *B. lampros* per m$^2$ compared with only 15.7 per m$^2$ on winter-sown plots. However, the prolonged overlap between egglaying activity on the open plots and the time of installation of arenas at the end of April, means that these emergence estimates are likely to substantially underestimate the true production of this species because at least part of the new egg population was excluded by installation of the arenas.

The proportion of the total egg population enclosed by the arenas may be estimated using information from dissection of female beetles trapped on the open plots as follows:

% of egg population excluded from arenas =

$$\frac{\sum_a^f p \times e}{\sum_l^f p \times e} \times 100 = 47.3$$

where: $p$ = proportion of old generation females with mature ovaries (stage III), $e$ = number of mature eggs per stage III female, $f$ = date of capture of the first stage III female, $a$ = date of arena installation, $l$ = date of capture of the last stage III female.

The complete egg production period of *B. lampros* throughout the season showing the proportion of eggs produced before arena installation is illustrated in Fig. 5. Approximately, 47% of total egg production for the season had been produced by the time arenas were installed. The overall ratio of

47:53 can be applied to estimate, approximately, the proportion of the newly emerging generation that was confined within arenas and to adjust total emergence density estimates. This procedure leads to revised mean emergence estimates of 90 *B. lampros* per m$^2$ from spring-sown plots and 33 per m$^2$ from winter-sown plots.

## 4. Discussion

Arena construction and installation are crucial to the success of the technique described. In the current study, no older animals were trapped inside arenas and the arena design seems effectively to have prevented beetle movement either into, or out of, the sampled areas. Experience during early development of the technique, suggested that the use of sand to ensure a good seal around arena walls and burial of walls to at least 15 cm depth was neccessary to acheive this success. Helenius (1995) utilised a quite labour intensive methodology to assess emergence involving the periodic movement of small trapping arenas (0.25 m$^2$) which were 'pushed' 5 cm into the soil tilth. Very high density estimates produced for some species using this technique e.g. 681 *Trechus discus* (Fab.) per m$^2$ (Helenius & Tolonen, 1994) suggest that complete isolation of trapped areas may not have been acheived for some species. Helenius (1995) moved trapping arenas on a regular basis in order to minimise any influence of altered microclimate on pupal survival inside enclosures. However, perhaps because rather larger arenas were used in the current study, survival was not obviously influenced by season-long enclosure, so far as can be judged, since a density estimate equivalent to almost 140 000 *P. melanarius* emerging ha$^{-1}$ on winter-sown plots seems realistic for a relatively large species. No comparable estimates for *P. melanarius* are available and further use of the technique is desireable to assess production of this species from other habitats. It is probable that the environment inside arenas was modified since crop height and vigour was noticebly greater than on the open field making it neccessary to trim crop height at the level of the arena cover. Much of this effect was probably due to above-ground shelter and possibly not so much due to altered soil conditions. Rainfall was not excluded by the flat mesh covers on arenas and for both species, beetle emergence inside arenas was not accelerated to any apparent degree, but closely coincided with appearance in open-plot traps.

Estimates of emergence densities for *P. melanarius* on winter and spring-sown plots suggest that spring soil cultivation produces a population reduction of approximately 80%. This reduction is of a similar magnitude to that observed in carabid populations following insecticide spray applications (Hassan *et al.* 1987). It is interesting to note that this effect was not demonstrated by pitfall catches made on open plots which showed exactly the opposite treatment effect with greater activity density occuring on spring plots following emergence of the new generation. As the quite small treatment plots were not barriered, and the rest of the field was winter-sown, it seems probable that the spring barley plots were very rapidly invaded by beetles actually emerging in much greater numbers from the surrounding field which was untilled in the spring. The very substantial dispersal ability of *P. melanarius* following emergence seems to lead to redistribution between fields within a matter of weeks (Fadl *et al.* 1996). Such dispersal ability is probably essential for the survival of species overwintering as larvae in cultivated land. Autumn ploughing was carried out on both the winter and spring-sown plots and seems to be less harmful, probably because very small early larval instars are more robust than large late larval instars and pupae. It must be pointed out that in the current experiment, spring-sown plots also differed from winter-sown plots in not having a crop cover during the winter months. This probably explains the greater activity of overwintering old generation beetles in the early spring on winter-sown plots and may also have had some additional influence on the survival of *P. melanarius* larvae in the soil. Any such effect seems much less likely to be as important in influencing the numbers of the emerging new adult population however, as the direct influence of additional soil cultivations prior to spring sowing.

