ARABLE FIELD MARGINS: FACTORS AFFECTING BUTTERFLY DISTRIBUTION AND ABUNDANCE

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ABSTRACT

The current status of butterfly ecology on arable farmland with specific reference to field margins is reviewed, including major studies with a substantial potential for butterfly conservation. The potential role of pesticides, adjacent habitats, and biotic and abiotic influences on butterfly distribution and abundance are considered, and possible future avenues of investigation discussed.

INTRODUCTION

Butterflies have an intrinsic appeal, even pest species. Historically, farmland was a rich habitat for butterflies but, following the intensification of agriculture since the late 1940's, it is now regarded as impoverished (Thomas, 1984). Farmers themselves have recognised the need to reduce the impact of farming practices on wildlife, a particularly successful example being the farmer-funded development of Conservation Headlands (Sotherton *et al.*, 1989). The change in emphasis in the management of farmland, particularly the permanent vegetation of the field margin, provides a substantial opportunity for the conservation of butterflies. This paper reviews the progress to date.

SPECIES FOUND IN FIELD MARGINS

British butterflies currently comprise sixty-one species, excluding rare migrants. Thirty-one species (51% of the British list) have been recorded from arable field margins, together with the rare migrant *Colias hyale* (Table 1). The majority of these species probably breed in field margins, with species such as *Argynnis aglaja*, *Argynnis paphia* and *Ladoga camilla* flying in from adjacent habitats to nectar or bask. Simple species lists do not, however, give any indication of the relative abundance of species, and many will be, at best, only occasional sightings (Table 1).

LARVAL HOSTS

Full details of the larval host plants of butterflies may be found in Dennis (1992), Emmett & Heath (1989) and recent work on some satyrids in Feber (1993). Marshall (1989) gives details of the flora of field margins. Not all larval hosts present in field margins will be exploited because of biotic and abiotic influences on adults such as shelter (Dover, 1990a), shade (Courtney, 1982), weather (Courtney & Duggan, 1983), micro-scale influences on oviposition cues (Dennis, 1983), size of hosts (Dennis, 1985), the propensity

for many species to lay on the outside of clumps (the 'edge-effect') (Courtney & Courtney, 1982; Dennis, 1984), and the physiological and nutritional status of the plants (Myers, 1985; Pullin, 1987). The cutting of verges can have catastrophic effects on larval survival (Courtney & Duggan, 1983), although this is most likely to be a problem in the margins of fields adjacent to roads.

TABLE 1. Butterfly species recorded in arable field margins in specific English counties, larval hostplants known to grow in field margins, probable breeding status, and relative abundance. Taken from Dover (1991), Feber (1993), Emmet & Heath (1989), Pollard *et al.* (1986)

Hesperiidae		Pieridae	
Ochlodes venata	G,Ha,Hu,Ox,*,L	*Anthocharis cardamines*	G,Ha,Hu,Ox,*,L
Thymelicus lineola	Ha,*,L	*Colias croceus*	G,Ha,*,#,I
Thymelicus sylvestris	G,Ha,Hu,Ox,*,L	*Colias hyale*	G,*,#,I
Lycaenidae		*Gonepteryx rhamni*	G,Ha,Hu,Ox,*,L
Aricia agestis	G,Ox,#,I	*Pieris brassicae*	G,Ha,Hu,Ox,*,A
Callophrys rubi	Ha,*#,I	*Pieris napi*	G,Ha,Hu,Ox,*,R
Celastrina argiolus	G,Ha,Hu,Ox,*,L	*Pieris rapae*	G,Ha,Hu,Ox,*,A
Lycaena phlaeas	G,Ha,Hu,Ox,*,L	**Satyridae**	
Polyommatus icarus	G,Ha,Hu,Ox,*,L	*Aphantopus hyperantus*	G,Ha,Hu,Ox,*,R
Quercusia quercus	G,Ha,Ox,*,#,I	*Coenonympha pamphilus*	G,Ha,Hu,Ox,*,L
Strymondia w-album	G,Ox,*,I	*Lasiommata megera*	G,Ha,Hu,*,L
Nymphalidae		*Maniola jurtina*	G,Ha,Hu,Ox,*A
Aglais urticae	G,Ha,Hu,Ox,*,A	*Melanargia galathea*	G,Ha,Ox,*,L
Argynnis aglaja	Ha,*,#,I	*Pararge aegeria*	G,Ha,Ox,*,L
Argynnis paphia	G,Ha,*,#,I	*Pyronia tithonus*	G,Ha,Hu,Ox,*,A
Inachis io	G,Ha,Hu,Ox,*,R		
Ladoga camilla	Ha,*,#,I		
Polygonia c-album	G,Ha,Hu,Ox,*,L		
Vanessa atalanta	G,Ha,Hu,Ox,*,L		
Vanessa cardui	G,Ha,Hu,Ox,*,L		

