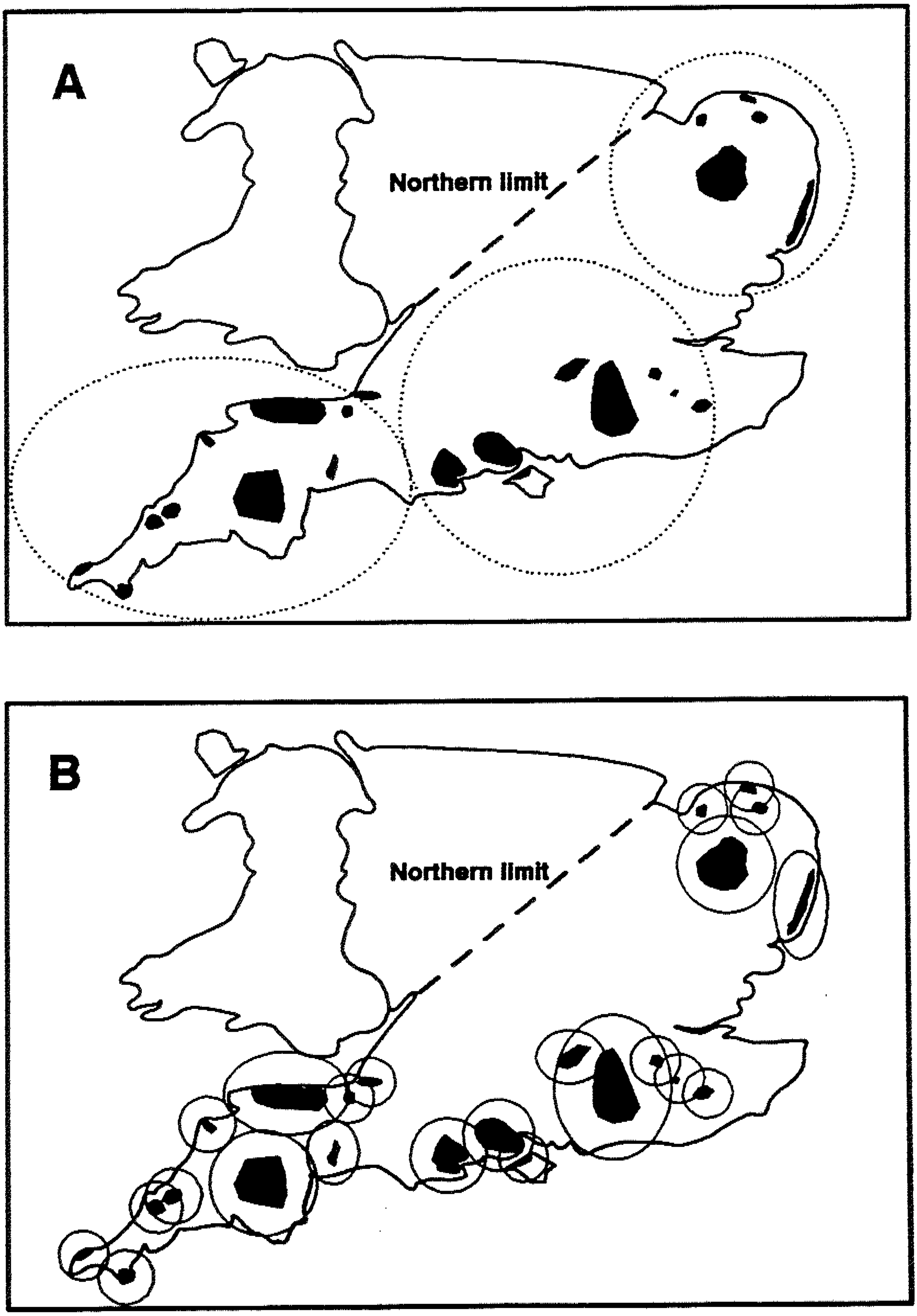
Figure 5.2 The occurrence of heather moorland in southern England.



At an even finer scale, heathland itself is heterogenous, consisting of several easily recognizable second-level biotope categories. A patch of heathland biotope often comprises a set of smaller patches (or islands) of second-level biotopes (Figure 5.4). If a species' habitat only existed within a certain second-level biotope, then the average probability of an animal leaving one of the three biotope patches and finding another, is twice that calculated for an animal leaving one of the seven habitat defined patches and finding another (Figure 5.4). We can then question whether it matters to that animal species whether the land separating habitat patches is defined by the observer as a different second-level heathland biotope or a completely different biotope, eg. farmland. The answer would be in the relative values of the 'hostility' parameter θ above.

The problem for invertebrates therefore, is one of mobility, scale (Doak *et al* 1992), colonization, and habitat definition compounded by temporal change. Apart from the spatial patchiness at any given time, variations in climate combined with natural catastrophe and vegetational successions has meant that all invertebrates have evolved to live in a temporally patchy environment.

Recently this has been confounded by the widescale interference of man, which has produced changes on a scale and at a rate probably rarely experienced in previous epochs. Take as an example the change in distribution of Dorset heathlands since 1759 (Figure 5.3B). Therefore, even in the case of species whose habitat is well defined and easily mapped it is hard to be sure whether the dispersal and other characteristics observed in current populations evolved to suit conditions before man's interference or have evolved as recent adaptations to man-made biotope.

The remainder of this section examines some empirical work on aspects of these problems and draws attention to areas that are relevant to conservationists responsible for managing populations of endangered invertebrates in a changing environment.

