ENVIRONMENTAL CHANGE AND THE DISTRIBUTIONS OF BRITISH BUMBLE BEES (*BOMBUS* LATR.)

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Introduction

Some species of organisms are considerably more widespread than others. Bumble bees are no exception, and differences between the distributions of the various species found in Britain have often been noted by natural historians. My own collecting trips have yielded six or seven species common to most of the localities I visited, while I found other species only in the far south of the country or only in the west and north.

Several authors[1,3,11,23,24] have reported the belief that bumble bee populations have been declining in recent years. Now that IBRA's Bumble Bee Distribution Maps Scheme has collected past (i.e. pre-1960) and more recent (1960-1976) records from throughout the British Isles[2], it is possible to examine further evidence for this trend.

Ecology has been described as the study of the interactions governing the distribution and abundance of organisms[4]. Hence, not only are the factors that influence the changing distributions of bumble bees of practical importance to pollination and conservation, but the mechanisms through which they act are of central theoretical concern in ecology. The aims of this article are to summarise general patterns of distribution, to discern the most likely factors affecting these patterns and to describe briefly a mechanism through which they may act. Any changes in distribution patterns with time are especially fortunate because they make it easier to eliminate the uncorrelated factors among those suggested as having an influence on bumble bee distributions.

Distribution patterns of bumble bees

Regional patterns

When bumble bees are classified by their regional distributions within Britain[44], the three major groups of species obtained resemble those from analyses of the distributions of bumble bee species in other parts of northern Europe[21, 28]. These groups are the 'Mainland' Species, the 'Southern' Species and the 'Widespread' Species.

The Mainland Species are composed of *Bombus hortorum* (L.), *B. ruderarius* (Müller), *B. pascuorum* (Scop.), *B. pratorum* (L.), *B. terrestris* (L) [=*B. lucorum* (L.)], *B. audax* (Harris) [=*B. terrestris* of earlier authors], and *B. lapidarius* (L.). These species are not generally at the limits of their potential latitudinal distributions within Britain.

The Southern Species, composed of *B. ruderatus* (F.), *B. muscorum* (L.) [=*B. humilis* Ill.], *B. sylvarum* (L.), and *B. subterraneus* (L.), reach their northern limits within Britain (Fig. 1, 2) and southern Scandinavia.

The Widespread Species, *B. laevis* Vogt [=*B. muscorum* of earlier authors], *B. soroeensis* (F.), *B. jonellus* (Kirby), and *B. monticola* Smith, are most strongly represented within Britain in the north and west (Fig. 2) and represent a subarctic element which is strongly represented in the north of Scandinavia. They are also present further south in Europe but mainly in the uplands and especially in the Alps.

