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Why are there so many species of bumble bees at Dungeness?

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WILLIAMS, P. H., 1989. **Why are there so many species of bumble bees at Dungeness?** Dungeness is unique in the British Isles in that it has more species of bumble bees than any other locality. Three ideas about what governs the number of species at a locality are examined by looking at patterns of flower visits at Dungeness in comparison with those at Shoreham, a species-poor locality also in Kent. The species of bumble bees that are present at Dungeness but absent from Shoreham show no association in their distributions among 2 km grid-squares in Kent with the species of food-plants that they prefer at Dungeness, nor is there any correlation between the diversity of bees and diversity of food-plants at Dungeness and Shoreham. From the information available, Dungeness is most likely to have more species of bumble bees because it has a particularly high density of the more nectar-rich flowers that bumble bees can use. Bumble bees feed most profitably from deep flowers because these contain more nectar than shallow flowers, although direct access to deeper flowers is ultimately limited by the length of each bee's proboscis. The distribution of worker proboscis lengths among species in the species-pool in Kent is clumped about a median of 7.9 mm. The best foraging conditions for the maximum number of species should be provided when flowers of similar depths are present in sufficiently large numbers for all foragers to make near-optimal flower choices. Although there is no difference in median between the distributions of the bees' proboscis lengths and the depths of the flowers they use at Dungeness, at Shoreham the flower depths used are shorter than the proboscis lengths. Among the food-plants at Dungeness, high densities of *Teucrium scorodonia* and *Echium vulgare* are likely to be especially important.

ADDITIONAL KEY WORDS:—*Bombus* – distribution – diversity – species assemblage – competition – community structure.

CONTENTS

INTRODUCTION

There are now more species of bumble bees at Dungeness (13 out of 16 *Bombus* species, Table 1) than are found together at any other locality in the British Isles (see maps in Alford, 1980). Seven of these species are more or less ubiquitous in

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TABLE 1. List of the species of bumble bees recorded at Dungeness and Shoreham with measurements of mean worker proboscis length (PL: glossa + prementum). The measurement for *B. ruderarius* from Stapel (1933) is preferred because it is much closer to estimates from small samples from Dungeness and Shoreham. Nomenclatural changes arising from problems outlined by Løken (1973) and Day (1979) are incorporated. *Bombus magnus* and *B. ruderatus* are names that have been applied to regional colour forms that occur in Britain, although it has not been established definitely that they do not interbreed with forms referable to the older names *B. terrestris* and *B. argillaceus* respectively, as parts of more widespread 'biological' species

Species of *Bombus* Latreille	Abbreviation	Mean proboscis length, PL (mm)	Authority
hortorum (L.)	ho	12.30	Medler, 1962a
ruderatus (F.) = ? *argillaceus* (Scopoli)	rt	10.62	Medler, 1962b
subterraneus (L.)	su	8.79	Medler, 1962b
pascuorum (Scopoli)	pa	8.54	Medler, 1962a
muscorum (L.) = *humilis* (Illiger)	mu	8.17	Medler, 1962b
ruderarius (Müller)	re	8.0	Stapel, 1933
sylvarum (L.)	sy	7.93	Medler, 1962b
laevis Vogt = *muscorum* of earlier authors	le	7.76	Pekkarinen, 1979
audax (Harris) = *terrestris* of earlier authors	au	7.61	Medler, 1962a
pratorum (L.)	pr	7.11	Medler, 1962b
lapidarius (L.)	la	6.96	Medler, 1962a
terrestris (L.) = *lucorum* (L.) = ? *magnus* Vogt	te	6.68	Medler, 1962b
jonellus (Kirby)	jo	5.99	Pekkarinen in Teräs, 1985

southern England, but the other six have declined throughout Britain (Williams, 1986) and are now of very restricted and local distribution in Kent (Williams, 1988).

The question of what governs the number of species that occur together in a local assemblage is a fundamental problem in ecology. It has been much discussed and only a few of the ideas are examined here. Hutchinson (1959) summed up a general belief: "If the fundamental productivity of an area ... is less than under more favourable conditions, then the rarer species in a community may be so rare that they do not exist". Bowers (1985) described the dynamic processes through which this may act on bumble bees, from a study of their distribution among subalpine meadows in Utah. He found that the number of species that colonized meadows in spring is related to meadow area, but that the success of these colonies in rearing young queens and males is related to the floral composition of each meadow and hence to the availability of food resources.

