

THE ACULEATE HYMENOPTERA OF AMBERSHAM AND IPING (WITH STEDHAM) COMMONS IN WEST SUSSEX, INCLUDING STATISTICAL PROCEDURES FOR ESTIMATING SPECIES RICHNESS

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Abstract. A total of 263 aculeate (230 solitary and 33 social) species, about 51% of the British list, were found on Ambersham and Iping Commons between 1974 and 1998. Using these data the Jaccard Index of similarity between the two sites was 64.8% for the solitary species and 78.8% for the social species. Three hypotheses are developed to explain these differences. Three non-parametric estimates of the potential number of species for each site are in general agreement and agree with the number of species recorded. Thus the species lists may be considered sufficiently complete to carry out further comparisons. Since species diversity estimates are not available for other inland sandy sites in south-eastern England, a species–area relationship method is used to justify further comparisons between these sites and the West Sussex sites. Species quality scores for good inland sandy sites in south-eastern England vary between 4.5 and 5.5. The narrow range in values of the cleptoparasitic load for the solitary wasps and bees supports Wcislo's hypothesis. There is a good representation of the aerial-nesting solitary species.

INTRODUCTION

The aims of this paper are, firstly, to give an account of the aculeate wasp, ant and bee fauna of Ambersham and Iping (with Stedham) Commons, both in West Sussex, and to develop hypotheses to account for any differences. Secondly, a subsample of the data for the solitary species is used to investigate three non-parametric statistical methods for determining potential species diversity for each site. Thirdly, having shown by the species diversity estimates that the solitary species lists are sufficiently complete, further comparisons using the summarising indices of cleptoparasitic load, aerial-nester frequency and quality assessment can be justified. Fourthly, a species–area procedure is used to justify comparisons between the two West Sussex and other inland sandy sites of south-eastern England.

Ambersham Common (212 ha, SU91) is situated about 3 km south-east of Midhurst, and Iping (with Stedham) Common (172 ha, SU82) is situated about 3 km west of Midhurst. Iping and Stedham Commons are continuous with each other and elsewhere in this paper are referred to as Iping Common.

Ambersham Common is owned by the Cowdray Estate who currently manage the Common under a Countryside Stewardship Agreement. For most of the time covered by the records used in this paper, however, it was essentially unmanaged and suffered increasing invasion by pine and loss of structure within the heathers. A sheltered section of old railway line has been altered dramatically through use as a forestry thoroughfare, leading to the total loss of an area of heath verge during the period covered by this paper. Likewise the heath verge along the road has suffered both by shading from trees and from trampling from the large number of polo ponies which are exercised here. The ponies have also churned up many of the trackways over the Common, rendering the former areas of open sand unsuitable as nesting

sites. These habitat changes have led to the apparent loss of several species which were recorded during the early 1970s. Such losses are, to some extent, off set by the appearance of newly recorded species during the 1990s. The Common has not experienced extensive fires during the study period.

In contrast, Iping Common was three-quarters burnt over during 1976, just after it was declared a Local Nature Reserve, under the management, initially, of West Sussex County Council and, latterly, The South Downs Board. This event, however, has not resulted in the loss of any of the species known for the area prior to the fire, whereas several species recorded during the period of the study appear to be currently extinct as the habitat which supported them is now not present. This loss is due both to succession to woodland over an area of open grassy habitat and to the cessation of use of this part of Stedham Common as a dumping ground for locally extracted timber which was unfit for use in the local sawmill. This area provided many records of aerial-nesting species at the start of the study period but is of little use to these insects now.

Ambersham Common has always had more areas of comparatively flower-rich heath verge than Iping Common, which off sets the historically greater opportunities for aerial-nesting species at Iping Common. Both these effects are, however, somewhat a result of having to set boundaries to the sites as most of the 'missing' species are known from areas nearby each Common. The loss of directly heathland-associated species such as *Nomada baccata* and *Andrena tarsata* due to changes in the nature of the heathland is far more serious from the conservation perspective. Fortunately, both sites are now under active management, which includes in its aims the conservation of the heathland-insect assemblages present.

