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Natural Resting Sites of the Peppered Moth (*Biston betularia*)

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SUMMARY

This project investigates the controversial issue of natural resting sites of the peppered moth (*Biston betularia*). Scientists' ignorance on this subject is often cited to discredit previous studies on the species, including Bernard Kettlewell's famous study. Here I analyse a data set, collected by Dr Michael Majerus, describing the resting positions of 154 moths of both sexes and 3 morphs. The majority of moths rested on the underside of lateral branches, confirming previous studies. Moths were also commonly found resting on the North side of vertical structures, particularly trunks. Moths were not more abundant at a particular height above ground level, or particular height as a percentage of total tree height, but rather were distributed throughout the branched part of the tree. Most moths rested on Oak trees, compared to other tree species. The Discussion addresses whether scepticism about the accuracy of previous experiments can be laid to rest, and how incorporation of these results may improve the reliability of future experiments on the species.

INTRODUCTION

The peppered moth, *Biston betularia (Linn.)*, has long been a textbook example of evolution by natural selection. Several studies have been conducted on the species, most famously the mark-release-recapture experiments carried out by Bernard Kettlewell (Kettlewell, 1955, 1956) into bird predation as the driving force of selection on the species. This current study is concerned with natural daytime resting sites of these moths. Kettlewell, and others after him (Clark & Sheppard, 1966; Bishop, 1972; Lees & Creed, 1975; Whittle *et al.*, 1976; Steward, 1977a), released his moths "onto available trunks and boughs" which he believed to be "their normal resting places" (Kettlewell, 1956). This assumption was based on little evidence as prior to his experiments, few peppered moths had ever been found at rest in the wild. The few experiments conducted since suggest that this species rests instead on the underside of lateral branches, and are almost never found on trunks. This has led to accusations that Kettlewell's data was biased and hence unreliable.

Most studies into the resting behaviour of the species have focused on differences in background selection of the 3 morphs: *typica* (pale), *insularia* (intermediate), and *carbonaria* (dark) (Howlett and Grant, 1987; R. C Steward, 1985) where it was assumed that moths select sites based on visual cues alone. Although visual cues are likely to be important in resting site selection, due to the cryptic nature of the species, "the selection of resting sites by

Biston betularia almost certainly involves cues in addition to background reflectance" (Howlett and Grant, 1987). There have been 3 previous studies investigating what these other cues might be: K. Mikkola (1984), Howlett and Majerus (1986) and Liebert and Brakefield (1987). These studies have not provided a definitive answer to where the species rests by day, for several reasons. They were not executed high up in the trees where moths are likely to be found, due to reduced exposure. I two (Mikkola and Liebert and Brakefield), moths were placed artificially on trees and their movements tracked rather than recording the positions of moths encountered in the wild. The same two experiments only concentrated on behaviour of only one sex. These aspects were improved by Howlett and Majerus(1986) but sample sizes were too small for detailed statistical analysis. In all three investigations few characteristics of moth resting sites were examined.

This current study is an analysis of the largest dataset yet collected on the natural resting sites of *B. betularia*. The data set describes in detail numerous characteristics of the natural daytime resting sites of 177 moths of both sexes and the 3 morphs were recorded. 4 questions were investigated:

1. Are Peppered moths randomly distributed with respect to tree species?
2. Are Peppered moths equally distributed between trunk, branch and twig?
3. Are Peppered moths randomly distributed over the surface of trunks branches and twigs?
4. Are Peppered moths randomly distributed with respect to height?

METHOD

Natural History of B. betularia and Study area

B. Betularia is univoltine in Britain, flying from late dusk until dawn with a flight season lasting from early May to late August. These were the months when the data were collected between 2001 - 2007. Flight pattern of males and females differs, with males flying most nights in search of females, and females often only on the first night before taking up a resting position and beginning calling. After copulation, pairs remain together for up to 24 hours as the male guards the female. Paired moths rest back to back so that they effectively share a resting site (Liebert and Brakefield, 1987). Various species of trees and shrubs serve as the larval food-plants of the species (Waring *et. al,* 2003), many of which are included in this study. The study area was an orchard in Cambridge, UK that was predominantly made up of Apple and Hawthorn trees, but also contained the following tree species: Ash, Birch, Blackthorn, Elder, Goat Sallow, Oak, Pear, Privet and Wild Plum.

Data Collection

Data collection was carried out by Dr Michael Majerus, of the Department of Genetics at Cambridge University, by climbing trees looking for moths. Individual trees were numbered. The date, sex and morph of each moth were recorded along with the following: Tree species, particular tree, height (in m) above the ground, part of the tree (Branch, Twig or Trunk), foliage level, and whether it was approximately vertical or horizontal. For vertical sites the position was measured, as a compass bearing. For horizontal sites the position was recorded as being on the top, mid-side or underneath. In cases of mating pairs the sex and Morph of both moths was recorded along with their pair status.

Data Analysis

For questions 1, 2 and 3 the relevant data were discrete and categorical (compass points for question 3 were assigned to the categories N, S, E and W for ease of analysis). In cases where moth number data was classified by only one variable, e.g. tree species, it was compared with expected numbers using the Chi-squared goodness-of-fit test. In cases where moth numbers were classified by 2 variables, e.g. tree species and sex, contingency tables were used. Where there was enough data in each category to give large enough expected values (no more than 20% < 5 and none < 1), the Chi-squared test of association was used. When expected values were too small, Fisher's exact test was used instead. For question 4, data was continuous and the following tests were performed: Kolmogorov-Smirnov test for normality, the Kruskal-Wallis test, and the t-test.

