



British Ecological Society

A Study of the Hibernation of Bumblebees (Hymenoptera:Bombidae) in Southern England

Author(s): D. V. Alford

Source: *Journal of Animal Ecology*, Vol. 38, No. 1 (Feb., 1969), pp. 149-170

Published by: British Ecological Society

Stable URL: <https://www.jstor.org/stable/2743>

Accessed: 05-12-2018 06:18 UTC

REFERENCES

Linked references are available on JSTOR for this article:

https://www.jstor.org/stable/2743?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Animal Ecology*

A STUDY OF THE HIBERNATION OF BUMBLEBEES (HYMENOPTERA: BOMBIDAE) IN SOUTHERN ENGLAND

BY D. V. ALFORD

Department of Zoology, Royal Holloway College, Englefield Green, Surrey

INTRODUCTION

In temperate parts of the world such as the British Isles, bumblebee colonies are annual, since only the young queens are able to survive the winter, while the old queens, workers and males all die. The young, fertilized queens produced during the summer months enter hibernation, and it is these bumblebees which reappear in the following spring and later form colonies of their own. In southern England the period of hibernation may last anything from 6 to 9 months, depending on the species and to some extent on spring temperatures. Hibernation is, therefore, an important yet neglected aspect of bumblebee biology.

Previous workers (Sladen 1912; Bols 1937, 1939) have indicated that well-drained banks or slopes with a north or north-west exposure are favourite sites for hibernating bumblebees, and both Wagner (1907) and Sladen (1912) have stated that bumblebees hibernate under trees, but do not give precise details. Bumblebees have also been recorded hibernating in rotten tree stumps (Frison 1926; Tkalcu 1960, 1961), under moss, leaves and piles or rubbish (Verrill, in Putnam 1864; Sladen 1912; and others), and in various other miscellaneous places. Plath (1927, 1934), Frison (1929) and Townsend (1951) have all reported the occurrence of many queens of the New World species *Bombus impatiens* (Cresson) hibernating in very close proximity to one another, and presumably in all these cases the queens were hibernating about the entrance to their maternal nest. However, much of the information on the hibernation of bumblebees so far published has accumulated from casual observations which have not been followed up by more critical data, and apparently only Sladen has investigated the subject of the natural hibernation of bumblebees in this country. In the present studies an attempt has been made to obtain data on various aspects of the natural hibernation of bumblebees and where possible differences between species or groups of species have been investigated.

METHODS OF LOCATING HIBERNATION SITES AND HIBERNATING BUMBLEBEES

Spring queens of both *Bombus Latreille* and *Psithyrus Lepeletier* species that are parasitized by the nematode *Sphaerularia bombi* Dufour do not initiate or invade young colonies but instead, return to their old or similar hibernation sites where they eventually die (Bols 1939; Cumber 1949). Such queens often occur in considerable numbers and so the localities where greater or lesser concentrations of parasitized bumblebees were found in the late spring or early summer were examined later in the year for hibernating queens, since such areas were almost certainly suitable hibernation sites and likely to be occupied.

Well-drained banks, tree-covered slopes and a wide variety of terrestrial undulations were searched in the late summer, autumn and winter, in order to locate hibernating bumblebees. In many instances the hibernation burrows of hibernating queens were located, while in other cases queens were obtained by selective digging in banks, under moss, leaf litter and so on. A few queens were seen searching for hibernation quarters and occasionally queens were observed in the act of excavating their hibernacula.

Most observations were carried out in the vicinity of the Department of Zoology, Royal Holloway College, Englefield Green, Surrey. Much of the region consists of open areas of rough grassland, and deciduous woodland composed principally of oak and birch trees, although areas of beech and Scots pine also occur. The soil is basically Bagshot sand with occasional outcrops of gravel. Studies were also conducted on the **beech-covered chalk slopes** of the Chiltern Hills at Tring, Hertfordshire, but few observations were made elsewhere.

THE HIBERNATION SITES OF BUMBLEBEES

The various sites chosen for hibernation quarters by 142 queens of ten different species are summarized in Table 1. Most queens were found in ground which was well drained and shaded from direct sunlight. Bumblebees of most species found hibernating in the soil tended to avoid overgrown ground, although a covering of litter or moss was no barrier. The number of individuals of each species hibernating under various ground covers is given in Table 2.

Table 1. *Number of hibernating bumblebees found in various sites*

Species	In banks, slopes, etc.	Under trees	Under herbage (away from trees)	Others
<i>Bombus terrestris</i>	1	5	—	—
<i>B. lucorum</i>	3	13	1	2
<i>B. lapidarius</i>	76	2	—	—
<i>B. pratorum</i>	—	2	—	—
<i>B. hortorum</i>	17	5	—	—
<i>B. agrorum</i>	—	—	3	—
<i>Psithyrus vestalis</i>	2	—	—	—
<i>P. barbutellus</i>	3	—	—	—
<i>P. campestris</i>	3	1	—	—
<i>P. sylvestris</i>	1	2	—	—

Table 2. *Number of hibernating bumblebees found below various ground covers*

Species	Condition of ground surface		
	Clear	Moss	Litter or herbage
<i>Bombus terrestris</i>	—	2	4
<i>B. lucorum</i>	2	1	14
<i>B. lapidarius</i>	57	19	2
<i>B. pratorum</i>	—	—	2
<i>B. hortorum</i>	9	10	3
<i>B. agrorum</i>	—	—	3
<i>Psithyrus vestalis</i>	2	—	—
<i>P. barbutellus</i>	3	—	—
<i>P. campestris</i>	4	—	—
<i>P. sylvestris</i>	1	2	—

Exposure

The approximate exposure of the banks, slopes and other terrestrial undulations in which hibernating queens were found is given in Fig. 1. Half of all queens found occurred in ground with a north-west exposure. The remainder were found mainly in sites with a west, north or north-east exposure. Although some queens were found in ground with a more southerly aspect, such sites were always well shaded. Further, queens occurred in southerly facing banks even when suitable, and occupied, north or north-west exposed sites were available nearby.

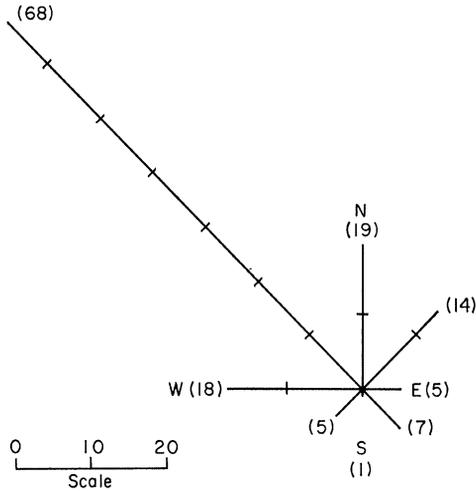


FIG. 1. Exposure of ground in which bumblebees were found hibernating. The number of individuals found in ground of a particular exposure is indicated in each case.

Hibernation in banks, slopes and other terrestrial undulations

Bumblebees were found hibernating in banks, in walls of ditches, in small undulations at the sides of paths and tracks, in more general slopes such as those under a mature beech canopy, and occasionally in isolated mounds of soil. In all instances the ground into which the queens had burrowed was shaded, usually by nearby trees. Most queens found in terrestrial undulations had burrowed into clear ground or through moss. Very few were found beneath litter or herbage. Of all habitats examined, those covered in this section provided the easiest conditions for finding queens since the entrances to subterranean hibernacula were often clearly visible at the surface.

Bombus lapidarius (L.) was by far the most common species present in the situations included in this section, and was found in all manner of places from the smallest undulation of only a few centimetres, to banks and slopes many metres in height. There appeared, in this species, to be little or no selection so far as the degree of slope was concerned. Some queens were found in steep banks and others in more gently sloping ground, even when this was inclined at less than 10° from the horizontal.