G - Gloucestershire, Ha - Hampshire, Hu - Huntingdonshire, Ox - Oxfordshire; * - hosts found in field margins; # - unlikely to be breeding in field margins; adult abundance, subjective score: I - infrequently found, L - low numbers, R - reasonable numbers, A - abundant

ADJACENT HABITATS AND GAME COVER

Field margin habitats such as hedgerows and verges are typically quite narrow and discrete entities, although they may form part of a wider hedgerow network. Other margin habitats such as woodland and railway embankments are frequently of considerably greater area. The transition between two habitat types, known as the 'ecotone' is where species characteristic of both habitats may be found. Hence, woodland specialist butterflies such as *Q. quercus*, *A. paphia* and *L. camilla* and grassland species such as *A. aglaja* and *M. galathea* are found associated with arable field margins exploiting some resources of the

ecotone, but ultimately returning to their primary habitat. The field margin ecotone may be important to habitat specialists, especially during dispersal or after failure of their principal resources.

On farms with a significant game interest some fields may have a strip of game cover between the field margin and crop. Cover crops on a north-Hampshire farm composed of *Helianthus tuberosus* (Jerusalem artichoke) and/or *Phalaris tuberosa* (canary grass) were found to be of high value for butterflies (Dover *et al.*, 1992). The cover crops studied were subject to relatively low levels of management, were in place for several years, and had been colonised by perennial and annual 'weeds' (Rew, 1988) providing both larval and adult resources.

CONSERVATION HEADLANDS AND EXTENDED FIELD BOUNDARIES

The crop margin management technique known as 'Conservation Headlands' (Sotherton *et al.*, 1989), where pesticide inputs to the outer 6m of cereal fields are prescriptively reduced and selective, has been shown to have a significant benefit for butterflies on farmland. Butterfly transects carried out over a five year period showed significantly more butterflies in field margins which had Conservation Headlands compared with crop margins sprayed according to normal farm practice (Dover, 1991). On average 68% of all butterflies seen on transects were found in Conservation Headlands. Of 57 statistical comparisons between the two experimental regimes, 45 significant differences were identified, of which only one showed significantly more butterflies in field margins sprayed according to normal farm practice (Dover, 1991).

Observations of butterflies revealed significant changes in the temporal and spatial distribution of flight, feeding, resting and interacting (mating) behaviours between field margins with Conservation or fully sprayed headlands; in the Conservation regime flight activity reduced, feeding increased as did resting and interactive behaviour. The shift in behaviour was principally due to the additional nectar resources present in Conservation Headlands and, for some pierid species, additional larval host plants (Dover, 1989a,b,1991, 1992). Nectar is a significant factor in the potential fecundity and longevity of adult butterflies (Watt *et al.*, 1974; Murphy *et al.*, 1983) and may be a limiting factor for butterflies in modern arable farmland.

Population trends of three satyrid and three pierid species on a study farm with half the cereal fields managed with Conservation Headlands were compared with regional data from the National Butterfly Monitoring Scheme (Pollard *et al.*, 1986) over a five year period. The 'open' (continual dispersal) population structure of the pierid species prevented the identification of differing population trends unlike the 'closed' (colony forming) structure of the satyrid species (*A. hyperantus*, *M. jurtina* and *P. tithonus*) which all showed increases in population trends at the study farm compared with regional data (Dover, 1991, 1992).

The impact of increasing the uncropped area of arable field margins by the inclusion of an additional 2m wide boundary strip, created by sowing with a grass and wildflower mixture or by allowing the existing seed-bank to develop (unsown), was examined by Feber (1993; this volume). The two sward types were manipulated by the use of different

cutting and hay removal regimes; additionally, some unsown plots were sprayed annually with glyphosate. This latter regime provided the poorest habitat for butterflies with fewer species and lower abundance. The sown sward performed better than the unsown sward as butterfly habitat; cutting in the summer decreased butterfly numbers compared with a spring and autumn cut, or no cut. Comparison of the expanded field margins with a nearby commercial farm with 'normal' margins showed increased abundance of butterflies at the experimental farm. Both the sown and unsown swards provided host plants for some butterfly species, but the sown sward in particular provided enhanced adult nectar resources.