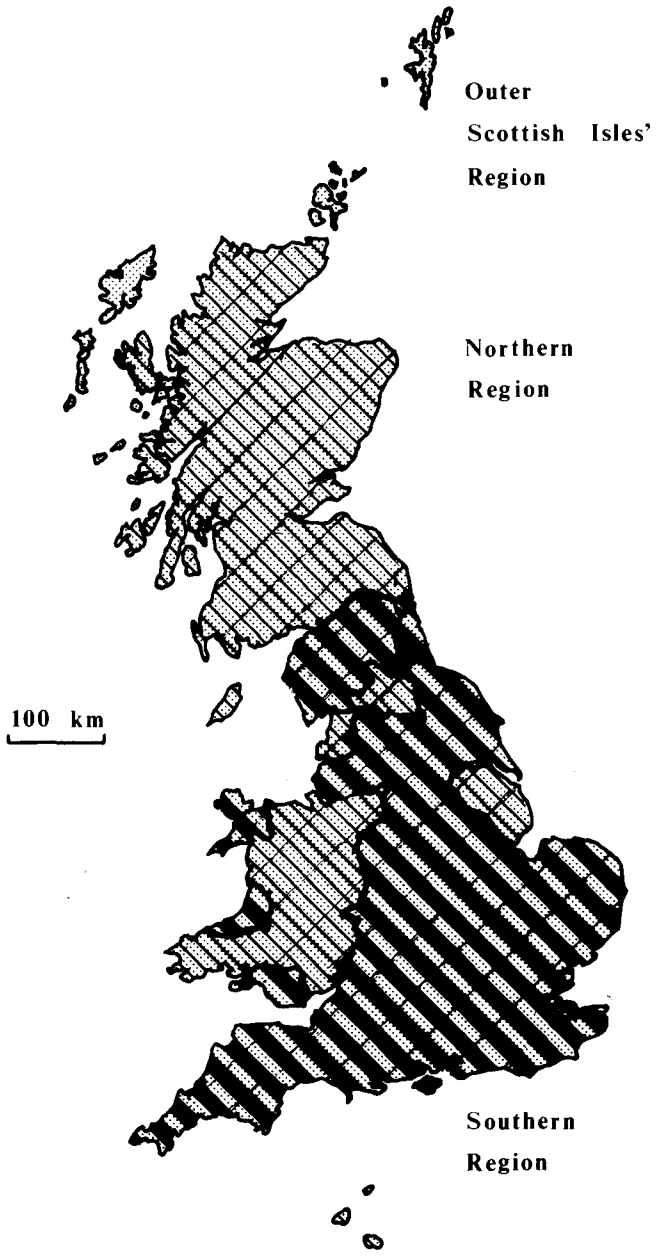

FIG. 1. Map of England, Wales and Scotland showing the pre-1960 biogeographic regions defined for their similar bumble bee faunas (based on pooled data for vice-counties[44]). Dots represent the Widespread Local Species; narrow lines the Mainland Ubiquitous Species; broad stripes the Southern Local Species.