Several *Psithyrus* species (*P. vestalis* (Geoffrey in Fourcroy), *P. barbutellus* (Kirby), *P. campestris* (Panzer) and *P. sylvestris* (Lepelletier) were found in similar situations to those selected by *Bombus lapidarius*, but only relatively few queens of this genus were encountered (Table 1). However, *Psithyrus* queens were not common at any time of the

year in the areas under investigation and surprisingly, in view of the commonness of its host *Bombus lapidarius*, no specimens of *Psithyrus rupestris* (F.) were seen.

Several queens of *Bombus hortorum* (L.) were found hibernating in banks, etc. but few specimens of other *Bombus* species. Most queens of *B. hortorum* were found in steep banks with or without a covering of moss. The virtual absence of common species such as *B. terrestris* (L.) and *B. lucorum* (L.) and the complete absence of the abundant species *B. agrorum* (F.) from these sites, was considered to be of significance.

Hibernation under trees

The ground surrounding trees in a wide variety of places was searched during the autumn and winter months for hibernating queens. Generally little or no outward sign of the presence of queens in such places is present since the ground around trees is often covered by leaf litter. This makes the location of bumblebees in such places more difficult than in banks. In all, a total of thirty queens of seven different species were found under trees (Table 1).

A few queens were found close to trees growing on steep banks. Others were found under trees in flatter areas at the edges of woods or plantations, adjacent to clearings, or in lightly wooded areas, but always where the ground was sloping and usually where the slope exposure was more or less north-west. Such sites were always well drained and there was also reasonable shade provided by the trees. In most cases the ground was covered by a layer of litter and was, at least near to the tree trunks, more or less free of living ground vegetation. No queens were found under trees in thickly wooded sites, and none was found under isolated trees in open country.

In order to confirm that queens under trees on general slopes were actually hibernating in relation to the trees, searches were also made in ground identical to that near the trees (at least as far as surface conditions were concerned), at some distance from the tree trunks, but under the tree canopy and therefore similarly illuminated. All such searches proved negative. Unlike queens of *B. terrestris*, *B. lucorum* and *B. pratorum* (L.), most *B. lapidarius*, *B. hortorum* and *Psithyrus* queens included in this section were found under trees which were growing on banks and not on general slopes. It is possible, therefore, that in these cases the hibernation position selected was not directly related to the presence of a tree.

Several queens were found in association with trees with diameters of 40 cm or more, but very dry soil, which often occurs close to the boles of such trees, was never frequented. Smaller trees were also selected by queens. The smallest 'occupied' tree had a diameter of only 15 cm. In one instance a *Bombus terrestris* queen and a *B. lucorum* queen were found beneath the same tree. Most queens were located in the ground on the downward side of the slope from the trees. Some, however, were found up the slope from the trees, even when this meant that they were on the south or south-east side of a trunk. Individuals of four species (*B. lucorum*, *B. pratorum*, *B. hortorum* and *Psithyrus campestris*) were found to have constructed their hibernacula against the bole of the selected tree. More usually, queens were found a short distance from the bases of the trees (mean distance from tree to centre of hibernation chamber 15.4 cm) (Table 3).

Hibernation under herbage or litter not in relation to trees

The absence of such a common species as *Bombus agrorum* from all of the previously examined sites led to the searching of other kinds of habitat. It was noticed that, in June, many *B. agrorum* queens flew low over the ground at the periphery of clearing in woods

Table 3. Distances from trees at which bumblebees were found hibernating

Species	0·0-4·9	5·0-9·9	10·0-14·9	15·0-19·9	20·0-24·9	25·0-29·9	30·0-34·9	35·0-39·9	40·0-44·9	45·0-49·9
<i>Bombus terrestris</i>	1	2	3	3	1	1	-	-	-	1
<i>B. lucorum</i>	-	1	-	5	1	-	-	-	-	-
<i>B. lapidarius</i>	1	-	-	1	-	-	1	-	-	-
<i>B. pratorum</i>	2	1	1	-	1	-	-	-	-	-
<i>B. hortorum</i>	1	-	-	-	-	-	-	-	-	-
<i>Psithyrus campestris</i>	-	-	-	-	1	-	-	-	1	-
<i>P. sylvestris</i>	-	-	-	-	-	-	-	-	-	-

or at the edges of woodland, in areas where there was a definite open but generally shaded piece of ground covered with grass clumps or low herbage such as bracken and brambles. Dissection of some of the queens revealed that they were, as expected, parasitized by *Sphaerularia bombi*. In the late autumn these areas were searched for hibernating queens by clearing the ground cover and examining the underlying soil. Searching in such ill-defined sites was difficult and, consequently, rarely successful. However, three hibernating queens of *Bombus agrorum* were found, two under grass and one in the soil immediately below a layer of bracken litter. In two cases the ground was more or less flat, although well drained. Quite by chance, a queen of *B. lucorum* was found hibernating under a grass sod in a shaded grass-covered slope in a lightly wooded area.

Hibernation near to the maternal nest

When a queen-producing colony was located in the field a search was also made in that area for hibernating queens. Similarly in areas where hibernating queens were known to occur, particular attention was paid throughout the spring and summer to searching for any nests that might be present.

The observed distribution within the study areas of all bumblebee nests and hibernating queens found from 1965 to 1967 showed a negative correlation even when data for all years were summated. In only one instance were queens found hibernating near to a nest. This particular case was of three *B. lapidarius* queens which were hibernating within 2 m of a queen-producing colony of the same species. Unfortunately no opportunity was afforded to mark any young queens from this colony, and it was not possible to confirm that the hibernating queens were actually from this nest. The colony was located on a slope which was known to be a suitable site for hibernating bumblebees and therefore it is doubtful if any significance can be attached to the spatial relationship of nest and hibernating queens in this instance, especially since queens of *B. lapidarius* and other species were found hibernating elsewhere on the slope, where there were no colonies. This nest was the only example located in a known hibernation site.

Miscellaneous sites

A wide range of miscellaneous sites in the field was examined for hibernating bumblebees but without success. However, by chance, two *B. lucorum* queens were found hibernating in the folds of a curtain in an unheated, north-facing first-floor bedroom.

Analysis of site selection data in Table 1

In selected cases, the accuracy of the null hypothesis that the relative number of queens of two given species (or groups of species) in one kind of hibernation site does not differ from the relative number of queens of the same two species (or groups of species) in another kind of site has been tested by using 2×2 contingency tables. The corrected method given by Bailey (1959), for results with low numbers but with expectations greater than 5 units, has been followed in each analysis.

Comparisons have been made of the number of queens of certain species found hibernating in banks, slopes, etc. or under trees, and in each case the null hypothesis is disputed (Table 4). The observed site selectivity by certain species is therefore upheld in that both *B. lapidarius* and *B. hortorum* show a preference for banks and slopes while *B. lucorum* tends to hibernate under trees. Further, as a group the species which emerge from hibernation earlier in the spring (*B. terrestris*, *B. lucorum* and *B. pratorum*) tend to hibernate under trees, in contrast to many later-emerging species (*B. lapidarius*, *B.*

hortorum and *Psithyrus* species) which principally hibernate in banks. Significance between these two groups is shown even when the relatively large *Bombus lapidarius* sample is omitted.

Table 4. Analysis of data summarized in Table 1 to test validity of observed site selectivity by queens of various species

Compared species	No. of individuals in each compared site		χ^2	Probability that null hypothesis is correct
	In banks, slopes, etc.	Under trees		
<i>Bombus lucorum</i>	3	13	55.567	$P < 0.001$
<i>B. lapidarius</i>	76	2		
<i>B. lucorum</i>	3	13	10.486	$P < 0.01$
<i>B. hortorum</i>	17	5		
<i>B. terrestris</i>	4	20	59.388	$P < 0.001$
<i>B. lucorum</i>				
<i>B. pratorum</i>				
<i>B. lapidarius</i>	102	10	17.827	$P < 0.001$
<i>B. hortorum</i>				
<i>Psithyrus</i> spp.				
<i>Bombus terrestris</i>	4	20	17.827	$P < 0.001$
<i>B. lucorum</i>				
<i>B. pratorum</i>				
<i>B. hortorum</i>	26	8		
<i>Psithyrus</i> spp.				