Feber (1993) also compared two grass leys on wider strips (7.2 to 9.6 m) of boundary; a conventional grass/clover mix and a more diverse mix including wildflowers. More butterflies were found on the margins with the diverse sward compared with the conventional ley, and fertiliser use diminished butterfly abundance in both. Neither sward type was as attractive to butterflies as the 2m margins described above.

BUTTERFLY DISTRIBUTION BETWEEN AND WITHIN FIELD MARGINS

Dover (1990a) carried out a mark-release-recapture experiment with *A. hyperantus, P. tithonus* and *M. jurtina,* in the field margins of a 66.5ha block of arable farmland. The field margins principally consisted of hedgerows and grass verges, some with associated farm tracks, and wood-edges. Records of biotic and abiotic parameters were made in a subset of the fields under study during the years 1988 and 1989. Butterfly captures and habitat data for 30m lengths and whole field margins were analysed by stepwise multiple regression. Factors affecting the distribution of butterflies between field margins included: shelter, a small uncropped area between a narrow copse and hedgerow field boundary traversed by a farm track, and nectar sources. Within field margins, distribution was affected by the *degree* of shelter, insolation, nectar sources, farm tracks and variables reflecting different aspects of habitat quality.

BUTTERFLY MOVEMENT AND COLONY COMPACTNESS

Dover, (1990a) and Dover *et al.* (1992) showed that *A. hyperantus, P. tithonus* and *M. jurtina* were capable of moving considerable distances, in excess of 1km, between marking stations in farmland habitats, although the frequency of such movements was low. Dover (1990b) demonstrated that pierid butterflies made use of field margins as flight corridors, apparently in preference to overflying crops. This may be due to the shelter associated with hedgerows and wood-edges, and the presence of adult and juvenile resources. Males of the territorial species *A. urticae* and *I. io* use field margins as territorial habitats in order to maximise their encounters with females searching for oviposition sites along them (Baker, 1972). Dennis (1986), Dover (1991), and Munguira & Thomas (1992) noted that wind buffeting may reduce the passage of species across an unsheltered area such as a gap in a hedgerow or a road. The flight tracks of butterflies are also affected by shade, and individuals can be observed flying along the contours of the shadows cast by hedgerows and hedgerow trees (Dover, personal observation), potentially reducing the time available for oviposition and nectaring.

Movements of *A. hyperantus, P. tithonus and M. jurtina* between field margins were studied by Dover (1990a) and Dover *et al*. (1992). Plots of flights between capture points in MRR studies demonstrated substantial interchange between nearby field margins within colonies. Movement between adjacent colonies of species was evident, suggesting that satyrids exhibit a metapopulation structure on arable farmland. The area of land required to support colonies of butterflies on farmland can be quite small; Dover (1991) showed that in one colony the butterflies were utilising just 0.67ha of field margin, approximately one-third of the total field margin habitat in the study area, or just 1% of the total study area. Thomas (1984) gives details of the minimum habitat area for British species.

Many farms are traversed by road systems, which may act as bottlenecks for movement between field margins. Dennis (1986) in a study of *A. cardamines* in the Bollin valley in Cheshire showed the M56 motorway to reduce overflights by 92%. However, Munguira & Thomas (1992) recorded nineteen species crossing 'A' class roads; these were not considered to impose significant levels of mortality or to prevent butterfly dispersal, although they restricted it in some species.

SPRAY DRIFT

Dover *et al*. (1990) speculated on the impact that reducing pesticide drift into field margins would have on butterflies, either through lower juvenile mortality from compounds with insecticidal activity, or reduced herbicide damage to larval host plants and adult nectar resources. Work on pesticide drift into field margins (Cuthbertson, 1988; Cuthbertson & Jepson, 1988) showed that, during autumn spraying of cereal crops, Conservation Headlands reduced pesticide levels on hedgebank vegetation by over 50%. The presence of a mature crop during summer spraying sheltered the basal vegetation of hedgerows from spray drift, reducing the loading by 75% compared with vegetation above the crop canopy.

Cilgi & Jepson (in press) using fourth instar *P.brassicae* and *P.rapae* larvae demonstrated that exposure for two hours to 1/16th of the field dose rate of the synthetic pyrethroid deltamethrin sprayed onto leaf surfaces resulted in mortality. Further experiments exposing larvae to low dose rates over long time periods demonstrated mortality and sub-lethal effects (eg. anti-feedant response and smaller size of adult at eclosion) at concentrations down to 1/640th of the full field dose rate.