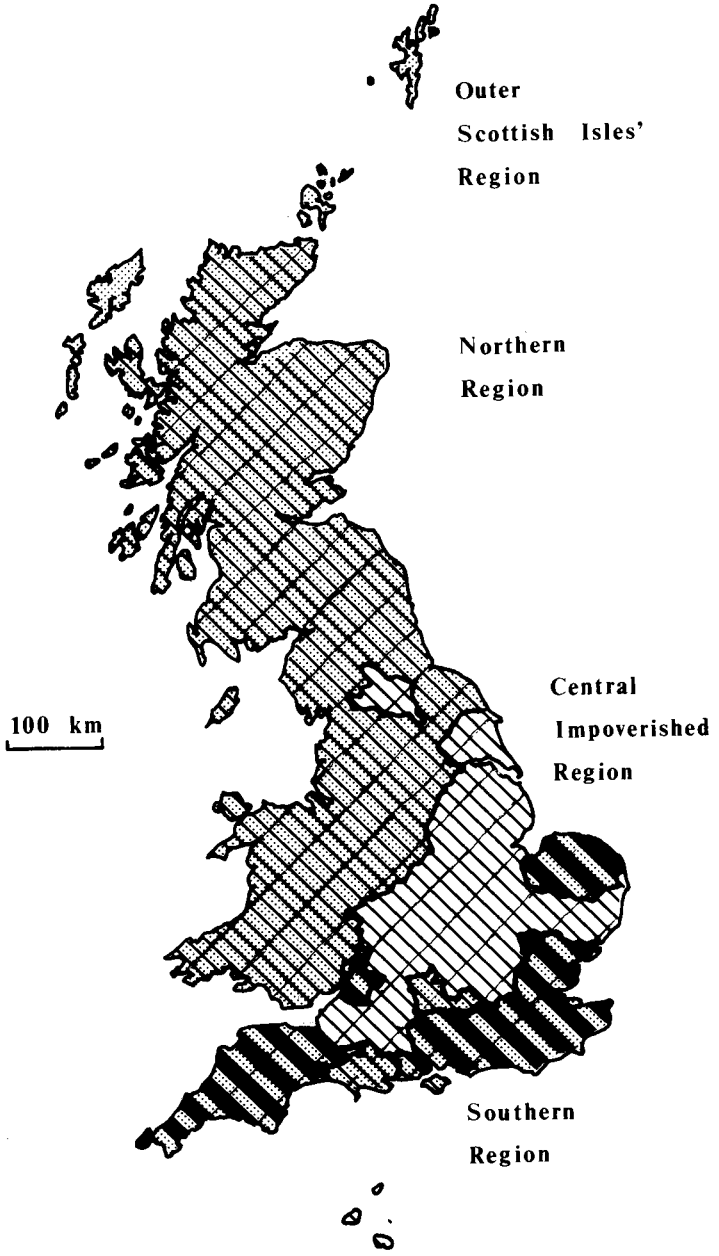

FIG. 2. Map of England, Wales and Scotland illustrating the post-1960 biogeographic regions defined for their similar bumble bee faunas (based on '1960 onwards' data for vice-counties[44]). Symbols as for Fig. 1..

Local patterns

In Britain, only the Southern Region now supports a strong representation of all three groups of species (Fig. 2). I have investigated local patterns of distribution within this region, in Kent, using fine-scale data (from 2 km^2 quadrats)[45, 46]. The various species of bumble bees tend either to be found nearly everywhere (i.e. they are *ubiquitous*) or to be very locally restricted. This pattern in Kent is related to their distributions throughout Britain; hence species found only in particular regions of the mainland after 1960 (Fig. 2) are very locally restricted within Kent; these are the 'Southern Local Species' and the 'Widespread Local Species'. In contrast, the only group of species to be well represented in all mainland regions since 1960 is almost ubiquitous in Kent and I refer to it as the 'Mainland Ubiquitous Species'. The local species in Kent are therefore near the edges of their distributions and are also generally less abundant even where they do occur. Furthermore they appear to be associated with particular areas, although there is no evidence for close mutual associations between species within these areas, except at Dungeness in the south of Kent.

Although all three major groups of bumble bees occurred widely in central and eastern England before 1960 (Fig. 1), the two groups of local species (Southern and Widespread) appear to have retreated subsequently, so that after 1960 a 'Central Impoverished Region' has emerged in which only the Mainland Ubiquitous Species remain well represented (Fig. 2). Thus it is the species nearest to the edges of their distributions that are declining in Britain. A similar relationship has been reported for changes in the occurrences of plant species in Holland[14].

Factors correlated with the changing patterns

Climate

The activity of bumble bees is strongly seasonal in most parts of their distributions. In the British Isles, the only surviving individuals between November and March are usually queens in hibernation. In this state they are very resistant to cold[1], so that their distributions are not expected to be affected by winter temperatures within the range normally experienced in Britain. The lack of correlation between regional distribution limits and January mean isotherms[42], which generally run from north to south within northern Europe, could therefore have been anticipated.

The length of the season during which bumble bees can forage and their colonies develop could present a constraint on their distributions. One way of measuring this period is by the number of days between the last and first frosts[8], known as the 'growing season'. Coastal areas around Wales and southern England have particularly long growing seasons[7], but while these areas may show some agreement with the distributions since 1960 of certain of the Southern Local Species (e.g. *Bombus muscorum*), this factor does not explain the pre-1960 distributions of these species in central England.

The climate within the available foraging season is likely to be important in determining when foraging can occur and how profitable it can be. From a study of bumble bee activity in relation to weather, Lundberg[22] concluded that foraging generally ceases when it rains and that the number of foragers is strongly influenced by temperature. Wind speed and light intensity have pronounced effects on foraging only when they reach extreme levels. The distribution limits of the various bumble bee species

were not clearly related to their responses to weather in these results. However, Hasselrot[15] found differing daily times of peak foraging activity between a more northern and a southern species where they coexist in Sweden which might have been related to physiological temperature optima. Teras[41] found an inverse relationship between precipitation and foraging activity, although he found no simple (linear) relationship of number of foragers with temperature, possibly because there is likely to be less foraging activity at both high and low temperatures.