χ^2 , with 1 d.f.

THE HIBERNATION QUARTERS OF BUMBLEBEES

Outward signs of the presence of queens

Normally queens hibernating under litter, as previously mentioned, leave no outward sign of their presence, although in the case of one *Bombus lapidarius* queen found under litter, some particles of soil were present on the surface. Queens burrowing directly into the soil, however, leave very clear signs on the surface which, until washed away by the rain, enable them to be located (Sladen 1912). Typically, a small pile of freshly excavated soil, surmounted by the entrance hole of the hibernaculum, is visible at the surface. The entrance hole of an occupied hibernaculum is usually less obvious than that of a deserted hibernaculum since, in the latter, little or no soil remains in the burrow, because it is forced out as the queen backs out of the ground. The entrance hole tends, therefore, to be more distinct and the pile of soil is often larger. Where a layer of moss covers the surface of the ground, the excavated soil may be particularly obvious.

Hibernacula

Although some of the hibernation chambers discovered were spherical in form—as described by both Sladen (1912) and Bols (1937, 1939)—others were distinctly oval. The size of a chamber naturally depends upon that of the queen. Those of *B. lapidarius*

had maximum diameters of about 26–30 mm, and those of *B. hortorum* a maximum of 25 mm. Where bumblebees hibernated in banks and directly into the soil in other situations, the hibernation chamber was connected to the surface by a straight burrow which was blocked by soil. Burrows of *B. lapidarius* were approximately 11 mm in diameter. Most burrows were formed more or less at right angles to the surface of the ground, but some were inclined somewhat horizontally. The hibernation chamber was usually found at the extreme inner end of the burrow, but sometimes it was at the end but to one side.

Bumblebees hibernating beneath a layer of litter fell into two distinct groups with regard to the position of the hibernation chamber. Some species (*B. terrestris*, *B. lucorum*, *B. pratorum* and *B. agrorum*) constructed their chambers immediately below the soil–litter interface, whereas others (*B. lapidarius* and *B. hortorum*) always burrowed down further into the soil before hollowing out their chambers (Fig. 2).

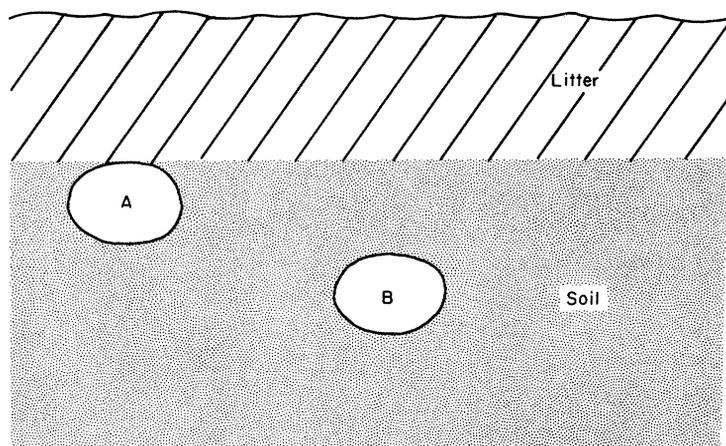


FIG. 2. Position of hibernation chambers of certain bumblebee species in relation to soil–litter interface. (A) *Bombus terrestris*, *B. lucorum*, *B. pratorum*, *B. agrorum*. (B) *B. lapidarius*, *B. hortorum*.

Hibernation depth

The depths at which hibernating bumblebees were found are summarized in Table 5. Measurements were made from the surface of the ground to the centre of the hibernation chamber along a line at right angles to the ground surface. Some queens were found as shallowly as 2 cm but only one individual was found deeper than 15 cm. The latter specimen, a *B. lapidarius* queen, had burrowed through 8 cm of pine needle litter to a depth of 20 cm. Queens were most frequently found at a depth of 8 cm. The depths at which many queens were hibernating could not be determined exactly, either due to the bees being brought to the surface whilst being exposed and the hibernaculum destroyed, or due to collapse of the soil containing the queen and hibernaculum, such as when digging in banks. However, it is possible to state that none of these queens was hibernating at a depth greater than 11 cm.

Although from Table 5 it would appear that some species may hibernate at greater depths than others, the small sizes of samples, coupled with the wide range in the depths at which individuals of each species were found, prevents any significance being shown between different species or groups of species. Further, some of the figures given in Table 5 are not strictly comparable since the depth of a queen hibernating under litter,

Table 5. Mean depths (cm) of bumblebees hibernating beneath various ground covers and in different soils

Species	Clear soil			Moss cover			Under litter	All bees
	Chalk	Intermediate*	Sand	Chalk	Intermediate*	Sand		
<i>Bombus terrestris</i>	-	-	-	2.0(1)	8.0(1)	-	4.8(4)	4.8 ± 2.0
<i>B. lucorum</i>	-	10.0(1)	5.0(1)	-	4.0(1)	-	6.5(13)	6.5 ± 2.3
<i>B. lapidarius</i>	5.6(18)	7.8(9)	9.5(2)	3.8(4)	7.6(10)	8.2(5)	14.0(2)	7.0 ± 2.8
<i>B. pratorum</i>	-	-	-	-	-	-	4.5(2)	4.5 ± 1.5
<i>B. hortorum</i>	3.5(2)	7.1(7)	-	2.0(1)	7.2(6)	10.0(1)	7.0(1)	6.2 ± 2.7
<i>B. agrorum</i>	-	-	-	-	-	-	8.0(1)	8.0
<i>Psithyrus vestalis</i>	-	-	7.0(1)	-	-	-	-	7.0
<i>P. barbutellus</i>	-	-	-	-	8.0(1)	-	-	8.0
<i>P. campestris</i>	4.0(2)	4.0(1)	15.0(1)	-	-	-	-	6.8 ± 5.0
<i>P. sylvestris</i>	10.0(1)	-	-	4.0(1)	11.0(1)	-	-	8.3 ± 3.1

* Soil heavier than sand but lighter than chalk.

Number of observations contributing to each mean given in parentheses.

and possibly other ground covers such as moss, may be influenced by the thickness of such a layer. No difference was found, however, between the depths of queens burrowing through moss or into clear soil for either the *B. lapidarius* or *B. hortorum* samples.

One factor with an effect upon the depth at which queens hibernate is the texture of the soil into which they must burrow. Queens of *B. lapidarius* were found at a mean depth of 5 cm in chalky soil (twenty-two queens sampled from Tring, Hertfordshire), and at a mean depth of 8 cm in more or less sandy soil (twenty-six queens sampled from Englefield Green, Surrey). The difference between the depths of these samples was significant ($P < 0.001$). Data for other species also suggest that queens will burrow deeper in a light soil than in a heavier one (Table 5).

THE BEHAVIOUR OF QUEENS AT HIBERNATION SITES

Before hibernation

Queens of *Bombus lapidarius* searching for hibernation quarters were observed from the time that they arrived at hibernation sites. Once in a suitable area, the queens flew slowly over the ground at a height of a few centimetres. They settled at intervals and then crawled over and occasionally scratched at the surface of the ground. On finding a suitable place to dig, a queen would start to burrow into the soil. Queens were so engrossed in their digging that they could be covered with a glass tube or pill box without being disturbed. A *B. lapidarius* queen burrowing into semi-chalky soil took 32 min from commencing to dig until disappearing from sight. This time agrees with the estimates of both Wagner (1907) and Bols (1937), but no doubt the speed at which a queen will burrow depends upon the hardness of the ground. Queens use their mandibles and legs whilst digging, and occasionally back out of the burrow to force loosened soil out of the way (Wagner 1907). This soil forms the mound at the entrance to the hibernaculum, while soil from the chamber serves to block up the burrow.