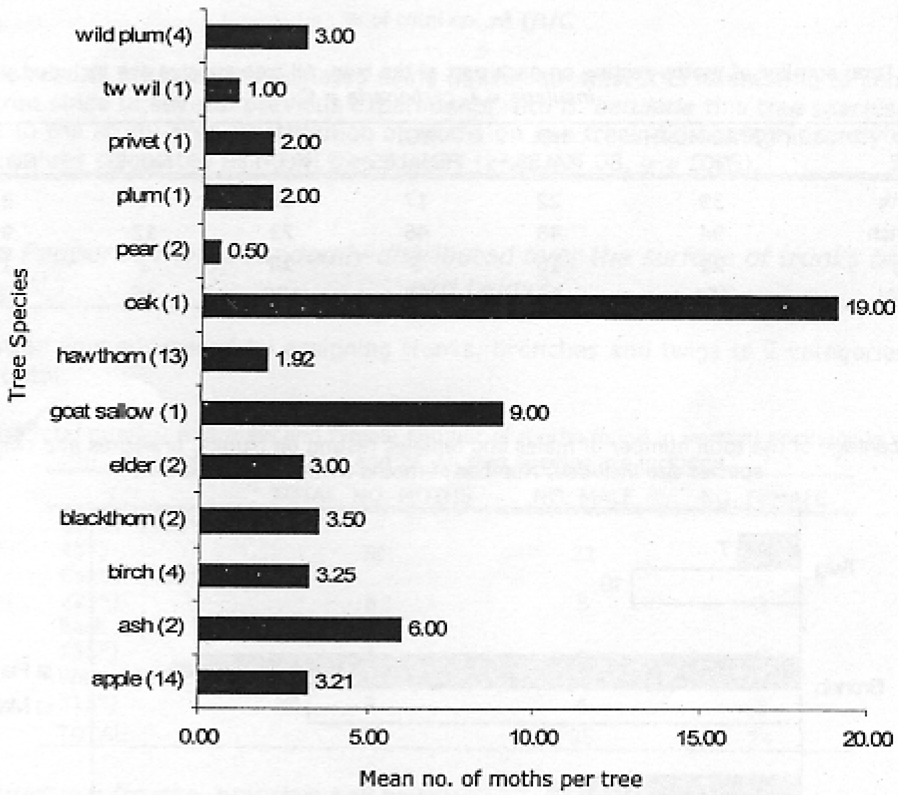
For each of the four questions posed, comparisons of the behaviour of males, females and the 3 morphs were made. The corroboration of the data set with conclusions drawn from previous studies on the subject (where such studies exist) was assessed. I analyse only un-paired moths since the position of paired male moths is determined by the female causing possible bias in analyses comparing behaviour of the sexes. Mixed mating pairs will also bias resting site comparisons between morphs. I also exclude calling virgins since females may rest in abnormal positions when releasing male-attracting pheromones (e.g. more exposed so they can be easily located by males).

RESULTS

The positions of 177 moths were recorded, including 22 mating pairs and 1 calling virgin which were excluded from analysis. 154 non-mating moths were analysed, comprising 86 males, 68 females, 126 *typica*, 15 *insularia*, and 13 *carbonaria*.

Are Peppered moths randomly distributed with respect to tree species?

Fig. 1 Comparison of the mean total number of moths found per individual tree for each of the 13 tree species in the study area. Number of trees of each species shown in brackets next to species name, Number of moths on each tree species written after the bar.



Proportionally more peppered moths were found on oak trees (Fig. 1). Chi-squared and Fisher's exact analyses of all 13 tree species was impractical especially when a species was represented by only 1 tree due to the resulting small expected values. Therefore, chi-squared analysis was performed only on tree species with more than 10 moths resting on them (Table 1).

Table 1: number of , male, female, *typica* (T), *insularia* (I), and *carbonaria* (C) moths resting on the 5 most abundant tree species . Number of trees of each species shown in brackets after species name. All chi-sqaure analyses carried out on this data uses expected values which compensate for the number of trees of each species.

TREE SPECIES	MOTH NUMBER					
	TOTAL	MALES	FEMALES	T	I	C
Apple (14)	45	27	18	31	8	6
Hawthorn (13)	25	12	13	21	2	2
Birch (4)	13	5	8	11	2	0
Wild Plum (4)	12	9	3	11	0	1
Ash (2)	12	7	5	10	1	1
Oak (1)	19	12	7	18	1	0

Moths were not randomly distributed with respect to tree species ($\chi^2_{(5)} = 86.18$, $p < 0.001$) so the higher number found on oak trees was significant.

Analysis of the same 6 tree species found that morphs were not randomly distributed between tree species (Fisher's Exact P=0.0000011 (<0.001)) unlike the two sexes ($\chi^2_{(4)} = 4.71$, $p > 0.05$).

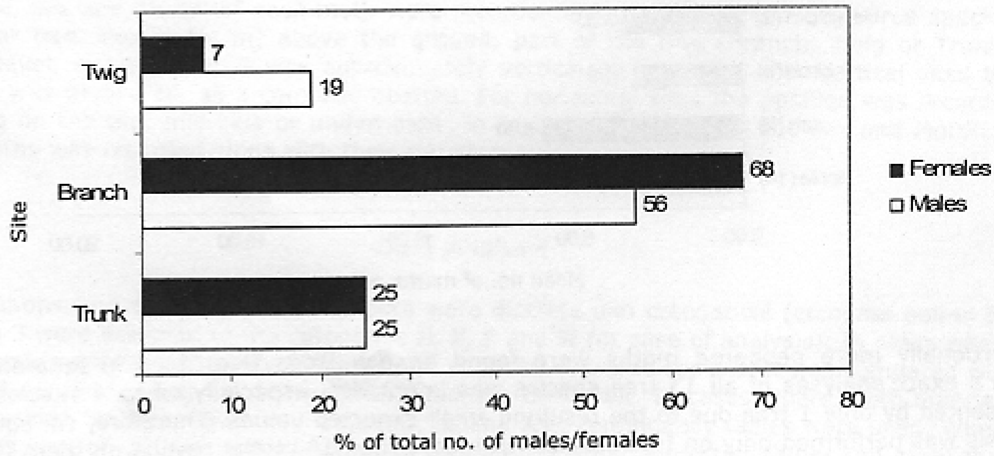
Are Peppered moths equally distributed between trunk, branch and twig?

Moths were not equally distributed between trunk, branch or twig ($\chi^2_{(2)} = 56.39$, $p < 0.05$). 60% of moths were found resting on branches, 25% of moths were found resting on trunks (Table 2).

Table 2: Total number of moths resting on each part of the tree. All tree species are included. *typica* =T, *insularia* = I, *carbonaria* = C

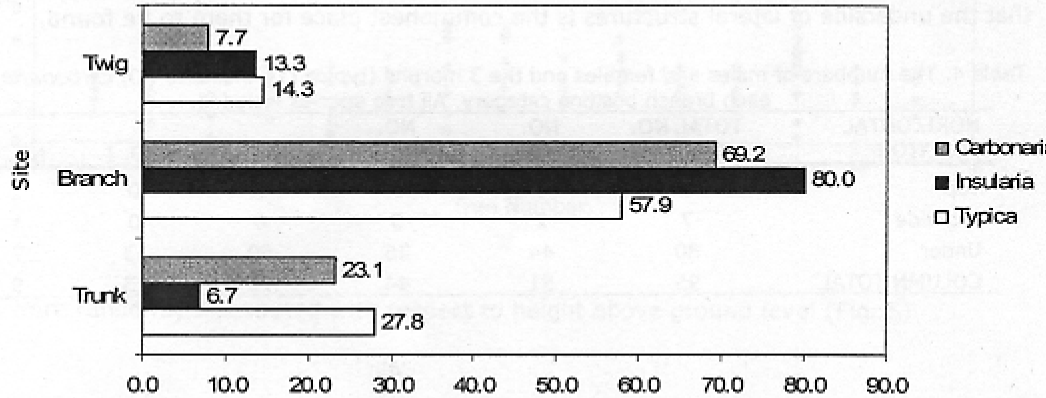
SITE	TOTAL MOTH NO.	NO. MALES	NO. FEMALES	NO. T	NO. I	NO. C
Trunk	39	22	17	35	1	3
Branch	94	48	46	73	12	9
Twig	21	16	5	18	2	1
TOTAL	154	86	68	126	15	13

Fig 2: percentage of the total number of males and females resting on trunks, branches and twigs. All tree species are included. Number of moths written after the bar.