For summer breeding species like *B. lampros*, overlap between emergence of the first individuals of the new generation and continued oviposition by the old generation creates difficulties in estimating a total emergence density. The likely extent of population under-estimation resulting from this overlap was estimated using information regarding egg production in the open plots. Use of this method to correct arena density estimates is dependent upon four basic assumptions:

i – the total number of old generation females on the plots remains constant throughout the egg-laying season despite variation in open-plot catches
ii – the catchability of gravid stage III females relative to other old generation developmental groups remains constant throughout the egg-laying season
iii – the number of eggs produced by females laying 'early' and 'late' in the season is similar
iv – 'early' and 'late' season eggs have an equal chance of survival.

The first of these assumptions is probably a reasonable one given the known biology of species which colonise crops from field margins at the beginning of the growing season and leave the open field again only in the autumn to find overwinter shelter as immatures of the next generation (Wallin 1989). The increase in open-plot catches in September is good evidence of increased activity by new generation beetles prior to their movement to field margins. Old generation development stages are probably not caught with equal ease but their relative catchability is less likely to vary with time. The third and fourth assumptions are more problematic and may not be strictly true. We have no direct information on the relative fecundity of 'early' and 'late' season females. Eggs may, in adverse circumstances be resorbed rather than laid, but since the last mature eggs were dissected in early July at a time when food availability is not likely to be limiting, this is unlikely to be a significant factor. We know nothing of survival between oviposition and pupal eclosion throughout the season. Despite this uncertainty, the ratio of egg production before, to that after arena installation, is probably quite a robust and accurately assessed statistic. The admittedly crude application of this ratio to estimate total pupal emergence is then, a questionably accurate, but probably fairly conservative way to revise an obvious under-estimation of the true population production. The revised population estimate of 90 *B. lampros* per $m^2$ on spring barley plots is similar to an estimate of 60–80 *Bembidion guttula* (Fab.) per $m^2$ in spring-sown cereals in Finland (Helenius, 1995) and to Scheller's estimate of 61 *B. lampros* per $m^2$ emerging from spring-sown cereals in Denmark (Scheller 1984). Scheller (1984) found his method using large emergence arenas measuring 4 $m^2$ did not trap out other species, including *P. melanarius*, probably because his arena walls were ineffective barriers to beetle movement.

Comparison of *B. lampros* incidence on treatment plots produced a less expected result. Almost three times as many beetles emerged from spring-sown plots compared with winter-sown. This result should probably be treated with caution. The most likely explanation is that individuals of the previous *B. lampros* generation showed selective preference for spring-sown plots when they returned to the field in the spring. If this was the mechanism, then the relatively small size of the spring-sown plots within the larger winter-sown field may well have distorted the effect seen by artificially concentrating ovipositing beetles on small spring-sown plot areas. The effect, in such circumstances, would be unrepresentative of real differences between winter and spring-sown fields. However, *B. lampros* and other summer-breeding species trapped in the survey described by Fadl *et al.* (1996) frequently showed a greater incidence in spring-sown compared with winter-sown fields (unpublished data). Low emergence from winter plots in the current study could, alternatively, be due to reduced survival of *B. lampros* in the presence of predation by nearly 14 late instar *P. melanarius* larvae per $m^2$ on winter-sown plots during May.

Increasingly, attempts are being made to understand carabid population dynamics in very heterogeneous and often hostile environments, to develop models of population processes and to predict the outcome of changing management practices such as increased pesticide use on carabid survival (Jepson & Thacker 1990). Todate, the major limitation in this approach has been the relative lack of field data to make such models realistic. We simply do not know enough about population processes because, in this context, the traditional pitfall trap is a very poor tool with which to seek information regarding population production and dispersal. In the current study, open pitfalls produced data difficult to reconcile with the emergence pattern of *P. melanarius*. Suggesting reasons for this can only be speculative. Probably a greater level of foraging activity on spring-sown compared to winter-sown plots followed very rapid dispersal from pupation, however, the physical structure of the two crop types at the time, in June, did not differ greatly. Many similar plot-based or even field-based studies are likely to produce results which are difficult to interpret if only activity density is measured. The emergence arena technique is one which can provide unequivocal evidence of population processes in any area of investigation where population production and mobility in a fragmented habitat is at issue.

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