Occasionally a queen would back out of the burrow she was excavating and start to dig another one a short distance away. Examination of these deserted burrows always showed that they abutted on a stone or root at a depth of only a few centimetres. No evidence was found to suggest that a queen would ever attempt to bypass underground obstructions. In several instances where deserted burrows were found, an occupied hibernaculum was found nearby.

During hibernation

When hibernating queens were disturbed in the late summer or early autumn, they quickly became active and vibrated their wings, producing an audible, low-pitched buzz. Such behaviour was exploited when searching in the soil for hibernating queens during dull weather or in dimly lit sites, since on many occasions queens could be heard long before they could be seen. The vibration of the wing muscles rapidly raised their body temperature and in a short time they were able to fly. When dug up in mid-winter, queens were in a torpor although they did become active when warmed in the palm of the hand. This has also been observed by Plath (1927, 1934). Although some queens were on their backs when found, as were those found by Bols (1937), others were in a crouched position. Due to the tendency of queens to alter their position when disturbed, especially in the early stages of hibernation, it was often difficult to say whether or not a queen was in its original position when finally exposed. However, torpid queens obtained in mid-winter were all found in a crouched position within their hibernacula.

After hibernation

Known hibernation sites were visited frequently at various times of the day from late February onwards, but no queens were observed to emerge from their winter quarters. Following their emergence, however, hibernated queens were commonly found foraging in adjacent areas. Cumber (1953) states that in cool weather, before colonies have been founded, spring queens often crawl beneath vegetation in the vicinity of their food plants and reappear when conditions become more favourable. The present writer observed several spring queens in foraging areas creeping into matted vegetation towards evening, presumably to spend the night. It should be emphasized, however, that hibernation sites were not used as night refuges and there was no tendency for healthy spring queens to assemble in such areas as described by Bols (1939). Queens parasitized by *Sphaerularia*, however, inhabited hibernation sites both in the spring and early summer. Some of these queens attempted to burrow directly into the ground while others flew slowly over the surface and occasionally forced their way under leaf litter or other dead vegetation. Queens in the earlier part of the spring were reasonably active and easily disturbed, but those present at a later date were more laboured in their movements and less easily disturbed. There was a distinct preference shown by parasitized queens of different species for particular types of hibernation site. Most *Bombus lapidarius*, *B. hortorum* and *Psithyrus* queens frequented slopes or banks, while *Bombus terrestris* and *B. lucorum* queens tended to occur on tree-covered slopes. In addition *B. agrorum* queens, and one *B. ruderarius* (Müller) queen, were observed in more open, flatter ground with a covering of bracken or rough grass, but within the shadow of adjacent trees. The site preferences of hibernating queens of various species (Table 1) are identical to those shown by the parasitized queens. These observations on queens parasitized by *Sphaerularia bombi*, therefore, support the specific site selection data already presented.

PHYSIOLOGY

Changes in weight and water content

The amount of water in queens prior to their entry into hibernation shows considerable variation, but generally represents between 60% and 70% of their total live weight. Water forms about 57% of the live weight of queens at the commencement of hibernation, and this figure remains relatively constant throughout the whole period of hibernation, during which time there is a reduction of approximately one-half in both the live and dry weight of queens. Immediately after hibernation, however, there is a marked increase in the relative amount of water in the body, following post-emergence feeding (Table 6).

Utilization of fat body reserve

Reserves of fat and glycogen, but not protein as is mistakenly implied by Palm (1948), are accumulated in the fat bodies of queens prior to their entry into hibernation (Alford 1967). At the start of hibernation fat forms from 11% to 16% of the total live weight of queens (mean 13%), and on average some 34% of their total dry weight. About 80% of the fat stored in queens is utilized during hibernation, most being used in the first half of the hibernation period (Table 6). Histochemical tests suggest that the glycogen reserves, unlike fat, may be more substantially reduced during the winter months than in the autumn.

L. J.A.E.

Table 6. Mean water and fat content of queens sampled during or immediately after hibernation

Species	n	Live weight (mg)	Dry weight (mg)	Fat (mg)	Water (mg)	Water (% live weight)
In hibernation: autumn						
<i>Bombus lucorum</i>	(1)	663.8	288.4	76.1	375.4	56.6
<i>B. lapidarius</i>	(5)	810.4	342.5	96.7	467.9	57.7
<i>B. hortorum</i>	(2)	634.5	277.2	99.4	257.3	40.6
In hibernation: winter						
<i>B. lucorum</i>	(2)	619.0	276.0	30.4	343.0	55.4
<i>B. lapidarius</i>	(1)	524.3	215.5	28.4	308.8	58.9
<i>B. hortorum</i>	(4)	426.2	177.0	31.0	249.2	58.5
In hibernation: spring						
<i>B. hortorum</i>	(2)	336.4	148.2	21.9	188.2	55.9
Immediately after hibernation						
<i>B. lucorum</i>	(5)	510.0	149.6	12.5	360.4	70.7
<i>B. lapidarius</i>	(5)	517.6	151.4	6.1	366.2	70.7
<i>B. hortorum</i>	(2)	361.2	118.0	6.4	243.2	67.3

n, Number of observations.

Utilization of honey stomach contents

The honey in the crop or honey stomach of hibernating queens contains 20% water and at the commencement of hibernation represents 23.3% of the live weight of queens. In some cases there may be more than 200 mg of honey in the crop (Table 7). During the

Table 7. Amount of honey in crops of bumblebees sampled from natural hibernacula at various times during hibernation

Month	Species	Total live weight (mg)	Honey (mg)	Honey (% live weight)
September	<i>Bombus terrestris</i>	883	154	18
	<i>B. lucorum</i>	760	165	22
	<i>B. lapidarius</i>	733	185	25
	<i>B. lapidarius</i>	838	170	20
	<i>B. lapidarius</i>	794	160	22
	<i>B. lapidarius</i>	862	194	23
	<i>B. lapidarius</i>	831	220	27
	<i>B. lapidarius</i>	811	168	21
	<i>B. lapidarius</i>	793	150	20
	<i>B. lapidarius</i>	840	200	24
	<i>B. lapidarius</i>	824	209	25
	<i>B. lapidarius</i>	705	228	32
	<i>B. lapidarius</i>	830	223	27
December	<i>B. terrestris</i>	605	77	13
	<i>B. lucorum</i>	593	98	17
	<i>B. lucorum</i>	645	127	20
	<i>B. lapidarius</i>	524	45	9
	<i>B. pratorum</i>	313	19	6
	<i>B. hortorum</i>	474	22	5
	<i>B. hortorum</i>	551	22	4
	<i>B. hortorum</i>	424	78	18
	<i>B. hortorum</i>	397	8	2
	<i>B. hortorum</i>	461	15	3
	<i>B. hortorum</i>	423	57	13
	<i>B. hortorum</i>	437	31	7
	March	<i>B. hortorum</i>	424	28
<i>B. hortorum</i>		249	13	5

autumn, the contents of the crop are considerably reduced and apparently, as with fat, more honey is utilized at this time than in the second half of the hibernation period. Although the relative amount of honey in the crop of queens at the start of hibernation was reasonably constant, the quantities present in individuals sampled in mid-winter showed considerable variation, ranging from 8 mg to 127 mg (Table 7).

THE EMERGENCE OF BUMBLEBEES FROM HIBERNATION

It is generally agreed that the emergence of bumblebees from hibernation is governed by temperature and it is known that some species appear earlier in the spring than others (Hoffer 1882–83; Sladen 1912; Plath 1934; and others). Both Siivonen (1942) and Stein (1956) have produced data which relate the emergence of bumblebees to spring temperatures. Stein (1956) also investigated ground temperatures at a depth of 20 cm and found that maxima were about 5–6° C at the time of appearance of *Bombus terrestris* and 9° C when *B. lapidarius* appeared. No details are given of the site chosen for the measurements and why a depth of 20 cm was chosen is not stated. The assumption usually drawn from observations made on the appearance of hibernated queens in the spring is that the various species have different threshold temperatures of arousal. The ecological conditions under which different species hibernate and any effect these may have on the influence of spring temperatures on the queens, however, are never taken into account. The present ecological studies have shown that the early-emerging species *B. terrestris*, *B. lucorum* and *B. pratorum* typically hibernate immediately below the soil–litter interface close to trees, while later-emerging species such as *B. lapidarius*, *B. hortorum* and *Psithyrus* species, usually hibernate directly in banks or slopes. In order to investigate the possible effect that these site differences might have on the emergence of queens, a study was made of the relationship of spring temperatures and subterranean temperatures in hibernation sites typical of early- or late-emerging species.