Sex did not significantly affect the distribution between branch, trunk or twig ($\chi^2_{(2)} = 4.40$, $p > 0.05$). The sex ratio does not significantly differ from 1:1 on branches and trunks (using Bonferroni correction; Branches: $\chi^2_{(1)} = 0.043$, $p > 0.017$, Trunks: $\chi^2_{(1)} = 0.64$, $p > 0.017$) but does on twigs ($\chi^2_{(1)} = 5.76$, $p < 0.017$) suggesting that moths found on twigs are more likely to be male. However, this outcome is very marginally statistically significant and not significant enough to affect the outcome of the original test of association (being male was found not to have an effect on resting site) so should be treated with caution. Morphs were not equally distributed between the three sites (Fisher's Exact, $P = 0.0011$ (< 0.05)).

Fig. 3 percentage of the total number of *carbonaria (C), insularia (I)* and *typica(T)* morphs resting on the trunk, branch and twig



The above results are means calculated using all tree species. It is interesting to consider only the oak tree since in several previous experiments with *B. betularia* this tree species was most abundant in the study area. Distribution of moths on oak trees did not significantly differ from expected values calculated using all tree species ($\chi^2_{(2)} = 5.08$, $p > 0.05$).

Are Peppered moths randomly distributed over the surface of trunks branches and twigs?

This question was addressed by assigning trunks, branches and twigs to 2 categories: vertical and horizontal.

Table 3. The total number and male and female number of moths found in vertical positions in each of the categories N,S,E and W. All tree species are included.

	TOTAL. NO. MOTHS	NO. MALE	NO. FEMALE
North (315° - 45°)	38	22	16
South (135° - 225°)	8	5	3
East (45° - 135°)	4	4	0
West (225° - 315°)	9	4	5
TOTAL	59	35	24

Vertical structures (trunks, branches and twigs):
Moths were not equally distributed between N, S, E and W sides ($\chi^2_{(3)} = 49.81$, $p < 0.05$). Most moths were found on the North side and the modal bearing was 20° (North). Morph significantly affected distribution between the 4 sides (Fisher's Exact, $P = 0.011$ (< 0.05)) as did sex (Fisher's Exact, $P = 0.0073$ (< 0.05)). The sex ratio did not differ significantly from 1:1 on any side (Using the Bonferroni correction; North: $\chi^2_{(1)} = 0.95$, South: $\chi^2_{(1)} = 0.50$, West: $\chi^2_{(1)} = 0.11$, East: $\chi^2_{(1)} = 4.00$; For all directions $P > 0.0125$).

There was a significant association between structure (Trunk, branch and twig) and orientation (N, S E and W) when not accounting for the incline (Table 4. - Fisher's Exact, $P = 0.00041$ (< 0.05)). Most moths found on vertical structure rested on trunks (37 out of 59 moths on vertical structures) where the highest number (24) rested on the North side.

Horizontal structures (branches and twigs):
Moths were not equally distributed between the top, mid-side, and underneath ($X^2_{(2)} = 110.66$, $p < 0.05$). Most moths were found on the underside for both sexes, and all 3 morphs. Sex significantly affected the distribution (Fisher's Exact, $P = 0.034$ (< 0.05)) as did morph (Fisher's Exact, $P = 0.015$ (< 0.05).

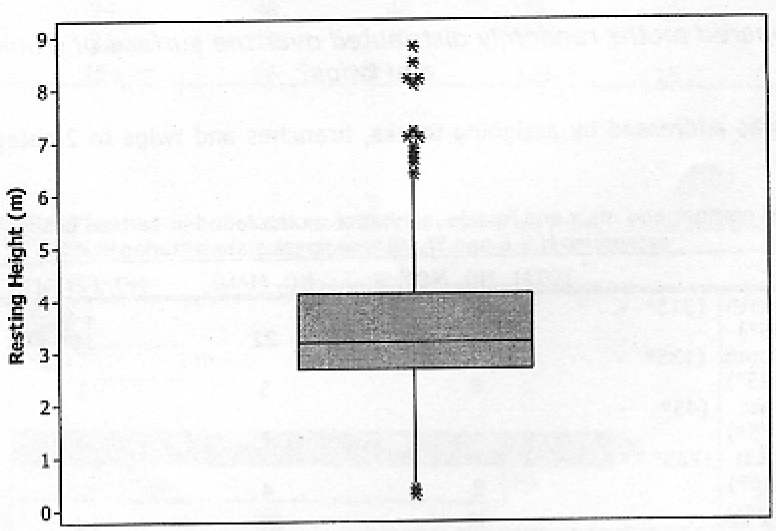
More moths rested horizontally than vertically (95 horizontal, 59 vertical) and more rested on the underside of branches than on the North side of trees (38 North, 80 under) suggesting that the underside of lateral structures is the commonest place for them to be found.

Table 4. The numbers of males and females and the 3 morphs (*typica* (T), *insularia* (I), *carbonaria* (C)) in each branch position category. All tree species included.