A good general agreement exists between bumble bee distribution limits and summer isotherms, which tend to run from south-west to north-east across northern Europe. For example, the July mean +15°C isotherm across Europe[42] closely follows the northern limit of the Southern Local Species[21,28]. The same pattern is clear within Britain, and fits the pre-1960 northern limit of the Southern Local Species (Fig. 1) more closely than the mean daily duration of bright sunshine because the isotherm also skirts the Welsh highlands[43]. The pattern of total annual precipitation across north western Europe[42] is very different from the pattern of bumble bee distribution, and the difference is unlikely to be excused by seasonal variation in precipitation[43].

The climate of Britain can hardly be considered as unchanging. A slight trend towards a general warming between the 1850s and 1930s followed by a trend towards a cooling has been blamed[35] for the expansion and subsequent contraction in distribution of the hornet, *Vespa crabro*. The trend towards a cooling could also have led to the apparent post-1960 declines in distribution of the Southern Local Species of bumble bees, if not the northward retreat of the Widespread Local Species. There is evidence that another reversal occurred around 1970, so that the current trend is towards a slight warming throughout the northern hemisphere[13]; furthermore, the hornet is spreading northward again, particularly following the warm, dry summer of 1976[5]. Perhaps a survey in another five to ten years of the Southern Local Species of bumble bees might also show more northerly distribution limits for them than at present.

Pesticides

Insecticides can have dramatic effects on bumble bee populations[26] and could have affected distribution since 1960. Mortality can be selective between species simply by the effect of the timing of insecticide application in relation to the time of emergence from hibernation of different species of bumble bees[31]. However, the persistence of all the Mainland Ubiquitous Species, with their rather diverse peaks of emergence[33, 45], suggests that the selective action of pesticides is not responsible for the impoverishment of the Central Impoverished Region in this way.

Herbicide application to field and road edges could be a particularly insidious problem because users may not be aware of the potential indirect hazard to bumble bee populations from herbicides which remove their food sources.

Predators and parasites

Reviews of the predators and parasites of British bumble bees have been provided by Sladen[36], Free and Butler[11] and Alford[1]. Although several of the organisms they mention (e.g. *Sphaerularia bombi, Aphomia sociella*) may have considerable effects on the sizes of bumble bee populations, there is no evidence that predators or parasites select directly

between the ubiquitous and local species, or that their population sizes have changed markedly.

Competition from the honeybee

Heinrich, observing an 'almost total overlap in resource utilisation'[16] between the introduced honeybees and indigenous bumble bees in North America, estimated that a single honeybee colony might reduce the number of bumble bee reproductives reared in a season by 38 400, re-kindling an old debate as to whether there is serious competition for food between these social bees. Inouye has pointed out that in Europe, where the honeybee (with a short proboscis) is native, bumble bees have longer proboscides than in North America[20]. Prŷs-Jones, working in Cambridgeshire within what is now the Central Impoverished Region for bumble bees (Fig. 2), found that the majority of visits by bumble bees were to plants that were not utilised by the honeybee[35]. In Britain, the honeybee is unlikely to have a major effect on bumble bee populations.

Habitat and land use

The sites to which the local species of bumble bees are restricted in Kent are characterised by a particularly narrow subset of the major vegetation formations present, namely saltmarsh, shingle, sand dune and old meadow[45, 46]. Results from more detailed investigations for differing habitat associations among the local species of bumble bees confirm the importance (particularly for the most restricted local species) of the large quantity of shingle habitat at Dungeness (Fig. 3.), but otherwise show only a general response by the remaining local species to the combined quantity of the other coastal vegetation and old-meadow vegetation. This sort of vegetation may be indicative of open habitats with a relative lack of certain types of disturbance created by man—such disturbance might be expected to promote dispersive weeds, which are often poor nectar sources. However, evidence from the Kent census is inconclusive as to whether locally restricted bumble bee species occur at sites with a higher proportion of nectariferous plants from (crudely determined) 'bumble bee flower' families. Nevertheless, at the Kent census sites where the local species were found, the combined abundances for the ubiquitous species alone were greater than for the sites where the local species were not recorded. These higher densities for the ubiquitous species could reflect generally higher levels of resources at sites supporting the local species.