Bumble bees are particularly suitable animals for the study of local species-richness, because they meet many of the assumptions for studies that use niche theory and optimal foraging theory (e.g. Inouye, 1977; Heinrich, 1979; Prŷs-Jones, 1982; Williams, 1985). It is likely that their populations are limited by nectar resources (the energy content of which is easily calculated) and by local climate. Nectar is most likely to be limiting when young queens and males are being reared (e.g. Bowers, 1985). During this period, all foraging for the colony is done by the workers, which carry out no other activity away from the nest. Workers continually adjust their foraging behaviour from their own experience of the changing distribution of resources. This 'tracking' of resources tends to maximize their individual contributions to the reproductive success of the maternal colony. Yet although all bumble bees feed on nectar, foragers of different species tend to choose different plants according to a simple relationship between their proboscis lengths and the flower depths. Hence patterns of resource use and interactions among species are relatively easy to measure.

The possibilities considered here are that the number of bumble bee species at a locality is limited primarily (1) by the presence of particular food-plant species, (2) by the diversity of food-plant species, or (3) by the abundance of food-plant species. Flowers visited for nectar at Dungeness are compared with those at another locality in Kent, Shoreham, where only the seven ubiquitous species of bumble bees are found. Both localities appear to lie within the same general climatic and faunal region (Williams, 1986).

METHODS

The survey area of 72 ha at Dungeness (grid ref. TR 0818) extends from The Pilot in the south-east to the Long Pits in the west and to the site of the disused railway loop and halt in the north. The Lydd road runs diagonally across this area and divides it nearly equally. To the north-east of the road, the area consists mostly of 'first class' shingle ridges (Fuller, 1985) with *Cytisus scoparius* (L.) Link, whereas much of the area to the south-west was excavated to a depth of about 3 m before 1950 and now supports *Salix* scrub. Worker bumble bees that were visiting flowers for nectar were recorded using a belt transect method (Banaszak, 1980). The transect followed the strips of vegetation on the shingle ridges. Transect data were collected during June, July and August, 1982. Only data from between 26 July and 8 August are used here, because this period included the maximum foraging activity by workers, when food resources are most likely to be limiting.

An area of 50 ha near Shoreham (grid ref. TQ 5260) was surveyed during the same period in 1983. The survey area consists of 34% wheat fields, 8% deciduous woodland and 58% grassland, including a golf course. The transect followed field and woodland borders, to which the flowers visited by bumble bees are restricted. No nectar 'robbing' was seen at either locality.

ANALYSIS & DISCUSSION

Number of species breeding in the survey area

Not all of the 13 species of *Bombus* recorded at Dungeness may have succeeded in reproducing within the survey area, because no young queens or males of *B. laevis* or *B. jonellus* were found (Fig. 1). Bowers (1985) found that not all of the species that colonized the meadows he studied succeeded in rearing young queens and males. Therefore, records of autumn queens or males may be better as indicators of habitat association for bumble bees than records of spring queens or even workers. Both *B. laevis* and *B. jonellus* probably do search for nest sites in the survey area because queens of both were found dead in a nest of *B. sylvarum*. Males of both species have been collected in neighbouring areas in other years. In 1984 *B. laevis* workers were much more abundant than those of *B. muscorum* at the adjacent South Brooks marshes, the reverse of the situation in the shingle area. Perhaps the presence of *B. laevis* and *B. jonellus* in the survey area is dependent on annual immigration. Nevertheless, this part of Dungeness has at least four more species in its local assemblage than most localities in Kent and this excess remains to be accounted for.