HORIZONTAL POSITION	TOTAL NO. MOTHS	NO. MALES	NO. FEMALES	NO. T	NO. I	NO. C
Top	8	5	3	7	0	1
Mid-side	7	2	5	6	0	1
Under	80	44	36	60	13	7
COLUMN TOTAL	95	51	44	73	13	9

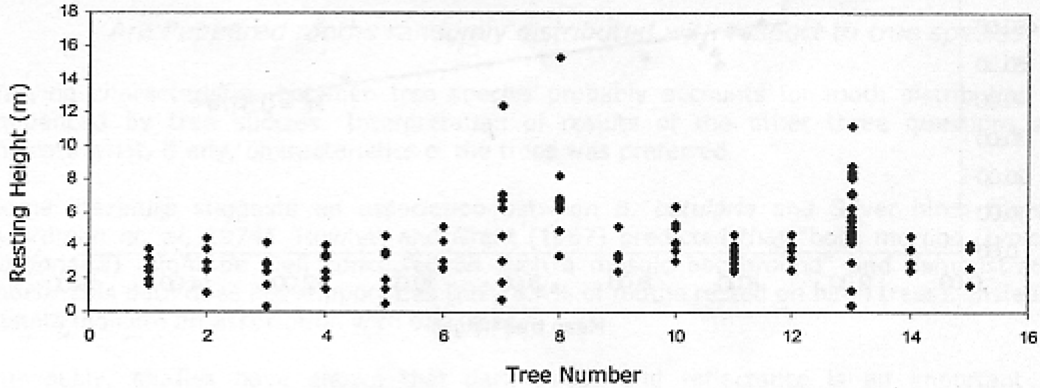
Are Peppered moths randomly distributed with respect to height?

Fig. 4 Box-plot showing skew and outliers in moth resting height data.



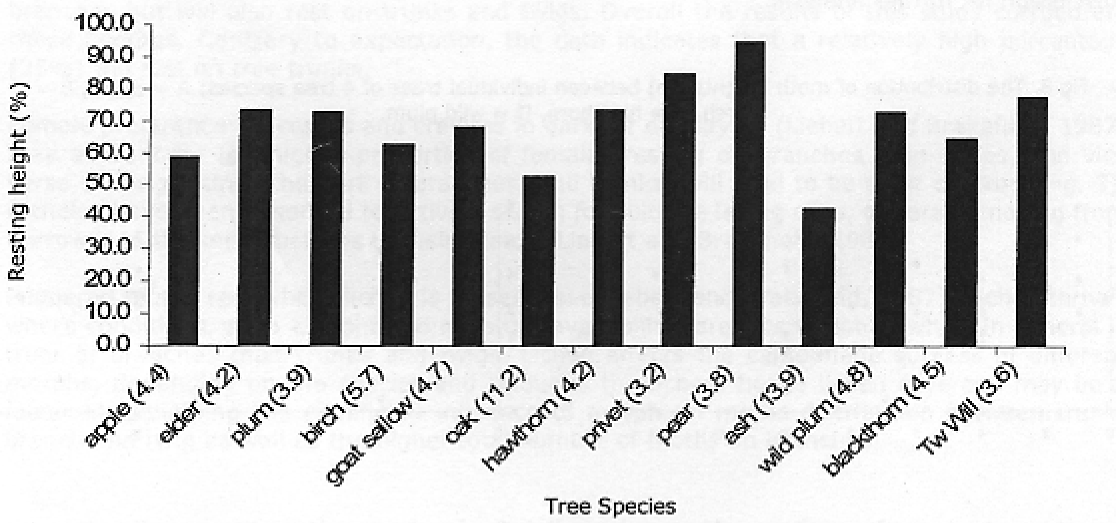
The data does not fit a normal distribution (Kolmogorov-Smirnov = 0.148, $P<0.05$), and is slightly skewed (Fig. 4).

Fig. 5. Scatter graph showing the resting heights (in m) for all trees with more than 5 moths resting on them. Species, number, and height of trees included are listed in the appendix (Pg 18.)



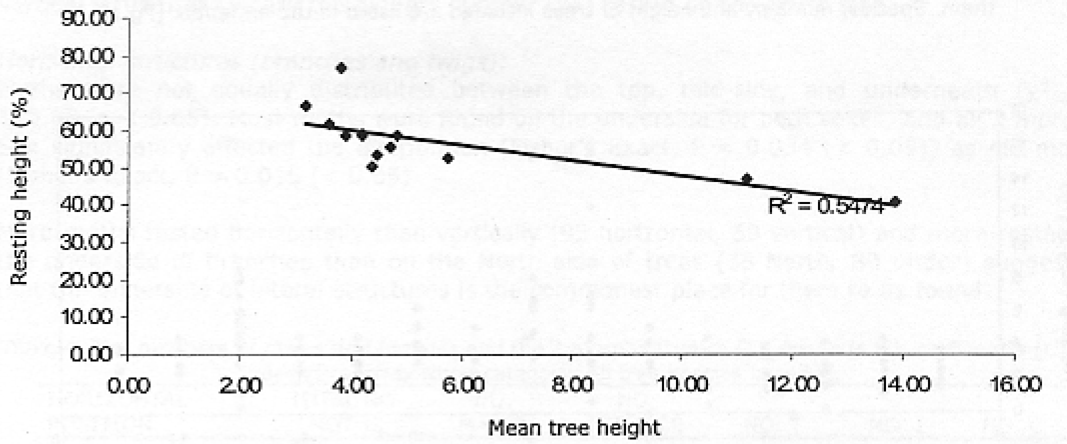
Moths were randomly distributed with respect to height above ground level (Fig. 5)

Fig. 6 The resting height of moths as a percentage of the total tree height was calculated for each moth. Here the mean resting height as a percentage of the total tree height is plotted for each tree species. The mean tree height is given in brackets after each tree species.