The soils of both sites are predominately free-draining and acidic, being derived from the Lower Greensand, and support a *Calluna vulgaris*/*Erica cinerea*-dominant dry-heath vegetation. Within these areas are heathy grasslands, often dominated by bracken, which has been the target of concerted conservation action during the latter part of the study period. There is a localised calcareous influence on both Commons, leading to a greater variety of flowering plants in some parts. This influence is due both to the effect of previous activity, such as the importation of chalk ballast for the railway line, and the presence of local veins of basic clay and calcareous streams arising at the base of the nearby South Downs. There are small areas of impeded drainage on both sites, giving rise to *Erica tetralix*-dominated wet heathland.

This paper has been mainly written by M.E. Archer (MEA), with M. Edwards (ME) providing a description of the sites, contributing to the three hypotheses concerning differences between the two sites, and providing the data of the species of aculeate Hymenoptera.

SAMPLING METHODS

Between 1972 and 1997 ME made 120 visits to Ambersham Common distributed throughout the year as follows: February (1 visit), March (8), April (5), May (11), June (29), July (26), August (34) and September (6). Most recording was carried out during the 1970s and 1997 with less recording in the intermediate years. Between 1974 and 1998 ME made 113 visits to Iping Common distributed throughout the year as follows: March (1), April (5), May (12), June (15), July (31), August (44), September (5). Most recording was carried out during the 1980s, 1996 and 1997 with less recording during the 1970s and early 1990s. During these visits specimens were usually collected with a hand net for identification, but a few specimens were trapped

with a Malaise trap and a very few specimens were bred from inside bramble stems. On a few visits to Ambersham Common ME was accompanied by the following people who contributed some records: G. Allen (2 visits), P. Chandler (1), S. Church (1), J. Field (1), J. Felton (1), R. Morris (1) and K. Side (1). The number of species recorded on each visit varied from one species to a more-or-less complete list of species encountered. For the species-diversity investigation the only visits used are those where the largest number of solitary wasp and bee species were recorded. From Ambersham Common 25 samples were selected which were distributed throughout the year as follows: March (2 visits), April (2), May (3), June (4), July (6), August (6) and September (2). From Iping Common 21 samples were selected which were distributed throughout the year as follows: March (1), April (1), May (3), June (3), July (6), August (6) and September (1).

SPECIES PRESENT

A full list of recorded species is given in the appendix, and, at the family level, Table 1 shows the taxonomic distribution of species. The total list of 263 species represents about 51% of the British list. The Pompilidae are particularly well represented with 71% of the British list and the Anthophoridae poorly represented with 36% of the British list.

Of the 230 solitary species (Table 1), 149 species were present on both sites, 41 species were only recorded from Ambersham Common and 40 species only recorded from Iping Common. The Jaccard Index (Ludwig & Reynolds, 1988), which depends

Table 1. The number of aculeate species recorded from Ambersham and Iping Commons

	Ambersham	Iping	Total
Solitary wasps			
Chrysididae	7	9	11
Tiphidae	3	2	3
Mutillidae	3	3	3
Pompilidae	25	23	29
Eumenidae	7	6	9
Sphecidae	51	65	71
Total solitary wasps	96	108	126
Solitary bees			
Colletidae	9	8	10
Andrenidae	32	23	33
Halictidae	24	24	27
Melittidae	0	2	2
Megachilidae	15	12	17
Anthophoridae	13	11	14
Xylocopidae	1	1	1
Total solitary bees	94	81	104
Total solitary wasps & bees	190	189	230
Social species			
Formicidae	13	14	15
Vespidae	5	7	7
Apidae	11	9	11
Total social species	29	30	33
Total aculeate species	219	219	263

upon the presence or absence of species, gives an index of 64.8% of species common to both Commons. Of the 33 social species (Table 1), 26 species were present on both sites, three species only from Ambersham Common and four species only from Iping Common. The Jaccard Index for the social species was higher than that for the solitary species at 78.8%.

Three hypotheses can be advanced to explain the differences in species lists between the two sites:

1) Species rarity—The populations of some species on the sites are so small and diffuse that the probability of recording them is very small. Such species may be reasonably expected to be recorded at only one site; greater recording effort may provide records for the second site. 2) Resource scarcity—The micro-habitats and resources for some species may be present only on one of the sites. 3) Recorder and sampling bias.—The possible effects of each of these hypotheses on the recorded species lists for the two sites is considered below.