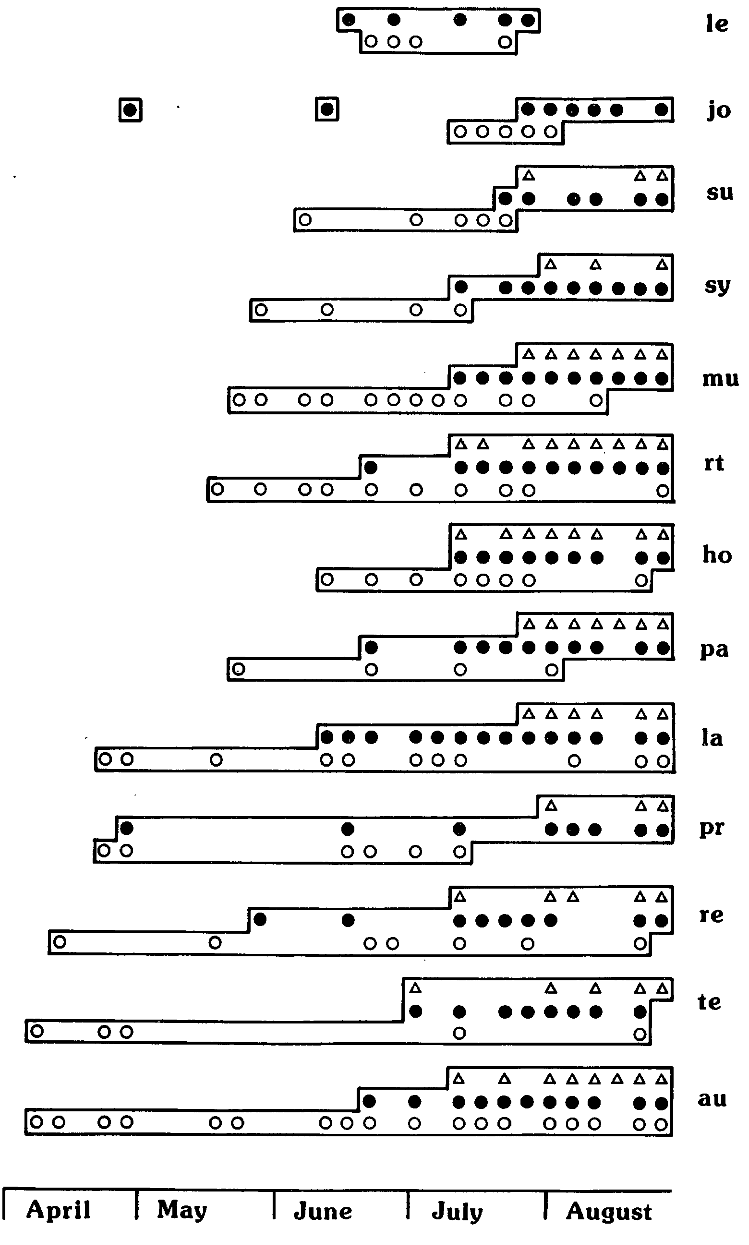

Figure 1. Phenological diagram for the foraging activity of bumble bees at Dungeness, including pooled records from 1974–1984 (positive records from a total of 69 days; no sampling was carried out after 28 August in any year, or on any days in 1980, 1981). Light circles represent the records for queens, dark circles the workers and triangles the males for each period of five days. See Table 1 for abbreviations of *Bombus* species.

Particular food-plants

The presence of a particular species of bumble bee at a locality, and, by extension, the local species-richness, might depend on the presence of a particular species of food-plant if the bees were obligate specialists.

Løken (1961, 1973) found that in Scandinavia *B. consobrinus* Dahlbom shows a strong preference for foraging from flowers of *Aconitum septentrionale* Koelle. Løken plotted the Scandinavian distribution of *B. consobrinus* and showed that it occurs only within the distribution of *A. septentrionale*. The bee is also found further eastwards as far as the Pacific coast of Russia and Løken believed that this distribution is completely within the distribution of species of the genus *Aconitum*.

One possibility is that food-plant specialization is also responsible for the restricted local distribution of some species of bumble bees in Kent. This can be examined by identifying the flower preferences of the local species at Dungeness and by then testing the correlation between the distributions of these bumble bee species and their preferred food-plant species in Kent. The frequencies of visits that would be expected if foragers were unselective and encountered the same flowers, but in proportion to the total numbers of recorded visits, can be calculated from the products of the marginal totals (from Table 4) divided by the total of all visits to all flowers. An index of preference for a species of food-plant is provided by the deviation of observed from expected frequencies of visits, divided by the expected frequency (Table 6). A high, positive preference could be the result of a highly specialized relationship with a food-plant. However, the distributions among 2 km grid-squares of these locally restricted bumble bees (distribution data from G. H. L. Dicker & E. G. Philp, unpublished, see Williams, 1988) and their preferred plants for nectar foraging (distribution data from Philp, 1982) are not associated in Kent (Fisher exact test, see Siegel, 1956, all $P > 0.05$). This does not support the view that narrow food-plant specialization plays a major role in governing the composition of bumble bee species-assemblages.

Extreme food-plant specialization is potentially disadvantageous for social species because it could unnecessarily restrict resource use in the neighbourhood of a fixed nest. Generalists could more fully exploit the changing resources through a long summer for the development of large colonies (e.g. Morse, 1982). However, the extreme specialist, *B. consobrinus*, occurs in subalpine habitats, where the foraging season is short. It has an exceptionally long proboscis and so can forage much more profitably from the very deep flowers of *A. septentrionale* than can most bumble bees. This is one of the most abundant food-plants in the subalpine habitat, so extreme specialization could arise solely as an optimal foraging solution. Longer-proboscis bumble bees also tend to collect pollen only from the same flowers that they visit for nectar (Prŷs-Jones, 1982).

Diversity of food-plants

The presence of a particular species of bumble bee might depend on the presence locally of food-plant species that are not depleted of resources too extensively by other bumble bees. The critical factor is expected to be that the overlap between two species in their use of a limiting resource must be small enough so that neither species is excluded by competition (see May, 1973). This idea has been extended to assemblages of many species as a theory of competitive 'species-packing' (see MacArthur, 1972).