Sinha *et al*. (1990) examined the impact of eight insecticides on two-day old *P. brassicae* larvae and demonstrated a x700 difference in toxicity levels. Davis *et al*. (1991) showed that *P.brassicae* was particularly suitable as an indicator species in bioassays, being more sensitive than *P. napi, P. tithonus* and *P. icarus*. Subsequent trials with the most toxic compound diflubenzuron, at the maximum field dose rate, and *P. brassicae* demonstrated high mortality (>95%) 16 m downwind of the spray boom with a windspeed of 5.3 m/second, but even at low speeds (2.5 m/second) 24% of larvae were killed at 24 m down wind (Davies *et al*., 1991).

The host-plants of many British butterflies (Dennis, 1992; Emmet & Heath, 1989; Feber, 1993) may be subject to herbicide drift. No information is currently available on the impact of such drift on butterfly populations. Marshall & Birne (1985) in a study of

seven herbicides showed a significant impact on the graminaceous host-plants of Hesperiidae and Satyridae, and the broadleaved host-plants of the Pieridae and Nymphalidae, as well as to some adult nectar plants. Death of a host-plant requiring the larva to find a new host, or premature scenescence of a plant, or part of a plant, may be sufficient to cause larval starvation resulting in mortality or the eclosion of less-fit adults (Courtney, 1981). Marrs *et al.* (1989) recommend that buffer zones of 5-10m be left between areas of sensitive vegetation when using herbicides. Most lethal effects occur within 2.5m of the spray boom, although transient effects and flowering suppression may occur on sensitive species up to 20m away from the sprayer (Marrs *et al.* (1989)). Although plants were found to recover from such sub-lethal effects, the impact on larvae and nectivorous adults may be substantial.

DISCUSSION

Information on the ecology of butterflies on arable farmland has increased considerably since the first paper on the subject by Rands & Sotherton (1986) and approaches such as Conservation Headlands and extended field margins have clear demonstrable, benefits for butterflies. However, much information is of a preliminary nature and begs further questions. For example, is the relatively poor abundance of some lycaenid species in field margins due to pesticide and cultural effects (including fertiliser drift) on the host plants and juvenile stages, disruptive impacts on mutualistic associations with ants, or a combination of the two? Several studies have shown the importance of nectar in butterfly longevity, fecundity and microdistribution, but precisely how important is it? Is nectar a limiting factor on arable farmland and if so what is the threshold value and does it differ between butterfly species? Can annual nectar sources in Conservation Headlands fully compensate for degraded perennial nectar sources in field margins? The information available on insecticide and herbicide drift is incomplete. There appear to be substantial differences in the toxicity of the main classes of insecticide to butterflies, herbicides have sub-lethal effects on non-target plants; what are the impacts on larval survival, how do the various factors interact? Information on the use of field margins as flight corridors by butterflies is sparse, but there appears to be a huge potential for the use of this group to explore the concept in a landscape ecological approach.

Using closed population species such as the satyrids it should be possible to develop a simulation model of the impact of habitat and crop management on butterfly distribution and abundance allowing the impact of current and future management options to be explored.

ACKNOWLEDGEMENTS

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FIELD MARGINS AS HABITATS, REFUGES AND BARRIERS OF VARIABLE PERMEABILITY TO CARABIDAE

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ABSTRACT

Carabidae may be sensitive indicators of the ability of fragmented landscapes to support invertebrate wildlife. There is evidence that natural populations undergo frequent extinctions and that the rate of extinction increases in cultivated areas. Little is known however, about the effects of landscape features such as field boundaries on population persistence. Interactions between carabids and field boundaries are complex and variable across the family but there is some evidence that they delay the inter-field movement of species that overwinter in the field. A simple model, incorporating diffusion and population growth rates for Carabidae demonstrates that the environmental resistance of the habitat, which is contributed to by field boundaries, could have a significant effect on recolonisation rates of depleted habitats. The potential of Carabidae to be exploited as indicators of habitat quality for invertebrates may only be realised when some key research questions have been answered.

INTRODUCTION

Linear features in the farming landscape may provide connections between non-crop habitats and assist colonisation and movement by wildlife (although the evidence that this occurs is patchy; Hobbs, 1992). To those organisms that complete their life-cycles within agricultural fields however, associations with the linear features such as field boundaries may be far more complex: the boundary may act as a habitat, a refuge or even a barrier, effectively restructuring the population into sub-units. Habitat fragmentation by field boundaries may have a variety of consequences. Small, sub-populations may suffer an increased risk of local extinction through amplification of stochastic effects. These populations may alternatively, benefit from fragmentation because they are partially protected from the consequences of random catastrophic events by being out of synchrony with other sub-populations (Kareiva, 1991). The degree to which the structure of the farming landscape affects the density and persistence of organisms inhabiting farmland remains one of the more interesting unanswered questions of agro-ecology.