Firstly, species rarity. The higher Jaccard Index for the social species, compared with that of the solitary species, would support this hypothesis, since each of the social species will be represented by more individuals than each of the solitary species (Archer, 1988). Further support for this hypothesis could be gained if it is considered that the cleptoparasitic species are represented by fewer individuals than their host species. The less well represented Anthophoridae, particularly the cleptoparasitic genus *Nomada*, can be used to support this hypothesis. The following species of *Nomada* have been recorded from only one of the Commons but their *Andrena* hosts have been recorded on both Commons: *N. baccata*, *N. fulvicornis*.

Secondly, resource scarcity. Evidence for this hypothesis is the presence of the pompilid *Anoplius concinnus* at Iping, where it hunts spiders at the edge of the lake in the old sand-pit workings, a habitat not present at Ambersham Common. The oligolectic bee *Melitta tricincta* was regularly found on the grassland of the old dumping ground until its food-plant, red bartsia (*Odontites vernus*), was swamped by the invading willow scrub. Red bartsia is unknown on Ambersham Common. The bee *Megachile circumcincta* is often associated with bird's foot trefoil on sandy sites; this habitat has never been present at Iping Common whilst it has been worked, but was plentiful at Ambersham Common before the destruction of road verge and old railway track—it has not been found since, despite several directed searches over a number of years.

Thirdly, recorder and sampling bias. Over the 26 years of study the recording effort, the reasons for recording and the search image have changed. The data were not collected with any idea of treating them statistically or with producing total lists for each day, although the very large sample helps to overcome this effect. It is well known anecdotal fact that two recorders at the same site will only have a partial overlap of species recorded on any day. With a long-term set of data as this, ME is aware that his ability to find particular species has varied over the years. His increasing experience, his changing search image and even the changing nature of his physical sight all interact to increase, or decrease, his ability to find a specific species. Hence, in some sense, over the period of the study ME can be regarded as two different recorders. This is relevant to the argument about whether the differences between sites are real or artefacts of the method, when it is realised that the data sets were not collected in parallel but that his attentions to the two sites occurred at largely non-overlapping times.

Evaluating the relative importance of the three hypotheses is not possible on the current set of data but would be an interesting study. It goes without saying that the effects of the third hypothesis would be the hardest to control.

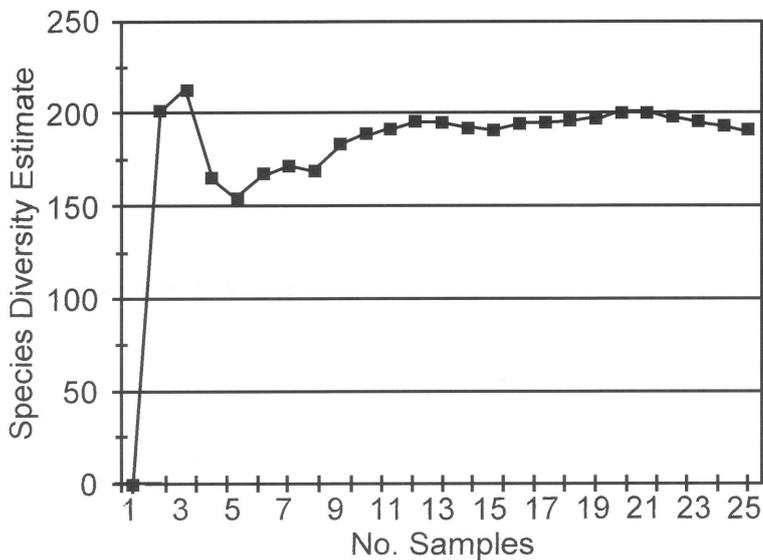


Fig. 1. Species-diversity estimate based on the presence/absence quantitative estimate of Chao for Ambersham Common.