Inouye (1977) applied the idea of limiting morphological similarity (Hutchinson, 1959) to the proboscis lengths of bumble bees. This followed the observation by Brian (1957) that species of bumble bees with different proboscis

TABLE 2. List of the species of plants visited for nectar during the Dungeness survey with measurements of mean exclusion depth of the flowers for bumble bee proboscides (see Williams, 1985). Samples consist of 20 measurements

Species of plant	Abbreviation	Mean flower depth FD (mm) ($\pm$S.E.$_{mean}$)
Linaria vulgaris Miller	Lin.vl	12.94 (0.30)
Dipsacus fullonum L.	Dip.fl	9.60 (0.10)
Lathyrus sylvestris L.	Lat.sy	7.78 (0.11)
Teucrium scorodonia L.	Teu.sy	7.13 (0.11)
Lotus corniculatus L.	Lot.cn	6.73 (0.12)
Ononis repens L.	Onn.rp	6.33 (0.07)
Echium vulgare L.	Ech.vl	5.30 (0.11)
Cirsium vulgare (Savi) Ten.	Cir.vl	4.65 (0.06)
Centaurea nigra L.	Cen.ng	4.10 (0.04)
Melilotus altissima Thuill.	Mel.at	3.64 (0.06)
Senecio jacobaea L.	Sen.ja	2.91 (0.07)
Chamaerion angustifolium (L.) J. Holub	Chm.an	2.40 (0.03)
Rubus fruticosus agg.	Rub.fr	1.40 (0.02)

lengths visited flowers of different depths. Inouye assumed that competitive overlaps between species in their use of a limiting resource must remain small. He suggested that the number of bumble bee species in a local assemblage might be linked to the number of plant species with suitable flowers, provided that a broad range of flower depths is present.

Contrary to what is expected from competitive species-packing, there is actually a lower diversity of food-plants, whether measured in numbers of species (Tables 2, 3), or in range of flower depth sizes (Fig. 3C, D), at Dungeness, the locality with more species of bumble bees. The evenness of the distribution of visits among these species of plants was similar at the two localities (Fig. 2). But again, the slope does appear to be slightly steeper (i.e. less even and less diverse) for the Dungeness data because of the exploitation of abundant *T. scorodonia.*

The maximum overlaps in nectar use between bumble bee species (index of Schoener, 1970) appear to be similar at Dungeness (0.88) and Shoreham (0.84),

TABLE 3. As for Table 2, but for the Shoreham survey

Species of plant	Abbreviation	Mean flower depth FD (mm) ($\pm$S.E.$_{mean}$)
Dipsacus fullonum L.	Dip.fl	11.17 (0.11)
Trifolium pratense L.	Trf.pr	9.93 (0.14)
Lamium purpureum L.	Lam.pu	9.18 (0.14)
Knautia arvensis (L.) Coulter	Knt.av	6.37 (0.25)
Cirsium vulgare (Savi) Ten.	Cir.vl	5.46 (0.05)
Medicago sativa L.	Med.st	5.30 (0.07)
Origanum vulgare L.	Ori.vl	4.73 (0.04)
Centaurea nigra L.	Cen.ng	4.56 (0.05)
Convolvulus arvensis L.	Con.av	4.31 (0.10)
Arctium minus Bernh.	Arc.mn	3.50 (0.04)
Senecio jacobaea L.	Sen.ja	3.46 (0.05)
Epilobium hirsutum L.	Epi.hi	3.30 (0.06)
Carduus acanthoides L.	Cad.ac	3.14 (0.07)
Chamaerion angustifolium (L.) J. Holub	Chm.an	2.54 (0.04)
Rubus fruticosus agg.	Rub.fr	1.47 (0.03)
Cirsium arvense (L.) Scop.	Cir.av	0.89 (0.05)
Clematis vitalba L.	Clm.vt	0.50 (0.06)