Figure 3 shows some of the shingle habitat at Dungeness which supports an exceptionally rich fauna of thirteen species of bumble bees. In the foreground are clumps of wood sage (*Teucrium scorodonia*), with blackberry (*Rubus* spp.) and sallow (*Salix* spp.) beyond. (Other flowers found at Dungeness and preferred by the rarer bumble bee species during the 1982 study[45] included common toadflax (*Linaria vulgaris*), common teasel (*Dipsacus fullonum*), viper's bugloss (*Echium vulgare*) and yellow melilot (*Melilotus altissima*).)

Vegetation can be profoundly influenced by land use and one of the largest proportional changes in Britain this century has been through rapid urbanisation[6]. This is not likely to have affected regional distribution data for bumble bees because few vice-counties (the units employed in the analysis) approach complete urbanisation. The Mainland Ubiquitous Species are all present, and are often abundant, in the domestic

FIG. 3. A view of Dungeness, Kent, showing the shingle habitat, and the CEGB nuclear power station.

gardens of low density suburbs around London and foraging bumble bees are not a rare sight even in the parks near the city's centre.

More than 80% of the total land area of Britain is used for agriculture[6], with a preponderance of arable farming (especially wheat) in central and eastern England, and livestock in the wetter west and north[7]. Two areas of field enclosure were distinguished by Rackham[34]. These are the 'Ancient Countryside' of western and south-east England, with irregular, often small fields enclosed in the period between the Bronze Age and about 1700 AD, and the 'Predominantly Planned Countryside' of central and eastern England, of post-1700 enclosure with regular fields and straight roads.

The blockades of the 1939-1945 war necessitated a policy in Britain of self-sufficiency in food. This became perpetuated as a doctrine of the 1947 Agriculture Act and subsequently, even under the Common Agricultural Policy, market subsidies and development grants have resulted in the intensification of agriculture with an acceleration of mechanisation. Inevitably, under this economic pressure much land that was previously considered to be of borderline profitability (especially wet grassland), and frequently allowed to remain relatively undisturbed, has been 'improved' in the north and west to take higher stock densities or has been reclaimed for cultivation in the central lowlands[27]. Field under-drainage, most extensive in central and eastern counties, has usually been the prelude to the conversion of pastures back to arable use and to the first-time cultivation of pasture land, including alluvial meadows and marsh[25]. The Midlands have been most affected by increases in the arable area[6] and, although the eastern counties have remained largely arable in their farming, field sizes have been increased to facilitate mechanisation, particularly by the removal of hedges[32]. The differentiation of the region of 'Predominantly Planned Countryside'[34], corresponding closely with the Central Impoverished Region for bumble bees, has thereby become enhanced since the 1940s by the regional effects of agricultural intensification—with an obvious loss of habitat diversity.

In the midst of the Central Impoverished Region, the bumble bees of Wicken Fen (Cambridgeshire) have been studied intensively, especially in the 1920s[37] and 1970s[33].

Fourteen species of *Bombus,* including all the Southern Local Species and Widespread Local Species (except *B. monticola*), were recorded during the 1920s, particularly in the vicinity of the rough land bordering the fen to the north east[38]. However, by 1978, when the fields beyond the fen borders were under regular cultivation, only the Mainland Ubiquitous Species persisted. The only area of Cambridgeshire where I found any of the local species to persist in any numbers during 1984 was in the flood zone of the Hundred Foot Washes.