5.2.1 Mobility and dispersal

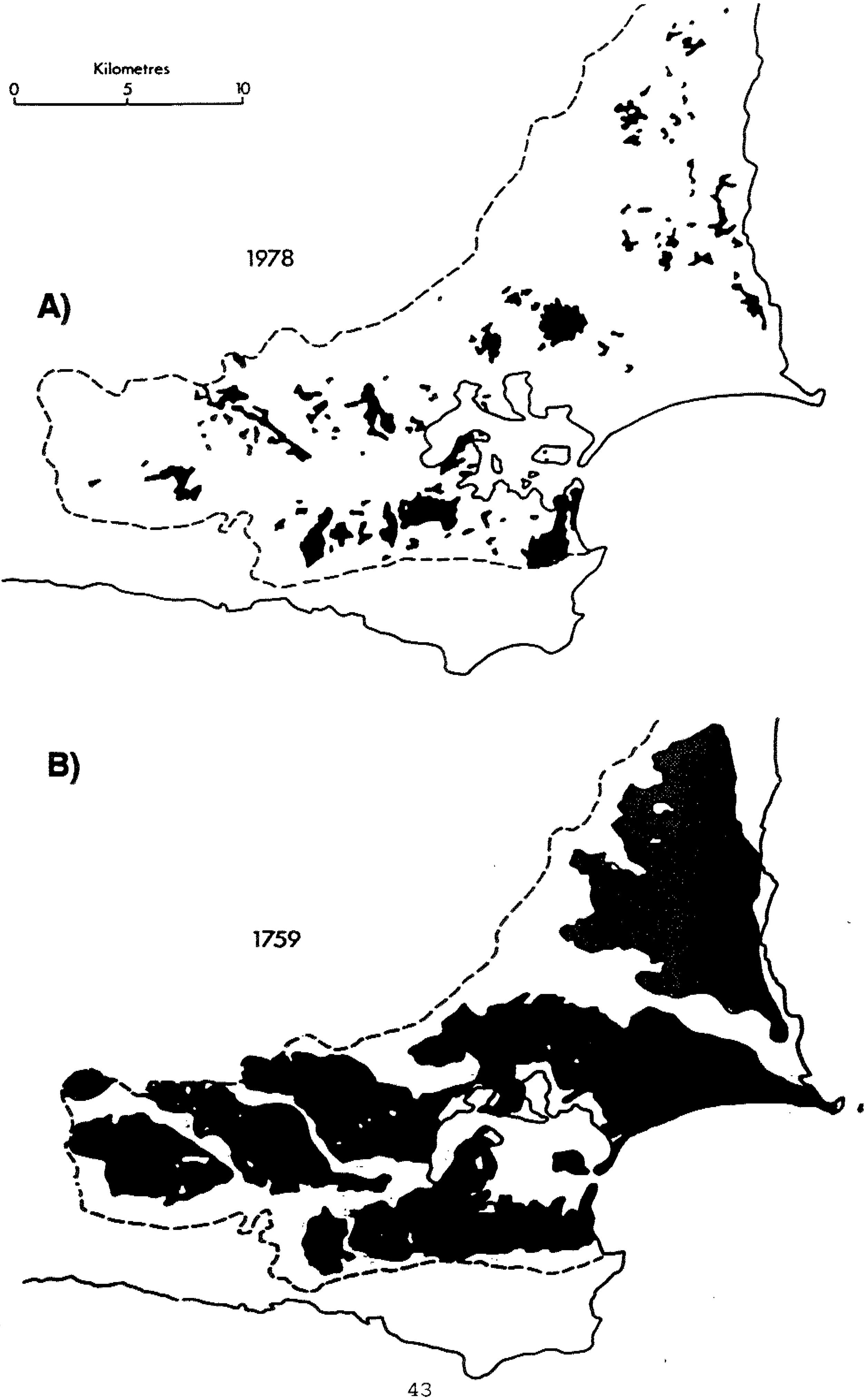
As a generalization, one can say that invertebrates are preadapted either for dispersal or for sedentary behaviour.

Consider a hypothetical insect whose entire reproductive progeny disperses (either as gravid females or parthenogenic individuals). Assuming no bias in the direction of migration, it can be calculated from Equation 5.1:

$$L \approx 0.6P * d \qquad \ldots\ldots\ldots \quad 5.2$$

If there were 3 new patches available, one 6m in diameter and 100m away, another 60m in diameter and 1km away and the third 6km in diameter and 100km away, there would be a 1 in 10 chance of finding each. An insect need only produce about 4 reproductives on average, for one to reach one of the three patches. Therefore, given no mortality factor due to distance *d*, reproductive rates need be fairly low for a population to survive as a metapopulation. However as soon as the probability of surviving the journey is considered the calculations change dramatically.

Figure 5.3 The heathlands of south Dorset.



Suppose the probability of surviving a journey of 100 m is 0.9, then 1 in 11 reach the 6m patch 100m away. The chances of surviving a 1km journey is 0.35 (0.9^{10}) so that only 1 in 30 would find the 60m patch. The chances of surviving a 10km journey are $<$ 1 in 30,000 and survival of a 100km journey is negligible ($1.8 * 10^{-46}$).

With the odds changed like this, the hypothetical species has several evolutionary alternatives. It can evolve to improve its chances of surviving a journey - if they improved one hundredfold to 0.999 the chances of surviving a distance of 100km are 0.3. It can evolve a higher reproductive rate, but because of the exponential nature of the relationship this alone cannot solve the problem of surviving long journeys (it would need to produce 300,000 individuals for one to find the patch 10km away). It could evolve abilities to search out new habitat from great distances (olfaction being the best solution), so that in the ultimate case the chances of reaching a new site are just the same as the probability of surviving the journey. Natural selection should optimize some combination of these characteristics that will depend upon the average temporal and spatial patchiness of habitat, and the innate characteristics of the animal, constrained by selection for other aspects of its life-history.

The resulting combination is unique to each species. At any scale the species is optimized either for moving between patches (dispersers) within some spatially defined cluster or for staying within patches (sedentary). Thus one species may appear sedentary at a spatial scale of $1km^2$ but be a disperser within patches of 0.1ha, whereas another that is a disperser at the 1km scale may appear sedentary at the 10km scale, which is the one normally perceived by man.