ESTIMATING THE POTENTIAL NUMBER OF SOLITARY WASP AND BEE SPECIES

One of the problems in the study of any site is the difficulty of not knowing how many more species are present at a site, but as yet are unrecorded. Recent advances in non-parametric statistical procedures offer a way of addressing this problem. Chao (in Colwell & Coddington, 1994) describes procedures to estimate the potential number of species (species richness) likely to be found on a site after a number of samples have been taken. The presence/absence quantitative estimate of Chao is based on the number of species that are observed in one (unique species) or two (two-occasion species) samples. Because some aculeate species are only active in the spring or summer it is advisable that samples be distributed throughout the months of adult activity. The software to carry out this statistical procedure was provided by Pisces Conservation Ltd.

The statistical procedure was run 20 times for each Common and the resulting estimates are given in figs 1 & 2. In practice the software takes 1, 2, etc. samples at random from the 25 samples of Ambersham or 21 samples of Iping Commons 20 times, each time calculating a mean estimate of species diversity. With a small number of samples the estimates are erratic, but as more samples are selected the estimates stabilise giving confidence in the estimates. The 95% confidence limits (meaning that there is a 95% chance that the potential number of species falls within this range) are given at the maximum sample size selection in Table 2. Thus the estimated species diversity with the 95% confidence limits for Ambersham Common is 190 (163–217) species and for Iping Common is 189 (162–217) species. The total number of solitary species of wasps and bees actually recorded from Ambersham Common during the 120 visits was 190 species and from Iping Common during the

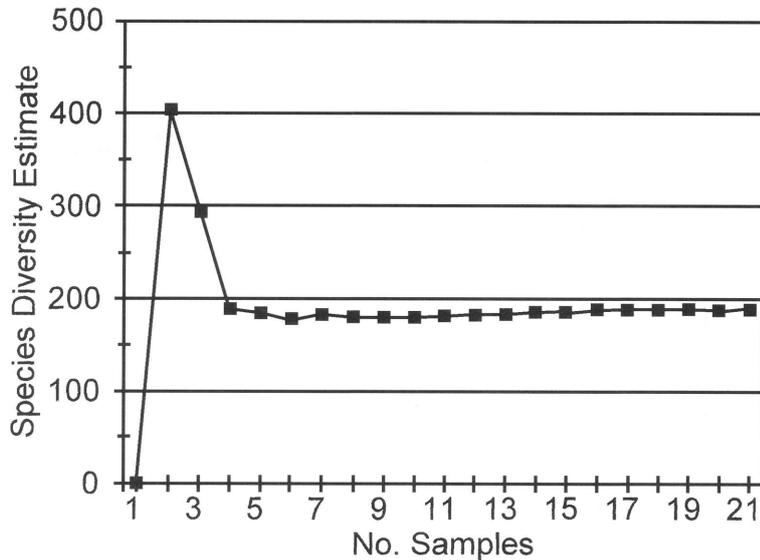


Fig. 2. Species-diversity estimate based on the presence/absence quantitative estimate of Chao for Iping Common.

113 visits was 189 species. Since the recorded species diversity for Ambersham and Iping Commons is within the 95% confidence limits, the Chao estimator is seen to be a good estimator of the potential species diversity.

Since the use of the Chao estimator is a relatively new statistical procedure caution is needed in accepting its estimates. Two further non-parametric statistical estimators are the jackknife (Heltshe & Forrester, 1983) and bootstrap (Smith & van Belle, 1984) procedures (software by Pisces Conservation Ltd). The jackknife procedure gives higher estimates than the Chao quantitative estimator (Ambersham 209 species, Iping 205 species) and the bootstrap procedure lower estimates (Ambersham 181 species, Iping 178 species). However the jackknife and bootstrap estimates are included within the 95% confidence limits of the Chao quantitative estimator so that the three estimates are in general agreement and confidence can be placed on the use of these relatively new statistical procedures.

A possible complication in making these estimates may be that some of the unique species were accidentally present, being outside their normal range (vagrant species). Vagrant species would artificially increase the estimate of species richness. Both authors have looked carefully at the unique species and do not regard any of them as vagrant species. Many of the unique species in the species diversity study cease to be unique species when the samples from all the visits are considered.