Changes in the bumble bee fauna have not been confined to the 'open field' counties of central England. For example, the Rother Levels in Kent underwent a pronounced change in drainage regime between 1966 and 1976 with embankment of the river and installation of flood control schemes[25]. In 1973, during the survey of Kentish bumble bees by Philp and Dicker, the seven Mainland Ubiquitous Species and three local species were recorded. I predicted[45, 46] from a lack of the associated plants persisting until a botanical survey in 1971-1980[30] that the habitat was no longer favourable to local bumble bee species, and indeed none of the local species of bumble bee found in 1973 were recorded again when I made a census of the site in 1983.

Peters has reported a parallel decline in the local species of bumble bees of E. Germany[29]. All the 'British' Widespread Local Species (only *B. monticola* is absent) and Southern Local Species are described as rare and declining, except for *B. sylvarum,* which is apparently rather more widespread there than in Britain. Although agriculture may have created favourable conditions for bumble bees in the past, Peters suggested that their decline in E. Germany could have been caused by a recent trend towards uniformity in agricultural landscapes and the use of pesticides. He considered that cold spells in the early summer of some years were of secondary importance (probably merely the '*coup de grace*' under conditions of decreased food availability). Unfortunately, he presents no information concerning the effects of habitat changes.

A marginal mosaic model

Animals and plants are generally more abundant near the centres of their distribution ranges than near the edges[17]. A species of bumble bee, for example, will be most efficient at harvesting resources under one broad set of climatic conditions, despite some variation, so that the more adverse climates towards the edges of its range might reduce foraging profits (e.g. through increased thermoregulatory costs) and, if energy were limiting, would result in decreased local abundances of bumble bees. Since different types of habitat have different levels of food resources available, the local abundances of bumble bees that they support might also be expected to differ, even in the region near the centre of the distribution range where the climate is most favourable. If other conditions are more or less constant, local abundances of bumble bees would then decrease in step between patches in a mosaic of these different habitat types as the climate deteriorates towards the edges of the species' distribution range. But bumble bees cannot survive in any locality if they are too rare, because there must be sufficient numbers in each colony to rear enough young queens to ensure that the species persists from year to year. The local numbers of bumble bees are likely to fall below the minimum number for survival within patches of the habitat type with lower food availability closer to the distribution centre, therefore the bees could have different distribution limits in

different types of habitat. For a mosaic of habitats, these differential limits might result in ubiquitous occupation of all habitats in the climatically favourable central region of the species' distribution, but beyond the species' limit within the poorer habitats there would be a marginal region where its occurrence would be restricted to those local patches of habitat with the highest availability of food[45, 46].

This marginal mosaic model describes a mechanism, dependent on the economics of energy, that accounts for many of the distribution patterns of bumble bees. It also provides another way of looking at the composition of local assemblages of species because it describes how some of the major factors interact to influence whether or not a species can survive at a particular locality. Thus if the availability of food at one site declines then, among the species affected by the food shortage, it should be those relatively furthest from their climatic optima (and therefore previously surviving on a lower margin of foraging profit) that are expected to die out first. This model has been more successfully predictive than earlier models of competitive exclusion[45].

Postglacial history of British bumble bees

Using the marginal mosaic model and information regarding past climatic changes, it is possible to speculate as to the postglacial history of distributions of British bumble bees. The subarctic/subalpine *B. monticola* may have persisted near the southern limit of the last glaciation, possibly together with species of the other presently arctic/alpine groups, such as *B. alpinus* (L.). However, most of the species of bumble bees in Britain now would probably have been absent from within the present boundaries of Britain, only spreading from the south east following the improvement in the climate and the retreat of the ice sheet 17 000 years ago[9].

Even after complete reafforestation about 9000 years ago[19], the distributions of some of the British bumble bees may still have been rather different from those today. The local species studied in Kent avoid closed canopy woodland[45, 46] where there may be few suitable flowers in the summer, and therefore in post-glacial times these bumble bees may have been restricted to open lowland areas, which were perhaps extensive only on some coasts. The absence of many bumble bee species from islands, and even Ireland[2], may indicate that dispersal across the Channel was probably infrequent after the severing of the land connection about 7000 years ago[9]. This isolation also marked the beginning of a rather warmer period than the present (the postglacial 'Climatic Optimum' of 7000-5000 years ago when temperatures were 2–3°C above recent averages[9]), which is also likely to have driven latitudinal distribution limits northwards, and could have been especially unfavourable to any *B. alpinus*, for example, persisting in mountains in the northern mountains. The forest clearance accompanying the spread of early agriculture between 6000 and 5000 years ago[9] probably assisted the spread of particularly the Southern Local Species inland to some newly-opened meadow habitats which provided more food than the surrounding forests. The climate then started to cool again and to isolate local fragments of populations of the Southern Local Species in smaller 'islands' of especially favourable habitat.