Often dispersal is at a juvenile stage, eg. many marine molluscs, spiders, sometimes adults disperse, eg. aphids, beetles and newly fecund ant queens. As a rule, good dispersers are common (often pest) species that inhabit a wide range of biotopes, often they can be classified as generalists. Dispersal may be active, usually winged flight) or passive, eg. young spiders drifting on strands of web. To a certain extent both rely upon chance factors, eg. wind direction and speed. Climate change resulting in generally warmer and more protracted summers might increase the dispersal of insects because increased ambient temperature is known to stimulate flight and movement. Increased dispersal might aid some species endangered by increased fragmentation of habitat but could endanger a more sedentary species if it stimulated greater emigration. Beetles and butterflies are probably the two insect groups for which dispersal has been most studied.

5.2.1.1 Examples from beetles

Work in The Netherlands on carabid beetles has been well documented (den Boer 1971, 1977). As expected from theoretical predictions, it was shown that carabids with high dispersal powers are good immigrants but risk local extinction. They are favoured as long as suitable habitats are amply available. Conversely, in a rapidly changing landscape, species with low dispersal powers are progressively endangered but were "good survivors" (den Boer 1985). In other words, anthropogenic and climate-induced changes should initially favour sedentary species, which after some period of change become extinct so that ultimately it is the dispersers that survive.

It is difficult to estimate actual dispersal powers. Luff (1987) estimated 5-20 m per day as the distance a walking carabid can travel. Estimates for flying beetles are best obtained from species whose range is known to be increasing. For example, *Leistus rufomarginatus*, a ground beetle of deciduous woodland that has been spreading across Europe, was first recorded in Kent in 1942. By 1992 it had reached Wales and Northeast England, a distance of 440km over 50 years. During the eight active months of those years the colonizers would have to fly an average 36m per day. It is not known whether individuals move by a series of short hops or episodic long distance flights. Similar estimates (38 m/day) can be made for *Harmonia quadripunctata* (the cream-streaked ladybird), which was first recorded in pine plantation in the East Anglian Breckland in 1937 and had reached SE Scotland by 1982. It is believed that *H. quadripunctata* arrived in Britain naturally from the continent but only became established once conifer plantations were made. In other words, its maximum dispersal flight might be in the order of 150-200 km.

Hammond (1974) cites *Aridus bifasciatus*, an Australian mould-feeding plaster beetle, which was first recorded in the UK in 1949 in London and being an active flyer, had reached Scotland by 1974. He felt that this and the previous examples indicated that the distribution of the British Coleoptera are most likely affected by human activities and that climate change would be of secondary importance.

The Great European spruce bark beetle, *Dendroctonus micans*, accidentally introduced into Wales, the West Midlands and Lancashire since 1972, was believed not to fly below temperatures of 23°C in continental Europe. However, British specimens initiate flight at 20°C and secondary flight can continue at 18°C and be sustained at temperatures as low as 14°C. It is not known whether there has been some sort of adaptation to the lower temperatures of Britain, however warmer summers should increase the dispersal abilities of this species. Climate warming would enable this species to extend its range northwestwards, where it would be a serious threat to plantations of Norway and Sitka spruce (*Picea abies* and *P. sitchensis*) and possibly also to Scots pine (*Pinus sylvestris*).

5.2.1.2 Examples from butterflies

Many butterflies migrate over vast distances, individuals travelling hundreds of miles during the coarse of a season. Other species are very restricted in local distribution and appear to be poor dispersers. Thomas *et al.* (1992) give data for the colonization pattern seen in four British species of butterflies. They measured sites where the butterflies occurred and sites which they believed contained suitable habitat and in which the butterflies did not occur.

In all four species the pattern was the same, sites that were close to an occupied site had a high probability of being occupied and the further away a site was from an occupied site the less chance it had of being occupied. The Silver studded blue (*Plebejus argus*) and the Silver-spotted skipper (*Hesperia comma*) are relatively widespread on calcareous grassland in southern Britain. In both cases, the many sites more than 1km from an occupied one had very little chance of being occupied themselves. Another grassland species, the Lulworth skipper (*Thymelicus acteon*) and the Heath fritillary (*Mellicta athalia*), a species of the earliest successional stages in coppiced woodland, both have more restricted ranges so that most potential sites were occupied, in both cases it was the furthest ones (1-10km away) that were usually empty. A slight effect of patch size, consistent with island theory was detected for *P. argus* and *H. comma*.

This distributional evidence was supported by data for *M. athalia* which showed the time taken for newly coppiced patches to be colonized. Patches within 200m of a source patch were colonized within one year while patches >500m away took 2-3 years. Similar data for a 5th species, the Black hairstreak (*Strymonidia pruni*) showed that patches of blackthorn (*Prunus spinosa*) within 500m of a source are colonized within 2-3 years whereas patches 500-1500 m from the source needed 5-15 years before successful colonization. Taken together these data give some idea of the metapopulation dynamics of butterflies with restricted mobility.

The conclusions are that very distant patches would need a very long period before they were colonized, even assuming the butterfly can travel that distance (see above). Using the *S. pruni* example, the butterflies seemed to manage a colonization event every 10 years when separated by 1km. Thus, assuming linearity a habitat patch 100km from a source might have to wait an average of 1000 years before it was colonized naturally. Anthropogenic changes will occur on a much faster time scale than this. The inference is that man may

have to assist colonizations in a rapidly changing environment to compensate for the rate of change created by himself.

5.2.2 Seeking, avoidance and barriers

5.2.2.1 Seeking

We have very little understanding of the multitude of stimuli that enhance dispersal behaviour in insects. It is very easy simply to assume it to be passive (as in the earlier calculations) but there are many examples of behaviours for seeking out habitat patches. For example *Scolytus* sp. easily find isolated elm trees. Dung beetles can be seen flying upwind towards cowpats. There are many records of sex pheromones attracting insects over great distances. Undoubtabedly many insects can detect food sources by similar means. This has the effect of increasing the effective diameter of a new habitat patch. For example, a herbivorous species might be attracted to a single plant from a distance of 100m, the plant then has an effective patch diameter of 200m rather than about 1m. An insect leaving a patch 1km away would have a probability of finding the plant equal to 1 in 8000 without attraction but a 1 in 30 chance if attracted from 100m away.