Methods

Subterranean temperature measurements at hibernation sites were obtained by using matched Grant thermistor thermometer probes (Type 'C'). Each probe consisted of a thermistor bulb enclosed at the tip of a stainless steel tube measuring 51 × 3 mm and was attached to a lead which led to where readings could conveniently be taken. Spot readings were made with a Grant thermistor thermometer (Model 'S'), and continuous recordings were obtained by Grant miniature temperature recorders. Under field conditions the power source supplied with the continuous recorders (mercury cells) proved wholly inadequate due both to failure at ambient temperatures below +4° C and to rapid loss of power during continuous operation at higher temperatures. Four Nife cells wired in series were substituted for the mercury cells on each recorder and these operated satisfactorily during continuous running under a wide range of ambient conditions. Recharged Nife cells were fitted every 2–3 weeks.

In March 1966, provisional data were obtained using two probes and recording temperatures from these with the Model 'S' thermometer. One of the probes was located in a bank and the other under litter near a tree. The position of each probe tip was intended to approximate to the centre of a natural hibernation chamber. Both probes were located in similar soil in known hibernation sites near the Department of Zoology, Royal Holloway College. In January 1967, in the same area, two probes (A and B) were dug into the soil of banks in which *Bombus lapidarius* queens were known to hibernate,

and two (C and D) were placed in the soil below the soil-litter interface under trees at sites where *B. lucorum* and other early appearing species had previously been found hibernating. The positions of the probes in both kinds of site are shown diagrammatically in Fig. 3. Probes A and C were later connected to the continuous recorders. Spring air temperatures were obtained from thermometers inside a Stevenson screen.

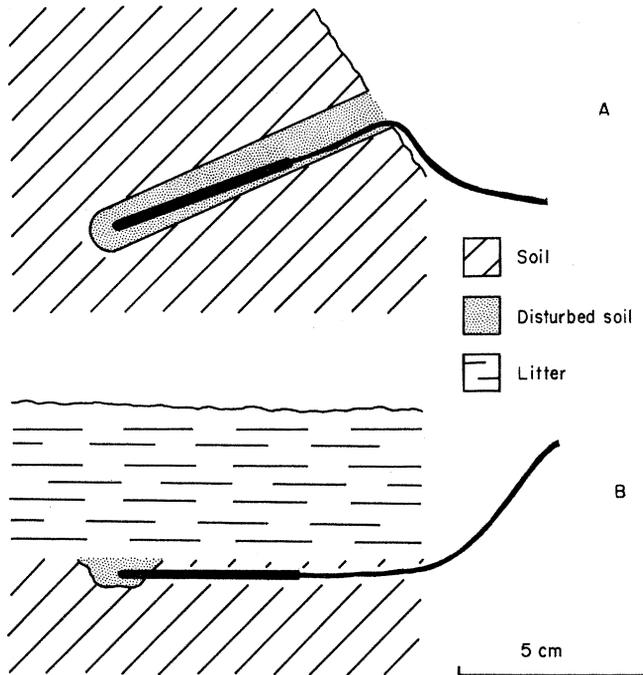


FIG. 3. Position of thermistor probes in two types of situation from which subterranean temperature records were obtained. (A) Probe in bank, (B) probe under litter.

Results

The daily maximum and minimum air temperatures for the period February–April, for 1965–67, are given in Fig. 4, and the day on which spring queens were first recorded in each year is also indicated. In Table 8 details of the first emergence dates for individual species are given. *B. terrestris* and *B. lucorum* were always the first species recorded, and both became relatively common in advance of other species with the possible exception of *B. pratorum* and *B. jonellus* (Kirby). Individuals of other species appeared more spasmodically, *B. agrorum* and *B. hortorum* becoming common slightly earlier than *B. lapidarius*. Data for other species, including *Psithyrus* queens, are unreliable because relatively few individuals were recorded at any time. In all three springs, queens of *Bombus lapidarius* were well out by the end of April, and in view of this, no temperature measurements were taken after this time.

The highest daily temperatures recorded by spot readings from a thermistor probe in a bank and a probe under litter near a tree, for the period 8–18 March 1966, are given in Fig. 5. The daily maximum air temperatures are also shown. The probe results are subject to error since without continuous recordings the true daily maxima may not be recorded. However, they do suggest that temperature differences between the two types of site

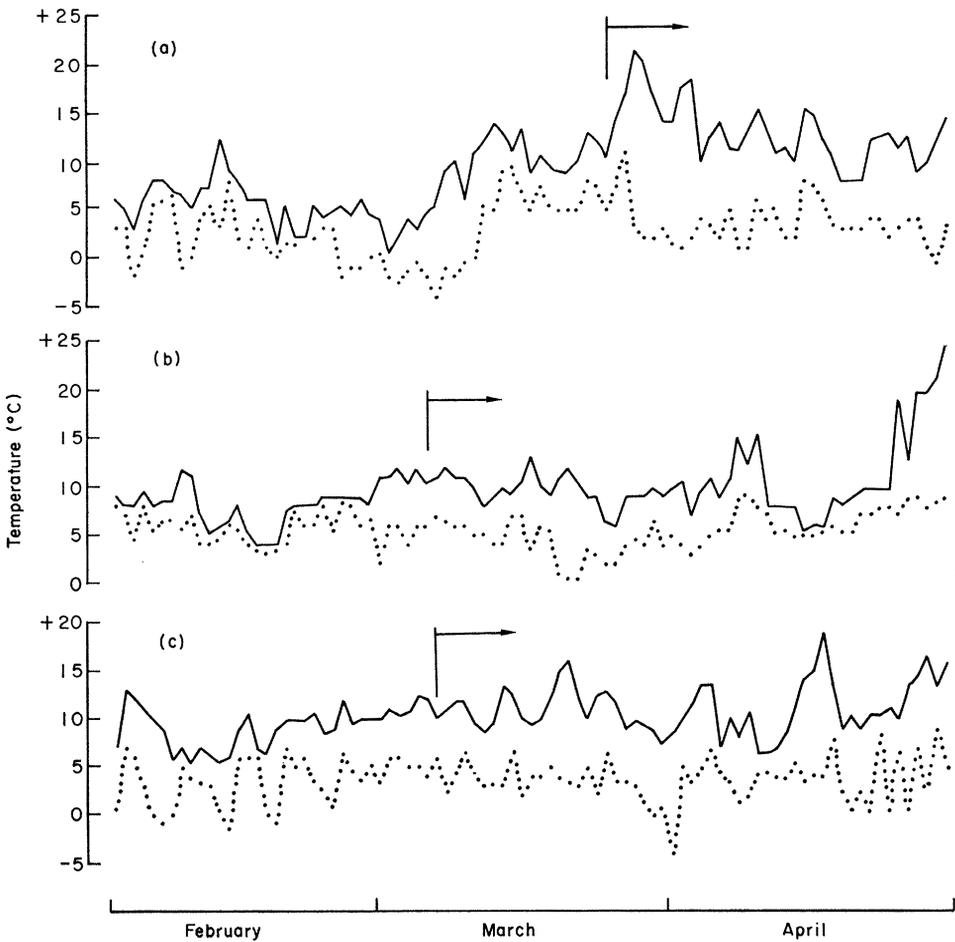


FIG. 4. Daily maximum (—) and minimum (· · ·) air temperatures in experimental area for the springs of (a) 1965, (b) 1966 and (c) 1967. The first appearance of hibernated queens in each year is indicated on the relevant graph.