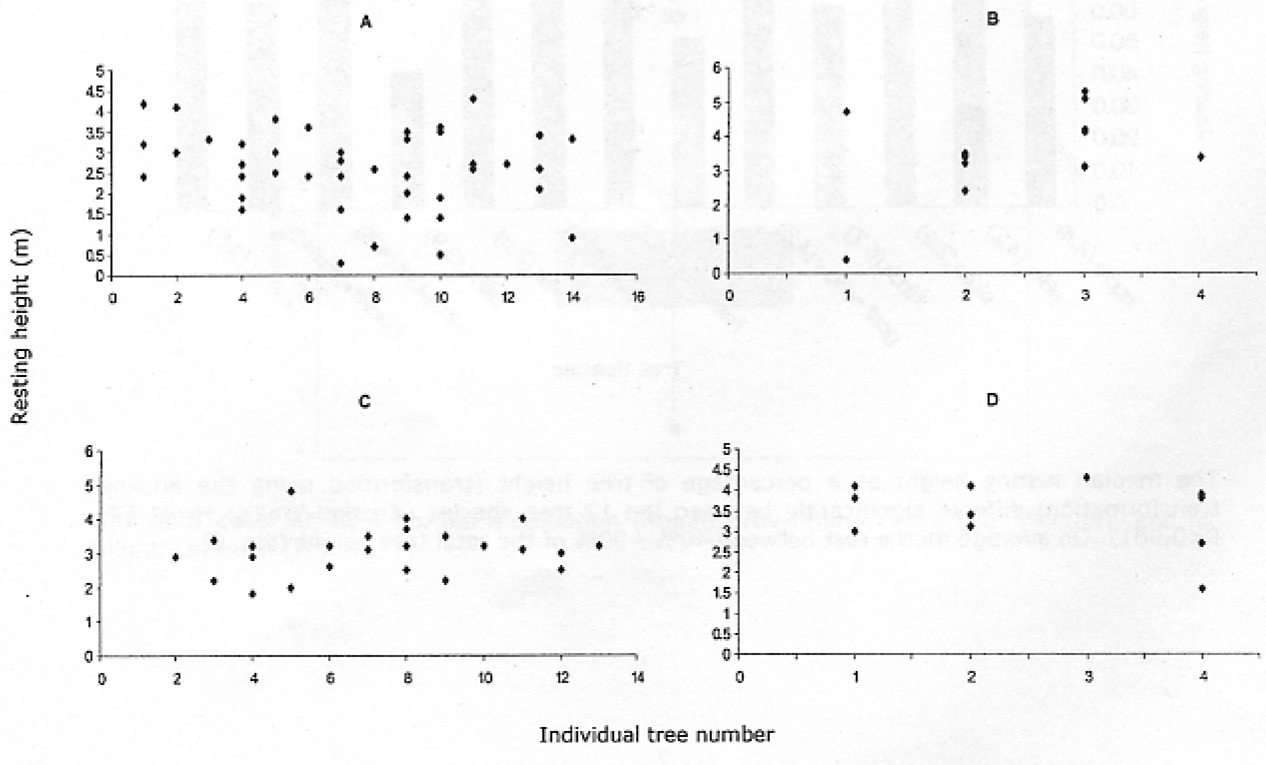
The median resting height as a percentage of tree height (transformed using the arcsine transformation) differed significantly between the 13 tree species (Kruskal-Wallis: H=41.52, P<0.001). On average moths rest between 40% - 90% of the total tree height (Fig. 6).

Fig. 7. Mean tree height (per species for all 13 tree species) against moth resting height as a transformed % of tree height.



On taller trees, peppered moths will rest at a mean height that is a smaller % of the total tree height, and vice versa for shorter trees (Fig 7). This indicates non-random distribution with respect to height above ground level but this was found not to be the case (Fig 5.) This could be due to outliers (fig. 4) affecting calculations of mean tree height for each species. The distribution of moths on individual trees, of different heights, of the same species was analysed to reduce this effect. This was only practical for the 4 most abundant tree species: apple, hawthorn, birch and wild plum trees (fig. 8). With the possible exception of Hawthorn trees (where almost all moths rested between 2 and 4 metres) the moths appear to be randomly distributed on the trees with respect to height. The pattern of distribution suggests that moth resting height is a result of branching pattern, for example on apple trees which commonly branch comparatively close to the ground the moths rest the lowest (0.4m) See discussion for further analysis.

Fig 8. The distribution of moth heights (m) between individual trees of 4 tree species: A = apple, B = birch, C = hawthorn, D = wild plum.



There is no significant difference between the mean resting heights (as a percentage of tree heights) of males and females (t-test$_{(152)}$ P=0.160 (P<0.05)).

DISCUSSION

Are Peppered moths randomly distributed with respect to tree species?

Varying characteristics between tree species probably accounts for moth distribution being influenced by tree species. Interpretation of results of the other three questions should indicate what, if any, characteristics of the trees was preferred.

Some literature suggests an association between *B. betularia* and Silver birch trees (see Boardman *et. al*, 1974). Howlett and Grant (1987) predicted that "both morphs (*typica* and *carbonaria*) might be well concealed on such a mosaic background" and demonstrated as much. This data does not support this (only 8.4% of moths rested on birch trees). Instead, the results indicate an association with oak trees.

Previously, studies have shown that bark colour and reflectance is an important factor affecting moth, particularly morph, distribution (Howlett and Grant, 1987, R.C. Steward, 1985), explaining why morph distribution differed between tree species. Studies found that the pale *typica* morph will rest on the palest available background, with the opposite being true for the dark *carbonaria* form (*insularia* morphs rest similarly to *typica* morphs (R. C Steward, 1985)). Having said this, there could be other factors such as predation, controlling the resting site of the 3 morphs. This will likely be true for all analyses of morph-specific resting site.

Are Peppered moths equally distributed between trunk, branch and twig?

Mikkola (1984) and Liebert and Brakefield concluded that moths predominantly rested on branches but will also rest on trunks and twigs. Overall the results of this study corroborate these findings. Contrary to expectation, the data indicates that a relatively high percentage (25%) will rest on tree trunks.

Female preference for cracks and crevices in bark for egg laying (Liebert and Brakefield, 1987) may account for the higher proportion of females resting on branches than males, and vice versa on twigs, since the bark of branches (and trunks) will tend to be most cracked (Fig. 3). Females have been observed to actively search for suitable laying sites, generally moving from narrower to thicker structures in their search (Liebert and Brakefield, 1987).

Peppered moths rest where lichen is present (see Liebert and Brakefield, 1987). Lichen thrives where conditions, such as light and moisture availability, are less variable, which in general is truer of branches than trunks and twigs. Lichen affects the camouflage success of different morphs, depending on the species and colour of the lichen, hence lichen coverage may be a factor in explaining the significant influence of morph on moths distribution between trunk, branch and twig as well as the higher total number of moths on branches.

Are Peppered moths randomly distributed over the surface of trunks branches and twigs?

Most moths were found on the underside of horizontal structures probably due to the advantage of being less visible to airborne predators. Moths were also commonly found on the North side of vertical structures, probably because there is relatively less sunlight on this side of trees in Britain, reducing the likelihood of overheating and shadow-effects (Majerus, 2004). Moths have been observed to move around trunks and vertical branches from sunshine into shade (Liebert and Brakefield, 1987). Variations in levels of sunlight on different sides of both vertical and horizontal structures will affect lichen abundance. Lichen coverage may again, be the key to why morph influenced distribution. It is unclear why sex influenced distribution, but it is possible that female oviposition behaviour may have had an affect.

Are Peppered moths randomly distributed with respect to height?

Studies into the preferred resting heights of peppered moth have, to my knowledge, not been carried out before this study. Expectation was that *B. betularia* "probably rest high up in the canopies" (Mikkola, 1984). Kettlewell suggests that the moths "under their own choice, would have taken up a position higher in the trees" (Kettlewell, 1955) than the trunks on which he placed them. Overall, this data supports these statements.

Moths were not more abundant at any particular height above ground level, nor at any particular height as a proportion of the tree height. On average moths are most likely to be found between 40% and 90% of the total height of the tree, but this is highly variable between species.