Real life examples are three species of weevil (*Cionus*) which colonized a small patch of *Scropularia* beside a garden pond, the nearest other patch being 5km away. Two species arrived seven years after the pond was planted and persisted for 6 years the other after 9 years and persisted only one year. Since extinction *C. scrophulariae* has re-colonized once more (Welch 1990).

Another example is the Knopper gall wasp *Andricus quercuscalicis* which has alternate asexual and sexual generations on alternate oak hosts. Parthogenetic females, which produce eggs of only one sex, emerging from galls on the acorns of *Quercus robur*, must find an introduced Turkey oak, *Q. cerris*, to lay their eggs in the developing catkins. The resulting males and females mate and the fertilized females must return to *Q. robur* to initiate a new cycle. The comparative rarity of *Q. cerris* in Britain indicates that the parthogenetic females must have an extremely effective means of detecting isolated Turkey oaks. Since its probable arrival during the 1950s, this gall wasp has rapidly spread throughout southern Britain.

5.2.2.2 Avoidance and barriers

It is probable that dispersing insects avoid some biotopes, particularly when actively migrating. Some butterflies will not fly long distances over water. Flying ants of *Lasius niger* and *L. alienus*, appear to avoid landing on unsuitable second-level biotope on heathlands: the former live in wet and humid heath and the latter on dry heath (Elmes *unpublished observation*), it is not certain whether the ants are detecting moisture, temperature or reflectivity of the soil surface, or are responding to some other stimuli. This is an area of study that needs further exploration.

At a finer scale, woodland, hedgerows, rivers and roads often act as barriers to insect dispersion. For example many butterflies will not fly over hedges or above woodland, while some species may find roads a barrier (Munguira & Thomas 1992). It is tempting to think of barriers as being definite obstacles to migration, but more likely they are cues which enable non-dispersing species to remain within a fairly discrete area. The role of barriers to insect dispersal is the opposite side of the coin to the concept of corridors and should be investigated in tandem.

5.2.2.3 Role of Corridors

Corridors, in the sense envisaged for some bird, mammal and aquatic species (eg. Saunders & Hobbs 1991, Hobbs 1992) probably do not exist for invertebrates. Even in the case of some adult aquatic insects that appear to fly upstream to oviposit, they are probably only returning to their original habitat, compensating for the downstream drift of the larvae. Hedgerows, may intercept migrating woodland insects, some of which may remain and breed there and even expand along them in later years, but there is little evidence that they actually follow them in the sense of using a corridor.

5.2.3 Non-dispersing species

Many rare species appear to be non-dispersers. For example, of the 196 spp of saproxylic coleoptera of pasture-woodland (Harding & Rose 1986), 68 are species known to have been found in recent times only in areas believed to be ancient woodlands (mainly pasture-woodlands such as Windsor, Sherwood Forest and Moccas Park). A large number of these appear to have virtually zero dispersal powers. A classic example is *Hypebaeus flavipes* (see Shirt 1987), which was first found in one tree at Moccas in 1934. By 1974 it was still present in the same tree and two other nearby oaks.

One idea that may explain these very restricted distributions is that many of Britain's rarer species might be using warm man-made refugia since the Holocene climatic optimum of 6000 years ago (Thomas *in press*). This idea supposes that some of the restricted rarer species of butterfly were more widely distributed and good dispersers at that time. As the climate cooled their natural habitat became restricted and, in the natural course of events, most species would have gone extinct. However, the change coincided with ancient man's agricultural expansion in northern Europe. Forest clearance and the establishment of permanent pasture created much warmer semi-natural biotopes, where the vegetation remains in an early successional stage. These acted as refugia for the species which have persisted at lower numbers than previously. The recent threat has been through man's new agriculture destroying ancient grasslands, meadows and managed woodlands. The same arguments could perhaps be applied to the rare saproxylic beetles which became restricted to pasture- woodland. Populations needed only find a new tree every few hundred years to survive while the pasture woodlands were being maintained.

In line with this idea is the evidence that dispersal ability can be readily selected against. Certainly, when habitat becomes fragmented and well separated there should be very strong selection pressure against dispersion (see above). Dempster *et al.* (1976) showed that the swallowtail (*Papilio machaon*) population at Wicken Fen had undergone changes in body size and shape, possibly as a result of increased habitat isolation about 1900. Dempster (1991) also gave evidence that as the range and potential habitat of *Maculinea arion* (Large blue butterfly) became restricted in southern Britain, selection produced races with less flight capability. Throughout northern Europe *M. arion* appears to be a poor disperser, yet the alpine race, which is found on large continuous areas of alpine meadow, lives at low densities and ranges over a large area.

Recent work in Italy has shown that an orthopteran species, *Conocephalus discolor* (the Long-winged cone-head) normally has long wings, but in hot summers, it produces extra macropterous individuals with better developed flight muscles and flies more actively (cf. Section 6.7 below). Therefore for many thermophilous species warming might actually increase both the potential habitat and the ability of a species to find it. For example, both the Short-winged cone-head (*C. dorsalis*) and Roesel's Bush cricket (*Metrioptera roeselii*) have significantly expanded their range in southern England during recent hot summers and moved into new habitat (eg. set aside farm land).

5.2.3.1 Conservation priority

Most of the rarer invertebrate species are poor dispersers whose range might be known precisely but whose specific habitat or niche may be poorly understood. For example the British Large blue (*M. arion*) was known to use both *Thymus* and red ant species during its life cycle. Until it was understood that the red ant had to be a specific *Myrmica* species, rather than any red ant all conservation attempts failed (Thomas 1980).