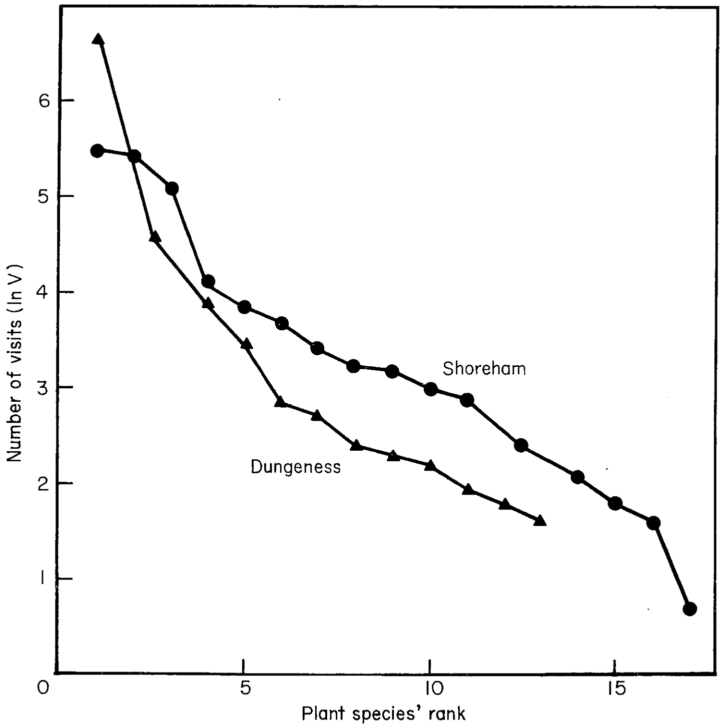

Figure 2. Plot of the evenness of the numbers of visits for nectar by worker bumble bees among flowers of different plant species. Triangles represent the plants at Dungeness and circles the plants at Shoreham.

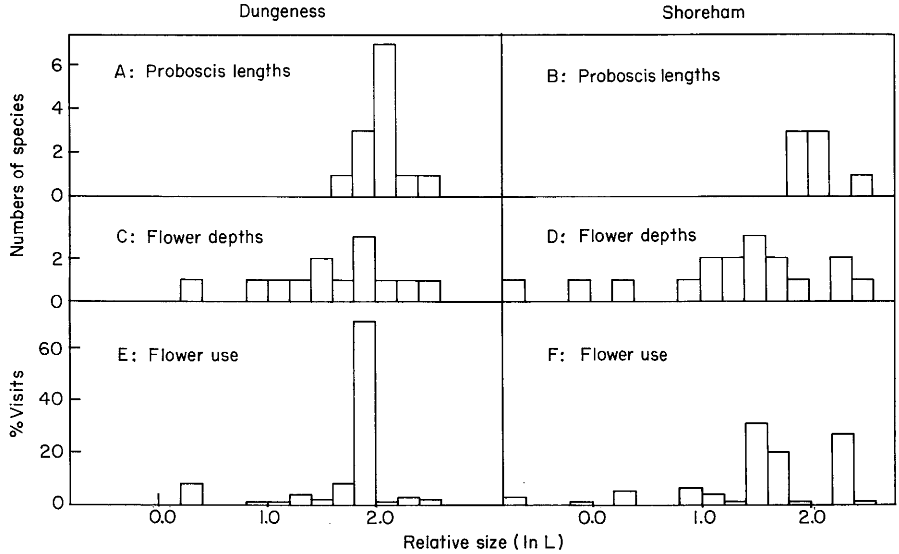

Figure 3. Histograms for the distributions of numbers by relative size. A. The bumble bee assemblage at Dungeness shown as the numbers of bumble bee species by mean worker proboscis length. B. As A at Shoreham. C. The nectariferous flora at Dungeness shown as the numbers of plant species visited for nectar by mean flower depth. D. As C at Shoreham. E. The flower use at Dungeness shown as the percentage of nectar visits by worker bumble bees by mean flower depth. F. As E at Shoreham.

although higher than expected from the theory (<0.7, see Williams, 1985). However, these differences cannot be tested because the overlaps are not independent observations. Either way these simple statistics are difficult to interpret in isolation and are of limited value (Connell, 1980). Yet it is worth noting that one possible reason for a discrepancy with the theory is that an additional resource (e.g. pollen) might also be under competition. In this case the median overlap should be lower at the locality with more species (see Rappoldt & Hogeweg, 1980). But on the contrary, the median overlap appears to be larger at Dungeness (0.33; cf. Shoreham, 0.13), where there are more species in the assemblage. This kind of result would be expected from a competitively neutral model.

If a relationship exists between choice of diet and morphology (reviewed by Hespenheide, 1973; Wiens, 1982), as confirmed below for these bumble bees, then competitive species-packing should have consequences for the relative sizes of the species that can coexist in a local assemblage, as a pattern of 'community structure'. Several previous studies of local assemblages of bumble bees have failed to find a pattern in the sizes of proboscides that deviates from the predictions obtained using competitively neutral models (Simberloff & Boecklen, 1981; Ranta, 1982, 1984; Ranta & Tiainen, 1982; Williams, 1985, 1988). Despite these results, there have been attempts to defend ideas of competitive species-packing while invoking non-equilibrium conditions (e.g. 'spatio-temporal heterogeneity' by Ranta & Vepsäläinen, 1981). In fact these ideas propose that the action of the competitive mechanism is normally suspended.