Despite their widespread distribution and abundance as members of the soil invertebrate community, populations of Carabidae (Coleoptera) are susceptible to local extinction in cultivated landscapes (den Boer, 1977; 1990a). Evidence to support this has arisen from an examination of the frequency distributions of population sizes: the form in which certain carabid species deviate from the expected

distributions in cultivated areas has been taken to indicate that small populations are being lost (den Boer, 1977). Carabidae within farmland may be more resilient than species that occupy uncultivated areas (den Boer, 1977; 1990a): recently however, cases of local extinction of species from the farmland community have been reported (e.g. Basedow, 1991; Burn, 1992). These events have been associated with intensive pesticide treatments however, the additional role that fragmentation of the agricultural landscape has played in the process of extinction is unknown.

Carabids are potential indicators of the side-effects associated with excessive pesticide use (Jepson, 1988; 1993). Their importance as ecological indicators may extend beyond this however: they may also be indicators of those levels of habitat fragmentation and types of field boundary that characterise habitats which are intrinsically less suited to support invertebrate populations in general. The first theoretical investigation to explicitly examine the importance of field boundary permeability in the local persistence of Carabidae (Sherratt and Jepson, 1993) revealed that there may be optimum field sizes, boundary permeabilities or rates of movement that maximise the chance that some species will persist in farmland with a given level of disruption by pesticides. The low reproductive rates and slow, cursorial dispersal of many Carabidae may make them good general indicators of the influence that landscape structure has upon population processes. The presence or absence of certain carabid species might be used to classify farming landscapes and patterns of land use in terms of their ability to support diverse invertebrate populations and withstand disruption by agricultural practices.

Given the increasing speculation that the fragmentation of cultivated habitats by roads, hedges and ditches has a major impact on the persistence of carabids and other invertebrates (Mader, 1990; den Boer, 1990; Sherratt and Jepson, 1993; Thomas, 1992), what evidence in support of this hypothesis can be derived from the literature?

TYPES OF CARABID INTERACTIONS WITH FIELD BOUNDARIES

It is known that some substrates and habitat types may directly impede carabid movement (den Boer, 1971; Speight and Lawton, 1976) and the rate of progress will be reduced if they cross rugged or densely vegetated terrain. Hedgerows, wooded strips and grass banks that border fields are likely to present more severe obstacles. These sub-divide the habitats of Carabidae that colonise arable cropping systems and are therefore the most commonly encountered impediments to movement. Do carabids coincide with field boundaries or complete parts of their life-cycles within them though?

There is a long history of research into the associations between Carabidae and field boundaries (Thiele, 1977). Initially, the fauna of dense, wooded strips bordering fields were investigated. These were found to contain an impoverished forest community that rarely entered agricultural crops (Tischler, 1958). Carabidae from adjoining agricultural habitats were at much lower levels of activity/density in the wooded strips. It may be inferred from data presented in Theile (1977) for example, that the activity/densities of *Pterostichus melanarius* Ill. in wooded strips was 20%

of that in the adjoining fields.

Later investigations have found a complex array of possible interactions between Carabidae and the more conventional hedgerow environment. In the spring to late summer, some of the most commonly occurring arable crop Carabidae are associated with the hedgerow, but not restricted to it (eg. *Nebria brevicollis* (F.), *Agonum dorsale* Pontoppidan): others however, only have limited associations with it (*P. melanarius, P. madidus, Harpalus rufipes* (DeGeer), *Bembidion lampros* (Herbst), *B. obtusum* Serville, *Trechus quadristriatus* (Schrank), *Loricera pilicornis* (F.) and *Notiophilus biguttatus* (F.)) (Pollard, 1968b). Pollard (1968a) concluded that the hedge or border zone impinged more upon the life-cycles of nocturnal Carabidae, active when crops are absent (eg. autumn-active *N. brevicollis*) than to diurnal species, active at the same time (eg. *B. obtusum*) or nocturnal species with a late summer peak, when crop cover was good (eg. *P. melanarius* or *H. rufipes*). This picture is complicated however by the finding that a sub-group of commoner species overwinter in the field boundary zone, penetrating the field in the spring (Greenslade, 1965; Fuchs, 1969; Sotherton, 1984). In addition, structural and vegetational properties of the field boundary are important in determining beetle composition and densities because of the narrow habitat preferences of many species (Sotherton, 1985).