Any future climate change producing overall warming, should in theory benefit many invertebrate species (with the exception of a limited number of montane species restricted to the west and north of Britain; see Chapter 6 below). The problem for conservationists will be that without some knowledge of their basic niche requirements, mobility and the potential for rapid selection for greater mobility, it will be very difficult to formulate management plans for protected populations.

Even if new habitat becomes available, it may be that the present species may be unable to find the habitat without active assistance (ie. introductions). If relict habitat is lost faster than new habitat is created then, even if a species has a potential to evolve greater dispersal powers, this might not happen fast enough to cope with the changing situation.

If the need for active participation in the management of the effect of climate change on rare invertebrates is accepted in Britain, conservationists will have to face a further challenge.

This is to protect similarly endangered species in continental Europe that are not present in Britain at this time. Without the influence of man, and the hypothesized selection for restricted mobility, a general northwards shift of climate should result in some of these species reaching Britain and occupying the vacated niches of our species that will have shifted northwards. Conservation policies in Britain will have given us many nature reserves where, under a warmer climate, continental species threatened on a global scale (eg *Maculinea alcon*) could thrive. The dilemma for conservationists and managers will be to decide to what extent Britain should meet international obligations by introducing such species into potential sites.

5.2.3.2 Need for research on non-mobile invertebrates

In order to evaluate the potential demands for intervention further work should be done to assess British and potential European colonizers in terms of the population regulating factors briefly outlined in this report. Initially this should be an "in depth" desk study which should research and review published information on this problem which should include consideration of the following:

1) Isolating factors in metapopulations, ie are individuals better dispersers in populations with "kinder" biotope between patches compared to similar populations with "harsher" intervening biotopes. Does this affect the dynamics and viability of populations?

2) The coincidence of biotope and habitat patches. Work being done by NR Webb's group (ITE Furzebrook) on habitat patches within heathland biotope could be supported. Similar examples can be found from grassland, particularly chalk grassland. Questions would involve: how important is the dynamics of patches? are populations with stable habitat patches more robust against extinction than populations with dynamic habitat patch within biotope. Does biotope patch size matter?

3) How can we extrapolate from these rather easily defined (and mapped biotopes) to more fragmented biotopes that are less easily defined. Can simply working at the biotope level be of any use to making predictions about rare species, living in these biotopes, whose habitat is not well known?

4) How adaptable is invertebrate dispersal? Could rare butterflies evolve greater dispersal abilities if more habitat became available? Is poor dispersal a cause of rarity or is it a means by which threatened species have been able to persist in diminishing habitat?

5) Is dispersal part of a fractal concept of space and time? For example, do populations of soil mites show the same sort of dispersal and metapopulation structures as butterflies (the difference being one of scale)? In other words would a mite with a specific niche requirement for reproduction (eg. *Steganacarus magnus* which breeds in fircones in pinewoods) take as long to colonize a new patch of forest floor 100m from a source population, as *S. pruni* takes to colonize a new patch of blackthorn 1.5 km away?

5.2.4 Conclusions

1. The concept of corridors as conduits to dispersal have little relevance to the dynamics of most invertebrate populations.

2. There is a confusion between biotope with habitat that colours thinking. For most invertebrate species the two are not synonymous.

3. For those species where habitat is well known, and can be defined and mapped precisely, concepts of island biogeography can be applied directly to islands of habitat (eg stepping stones, patch size, distance).

4. When the habitat of enough invertebrates is sufficiently well known, it will probably be shown that most exist as local metapopulations. The relevant theory can then be applied to those populations.

5. In cases where the biotope normally associated with a particular species can be defined, but the habitat of the species is known imprecisely, metapopulation theory becomes less relevant.

6. Patchy habitat selects either for dispersal or for sedentary behaviour and their associated secondary characteristics. Most

rare species either are intrinsically poor dispersers or have recently undergone selection against dispersal as a response to man's activities.

7. Dispersal, colonization time and population persistence time may all be related to the spatial perception of individual species. We need to investigate whether ecological theory can be applied at all spatial scales Further investigation is needed to quantify and compare the isolation of patches of habitat separated by "seas" of non-habitat of varying threat to an individual trying to cross it.

5.3 METAPOPULATION DYNAMICS THEORY AND PLANTS

5.3.1 Dispersal strategies

Animals, of course, are not only mobile but have some choice of where they colonize and settle. Plants on the other hand neither move nor consciously choose where they settle, but are moved by processes such as herbivore feeding, attachment to animals, and transport by wind and water (Welch, Miller & Legg 1990). Plant species have "chosen" the dispersal strategy which optimizes their chances of landing in a colonizable site through the process of evolution (Brown 1951, Southwood 1962, Venable & Brown 1988). The dispersal strategies of most of the native plant species of the British Isles evolved in a landscape which was completely different to the one we see today. For many species the landscape has become more fragmented, with habitable sites becoming further apart. Species' dispersal capabilities are likely to change so slowly that they face extinction before they are likely to be rescued by this factor (den Boer 1977).

If we consider the present distribution of British native plants it is, as Harper 1980 indicated, ".. not unreasonable to suppose that habitable sites are present within Britain in a particular vice-county or 10km square, suitable for occupation by many of the species listed in The Red Data Book but that seed dispersal fails too reach them." Species will become threatened if the colonization of new sites falls below the rate at which populations on existing sites die.

5.3.2 Can plants use corridors?

It is unclear whether wind-dispersed plant species and plant species that typically reproduce only vegetatively would benefit from a habitat corridor (but see section 4.4). Imagine two woods, A and B, connected by a corridor which we will assume is a habitable site. A woodland species eg. wood anemone (*Anemone nemorosa*) would take many years to creep along the corridor from woodland A to woodland B for example. Most woodland species are poorly dispersed and the chance of a seed dispersing direct from woodland A to woodland B is minimal. If we assume seeds do disperse from woodland A, the random nature of the angle of dispersal suggests that only a very small proportion will disperse in a direction along the corridor towards woodland B. (for a more detailed discussion see section 5.2). This also implies it would take many years for a species to reach woodland B along the corridor. Some species like oxlip (*Primula elatior*) almost never move out of woods into hedges and would generally fail to get from woodland A to woodland B along a hedge-like corridor (Verkaar 1990).