SPECIES-AREA RELATIONSHIP

Another problem in the study of any site, particularly when the potential estimate of the number of species is greater than the number of species recorded, is the difficulty of knowing when the species list is sufficiently complete so that comparisons with other sites may reasonably be carried out. This is less of a

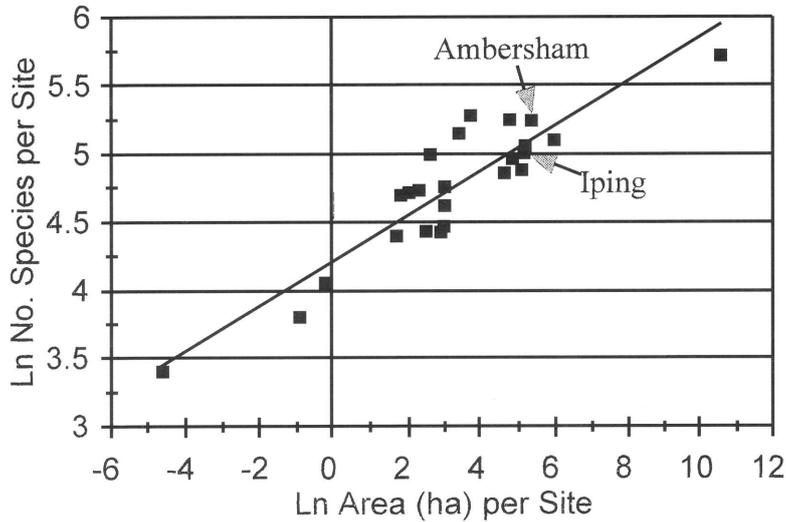


Fig. 3. A species-area relationship plot based on the solitary aculeate species from 24 inland sandy sites in south eastern England.

problem for Ambersham and Iping Commons since the recorded number of species and species-diversity estimates are in agreement with each other. However, for other sites from south-eastern England species-diversity estimates are not available so some other method must be used. In these circumstances one way to resolve this problem is the use of the species-area relationship where the number of species and the area of the sites, both expressed as natural logarithms (ln), can show a positive linear relationship (Usher, 1986). If the number of species in relation to the area of a site falls within the range of other sites which show a statistically significant species-area relationship, then the site may reasonably be compared with other sites. If the number of species in relation to the area of the site falls below the values of the other sites then this could indicate either many more species could be found on that site, or that the site consists of habitats which are particularly unfavourable for aculeates (Archer, 1999b). If the number of species in relation to the area occurs above the values of the other sites, then the site is more favourable for aculeates, perhaps because the local climate is more favourable or the habitats present at the site are particularly variable and favourable for aculeates.

With the help of many entomologists a species-area plot of 24 inland sandy sites, including Ambersham and Iping Commons, using only the solitary species of wasps and bees, has been constructed for south-eastern England (fig. 3). The other 22 sites are from Bedfordshire (Cooper's Hill, V.H. Chambers, pers. comm.), Suffolk (Elvedon, B. Collins, S. Falk, pers. comm.), Essex (Mill Wood Pit, Mill Land Fields, Alphamstone Pits, Broom Hill, Kent Road, Alsa Sand Pit, P. Harvey pers. comm.), Oxfordshire (Shotover, Steel 1984, Dry Stanford and Hitch Copse, C. O'Toole, pers. comm.), Dorset (Holt Heath, S. Roberts, pers. comm.), Hampshire (New Forest, Archer 1999a, M. Harvey, pers. comm., C. Palmer, pers. comm. and B.J. Pinchen, pers. comm.), London (Mitcham Common, Morris 1997), Surrey (Horsell Common, Bagmoor Common, Mare Hill Common, Ham Common, Sheepleas, Thursley

Common, D. Baldock, pers. comm.) and Kent (Tunbridge & Rusthal Common, I.C. Beavis, pers. comm. and Thameside, P. Harvey, pers. comm.). Bagmoor and Thursley Commons are treated as separate sites although they are continuous with each other. Data from other sites, e.g. Chobham Common and Oxshott Heath, Surrey (Guichard, 1977), could not be used because the recording area of these sites is unknown.