The variation seen indicates that the height at which peppered moths rest is more a consequence of branching pattern since most moths were found on branches (Fig.8). Abundant lateral branching occurs at different heights on different tree species, accounting for differences in height distribution between tree species. For example, commonly apple trees begin branching relatively close to the ground and branch density is comparatively constant throughout the tree. This may explain why moths were found on a larger portion of apple trees, and lower down. Contrastingly, birch trees have fewer lateral branches, abundant vertical branches (in the upper portion), and a large proportion of the tree is trunk, hence on these trees, moths tended to rest comparatively lower and on a smaller portion of the tree.

Sources of error in data collection method

Some aspects of data collection may have caused error or bias in the results. Firstly, the data was collected at the same time as a separate predation experiment was conducted so moths were recorded as they were encountered rather than after prolonged searching, hence some moths may have been overlooked. Climbing trees may have caused bias towards the, more visible, underside of horizontal structures. Furthermore, very high parts of trees were inaccessible, possibly causing bias towards lower resting heights. Climbing may also have scared away some moths. Moths resting in exposed positions were more visible, possibly explaining why few moths (7) were found resting in non-exposed positions. Well camouflaged moths were less visible, possibly resulting in more moths being found on abnormal resting backgrounds, skewing morph data. There may have been errors in species/form/or sex recognition but Dr Majerus' extensive experience working with peppered moths makes the likelihood of such errors small. Another source of bias is that tree heights were only measured once in the 7 years data collection period so growth was not accounted for. Consequentially, calculations of resting height as a percentage of total tree height may be inaccurate. Lastly, some tree species in the orchard were only represented by a single tree (e.g. Oak). Without being able to compare to other trees of the same species it is not possible to determine if other characteristics, apart from species, had a large effect on moth distribution on that tree.

Improvements and Further Study

Similar future studies could include several improvements. If carried out under more controlled conditions the subtle effect, on moth distribution, of some factors may be made clearer. Other factors could be measured, which may support conclusions made here or answer other relevant questions, such as:

- Diameter/ Surface area of the trunks, branches, and twigs. It is possible that more moths rest on oak trees because they have larger structures, hence this could be tested.
- Branching pattern – Allowing detailed analysis of how moth distribution reflects branching patterns (currently this observation is speculative based on descriptions of common tree species).
- Relative tree position - To analyse the effect of shading by neighbouring trees.
- Bark colour/reflectance - Allowing detailed comparisons of morph resting behaviour to test the hypothesis that peppered moths naturally rest where best camouflaged.

- Lichen coverage - To test if this affects moth (particularly morph) distribution as proposed here.

Further study might focus on the following areas in order to draw conclusions that will specifically allow judgement on the accuracy of previous predation experiments:

- Distribution on oak trees - Implications for field studies conducted on peppered moths in predominantly oak woodlands, such as Kettlewell's Birmingham experiments (Oak to Birch in ratio 10:1), and Liebert and Brakefield (1987).
- Wider geographical area and spatial distribution – Wider study areas would allow confirmation of these results, strengthening conclusions made here, and comparison of polluted and unpolluted sites like Kettlewell's. The currently not well understood spatial distribution of the species could also be determined using GIS analysis if co-ordinates of each moth are recorded.
- Moth preference by choice vs. Selection (predation) affects – This study does not discriminate between these two possible hypotheses to explain the distribution seen.

Implications of this Study

The results of this study show that a substantial proportion of moths (25%) do rest on trunks, so results of previous predation experiments, where moths were placed on trunks, should not be disregarded and may be less biased than previously feared. Having said this, calculations of morph frequencies from such experiments do not accurately fit expected frequencies from computer models based on selection coefficients. Attempts at improving the fit by incorporating non-visual selective factors and number-dependent selection into the model have had little success. Howlett and Majerus (1986) suggested that the fit can be greatly improved by incorporating more accurate data on natural resting sites. The results of this current study could serve as this data.

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APPENDIX

RAW DATA

Moth No.	Date Recorded	Morph	Sex	Tree Species	Height	Trunk/ Branch/ Twig	Compass Bearing	Horiz. Position	Twig foliage level	Exposure	Paired/ Single (blank)	Horizontal Vertical
1	14/05/1997	typ	male	ap 4	3.2	br		under				horiz
2	22/05/1997	typ	male	wd pl 2	4.1	tr	330					vert
3	05/06/1997	typ	female	ap 6	3.6	br		under				horiz
4	06/06/1997	ins 1	female	ap 1	2.4	br		under				horiz
5	18-Jun	typ	male	haw 7	3.1	tw		under	bare twig			horiz
6	20/06/1997	typ	female	haw 8	4	br		under				horiz
7	24/06/1997	typ	male	b 3	5.1	br		under				horiz
8	25/06/1997	carb	male	ap 4	2.7	br		under				horiz
9	27/06/1997	typ	male	oak	6.3	tr	20					vert
10	01/07/1997	typ	female	eld 2	3.3	br	290					vert
11	03/07/1997	carb	male	ap 13	2.1	br		under				horiz
12	06/07/1997	ins 2	female	b 2	3.2	tr	290					vert
13	07/07/1997	typ	male	g s	3.8	br		under				horiz
14	17/07/1997	typ	male	ap 9	1.4	br		under				horiz
15	22/07/1997	typ	female	haw 10	3.2	tr	330					vert
16	02/05/1998	typ	female	haw 4	2.9	tw		under	bare twig			horiz
17	05/05/1998	typ	female	ap 1	4.2	br		under				horiz
18	12/05/1998	typ	male	oak	4.4	tr	10					vert
19	15/05/1998	typ	female	ash 1	6.3	br		under			pair	horiz
20	15/05/1998	typ	male	ash1	6.3	br		under			pair	horiz
21	25/05/1998	typ	male	blk 1	2.8	tw		under	bare twig			horiz
22	01/06/1998	typ	male	wd pl 4	3.8	br	280					vert
23	03/06/1998	carb	male	ap 2	4.1	br		under				horiz
24	04/06/1998	typ	female	plum	2.7	br		under				horiz
25	07/06/1998	typ	male	b 1	0.4	tr	90					vert
26	10/06/1998	typ	female	ap13	2.9	br	30					vert
27	11/06/1998	carb	male	haw 12	2.5	tr	0					vert
28	13/06/1998	carb	male	ash 1	1.8	br		under			pair	horiz
29	13/06/1998	typ	female	ash 1	1.8	br		mid side			pair	horiz
30	17/06/1998	typ	female	ap 5	3	br		top				horiz
31	22/06/1998	typ	male	ap 9	2	br	280					vert
32	29/06/1998	typ	male	oak	8.2	tw		under	bare twig			horiz
33	02/07/1998	typ	female	g s	2.4	tr	10					vert
34	08/07/1998	ins 3	male	ap 11	4.3	br		under				horiz
35	17/07/1998	typ	female	haw 5	4.8	tw		under	leaves			horiz
36	01/08/1998	typ	male	wd pl 4	3.9	tw		under				horiz
37	10/05/1999	typ	male	blk 2	2	br	40					vert
38	15/05/1999	typ	male	eld 2	3.2	tw	170		leaves	shaded leaves		vert
39	17/05/1999	typ	male	oak	7.1	tw		under				horiz
40	18/05/1999	typ	male	privet	2.8	tw	20		bare twig			vert
41	26/05/1999	typ	female	ap 14	3.3	tr	10					vert
42	28/05/1999	ins 2	female	haw 12	3	br		under				horiz
43	03/06/1999	typ	male	ash 2	6.2	br		under				horiz