With this array of possible interactions with field boundaries, it therefore seems likely that the presence of at least some boundary types might alter the rate of diffusion of Carabidae through farmland.

FIELD BOUNDARIES AS BARRIERS TO MOVEMENT

What are the consequences of the sub-division of fields by hedgerows therefore likely to be for dispersal rate? In agricultural habitats, several investigations have attempted to quantify the extent to which movement between habitats is impeded in the short-term, by features such as dirt, gravel and tarred roads, grass strips and railway tracks (Duelli, Studer, Marchand and Jakob, 1990; Mader, Schell and Kornacker, 1990). The species most commonly investigated represented the larger Carabidae such as *P. melanarius* and *H. rufipes,* rather than the complete spectrum of body sizes however, a range of permeability levels (defined as the proportion of individuals that cross the hedgerow when incident with it) can be derived from these studies (Table 1). In addition, it can be assumed that certain barriers such as irrigation ditches, rivers and canals and brick walls will have zero permeability to epigeal species.

The reduction in recolonisation and recovery rates generally caused by field boundaries will tend to extend the duration of population reductions after harmful interventions such as pesticide spraying (Jepson and Thacker, 1990). Whether or not this has positive or negative long-term implications for population persistence in an area depends upon how adverse the conditions are in the field that might be entered and upon the dispersal rate of the species in question (Sherratt and Jepson, 1993).

MEASURING INTER-FIELD DIFFUSION AND RECOLONISATION RATES

For those species that overwinter in grass banks or hedgerows, there may be a high level of exchange between neighbouring crops between seasons: the importance of the physical features of the boundary in determining the likelihood of exchanging crops is unknown for these species. Up to 50% of the population in a given field might transfer to another field as a result of the reassortment that takes place after the use of hedgerows as an overwintering refuge. There will be also however, be a reduction in the overall displacement rate of these species, because these species preferentially colonise the open field in the spring and summer. This reduction in diffusion rate may however, be ameliorated by the apparently rapid diffusion along the hedgerow/crop junction by members of the boundary-overwintering guild (Jensen, Dyring, Kristensen, Nielsen and Rasmussen, 1989).

TABLE 1. Estimated habitat boundary permeabilities to certain Carabidae, calculated from data in the literature or guessed for extreme cases.

Ref. number	Boundary Type	Percentage permeability	Carabid species
1.	10m woodland strip	20	*P.melanarius*
2.	3m dirt road	51	smaller spp.
	6m tarred road	40	"
	grass strip	141	"
3.	1.2m grass track	55	*P.melanarius* and others
	1m gravel track	15	"
	0.5m paved road	23	"
	5.7m railway embankment	9.8	"
	"	17.4	*P.melanarius*
	"	0	*N.brevicollis*
guesses	canal or irrigation ditch	0	all species?
	crop:same crop interface (strip cropping)	100	"
	overwintering boundary	50	boundary overwintering spp.

References:1 (Thiele, 1964); 2 (Duelli *et al.*, (1990);3 (Mader *et al.*, 1990). For 1-3, % permeabilities are estimated rates of entry or crossing the given boundary types for Carabidae from arable crops: see these papers for details.

For field-overwintering species, the effects of field boundaries upon movement depend upon the level of interaction with the field boundary over the insect's life-cycle

and upon the structure of the boundary itself. The level of interaction with the boundary is dependent upon prevailing environmental conditions (Fuchs, 1969), food availability (Williams, 1959) and the habitat requirements over the complete life cycles of different species. Some Carabidae seem to exploit a secondary habitat as part of their life cycle, thus *P. melanarius*, a field-active species, may enter hedgerows during hot, dry, periods (Fuchs, 1969) and may spend part of it's life-cycle in other habitats adjoining wheat crops (Wallin, 1985). This species is however preferentially associated with the centre of the crop and larvae are mostly found in this zone (Wallin and Ekbom, 1988): a distribution that may reflect avoidance of competition and facilitate early exploitation of the crop habitat each season. Use of secondary habitats, requiring field boundaries to be crossed, may only therefore be for those adults that survive the reproductive phase in the field (Lyngby and Nielsen, 1988).

To estimate the degree of inter-habitat diffusion empirically, it is not therefore sufficient to measure boundary permeability over short time-intervals as was done in the recent studies reported above. The degree of interchange must me measured over a whole generation and is likely to be a product of intrinsic phenological characteristics and behavioural responses to conditions in the field, as well as the physical permeability of the boundary itself. A simple 'permeability' term may be adequate for general models, designed to explore the possible significance of field boundaries for local population persistence in Carabidae: it will not be sufficient however for predictions that relate to individual species. This problem is considered further in Jepson (1994).