The correlation coefficient of the species–area relationship of the 24 sites indicates a highly significant linear relationship ($r=0.91$, $p<0.001$) with 83% of the variation of the number of species between sites being explained by the variation in the area of the sites. The species–area regression equation is: \ln number of species = $4.22 + 0.164 \times \ln$ area (ha). The dots for Ambersham and Iping Commons fall within the range of the other 22 sites, and so the species lists for the 24 sites, including Ambersham and Iping Commons, can be considered sufficiently complete to make valid comparisons between them. Two other statistics from this regression equation are: 1. the mean number of species of solitary wasps and bees expected to be found on one ha is 68 species (anti- \ln 4.22) and, 2. to double the number of solitary species of wasps and bees the mean area would need to be increased about 69-fold (2 raised to the power of $1/0.164$). Possible reasons why the number of species should increase in relation to area are discussed by Archer and Burn (1995).

The species–area relationship is likely to be different for different regions of the UK. Thus, the mean number of species of solitary wasps and bees expected to be found on one ha from a sample of 19 sites from the north and north midlands of England is lower (47 species) than on the sites from south-eastern England, and the mean doubling factor is higher at about 475-fold (Archer, 1999b). These differences may be called the latitude variable and almost certainly reflect the more favourable climate in south-eastern England for aculeates.

For the Channel Islands a mean of 97 species of solitary wasps and bees are expected to be found on one ha which is higher than that expected for south-eastern England, again reflecting a further improvement in climate (Archer, unpublished). The mean doubling factor for the Channel Islands is about 66-fold which is similar to that of south-eastern England.

Other variables, e.g. altitude and habitat differences between sites, are also likely to affect the species–area relationship, although more information is needed before the effects of these variables can be tested. Archer (1999b) found that, for the north and north midlands of England, open habitats from inland and coastal sandy sites and calcareous, clay and silty sites could all be grouped together into a single species–area relationship, so here the habitat variable would seem to be less important.

SPECIES QUALITY

The status of each solitary species recorded from Ambersham and Iping Commons is given in the appendix. These statuses are the Archer's national statuses (Archer, 1999) rather than those given in Shirt (1987) and Falk (1991), since all species are considered, not just national priority (Simonson & Thomas, 1999), RDB or nationally scarce species. In addition, up-to-date information on distribution from the Newsletters of the Bees, Wasps and Ants Recording Society has been used. Caution must be exercised in the use of statuses since the status for a species is not fixed and can change as knowledge of the distribution of species improves or the species undergoes changes in range.

Species with very rare, rare and scarce statuses are called the high-quality species and are regarded as those species in most need of conservation. Overall, 59

Table 2. Non-parametric estimates of species richness of solitary wasps and bees at Ambersham and Iping Commons based on the species-diversity samples and using the presence/absence Chao quantitative estimator

	Ambersham	Iping
No. species in species-diversity samples	154	152
Estimated	190	189
95% confidence limits of estimated	163–217	162–217
Total species recorded	190	189

high-quality solitary species (9 very rare, 20 rare, 30 scarce) have been recorded from both sites.

Summing the status values for the solitary species gives the quality score for the site (Table 2). Dividing the site quality score by the number of solitary species recorded from a site gives the species quality score (SQS) 4.5 for both Ambersham and Iping Commons.

The investigation of species quality of aculeate wasps and bees has not been published for other sites in south-eastern England although Morris (1997) used another kind of site score and site quality index. Archer (unpublished) has carried out species quality investigations for Bagmoor Common and Thursley Common, Surrey and Holt Heath, Dorset. From Bagmoor Common 148 solitary species have been recorded with a quality score of 730 and a SQS of 4.9; from Thursley Common, 163 species with a quality score of 756 and a SQS of 4.6; and from Holt Heath 189 solitary species with a quality score of 1041 and a SQS of 5.5. Thus a SQS for the solitary aculeate species of between 4.5 and 5.5 is to be expected from a good inland sandy site in south-eastern England.

Sites from the north and north midlands of England usually have lower SQSs of between 1.5 and 3, although the SQS of the Ainsdale–Formby sand dunes is exceptionally large at 3.8 (Archer, 1999b). The variation of SQSs between northern and southern England is a latitude variable and is probably a consequence of a more favourable climate in southern England.