Corridors do provide habitable sites for species of plants but often the corridor itself provides a large proportion of the habitat available to the species. Railway lines, roadside verges and tracks account for a large proportion of the habitat for species occupying open bare ground eg. Oxford ragwort (*Senecio squalidus*) and bearded fescue (*Vulpia ciliata* ssp. *ambigua*). Roadside verges and railway embankments also provide grassland corridors, if they are cut regularly, for species such as cowslip (*Primula veris*) and primrose (*P.vulgaris*).

5.3.3 Generic metapopulation models

To make accurate predictions of how metapopulations of different species will behave we need detailed autecological studies of the species to determine the dispersal rates of the species in space and time (seed banks). Gaining this information for all the British flora would be a daunting task and making metapopulation models for them is even more daunting. To make the task easier metapopulation models could be envisaged for groups of species with certain characteristics. Such generic models have been produced by Hanski (1991). He distinguishes between four kinds of species with respect to their local abundance (N) and the fraction of occupied habitable sites (p). There are **core species** with large values of N and p, **satellite species** with small N and small p, **rural species** with small N but large p, and **urban species** with large N and small p.

According to Hanski's model each of the four categories should have certain characteristics. Core species should have a high local growth rate, eg. vegetative growth and good dispersal capabilities. Satellite species should have low local growth rate and poor dispersal capabilities. Rural species should have a low growth rate and low ratio of extinction to colonization, whilst urban species should have the opposite attributes. Increasing the mortality rate of seeds may turn a core species into a satellite species.

These ideas have been applied by Söderstrom (1989) to a study of the occurrence of epixylic bryophyte species in late successional stands of spruce. Local abundance was estimated as percentage cover on available logs in occupied forest stands. Söderström identified three urban species (large N small p) all of which had high local growth rate and low dispersal rate. There were seven core species (large N and p) which had high local growth rate and high dispersal rate. The seven satellite species (small N and p) had a high dispersal rate but because they did not spread through vegetative growth probably had a low local growth rate. The only rural species (small N large p) had intermediate dispersal and growth rates.

The model of Hanski (1991) with future development could enable us to classify species as core, satellite, urban and rural and thus allow us to predict which would be most affected by fragmentation of the habitat (satellites and to a lesser extent urban species) and which core species would become satellite species.

5.3.4 Conclusions

1. The distance between habitable sites and their size are vital in determining the distribution of species.

2. The idea that habitat corridors aid plant dispersal is not necessarily valid.

3. We need considerably more information on the population dynamics and dispersal capabilities of plant species in order to determine their likely response to climate change.

6 THE STATUS OF SPECIES AND BIOTOPES IN RELATION TO DISPERSAL ALONG CORRIDORS AND IN PATCHY HABITATS

B C Eversham, A Buse, H R Arnold & M G Telfer

6 THE STATUS OF SPECIES AND BIOTOPES IN RELATION TO DISPERSAL ALONG CORRIDORS AND IN PATCHY HABITATS

6.1.1 The Biological Records Centre

The computer database held by the Biological Records Centre (BRC) now contains over 6 million records of some 10,000 species. It currently forms a focus for a wide-ranging research programme on such themes as biodiversity hotspots, patterns of rarity, and the effects of land-use and climate change, in addition to fundamental biogeographic studies and the production of national species atlases (Eversham *et al.* 1993).

6.1.2 Biological Records Centre data for conservation planning

With access to these data BRC is able to quantify the present status and recent declines of individual species, thereby establishing the importance of corridors and habitat-patches for species dispersal under changed climate. In particular the Biotope Occupancy Database (BOD) highlights those biotopes containing greatest numbers of threatened or declining species. Using coincidence mapping for suites of characteristic species, the current extent of each major biotope can be measured. The presence of uncommon and stenotopic species is an important criterion for conservation evaluation (Usher 1986), so a species-based technique such as coincidence-mapping has added value because it provides a 'bioassay' which integrates elements of habitat quality as well as reflecting simple areal extent. Using historical data on species distribution, it has proven possible to quantify the relative decline of each major biotope in each region. For a few species which are known to be expanding their range rapidly at present, it may be possible to examine the mode of expansion, from which some empirical data on the role of corridors and stepping-stones may be derived.

This section of the report thus addresses the following:-

- Species status, past decline and future vulnerability
- Biotope occupancy of threatened species
- Current extent of major biotopes
- Declines in major biotopes
- Mode of expansion of currently-spreading species.

As well as providing a broad picture of past changes for all biotopes, one example is examined in more detail. The mountain-top grassland and snow-patch biotope has been chosen for this, because it is among the most seriously threatened by climate change.

To screen every rare or threatened species for its response to climate change and its potential use of corridors and habitat patches in dispersal would be a major undertaking. Hence, other techniques are described, and a small number of worked examples is provided to illustrate what would be possible. In particular, the criteria for selecting species for future research are examined.

6.1.3 Choice of groups for analysis

Not all taxa are equally useful when considering climate change impacts and corridor dispersal. Some taxa are so poorly known that they can provide little insight into past and current landscape patterns; and conversely, such taxa are very difficult to characterize in order to plan for their conservation. A range of the better-known animal and plant groups has been selected for this study. Each group meets the following criteria:-

- A published Red Data Book or equivalent list giving definitive categories of threat;
- A broad range of ecological and habitat requirements;
- A range of dispersal and mobility characteristics;
- Wide geographic distributions;
- Adequate data on current distribution in the national biogeographic data bank;
- Adequate biological information accessible in the literature and through contact with specialists;
- A reasonable level of public awareness or interest.

After considering a wider range, the following groups were chosen:
Vascular plants
Non-marine molluscs
Millipedes
Centipedes
Dragonflies (Odonata)
Orthoptera
Butterflies
Macro-moths
Woodlice
Amphibians
Reptiles
Mammals.