Diversity of bumble bees is associated with the diversity of food-plants among some localities (Ranta & Tiainen, 1982), as predicted by Inouye (1977). This may be necessary to support the idea of competitive species-packing, but it is not sufficient. A correlation could arise from optimal foraging behaviour alone, if bumble bees with a broader range of proboscis lengths exploited a broader range of flower depths. This is not to deny that interspecific competition affects patterns of foraging by bumble bees, which has been demonstrated by the effect of competitor removal (e.g. Inouye, 1978; Plowright, Pendrel & McLaren, 1978; Plowright & Rodd, 1980; Pleasants, 1981). It is concluded only that interspecific competition does not appear to govern the composition of local assemblages of bumble bee species in the manner predicted by the theory of species-packing.

Abundance of food-plants

The presence of a particular species at a locality is likely to depend on the balance of the effects of resource levels and various 'costs', which may be influenced by the local climate. The local reproductive economics of each species need not depend critically on any effects of other species in a local assemblage (i.e. the situation could be competitively neutral).

Andrewartha & Birch (1954: 656) described how climate could affect populations through their rates of increase and the length of the annual growing season. For bumble bees, rate of increase is likely to be strongly influenced by the overall rate of profit that is returned by foraging workers to the colony. In some regions the climate is likely to be suboptimal for a species because there are prolonged periods when the weather is unfavourable for foraging (this applies both near northern and southern distribution limits). However, the effective duration of these periods may be reduced by facultative thermoregulation (at least at low temperatures), though perhaps often at considerable cost in energy (see Heinrich, 1979). Species might then persist at a locality in a region with suboptimal climate only if the local resource level were sufficiently high to compensate for either the restricted foraging periods, or for the increased thermoregulatory costs, and so ensure adequate overall profit rates for the reproductive success of their colonies. Hence a species could be nearly ubiquitous near the centre of its distribution, where it is near its climatic optimum, but restricted to only the most resource-rich localities in the marginal regions of its distribution. This 'marginal mosaic model' for bumble bees (Williams, 1988) is based on descriptions of general patterns in distributions of animals across continents (e.g. Andrewartha & Birch, 1954; Hengeveld & Haeck, 1981, 1982; Brown, 1984; Schoener, 1987).

It is very difficult to measure reliably, and over sufficiently large areas and long periods of time, the quantity, profitability and variability of resources that are available from flowers of all ages for a direct comparison of localities (Connell, 1980; Pleasants, 1981; Tepedino & Stanton, 1981, 1982; Zimmerman & Pleasants, 1982). However, it is possible to compare food-plants between localities indirectly for profitability using criteria based on optimal foraging theory and the observed patterns of flower use by bumble bees. Optimal foraging theory (reviewed by Pyke, 1984) has been applied to bumble bees for the currency of net rate of energy profit (e.g. Heinrich, 1976, 1979; Pyke, 1980; reviewed by Plowright & Laverty, 1984; Cheverton, Kacelnik & Krebs, 1985). Many factors influence flower choice by bumble bees (e.g. Brian, 1957; Prŷs-Jones, 1982; Morse, 1982; Harder, 1985; Teräs, 1985), but one way in which it has been shown to be optimized for profit rate is by foragers learning to visit flowers of depths similar to their own proboscis lengths. This results from a trade-off between sugar reward (Prŷs-Jones, 1982) and cost in handling time (Harder, 1983). Profit rates are expected to be more favourable for all bumble bee species when there are enough flowers of all depths available for each bee to be able to forage mainly from the flowers of similar depth to its own proboscis length. So the difference between the distribution of proboscis lengths for the regional species-pool of bumble bees (in Kent this is identical to the Dungeness assemblage) and the distribution of flower depths used is expected to be less at Dungeness than at Shoreham.

There is indeed less of a difference between proboscis lengths and flower use for bumble bees at Dungeness than at Shoreham. The two assemblages of bumble bees do not differ in the medians of their proboscis length distributions (Fig. 3A, B), even between the species of Shoreham and the additional species at Dungeness alone (randomization test, $P=0.89$). Flower choice, as shown by mean (from the frequency of visits) flower depth visited by each species of bumble bee, is related to proboscis length at both localities (data in Tables 1–5: Dungeness, product-moment correlation $r=0.65$, slope of linear model by regression $=1.27\pm0.45$, $P<0.025$; Shoreham, $r=0.80$, slope $=1.89\pm0.63$, $P<0.025$). But whereas the distribution of resource use by flower depth does not differ from the distribution of bees' proboscis lengths at Dungeness (Fig. 3A, E: median test, $P>0.20$), these distributions do differ significantly at Shoreham (Fig. 3B, F: median test, $P<0.025$). Foragers at Shoreham are apparently unable to find enough of the most suitable, deeper flowers and so are obliged to