Only the ant *Formica sanguinea* among the social species is a high-quality species, probably with a scarce status.

Table 3. The Archer national quality scores of the species of solitary wasps and bees recorded from Ambersham (AC) and Iping (IC) Commons (species quality score 4.5 for both Commons)

Status	Status value (A)	No. species (B)		Quality scores (A × B)	
		AC	IC	AC	IP
Universal	1	70	71	70	71
Widespread	2	64	65	128	130
Restricted	4	14	13	56	52
Scarce	8	22	21	176	168
Rare	16	13	11	208	176
Very rare	32	7	8	224	256
Total		190	189	862	853

Table 4. The relative frequency of the cleptoparasitic (or parasitoid) species among the species of solitary wasps and bees from Ambersham (AC) and Iping (IC) Commons

	No. hosts (H)		No. cleptoparasites (C)		Cleptoparasitic load CL = $100 \times C/(H + C)$	
	AC	IP	AC	IP	AC	IP
Solitary wasps	78	92	15	13	16.1	12.4
Solitary bees	73	62	21	19	22.3	23.5

CLEPTOPARASITIC LOAD

The cleptoparasitic load (CL) is the percentage of aculeate species that are cleptoparasites (or parasitoids) on other host aculeates. Weislo (1987) showed that parasite behaviour among aculeate Hymenoptera correlated with geographical latitude. Thus the parasitic rates are higher in temperate regions as host populations are more synchronised in their life-history characteristics. This finding probably does not hold for desert climates where the occurrence of rainfall would tend to synchronise life history characteristics. From a review of the literature Weislo (1987) found that the CLs for bees in Europe varied between 16% and 33%, a range of 17%. The solitary bee CL for Ambersham Common is 22.3% and Iping Common 23.5% (Table 3). These values are within the range of values for Europe and thus support Weislo's speculation.

Weislo (1987) gives no CL values for wasps, but Archer (1999b) found that values for solitary wasps varied between 10% and 22%, a range of 12%, for sites from northern and the north midlands of England. The solitary wasp CL for Ambersham Common is 16.1% and Iping Common 12.4% (Table 3) which fall within the range for northern and the north midlands of England. Thus Weislo's speculation for bees could also apply to solitary wasps. Archer & Burn (1995) discussed why the CLs for the solitary bees are higher than the CLs for the solitary wasps. They argue that it is probably a consequence of food-chain relationships.

All the social species are host species, except for the species of *Psithyrus*, which are social parasites on the species of *Bombus*.

AERIAL-NESTER FREQUENCY

The aerial-nester frequency (AF) is the percentage of host aculeate species that have aerial nest sites. Aerial nesters use old beetle burrows in dead wood, central

Table 5. The nesting habits of the host species of solitary wasps and bees recorded from Ambersham (AC) and Iping (IC) Commons

	No. aerial nesters (A)		No. subterranean nesters (S)		Aerial-nester frequency AF = $100 \times A/(A + S)$	
	AC	IP	AC	IP	AC	IP
Solitary wasps	30	39	48	53	38.5	42.4
Solitary bees	17	13	56	49	23.3	21.0

stem cavities (e.g. bramble), old snail shells, or crevices in cob wall, old mortar or exposed on the surface of rock or other hard material. Subterranean nesters nest in the soil, usually in burrows dug by themselves, but sometimes holes and crevices are used after being altered.

The AFs for the solitary wasps and bees from Ambersham and Iping Commons are given in Table 4. The AFs for all the British species of solitary wasps is 46.2% and solitary bees is 17.9%. Thus the AFs for both Ambersham and Iping Commons are similar to the national values indicating that Ambersham and Iping Commons have a good representation of aerial nesters. It might be considered that sandy habitats could be poor in aerial-nesting species, but this observation does apply to Ambersham and Iping Commons.

The ants and host species of *Bombus* are subterranean nesters. Of the social wasps, *Vespa* species are usually subterranean nesters and *Dolichovespula* species aerial nesters, except for *D. sylvestris* which on heathland can be a subterranean or aerial nester.