Table 8. *Date of first recorded appearance of spring queens of various bumblebee species following their emergence from hibernation (1965–67)*

Species	1965	1966	1967
<i>Bombus terrestris</i>	25 March	7 March	7 March
<i>B. lucorum</i>	25 March	8 March	7 March
<i>B. lapidarius</i>	30 March	8 March	22 March
<i>B. pratorum</i>	26 March	6 March	20 March
<i>B. jonellus</i>	29 March	9 March	14 March
<i>B. hortorum</i>	29 March	9 March	22 March
<i>B. ruderarius</i>	29 March	10 April	22 March
<i>B. agrorum</i>	29 March	7 March	20 March
<i>Psithyrus sylvestris</i>	31 March	18 March	—

exist. Spot readings from the four probes used in 1967 are given in Table 9. Although these readings are subject to the same errors as those taken in 1966, they suggest that the temperature in banks is lower than that under litter.

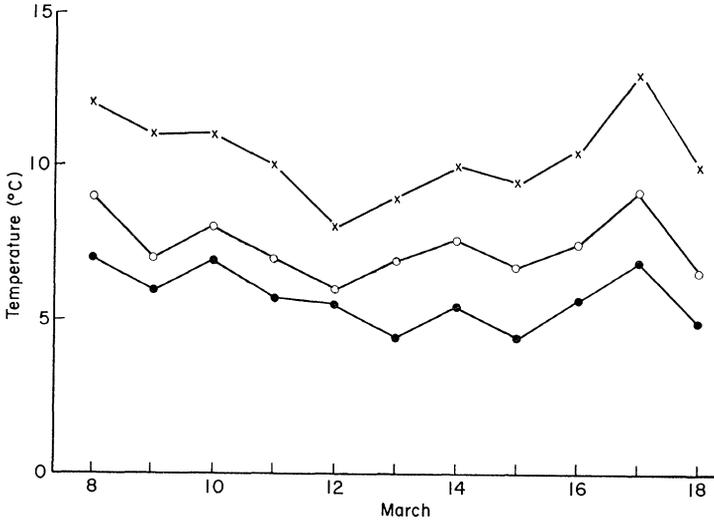


FIG. 5. Maximum recorded temperatures from Stevenson screen (x), thermistor probe under litter (o) and thermistor probe in bank (●), for March 1966.

Table 9. *Spot readings of thermistor probe temperatures (1967)*

Date and approximate time of readings (hours, G.M.T.)		Air temperature (°C)	Probe temperatures (°C)			
			In bank		Under litter	
			A	B	C	D
February						
6	08.30	3.0	2.75	1.5	3.5	3.5
6	15.00	7.5	3.8	3.3	4.9	4.9
7	14.00	6.0	4.0	4.0	5.0	5.2
8	14.00	6.0	2.75	2.0	3.75	3.5
9	13.45	6.0	2.5	2.5	4.0	4.0
13	08.30	1.0	1.5	0.25	2.0	1.7
13	14.45	4.0	2.25	0.6	2.5	2.3
14	11.00	1.0	0.5	-0.3	1.25	1.25
15	14.00	7.0	2.7	2.0	4.0	3.75
20	15.00	7.0	5.0	5.0	5.7	5.5
21	10.30	9.0	5.0	5.0	5.9	5.9
23	11.15	6.5	5.2	5.0	5.2	5.4
24	10.20	6.5	3.0	2.0	4.0	4.0
24	14.45	7.0	4.4	4.3	5.8	4.8
27	09.30	-	4.1	3.4	4.6	4.2
March						
1	15.30	8.5	5.5	4.6	6.0	5.6
2	14.15	-	5.5	5.5	7.0	6.0
6	08.45	8.5	6.2	5.5	6.2	5.75
6	13.15	9.0	7.7	7.7	8.2	7.0
8	10.45	7.0	5.9	6.0	7.5	6.25
14	12.00	-	6.3	6.25	7.1	7.3
21	12.40	-	6.6	7.0	9.0	8.75

The continuous recordings obtained from probes A and C in 1967 enable the actual daily maxima to be obtained and these are shown in Fig. 6, along with the daily maximum air temperatures. Readings from probe C were ended on 25 March because the litter cover was disturbed during the night, probably by a small mammal. The gap in the trace from probe C at the beginning of February was due to the jamming of the chart winding mechanism and that in the bank trace at the end of March, to battery failure. When

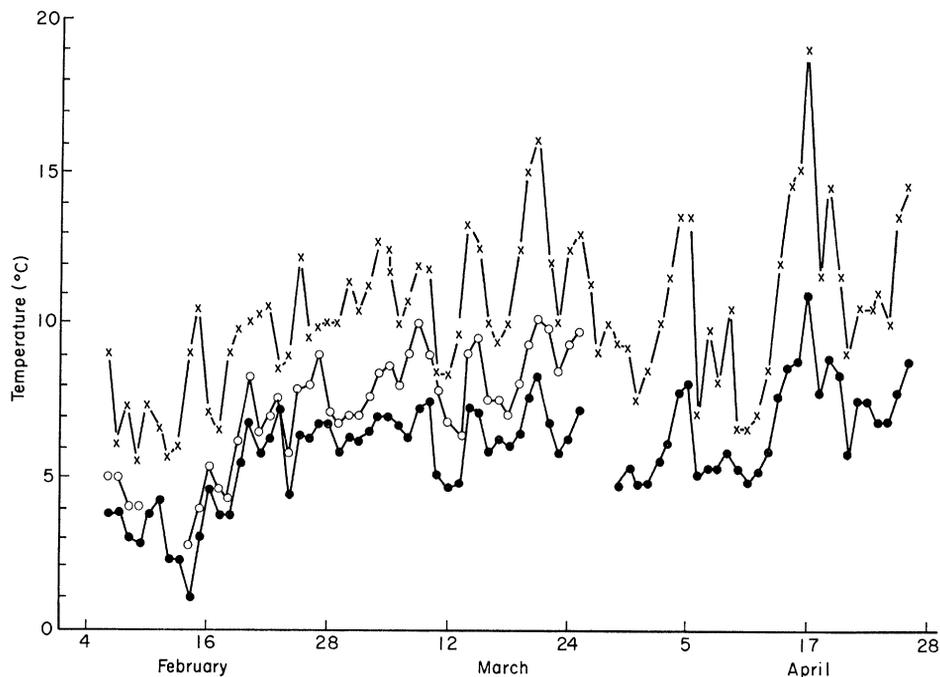


FIG. 6. Maximum recorded temperatures from Stevenson screen (\times), thermistor probe C (under litter) (\circ), and thermistor probe A (in bank) (\bullet), for the period February–April 1967.

readings were ended, it was confirmed that each probe was still in its original position. Throughout the 1967 experimental period the daily maximum temperatures recorded from probe C were above those from probe A (Fig. 6). The mean daily difference for February was $1.05 \pm 0.50^\circ \text{C}$ and for March $1.80 \pm 0.70^\circ \text{C}$. The trace obtained from probe A was gently undulating, showing that temperature changes were gradual, and the daily maxima were generally reached in the late afternoon or early evening. The trace from probe C was similar, except that, especially in response to rising temperatures, it was more uneven and the maximum point was reached an hour or more ahead of that of probe A. These results confirm those from spot readings which indicated that daily maximum spring temperatures were higher under litter than in banks, and suggest that queens hibernating in banks may be aroused later in the spring than those under litter, since a given threshold temperature will not be reached in a bank until later in the season.

DISCUSSION

In southern England, and elsewhere (Hoffer 1882–83; and others), *Bombus pratorum* is one of the first species to enter hibernation. Colonies of this species are normally at

an end by mid-July or even earlier, which is often long before some species produce queens. *B. lapidarius* queens were observed entering hibernation from July onwards, showing, in support of other writers such as Plath (1934), that initiation of hibernation is not governed by the onset of autumn weather as erroneously thought by Wagner (1907) and Stein (1957).