TABLE 4. Numbers of worker bumble bees visiting flowers for nectar during the Dungeness survey. Species of bumble bees ranked by mean worker proboscis length (abbreviations & measurements from Table 1), plants by mean flower depth (abbreviations & measurements from Table 2)

	jo	te	la	pr	au	le	sy	re	mu	pa	su	rt	ho
Lin.vl	—	—	—	—	—	—	1	—	6	2	—	7	1
Dip.fl	1	—	1	—	4	1	4	—	5	5	4	3	3
Lat.sy	—	—	—	—	—	—	1	3	3	2	—	—	—
Teu.sc	2	11	122	13	540	—	6	1	50	16	—	2	4
Lot.cn	—	—	1	—	—	—	2	—	6	1	—	—	—
Onn.rp	—	—	—	—	—	—	1	—	3	1	—	—	—
Ech.vl	—	2	3	5	11	2	8	6	12	16	1	15	14
Cir.vl	—	—	3	—	5	—	2	1	4	—	—	—	—
Cen.ng	1	—	6	—	1	—	1	—	1	—	—	—	1
Mel.at	2	—	5	1	2	—	10	—	22	5	—	—	—
Sen.ja	—	—	3	—	3	—	—	—	—	—	—	—	—
Chm.an	—	5	2	—	—	—	—	—	—	—	—	—	—
Rub.fr	17	4	3	12	34	—	4	1	15	5	—	—	—

visit shallower and less rewarding flowers (this is also shown by the greater deviation of the FD/PL regression from a slope of 1.0 at Shoreham). Interspecific competition is particularly likely to be demonstrable in this situation (Williams, 1985).

The likely consequences for local profit rates of the differences between local patterns of flower use can be examined using some simple relationships (cf. Pyke, 1980), even though the rewards and costs of foraging have not been measured directly. Prŷs-Jones (1982) found that sugar content increases exponentially with relative (log) flower depth and Harder (1983) showed that handling costs change little as long as the depths do not exceed proboscis length. For the food-plants at Dungeness, flower depth is independent of how clumped flowers are within an individual plant (Kendall tau$=0$, $P>0.05$), so at this locality the many species of plants with the deeper flowers that bumble bees can use are

TABLE 5. Numbers of worker bumble bees visiting flowers for nectar during the Shoreham survey. Species of bumble bees ranked by mean worker proboscis length (abbreviations & measurements from Table 1), plants by mean flower depth (abbreviations & measurements from Table 3)

	te	la	pr	au	re	pa	ho
Dip.fl	—	—	—	—	1	5	—
Trf.pr	—	—	—	1	1	9	—
Lam.pu	—	—	—	2	22	213	2
Knt.av	—	—	—	—	—	2	—
Cir.vl	3	3	—	3	—	21	—
Med.st	5	—	—	11	6	139	—
Ori.vl	12	1	—	13	—	13	—
Cen.ng	1	9	—	—	—	14	—
Con.av	60	58	—	91	2	13	—
Arc.mn	—	—	—	—	—	5	—
Sen.ja	2	4	—	1	—	1	—
Epi.hi	—	—	—	1	—	17	—
Cad.ac	—	—	—	1	—	19	—
Chm.an	15	—	4	11	—	28	—
Rub.fr	6	1	—	8	—	31	—
Cir.av	1	3	—	1	—	6	—
Clm.vt	14	—	—	7	—	4	—

Table 6. Deviations of observed frequencies of visits by the locally restricted species of bumble bees to flowers of plants during the Dungeness survey from those expected for unselective foragers encountering plants at random (see text, abbreviations from Tables 1 & 2). Strongest preferences are shown by the largest positive deviations, which are underlined

	jo	le	sy	mu	su	rt
Lin.vl	−0.59	−0.21	0.50	2.92	−0.28	10.27
Dip.fl	0.45	3.17	2.74	0.78	10.36	2.60
Lat.sy	−0.43	−0.16	1.19	1.95	−0.20	−0.47
Teu.sc	−3.47	−1.44	−4.10	−4.00	−1.85	−3.85
Lot.cn	−0.45	−0.16	2.74	4.55	−0.21	−0.49
Onn.rp	−0.32	−0.12	1.94	3.22	−0.15	−0.35
Ech.vl	−1.40	3.45	2.49	0.36	0.88	8.37
Cir.vl	−0.56	−0.20	1.99	1.75	−0.26	−0.60
Cen.ng	1.62	−0.17	0.96	−0.23	−0.22	−0.52
Mel.at	1.05	−0.36	6.40	7.19	−0.46	−1.07
Sen.ja	−0.35	−0.13	−0.46	−0.83	−0.16	−0.38
Chm.an	−0.38	−0.14	−0.50	−0.89	−0.18	−0.41
Rub.fr	10.74	−0.51	0.32	1.27	−0.65	−1.52

likely to provide higher profit rates. The effect can be estimated crudely by using the regression fitted by Prŷs-Jones (1982). For an arbitrary 100 visits (distributed as observed in Fig. 3E, F), the gross reward expected at Dungeness would be 3.03 mg sugar equivalent and at Shoreham, 2.51 mg. So the gross yield ratio between the localities would be about 1.2. However, if total foraging costs were