A SIMPLE MODEL OF 'ENVIRONMENTAL RESISTANCE'

A general population model for exploring the role of differing boundary permeabilities on the local population persistence of Carabidae has been developed by Sherratt and Jepson (1993). This model does not however, incorporate detailed population dynamics, phenological patterns or habitat requirements that might determine the likelihood of entering and crossing a field boundary. Some of this detail would be required if the model was to be used to generate specific predictions. At present, research into movement patterns of epigeal species over farmland is still lacking however, some general predictions of the way in which different types of field boundary might affect the displacement of Carabidae can be made by building simple mathematical models based upon the small amount of information that is available (Jepson, 1994). The example below concerns the special case of the rate at which Carabidae might enter an area from which populations have become extinct. It avoids the complexity of considering competition for food resources by colonists entering habitats that are already occupied.

On theoretical grounds, it may be argued that the rate of radial expansion of a population moving by random diffusion approaches an asymptote over long time intervals (Skellam, 1951). Andow, Kareiva, Levin and Okubo (1991) have developed a tractable test of this hypothesis for a range of invertebrates and vertebrates. The asymptotic velocity of the advancing wave-front of organisms is estimated from measurements of diffusion coefficients and intrinsic rates of population increase when resources are not limiting (hence the need to consider Carabidae entering a carabid-depleted habitat). Within certain limitations of the phenology of the population in question, the asymptotic velocity of the reinvading population front may be estimated as:

$V_F = \sqrt{4\alpha D}$ (from Andow *et al.*, 1991)............ function 1

Where V_F is velocity (distance/time), α is the intrinsic rate of population growth and D is the coefficient of diffusion.
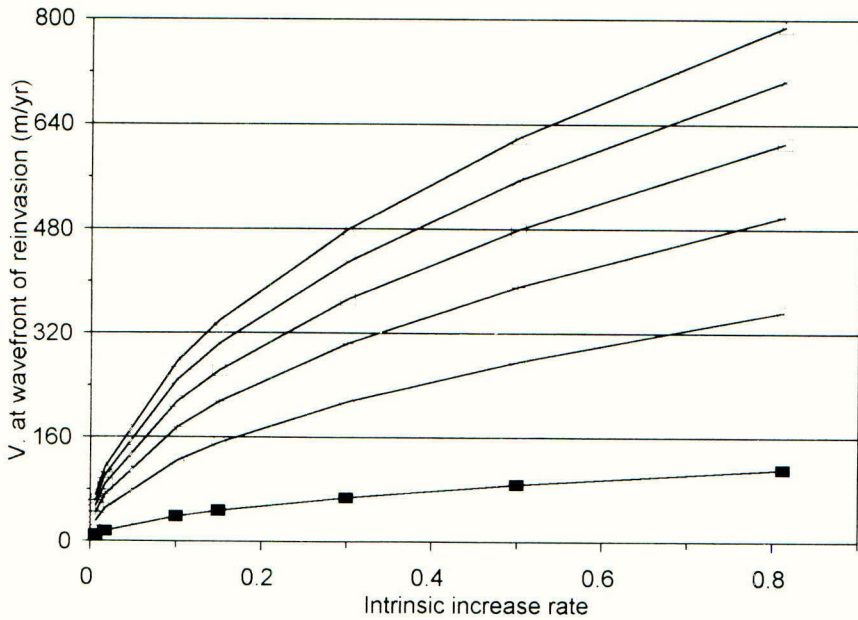

Fig. 1: Velocity of advance of the wave front of carabid colonists re-entering a system where pesticides have caused extinctions. Increase rates represent the range measured in cultivated land for 24 common species. Velocity is calculated for a range of net values of boundary permeability (see text). The upper line is for a net permeability of 100%. The other lines are 80%, 60%, 40%, 20% and 2% respectively.

Data is available to satisfy the requirements of this expression assuming that the rate of progress of the carabid population is effectively a random walk that can be predicted from the maximum daily displacement (see Jepson, 1994). Accepting these assumptions, the diffusion coefficient can then be derived from:

$$D = \frac{Ms\,(t)}{4t} \quad \text{(from Andow \emph{et al.}, 1991)} \dots\dots\dots\dots\text{function 2}$$

Where D is the coefficient of diffusion, Ms is the mean of the squared displacements and t is the number of time intervals. From the records of maximum displacement in the literature (N=8) (given in Jepson, 1994), the estimate of mean of squared displacement is 4806 and D is therefore 1202 m^2/day (function 2). Den Boer (1990b) gives mean population increase rates for established populations of 24 species of Carabidae. The range of ln (R) (where R was the total trap catch in year N+1 divided by the total catch

in year N) calculated from the mean R values for the 24 species, was 0.0065 to 0.8122. These were taken to represent the range in intrinsic increase rates attainable by carabid populations in farmland.