This study covers only England, Scotland and Wales, with an emphasis on England.

6.2 SPECIES STATUS AND DECLINE

6.2.1 Conservation status

The conservation status of the most threatened British species of plants and animals has been assessed by the authors of Red Data Books (RDBs), in which information on those species believed to be in danger of extinction in Britain is compiled. Four British Red Data Books have been published to date, covering vascular plants (Perring & Farrell 1977, 1983), insects (Shirt 1987), other invertebrates (Bratton 1991) and birds (Batten *et al.* 1990). Information on other groups can be obtained from other publications (Anon 1989a, b; Harris & Jefferies 1991).

The groups listed in 6.1.3 contain a total of 508 Red Data Book species. Each species is rated according to the following categories:

RDB 1 Endangered
RDB 2 Vulnerable
RDB 3 Rare
RDB 4 Out of Danger
RDB 5 Endemic

RDB App.	Formerly native, but believed to have become extinct before 1900
RDB K	Insufficiently known - believed to fall into one of RDB categories 1-3.

The number of species in each taxonomic group in each category is summarized in Table 6.1.

Table 6.1 Numbers of Red Data Book (RDB) species in each taxonomic group, with their RDB status categories. Status categories are 1 Endangered, 2 Vulnerable, 3 Rare, 4 Out of danger, 5 Endemic, App. Extinct, K Insufficiently known, X Not yet assigned.

	Status Category								
Group	1	2	3	4	5	App	K	X	Total
Ferns	3	2	3						8
Flowering plants	66	91	148						305
Non-marine molluscs	10	7	11				1		29
Millipedes							2		2
Centipedes							3		3
Odonata	4	2	3						9
Orthoptera	3	2	1						6
Butterflies	2	3	2	2	2	3			14
Macromoths	21	12	53			13			99
Micromoths	4	7							11
Woodlice	1					1		2	4
Amphibians								1	1
Reptiles							2	2	4
Bats	3	10	2						15
Rodents	1							1	2
Carnivores		1							1
Total	116	139	223	2	2	17	8	6	513

6.2.2 Quantification of decline

The records held by BRC extend back to 1850, or earlier, for most of the groups chosen. There is sufficient information to provide a pre-1900 baseline dateclass for most groups. Dividing 20th-century records into four date periods (1900-1940, 1941-1960, 1961-1975, post-1975) gives a five-point framework within which to assess species status. In each of the five dateclasses the ratio of records for each species to the total number of records for its taxonomic group has been computed to provide a comparative measure of status. By taking the ratio rather than the absolute number of occurrences, the influence of geographical and temporal variation in recorder effort has been minimized (Eversham *et al.* 1993, Preston & Eversham in preparation).

To reduce the effects of recorder bias, the recorded area of occupancy (Gaston 1991) of each species in each dateclass has been calculated, rather than the number of records in the database. The area of occupancy is defined as the number of 10 km squares of the Ordnance Survey national grid in which the species is recorded in a specified dateclass.

Linear regression can be used to provide a simple index of change in species status. A strongly negative correlation coefficient indicates a severe decline, and a positive correlation coefficient suggests that the species has increased.

Overall changes cannot easily be detected without quantitative monitoring, eg. the Butterfly Monitoring Scheme (Pollard *et al.* 1986). Nevertheless careful analyses of semi-quantitative historical data can sometimes reveal trends in suites of species, eg. the levels of weed seeds in cereal crops (Firbank 1988; Wilson 1992). Also trends in common species may be apparent for a few well-recorded sites, eg. the flora of Upper Teesdale (Bradshaw 1978; Bradshaw & Doody 1978). For individual species, a resurvey of historical sites may quantify the degree of decline more precisely (eg. Moore 1980 for the damselfly *Lestes dryas*). With some species, estimates of population changes with time are possible (eg. Jefferies 1989 for the otter *Lutra lutra*).

The analysis using five dateclasses could not be applied to non-marine molluscs or macro-moths since the BRC database does not yet contain precisely dated records. A simpler, two-dateclass analysis was used calculating the proportions of records of each species in both dateclasses as before. A test statistic comparing two independent population proportions (Z_t) (Cox 1987) was calculated using the pre- and post-date proportions. The cut-off dates used for the two dateclasses were dictated for each group by the available data: pre- and post-1960 was used for macro-moths and 1950 for molluscs.

The two-dateclass method has been used in part of the calculation of a 'threat number' in the vascular plant Red Data Book (Perring & Farrell 1983). An elaboration was devised for water beetles (Foster 1983) using an 'index of continuity' and an 'index of decline'. More precise analyses of long-term trends of Dutch insects, with up to 11 decade dateclasses, have been carried out for selected Carabid beetles (Turin & den Boer 1988; Aukema 1990) and for Odonata (Geijskes & van Tol 1983). However none of these previous analyses have considered such a large number of species or such a wide range of groups as the present study.

As an example of the use of this technique, Table 6.2 shows the decline statistics for the resident butterfly species. For most of these, the decline measured by proportion of records is in agreement with the published histories of the distributions (Heath *et al.* 1984).