Details of the stimuli responsible for initiating a queen's entry into hibernation are unknown. According to Detinova (cited by Lees 1955) there appears to be in *Anopheles maculipennis* Meig. an association between the inactivity of the corpus allatum and hibernation, and a similar association has been demonstrated in the Colorado beetle (de Wilde 1953). Since in bumblebees the corpora allata are inactive until the final stages of hibernation (Palm 1948), there may be a connection between their inactivity and hibernation. The corpora allata of spring queens parasitized by *Sphaerularia* are also apparently inactive (Palm 1948) which is indicative of similarities in the physiology of these queens and those approaching hibernation. This may explain why the behaviour of parasitized spring queens is similar to that of autumn queens about to enter hibernation.

Queens entering hibernation have considerable reserves of fat and glycogen in their fat bodies, and are normally fertilized. Cumber (1954) found that all the queens he dissected in the spring were fertilized, and all hibernating queens and spring queens dissected in the present studies were mated. The absence of unfertilized queens in the spring may be explained in several ways. Either unmated queens are usually unable to survive the winter or do not normally enter hibernation, or the chances of a queen mating are very high, so that few, if any, queens remain unfertilized. The development of fat bodies in young queens is not dependent upon previous fertilization (Free, in Free & Butler 1959) and in any case the reserves mainly accumulate in the first few days of adult life (Alford 1967), that is, before the normal time of mating. This strongly suggests that there is no reason why unmated queens should not survive the winter, and Cumber (1953) found unfertilized queens surviving among the bumblebees he was overwintering under artificial conditions. It is possible that an unmated queen is reluctant to enter hibernation but there is no evidence to show that such a queen will not do so. However, if, as seems likely from the evidence of dissections, the chances of young queens becoming fertilized are very high, then this is sufficient to explain the absence of unfertilized individuals in and following hibernation.

Many insects lay down reserves of fat and glycogen in their fat bodies before their entry into hibernation (Lees 1955) and according to El-Hariri (1966) glycogen instead of fat is consumed by hibernating coccinellid beetles during periods of very low temperature, although in these insects, in common with many others, fat is the most important stored source of energy. Since glycogen reserves in bumblebees appear to be consumed mostly during the winter months, this reserve may be important for their survival during periods of colder weather.

Before leaving the maternal colony in order to enter hibernation, a queen fills her crop with honey (Sladen, 1912). Sladen considered that this honey was especially needed as a source of food '... during September, when the ground is often very dry and warm.' It is at this time that a queen's metabolic rate will probably be somewhat higher than during most of the hibernation period and results have shown that most of the honey in the crop is used up during the autumn, as suspected by Sladen. It is unlikely, however, that the water content of the honey is of importance in offsetting desiccation since sufficient metabolic water will be available from the breakdown of the fat body reserves.

The honey remaining in the crop during the winter is probably particularly important as a source of energy from the end of diapause until the queen is able to forage.

The situations in which queens hibernate are varied but are typically well drained and shaded from direct sunlight. Hence sloping sites with a north-west exposure predominate. Sladen (1912) has suggested that such sites are most suitable because they will not tend to be warmed by the winter sunshine and so queens will remain undisturbed until the warm days of spring. Bols (1939) has referred to the numerous natural hazards faced by hibernating queens, but what percentage of those entering hibernation actually survive is unknown and in natural populations would be difficult to measure. The relative merits of the different types of hibernation site selected by queens are also hard to assess. Some species, as has been shown for *Bombus lucorum*, are somewhat adaptable in their choice of a hibernation site, but an element of preference within this, and other, species is usually found, which may be related to the normal time of appearance in the spring of hibernated queens of that species. Thus, *B. terrestris*, *B. lucorum* and *B. pratorum* typically hibernate immediately below the soil-litter interface close to trees, and all emerge earlier in the spring than *B. lapidarius*, *B. hortorum* and *Psithyrus* species, which usually hibernate in banks or slopes. There is apparently little or no relationship between the type of site chosen for hibernation and that selected for nesting, since the species that form colonies deeper in the ground than others (for example the subterranean-nesting species *Bombus terrestris*) are often found hibernating in the more superficial types of site. The present work has established that queens do not normally hibernate close to their maternal nests, and shows that Plath (1934) is not justified in concluding from Sladen's (1912) observations on *B. lapidarius* that this species usually does so. There would appear to be no reason why queens should hibernate next to their old nest, unless the colony were situated on or in a suitable hibernation site. Few positive data have been accumulated on the hibernation habits of the surface-nesting species or 'carder-bees' such as *B. agrorum*, *B. ruderarius* and *B. humilis* (Illiger), but it is possible that these species may all hibernate in similar situations to those in which *B. agrorum* queens were found. Presumably carder-bees rarely, if ever, hibernate in banks or under trees, since none was found in such sites in the present studies and Bols (1937, 1939) recorded very few specimens from the hibernation slope he investigated in Belgium. Observations made on queens parasitized by *Sphaerularia* support this view.

Some earlier writers on the hibernation of bumblebees (Huber 1802; Hoffer 1882-83; Sladen 1900; Wagner 1907) considered that queens overwintered in the ground at considerable depths from the surface. These early opinions, which are now known to be incorrect, were no doubt based on the assumption that queens would not be able to survive at low temperatures and would therefore need to burrow down deeply into the ground below the frost line, in order to survive the winter. The depths at which later workers have recorded bumblebees (2.5-7.5 cm by Sladen (1912) and 10-13 cm by Bols (1937)) are in accord with the present findings.

Since the appearance of queens in the spring is related to temperature, it follows that the conditions under which individuals hibernate will have an effect upon emergence. Results from temperature measurements in hibernation sites have indicated that hibernacula of species hibernating immediately below the soil-litter interface close to trees are subjected to higher daily maximum temperatures in the spring than chambers in banks or slopes. It is significant that the warmer sites are typical of early-emerging species, while the later-emerging species generally hibernate in banks or slopes. Later-emerging species may tend to hibernate at greater depths than early-emerging species, but this could not

be positively demonstrated. It may be that both an effect due to hibernaculum position and to specific physiological differences is involved in governing when a queen of a particular species will emerge from hibernation. However, although the suggestion that different bumblebee species have different arousal threshold temperatures cannot be ruled out, ecological conditions alone could explain this phenomenon.

It is unlikely that minimum or mean daily temperatures influence the time of emergence of bumblebees, since queens will appear on warm days whether nights are cold or not, so long as their hibernation quarters warm up sufficiently. Also, as previously mentioned, hibernating queens will become active, even in mid-winter, if warmed artificially. Further, it has been shown by Soulié (1957) that the hibernation of ants (*Crematogaster scutellaris* Ol.) may be disrupted by frequently repeated temperature maxima and that neither mean nor minimum temperatures are involved.

Inevitably, local topographical features will affect the time of emergence of spring queens, by influencing ambient temperatures. Also, queens hibernating in sandy soil will probably be aroused earlier than queens in similar situations, but in damper, heavier soil. A tendency for queens to burrow deeper in sandy conditions, because of the ease of burrowing, would close the gap between emergences in such cases, and it is interesting to find that queens in sandy soil were deeper than those in chalky sites.

Observations by Latter (in Fox-Wilson 1946) suggest that light penetrating into the hibernaculum may be effective in arousing hibernating wasps. Most bumblebees hibernate in the dark and will not be affected by light. However, occasionally bumblebees do hibernate in places where light may penetrate, as did the *Bombus lucorum* queens found in the folds of a curtain, and light may influence the time of emergence in such cases.