The pre-1960 regional distributions (Fig. 1) indicate that only the Southern Local Species clearly reached a latitudinal limit within Britain. The close agreement between their northern distribution limits across Europe and the pattern of the summer isotherms

is explained by considerations of the economics of energy as embodied in the marginal mosaic model. Under the prevailing climate of the present century, this regional distribution pattern could represent an approximate equilibrium for their potential latitudinal limits in habitats with high food availability.

Realisation of this latitudinal limit by partial occupation of the adjacent marginal region of distribution would of course be dependent on the persistence of sufficiently large patches of favourable habitat. Intensification of agriculture since the 1940s has brought much land into cultivation which had previously been little disturbed. Very probably these modern agricultural practices have reduced the availability of food for bumble bees in many formerly species-rich areas, resulting in an erosion of the northern limit for the Southern Local Species and disrupting the distribution of the Widespread Local Species, which are near their southern limit in the lowlands. Thus a Central Impoverished Region has emerged since 1960 (Fig. 2) which corresponds closely with the area of 'Predominantly Planned Countryside' described by Rackham[34], where the post-1940 changes in agricultural land use have been most profound.

Coastal areas probably remain especially favourable as refuges for bumble bee species at the margins of their distributions in southern Britain, because the soils of saltmarsh, shingle and sand dune are particularly unsuitable for agriculture, so that these sites enjoy lower levels of disturbance by man. In addition, the sites have more protracted growing seasons with a less extreme climate for colony development. The extensive shingle at Dungeness (Fig. 3) may, therefore, have protected the many local bumble bees while the marshes to the north and west were largely drained and, more recently, ploughed. A more permanent safeguard could prove to be the nuclear power station at Dungeness which may discourage further development.

Implications for farming

Stephen[40] believed that encroachment of agriculture upon the habitats of native pollinators, such as bumble bees, in Manitoba, Canada, had led to a fall in their populations and a fall in the resultant seed yields from alfalfa to the point where cultivation for seed crops was becoming uneconomic. Bumble bees can be economically very important as pollinators, particularly for leguminous seed crops and certain tree fruits[10]. They have advantages over honeybees to farmers (especially in northern Europe where their activity under cooler conditions than honeybees is at a premium) because bumble bees are attracted to visit crop flowers with a greater corolla depth than can be reached effectively by honeybees, and also will visit flowers at a higher rate than honeybees[18, 39].

The decline of the Southern Local Species and Widespread Local Species of bumble bees in Britain could continue if the agricultural practices followed in central England are applied more intensively in the west and south east. The decline of these local species alone is unlikely to have noticeable economic effects (i.e. through crop pollination) because they are not generally abundant even where present. However, their presence is correlated with higher abundances of the common species and, at the very least, their decline is a warning of the fate awaiting the 'ubiquitous' species if the removal of their food sources and nest sites continues.

Goral[12] noted that the numbers of bumble bees as the major pollinators of certain

clover crops in Poland increased with the proximity of forests, meadows and pastures to the crops. The analysis of habitat associations in Kent suggests that certain open habitats, such as old meadows with their rich growth of flowers, are especially favourable to bumble bees. A small amount of rough land without a closed canopy of trees, perhaps in corners of fields, can provide bumble bee nest sites and encourage a seasonal succession of the longer-corolla 'bumble bee' forage plants—and thereby help to secure adequate numbers of bumble bees for crop pollination.

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