6.2.3 Vulnerability of rare species to direct climate change effects

Each species under consideration has been recorded from the 10 km squares in Britain. Its areal extent or range envelope (Gaston 1991)

Table 6.2 Decline statistics for the resident butterfly species

Species	Gradient	Species	Gradient
Small tortoiseshell	1.098***	Mazarine blue	-0.135**
Meadow brown	0.973***	White-letter hairstreak	-0.139
Large white	0.906***	White admiral	-0.144
Small heath	0.893***	Silver-spotted skipper	-0.160*
Green-veined white	0.842***	Northern brown argus	-0.164
Small copper	0.753***	Comma	-0.164
Common blue	0.546***	Green hairstreak	-0.165
Small white	0.521***	Heath fritillary	-0.195
Orange tip	0.495	Chalkhill blue	-0.197
Wall brown	0.424	Dingy skipper	-0.214
Peacock	0.394	Brown hairstreak	-0.217
Gatekeeper	0.337	Brown argus	-0.226
Small skipper	0.307	Smll pearl-bordered fr.	-0.232
Large skipper	0.307***	Purple hairstreak	-0.235
Ringlet	0.215	Black-veined white	-0.258**
Brimstone	0.153	Grizzled skipper	-0.263
Speckled wood	0.107	Swallowtail	-0.273
Essex skipper	0.072	Duke of Burgundy fr.	-0.281
Scotch argus	-0.004	Marbled white	-0.285
Mountain ringlet	-0.009	Dark green fr.	-0.298
Silver-studded blue	-0.014*	Grayling	-0.350
Black hairstreak	-0.021	Purple emperor	-0.395
Large copper	-0.031**	Small blue	-0.405
Holly blue	-0.035	Silver-washed fr.	-0.435
Glanville fritillary	-0.039	Pearl-bordered fr.	-0.442
Lulworth skipper	-0.059	High brown fr.	-0.457
Chequered skipper	-0.084*	Wood white	-0.485
Large heath	-0.112	Marsh fr.	-0.520
Large blue	-0.117**	Large tortoiseshell	-0.711
Adonis blue	-0.126		

*** these species were under-represented in the earlier dateclasses which may increase their gradient values.

** species became extinct in the nineteenth century.

* these species have been the subject of intensive surveys in recent years, possibly masking their decline.

Note 'Gradient' refers to that of the regression line of relative frequency against time is a measure of changing status.

can be represented by a convex polygon connecting the outermost record points (Rapoport 1982). It is assumed that this range is determined by tolerance of prevailing climatic conditions. This has been discussed by palaeoecologists interpreting post-glacial range changes (Atkinson *et al.* 1986, 1987). Red Data Book species are restricted to a small number of rather special sites or regions. It is assumed that the ability and/or opportunity for extension of range under current conditions is negligible. Given these assumptions, the question 'How vulnerable is a species to climate change?' can be more precisely stated as 'What percentage of a species' range will remain occupiable after climate change?'.

A species occurring in at least one of the climatically extreme 20% of British squares was assumed not to suffer by an extension of the British climate beyond that extreme, eg. species occurring in the driest fifth of Britain are assumed to be unaffected by decreased mean annual rainfall (scenario 1 in Table 6.3) and their ranges remain 100% occupied. These taxa, which are mostly clustered around the south and east coast of England, are prime candidates for potential range extension under climate warming.

The climate range represented by currently-occupied squares was calculated for each species, in terms of the three key climate measures, mean annual rainfall, mean annual temperature, and 'continentality' (Table 6.3). The percentage of squares which would remain within the range of each climate measure under changed climate was then calculated for each of the 3 climate measures under the 5 scenarios.

Table 6.3 Climate change scenarios

	Change in:-		
Scenario	Mean annual rainfall (mm)	Continentality (°C)	Mean temperature (°C)
1. Hot & dry	-100	0	+2.0
2. Warm wet summers	0	+1	+0.5
3. Wet milder winters	+200	-1	+0.5
4. Dry summers, wet winters	+200	0	+1.0
5. Hot dry summers, cold wet winters	0	+3	+0.5

Note Continentality is difference between mean daily temperature figures for July maxima and January minima.

The impact of climate change on each species is represented by three 'occupiability percentages' (the percentage of the current area of occupancy which would remain within the species' range) for each scenario. The interrelationships between change in mean annual rainfall, change in mean temperature and change in continentality, and their combined effect upon each species are unknown, precluding the calculation of a 'mean' occupiability percentage. However, in order to present the climate change impact data more concisely, the 'worst case' occupiability percentage (the lowest of the three figures) was taken for each species under each scenario.

Further, an overall vulnerability to the direct effects of climate change in the broad sense can be calculated as the mean of the five worst case occupiability percentages for each species. The occupiability percentage is a measure *only* of the *detrimental* effect on the species, and the overall vulnerability represents an estimate of the average *attrition* of a species range as a result of climate change effects. Separate analyses would be needed for each scenario if an attempt were made to predict positive responses by threatened species. As an example, Table 6.4 shows the vulnerability statistics for a selection of Lepidoptera. Species expected to become more abundant and/or increase in geographic range are those for which corridor dispersal and stepping stones have most to offer.

6.2.4 Vulnerability of rare species to inundation by sea water

The best estimate of global sea level rise is about 20 cm by the year 2030 and 30 cm by 2050. This estimate must be adjusted for ongoing vertical land movements in specific coastal localities (UK Climate Change Impacts Review Group 1991).

Altitude data are available from a dataset containing point heights for each 2 km square (tetrad), from which a mean altitude above Ordnance Datum (a.O.D.) was calculated for each 10 km square of the national grid (Figure 6.1). For each species, the percentage of its area of occupancy (*sensu* Gaston 1991) lying in squares of mean altitude less than 5 m, and those between 5 m and 10 m, were calculated. Many RDB species occur in a few sites within this area, but most have other, more secure sites elsewhere.

Those species considered to be most at risk are listed in Table 6.5. Many of those species are unlikely to be directly at risk from the small rise in mean sea level; the major threat derives from the combination of rising sea level and any possible increase in the frequency of extreme storm events breaching coastal defences. In many cases, species vulnerability will be a function of the resources allocated to improving coastal defences. Conversely, some species associated with particular types of soft coastline, eg. saltmarsh, may be vulnerable to sea-defence engineering.

6.3 BIOTOPE OCCUPANCY OF RED DATA BOOK SPECIES

6.3.1 The Biotope Occupancy Database

The Biotope Occupancy Database (BOD) has been derived from an extensive literature search, and consultation with a wide range of specialists in the different groups of plants and animals being considered (Eversham *et al.* 1993). All major biotopes (habitats and land-management classes) are listed. Rare and specialized species may occupy a single biotope, whereas more widespread or eurytopic species may occur in five or more.