44	06/06/1999	typ	male	g s	3.4	tr	30					vert
45	17/06/1999	typ	female	b 3	4.1	tr	140			exposed		vert
46	18/06/1999	typ	female	ap 11	2.7	br		under				horiz
47	24/06/1999	carb	male	haw 9	3.5	tw		under	leafy twig			horiz
48	02/07/1999	typ	male	oak	4.7	br		under				horiz
49	05/07/1999	typ	male	ash 2	4.9	br		under				horiz
50	12/07/1999	ins 1	female	haw 7	3.1	br		under				horiz
51	16/07/1999	typ	female	ap 6	2.4	br		mid side				horiz
52	03/05/2000	typ	male	wd pl 1	3	tr	350					vert
53	06/05/2000	typ	female	wd pl 2	3.4	br		under				horiz
54	07/05/2000	typ	male	blk 2	1.4	tr	20					vert
55	12/05/2000	typ	male	haw 6	3.2	tw		under	bare twig			horiz
56	18-May	typ	male	ash 1	6.8	br	10					vert
57	26/05/2000	carb	male	g s	3.2	br		mid side				horiz
58	30/05/2000	typ	female	ap 13	3.4	br		under				horiz
59	31/05/2000	typ	female	ap 10	0.5	br	20					vert
60	31/05/2000	typ	male	wd pl 4	1.6	tr	330					vert
61	02/06/2000	carb	female	blk 1	3.1	br		under				horiz
62	05/06/2000	typ	female	b 3	4.1	br		top				horiz
63	12/06/2000	typ	male	ap 2	3	br		under				horiz
64	14/06/2000	typ	male	ap 4	2.4	tr	320					vert
65	15/06/2000	ins 1	male	ap 10	3.6	br		under				horiz
66	28-Jun	typ	male	oak	4.2	tr	160			shaded ivy		vert
67	06/07/2000	typ	male	ap 12	2.7	br		under				horiz
68	14/07/2000	typ	female	b 4	3.4	br		under				horiz
69	18/07/2000	ins 2	female	blk 1	3.6	tw		under	bare twig			horiz
70	28/07/2000	typ	male	haw 9	2.2	br		under				horiz
71	03/05/2001	typ	male	ap 5	1.1	br	50				pair	vert
72	03/05/2001	typ	female	ap 5	1.1	br	50				pair	vert
73	04/05/2001	carb	female	oak	0.4	tr	320				calling virgin	vert
74	07/05/2001	typ	male	ap 11	2.6	br		under				horiz
75	12/05/2001	typ	female	b 2	3.4	tr	0					vert
76	15/05/2001	ins 1	female	ash 1	7.1	br		under				horiz
77	18/05/2001	typ	male	wd pl 1	3.8	br		under				horiz
78	18/05/2001	typ	male	ash 1	3.1	tr	30					vert
79	22/05/2001	typ	male	oak	5.6	tr	190			shaded ivy		vert
80	29/05/2001	carb	male	wd pl 2	3.1	br		under				horiz
81	01/06/2001	carb	male	haw 2	3.3	br		mid side			pair	horiz
82	01/06/2001	typ	female	haw 2	3.3	br		mid side			pair	horiz
83	04/06/2001	typ	female	ap 8	2.6	tr		under				horiz
84	06/06/2001	typ	male	b 2	3.5	br		top				horiz
85	12/06/2001	typ	female	oak	4.4	br		under				horiz
86	17/06/2001	carb	female	ash 1	4.6	tr	10					vert
87	23/06/2001	typ	female	eld 2	3.5	br	0					vert
88	28/06/2001	typ	male	g s	4	tr	220					vert
89	03/07/2001	typ	male	ap 9	2.4	tr		under				horiz
90	04/07/2001	typ	male	plum	3	br		under				horiz
91	05/07/2001	typ	female	g s	3.6	br		under				horiz
92	10/07/2001	typ	male	oak	8.8	tr	30					vert