Accounts of the behaviour of queens following their emergence from hibernation are confused because observers have usually neglected to determine whether healthy or *Sphaerularia*-infected queens were being studied. Many of the habits of parasitized individuals have, therefore, been credited to healthy queens as well, as in Bols (1937). Réaumur (1742) found queens digging into the soil of a slope during the spring and Plath (1927) suggested that these observations were actually made on queens that were about to enter hibernation and that Réaumur had '... placed them in the spring by mistake.' In his later review of bumblebee hibernation, Plath (1934) alternatively suggests that Réaumur was observing queens that had overwintered and were digging into the ground to spend the night. It is more likely, however, that these queens were parasitized by *S. bombi* and had returned to a hibernation site. Between the time of their emergence from hibernation and the founding of colonies, queens pass the night in any convenient sheltered situation, especially to avoid the dangers of a night frost. They do not attempt to find, or habitually return to, special sites each night. Burrowing into the soil would appear quite unnecessary and since the duration of their stay may be measured in hours rather than in weeks or months, there would appear to be no great ecological requirement of such a site other than that it should offer a certain degree of protection.

ACKNOWLEDGMENTS

This work was carried out during the tenure of a Science Research Council studentship and forms part of a thesis approved for the degree of Doctor of Philosophy in the University of London. It is a pleasure to thank Dr A. J. Pontin for his interest and advice throughout this study and Professor P. M. Butler for providing facilities at the Department of Zoology, Royal Holloway College.

SUMMARY

1. The ecological conditions under which bumblebees hibernate have been investigated and differences noted in the type of site chosen for overwintering by certain species. *Bombus lapidarius* (L.), *B. hortorum* (L.) and *Psithyrus* Lepeletier species typically hibernate in banks or slopes, while *Bombus terrestris* (L.), *B. lucorum* (L.) and *B. pratorum* (L.) usually hibernate below the soil-litter interface close to trees.

2. It is confirmed that shaded, well-drained sites with a north-west exposure are most frequented, and that queens do not normally hibernate about the entrance to their maternal nest.

3. Bumblebees were most frequently found hibernating in the soil in spherical or oval chambers at a depth of 8 cm, but the depths at which queens occurred varied considerably according to ground conditions. Thus, *B. lapidarius* queens were found at a mean depth of 5 cm in chalky soil and 8 cm in lighter, sandy soil.

4. The behaviour of queens at hibernation sites before, during and after hibernation is described and that of spring queens parasitized by *Sphaerularia bombi* Dufour is discussed. Healthy spring queens do not habitually use hibernation sites as night refuges, prior to founding colonies.

5. A brief account of the physiology of hibernating queens is given. Most reserves of honey and fat present in queens at the commencement of hibernation are utilized in the autumn. Glycogen reserves, however, are apparently consumed mainly in the winter months.

6. Studies of the spring emergence of bumblebees have demonstrated that spring temperatures in hibernaculum positions typical of early-emerging species such as *Bombus lucorum* show higher daily maxima than subterranean temperatures in positions typical of later-emerging species such as *B. lapidarius*. The effect of ecological conditions on the emergence of bumblebees from hibernation is discussed.

REFERENCES

- Alford, D. V. (1967). *Some studies on the biology of bumblebees (Hymenoptera: Bombidae)*. Unpublished Ph.D. thesis, University of London.
- Bailey, N. T. J. (1959). *Statistical Methods in Biology*. London.
- Bols, J. H. (1937). Observations on *Bombus* and *Psithyrus*, especially on their hibernation. *Proc. R. ent. Soc. Lond.* (A), **12**, 47–50.
- Bols, J. H. (1939). Un remarquable terrain d'hivernation de *Bombus* et de *Psithyrus* près Louvain, à Lubbeek, en Belgique. *Verh. VII int. Congr. Ent.* 1048–60.
- Cumber, R. A. (1949). Humble-bee parasites and commensals found within a thirty mile radius of London. *Proc. R. ent. Soc. Lond.* (A), **24**, 119–27.
- Cumber, R. A. (1953). Some aspects of the biology and ecology of humble-bees bearing upon the yields of red-clover seed in New Zealand. *N.Z. Jl Sci. Technol.* B, **34**, 227–40.
- Cumber, R. A. (1954). The life-cycle of humble-bees in New Zealand. *N.Z. Jl Sci. Technol.* B, **36**, 95–107.
- El-Hariri, G. (1966). Studies of the physiology of hibernating Coccinellidae (Coleoptera): changes in the metabolic reserves and gonads. *Proc. R. ent. Soc. Lond.* (A), **41**, 133–44.
- Fox-Wilson, G. (1946). Factors affecting populations of social wasps, *Vespa* species, in England (Hymenoptera). *Proc. R. ent. Soc. Lond.* (A), **21**, 17–27.
- Free, J. B. & Butler, C. G. (1959). *Bumblebees*. London.
- Frisson, T. H. (1926). Contribution to the knowledge of the inter-relations of the bumblebees of Illinois with their animate environment. *Ann. ent. Soc. Am.* **19**, 203–36.
- Frisson, T. H. (1929). A contribution to the knowledge of the bionomics of *Bombus impatiens* (Cresson) (Hym.). *Bull. Brooklyn ent. Soc.* **24**, 261–85.
- Hoffer, E. (1882–83). *Die Hummeln Steiermarks. Lebensgeschichte und Beschreibung derselben*. Graz.
- Huber, P. (1802). Observations on several species of the genus *Apis*, known by the name of humble-bees, and called Bombinatrices by Linnaeus. *Trans. Linn. Soc. Lond.* **6**, 214–98.

- Lees, A. D. (1955). *The Physiology of Diapause in Arthropods*. Cambridge.
- Palm, N. B. (1948). Normal and pathological histology of the ovaries in *Bombus* Latr. (Hymenopt.). *Opusc. ent.* (suppl.) 7, 1–101.
- Plath, O. E. (1927). Notes on the hibernation of several North American bumblebees. *Ann. ent. Soc. Am.* 20, 181–92.
- Plath, O. E. (1934). *Bumblebees and their Ways*. New York.
- Putnam, F. W. (1864). Notes on the habits of some species of humble bees. *Proc. Essex Inst., Salem. Mass.* 4, 98–104.
- Réaumur, [R. A. F.] de (1742). Histoire des Bourdons velus, dont les nids sont de mousse. In: *Memoires pour servir a l'Histoire des Insectes*. 6, 1–38.
- Siiivonen, L. (1942). Zur Phänologie des Frühjahrsauftretens der Hummel (*Bombus*, Hym., Apidae). *Suom. hyönt. Aikak.* 8, 83–102.
- Sladen, F. W. L. (1900). Humblebees in winter. *Br. Bee J.* 28, 72–4.
- Sladen, F. W. L. (1912). *The Humble-bee, its Life History and How to Domesticate it*. London.
- Soulié, J. (1957). Quelques notes sur l'hibernation chez la fourmi *Cremastogaster scutellaris* Ol. et chez une espèce voisine *Cremastogaster auberti* Em. (Hymenoptera—Formicoidea). *Insectes soc.* 4, 365–73.
- Stein, G. (1956). Beiträge zur Biologie der Hummel (*B. terrestris* L., *B. lapidarius* L. u.a.). *Zool. Jb.* 84, 439–62.
- Stein, G. (1957). Über das Verhalten von Hummelköniginnen bei experimentell verhindertem Winterschlaf. *Verh. dt. zool. Ges.* 1957, 106–11.
- Tkalcu, B. (1960). Sur l'hibernation des bourdons. *Bull. Soc. ent. Mulhouse*, 1960, 96–7.
- Tkalcu, B. (1961). Deuxième contribution sur l'hibernation des Bourdons. *Bull. Soc. ent. Mulhouse*, 1961, 105–6.
- Townsend, L. H. (1951). The hibernation of *Bombus impatiens* Cresson (Hymenoptera: Bombidae). *Ent. News*, 62, 115–16.
- Wagner, W. (1907). Psycho-biologische Untersuchungen an Hummeln mit Bezugnahme auf die Frage der Geselligkeit im Tierreiche. *Zoologica, Stuttg.* 19, (Heft 4b) 1–239.
- Wilde, J. de (1953). Provisional analysis of the imaginal diapause in an insect (*Leptinotarsa decemlineata* Say). *Acta physiol. pharm. néerl.* 3, 141–3.

(Received 23 April 1968)