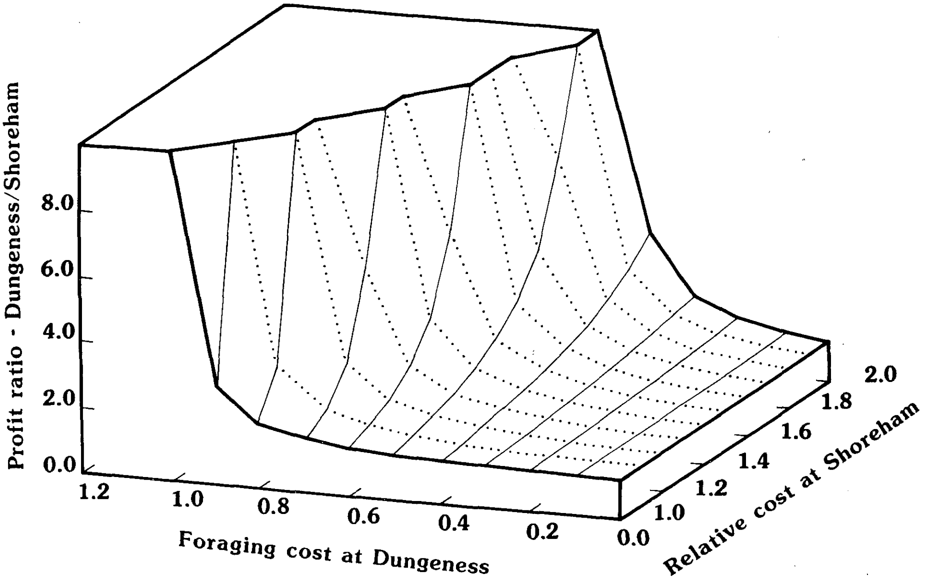

Figure 4. Surface plot to examine a simple model for the ratio of net foraging profit rate at Dungeness in comparison with Shoreham, for a gross sugar-yield ratio of 1.2 (see text). The advantage of greater profit rate at Dungeness increases (z-axis) as the absolute foraging costs increase at both localities (x-axis, expressed for Dungeness as a proportion of the gross yield at Shoreham) and also with increasing relative cost at Shoreham (y-axis), where remunerative flowers appear to be further apart. Realistic values of x and y are likely to lie away from the lower right corner of the x, y plane, so that foraging at Dungeness should generally be much more profitable than foraging at Shoreham (shown by high z values).

to consume similar, large amounts of this yield (e.g. 2.4 mg) in the same time, then the profit ratio could be much higher (5.7, see Fig. 4). In fact the largest component of total cost in the economics of the 'central place' foraging of bumble bees is the time spent travelling (see Heinrich, 1979), so the density of rewarding flowers near the nest is very important. At Shoreham almost all of the flowers visited by bumble bees are restricted to field edges, whereas at Dungeness the profusely flowering patches of *T. scorodonia* are rarely more than a few metres apart throughout most of the survey area. Thus the travelling cost could be much less at Dungeness, which is likely to further increase the mean profit rate at this locality in comparison with Shoreham (Fig. 4). Elsewhere in Kent, other localities that have many species of bumble bees may also be characterized by generally higher profit rates from foraging, because the density of even the ubiquitous species of bumble bees alone is higher at these localities (Williams, 1988).

This distribution-centred model is also more successful than competitive species-packing in accounting for the composition of local assemblages of bumble bee species at what are assumed to be depauperate localities (Williams, 1988). The species-poor assemblage at Shoreham is typical of the majority of localities in the county of Kent. The Shoreham assemblage deviates from a neutral model of species assembly in that it consists of the species that are furthest from their latitudinal limits in Britain. At Shoreham, lower resource levels may be inadequate to support the species in the marginal regions of their distributions, where suboptimal climatic conditions are likely to have already reduced profit rates for them.

Differences in foraging activity have been found among bumble bee species at the same locality with changes in the weather, especially with temperature (e.g. Reinig, 1972; Teräs, 1976), that may reflect differences in their climatic optima. Prŷs-Jones (1986, see also Prŷs-Jones & Corbet, 1987) found differences in the activity of substrate-cycle enzymes among some of these species. These enzymes are among the factors that are likely to affect local thermoregulation costs, and possibly the local reproductive success, climatic optima and the regional distribution of each species.

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