The effects of introducing impediments to movement such as hedgerows, may then be estimated by varying D (function 2) in proportion to the known permeability of field boundaries. This assumes, for a radially dispersing wave front, that the encounter rate with hedgerows will be the same in all directions. Figure 1 expresses the velocity of the reinvading wave front as a function of increase rates (across the full range measured by den Boer (1990b)), varying boundary permeability. Here, the measure of boundary permeability may be read as a net value, independent of the number of encounters with boundaries per annum. A value of 0.02 could be arrived at by a single encounter with a substantial obstacle or by several encounters with less severe features (eg. two encounters with boundaries of permeability 0.14 or three with a permeability of approximately 0.27). The figure may be interpreted as indicating that the rate of recolonisation of a particular habitat by Carabidae could be strongly affected by the net rate of displacement over the range of population increase rates reported in the literature. Thus, in a habitat with relatively impermeable field boundaries from which Carabidae have been rendered extinct or substantially reduced, the likelihood that a population might be reestablished will be reduced. This is discussed further in Jepson (1994) and Sherratt and Jepson (1993) however, the values given in Figure 1 represent the first estimates of the effects that field boundary permeability has on the overall scale and rate of movement by ground beetles.

AGENDA FOR RESEARCH

For an invertebrate family that is so sensitive to landscape characteristics, the potential for exploitation of Carabidae as indicators of adverse features, that might increase local extinction rates in the invertebrate fauna in general, should be explored. The ecological justification for this is that although the Carabidae are frequent colonists of disturbed land, their low reproductive rates and limited dispersal powers may make them amongst the most sensitive organisms to anthropogenic effects such as habitat fragmentation or excessive pesticide use (Jepson, 1988; Jepson, 1993). This hypothesis however needs to be tested by devising testable predictions concerning the patterns of presence and absence of Carabidae in different landscapes. These predictions would be based upon comparisons of the expected species composition in different habitats (determined largely by the physical characteristics of each habitat) with the composition predicted once anthropogenic activities have been imposed.

Several key research questions need to be answered in order to make these predictions possible:

1. Investigations are required of the components of field boundary permeability, over the life-cycles of selected species. These investigations would have to include representatives from the carabid guild that overwinters in the field boundary, as well as the guild that overwinters within the crop.

2. Mathematical models are then required to explore the consequences of differing levels of field boundary permeability for the local population persistence of carabid species, within agricultural habitats subjected to different patterns of land use (ie. differing degrees

of fragmentation, cultivation or pesticide use). These might be based upon the basic model presented by Sherratt and Jepson (1993).

3. Research is also needed to furnish predictions of the composition of the carabid community in different agricultural habitat types from the physical characteristics of that habitat. Physical factors determine the distribution and composition of carabid assemblages over long time scales (Hengeveld, 1985), over large spatial scales (Luff, Eyre and Rushton, 1989) and even within a given habitat type (Eyre, Luff and Rushton, 1990; Gardiner, 1991) and are likely to be the most important factor that underlie the distribution and abundance of different species.

4. Predictions of the likely carabid assemblages in habitats with differing degrees of fragmentation and disruption by agricultural practices could then in theory, be made. Sites could then be selected to test these predictions and investigate the degree to which species were lost in different systems. For the first time in might then be possible to properly determine the role of field boundaries on the distribution and abundance of Carabidae and also the degree to which loss of carabid species is a good general indicator for sites with depleted invertebrate faunas.

CONCLUSIONS

Most ecological research takes place on a small scale and investigates small numbers of organisms, commonly individual species. If we are to be able to understand the role that field boundaries play in the ecology of farming landscapes however, research must focus on much larger spatial scales and consider larger assemblages of organisms, even whole communities. This does not however imply vagueness or a departure from scientific rigour. Detailed mechanistic studies are needed, that permit testable predictions, supported by relevant ecological theory, to be made and to justify the assertion that some ecological processes can only be properly understood by considering this larger perspective. It has perhaps been too tempting to assume that field boundaries act as essential corridors for wildlife and that the most diverse and resilient farmland flora and fauna can only be maintained in habitats with the maximum quantity of field boundary per unit area. This assumption has ignored the possibilities that field boundaries could have negative consequences for some organisms or that qualitative characters, that determine permeability for example, might be important.

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