93	12/07/2001	carb	male	ap 4	1.9	br		top				horiz
94	01/08/2001	typ	male	haw 8	3.2	br		under				horiz
95	06/08/2001	typ	male	ap 7	0.3	br		under				horiz
96	28/04/2002	typ	male	ash 1	0.7	tr	70				pair	vert
97	28/04/2002	typ	female	ash 1	0.7	tr	80				pair	vert
98	02/05/2002	typ	female	b 2	2.4	br	290					vert
99	04/05/2002	typ	male	oak	1.3	tr	20				pair	vert
100	04/05/2002	carb	female	oak	1.3	tr	20				pair	vert
101	07/05/2002	typ	female	wd pl 3	4.3	tr	150			exposed		vert
102	07/05/2002	typ	female	ash 2	6.6	tr	0					vert
103	10/05/2002	ins 3	male	oak	5.8	br		under				horiz
104	12-May	typ	male	b 3	4.2	br		under				horiz
105	13/05/2002	ins 3	male	ap 3	3.3	br		under				horiz
106	13/05/2002	typ	female	g s	2.9	br	30					vert
107	13/05/2002	carb	male	eld 1	2.5	br	60					vert
108	15/05/2002	typ	female	blk 2	3.1	br		under				horiz
109	15/05/2002	typ	male	ap 11	3.1	tw		under	bare twig		pair	horiz
110	15/05/2002	typ	female	ap 11	3.1	tw		under	leaves		pair	horiz
111	18/05/2002	typ	male	haw 6	2.6	tw		under	bare twig			horiz
112	23/05/2002	typ	male	ap 2	3	br	330					vert
113	25/05/2002	carb	male	ap 5	2.5	br		under				horiz
114	29/05/2002	typ	female	haw 13	3.2	br		under				horiz
115	02/06/2002	typ	female	ap 10	3.5	br		under				horiz
116	06/06/2002	typ	male	b 3	5.3	br		under				horiz
117	11/06/2002	typ	male	oak	4.8	tr	210					vert
118	13/06/2002	typ	female	ash 2	3.4	tr	340					vert
119	14/06/2002	typ	male	privet	2.6	tw		under	bare twig			horiz
120	17/06/2002	typ	female	blk	4	br		mid side				horiz
121	21/06/2002	typ	female	oak	5.5	br		under				horiz
122	21/06/2002	typ	male	tw wil	2.8	tw	270		leafy twig			vert
123	22/06/2002	ins 1	male	wd pl 1	2.5	br		under			pair	horiz
124	22/06/2002	carb	female	wd pl 1	2.5	br		under			pair	horiz
125	28/06/2002	typ	male	oak	4.5	tr	290					vert
126	30/06/2002	ins 2	male	ap 7	3	br	350					vert
127	02/07/2002	typ	male	ap 10	1.4	br	60					vert
128	02/07/2002	typ	female	oak	4.4	br		under				horiz
129	07/07/2002	typ	male	ash 2	6.4	br		under				horiz
130	10/07/2002	typ	male	haw 11	3.1	br		under				horiz
131	11/07/2002	typ	female	haw 3	2.2	br		under				horiz
132	20/07/2002	carb	female	ap 7	1.6	tr	210			shaded leaves		vert
133	24/07/2002	typ	male	oak	4.9	br		under				horiz
134	29/07/2002	typ	female	eld 1	2.8	br		top				horiz
135	02/08/2002	typ	male	g s	3	tr	10					vert
136	08/05/2003	typ	female	oak	8.5	br		under				horiz
137	11/05/2003	typ	female	haw 3	3.4	br		under				horiz
138	14/05/2003	typ	male	ash 2	6.9	tw		mid side	bare twig			horiz
139	19/05/2003	typ	female	oak	7.2	br		under				horiz
140	21/05/2003	typ	female	wd pl 3	4.3	tr	230					vert
141	26/05/2003	typ	female	ap 13	2.6	br	20					vert
142	28/05/2003	typ	male	ap 14	0.9	tw		under	bare			horiz

									twig		
143	02/06/2003	typ	male	ap 14	0.9	br		top			horiz
144	06/06/2003	ins 2	female	b 3	3.1	br		under			horiz
145	11/06/2003	typ	female	eld 2	3.2	br		under			horiz
146	11/06/2003	typ	female	b 1	4.7	tr	0				vert
147	12/06/2003	typ	female	ap 1	3.2	br		under			horiz
148	15/06/2003	typ	male	ap 5	3.8	br		under			horiz
149	22/06/2003	typ	male	ap 7	2.8	tr	30				vert
150	24/06/2003	typ	male	haw 4	1.8	br		top			horiz
151	01/07/2003	typ	female	haw 7	3.5	br	340				vert
152	07/07/2003	typ	male	haw 2	2.9	tw	320		leafy twig		vert
153	14/07/2003	typ	female	oak	3	br		under		pair	horiz
154	16/07/2003	ins 1	male	oak	3	br		under		pair	horiz
155	20/07/2003	typ	female	pear 2	3.6	br		under			horiz
156	25/07/2003	ins 1	male	ap 9	3.5	tw		under	leaves		horiz
157	31/07/2003	typ	male	haw 8	2.5	br		under			horiz
158	03/08/2003	typ	female	ash 2	8.2	br		mid side			horiz
159	08/05/2004	typ	female	ap 4	1.6	tr	40				vert
160	12/05/2004	typ	female	ap 9	3.3	br		mid side			horiz
161	13/05/2004	typ	female	haw 11	4	br		under			horiz
162	16/05/2004	typ	male	wd pl 4	2.7	br	20				vert
163	19/05/2004	typ	male	ap 12	4.5	tw		under	bare twig	pair	horiz
164	19/05/2004	typ	female	ap 12	4.5	tw		under	bare twig	pair	horiz
165	21/05/2004	typ	male	haw 4	3.2	br		top			horiz
166	24/05/2004	typ	male	ap 10	1.9	tr	40				vert
167	28/05/2004	typ	male	ash 2	6.7	tr	70				vert
168	29/05/2004	ins 2	female	ap 8	0.7	br		under			horiz
169	30/05/2004	typ	male	b 3	3.7	tr	0			pair	vert
170	30/05/2004	typ	female	b 3	3.7	tr	0			pair	vert
171	06/06/2004	typ	female	oak	8.1	tr	270				vert
172	06/06/2004	ins 3	male	ap 7	2.4	br		under			horiz
173	12/06/2004	typ	female	haw 5	2	tw		under	leaves		horiz
174	13/06/2004	typ	female	haw 8	3.7	tw		mid side	bare twig		horiz
175	17/06/2004	typ	female	g s	2.6	br		under			horiz
176	25/07/2004	typ	male	wd pl	4.1	br	20				vert
177	10/08/2004	typ	female	oak	5.2	tr	0				vert

LIST OF TREES AND TREE HEIGHTS

TREE SPCEIS AND NUMBER	TREE HEIGHT (m)
apple 1	5.1
apple 10	4.6
apple 11	5.2
apple 12	5.5
apple 13	3.8
apple 14	3.8
apple 2	5.3
apple 3	4.2
apple 4	3.8
apple 5	4.4
apple 6	4
apple 7	4.2
apple 8	3.2
apple 9	4
ash 1	12.4
ash 2	15.3
birch 1	5.8
birch 2	5.2
birch 3	6.4
birch 4	5.5
blackthorn 1	4.4
blackthorn 2	4.5
elder 1	3.9
elder 2	4.5
goat sallow	4.7
hawthorn 1	3.3
hawthorn 10	4
hawthorn 11	4.7
hawthorn 12	3.8
hawthorn 13	5.1
hawthorn 2	3.8
hawthorn 3	3.9
hawthorn 4	3.6
hawthorn 5	5.4
hawthorn 6	3.7
hawthorn 7	4.2
hawthorn 8	4.7
hawthorn 9	4.3
oak	11.2
pear 1	3.2
pear 2	4.4
plum 1	3.9
privet 1	3.2
wild plum 1	4.6
wild plum 2	5.2
wild plum 3	5.4
wild plum 4	4.1
Twisted Willow	3.6

TABLE FROM FIG 4.

(Numbers correspond to numbers on graph)

NUMBER:	TREE:
1	apple 4
2	apple 5
3	apple 7
4	apple 9
5	apple 10
6	apple 11
7	ash 1
8	ash 2
9	birch 2
10	birch 3
11	goat sallow
12	hawthorn 8
13	oak
14	wild plum 1
15	wild plum 4