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APPENDIX—Species list for Ambersham (A) and Iping (I) Commons with national statuses as Universal (U), Widespread (W), Restricted (RE), Scarce (S), Rare (R), Very rare (VR)

- Chysididae: *Omalus auratus* (L.) (A,W), *O. panzeri* (Fab.) (A,I,W), *Hedychridium ardens* (Latreille in Coquebert) (A,I,U), *H. roseum* (Rossius) (A,I,RE), *Chrysis angustula* Schenck (I,W), *C. helleni* Linsenmaier (I,S), *C. impressa* Schenck (A,I,U), *C. gracillima* Förster (I,VR), *C. rutilans* Dalhobom (A,R), *Trichrysis cyanea* (L.) (A,I,U), *Cleptes nitidulus* (Fab.) (I,R).
- Tiphiidae: *Tiphia femorata* Fab. (A,I,RE), *T. minuta* Vander Linden (A,S), *Methocha ichneumonides* Latreille (A,I,S).
- Mutillidae: *Myrmosa atra* Panzer (A,I,W), *Mutilla europaea* L. (A,I,S), *Smicromyme rufipes* (Fab.) (A,I,S).
- Formicidae: *Myrmica rubra* (L.) (I), *M. ruginodis* Nylander (A,I), *M. sabuleti* Meinert (I), *M. scabrinodis* Nylander (A,I), *Leptothorax acervorum* (Fab.) (A,I), *Tetramorium caespitum* (L.) (A), *Formica cunicularia* Latreille (A,I), *F. fusca* L. (A,I), *F. rufa* L. (A,I), *F. sanguinea* Latreille (A,I), *Lasius alienus* (Förster) (A,I), *L. flavus* (Fab.) (A,I), *L. fuliginosus* (Latreille) (A,I), *L. niger* (L.) (A,I), *L. umbratus* (Nylander) (A,I).
- Pompilidae: *Dipogon variegatus* (L.) (A,U), *Caliadurgus fasciatus* (Spinola) (A,I,RE), *Priocnemis agilis* (Shuckard) (A,S), *P. exaltata* (Fab.) (A,I,U), *P. fennica* Haupt (A,W), *P. gracilis* Haupt (A,I,S), *P. hyalinata* (Fab.) (I,S), *P. parvula* Dahlbom (A,I,U), *P. pusilla* Schiödte (A,I,W), *P. schiödtei* Haupt (A,I,U), *P. coriacea* Dahlbom (A,R), *P. perturbator* (Harris) (A,U), *P. susterai* Haupt (A,I,RE), *Pompilus cinereus* (Fab.) (A,I,U), *Agenioideus cinctellus* (Spinola) (A,I,R), *Arachnospila anceps* (Wesmael) (A,I,U), *A. trivialis* (Dahlbom) (A,I,W), *A. wesmaeli* (Thomson) (I,R), *A. minutula* (Dahlbom) (A,I,S), *A. spissa* (Schiödte) (A,I,U), *Evagetes crassicornis* (Shuckard) (A,I,U), *E. dubius* (Vander Linden) (A,I,R), *Anoplius concinnus* (Dahlbom) (I,S), *A. nigerrimus* (Scopoli) (A,I,U), *A. infuscatus* (Vander Linden) (A,I,W), *A. viaticus* (L.) (A,I,W), *Episyron rufipes* (L.) (A,I,W), *Aporus unicolor* Spinola (I,R), *Ceropales maculata* (Fab.) (A,R).
- Eumenidae: *Eumenes coarctatus* (L.) (A,I,S), *Gymnomerus laevipes* (Shuckard) (A,R), *Microdynerus exilis* (Herrich-Schäffer) (I,S), *Ancistrocerus gazella* (Panzer) (A,I,W), *A. nigricornis* (Curtis) (A,S), *A. oviventris* (Wesmael) (A,U), *A. trifasciatus* (Müller) (A,I,U), *Symmorphus gracilis* (Brullé) (A,I,W), *S. bifasciatus* (L.) (I,U).
- Vespididae: *Dolichovespula media* (Retzius) (I), *D. norwegica* (Fab.) (A,I), *D. saxonica* (Fab.) (A,I), *D. sylvestris* (Scopoli) (A,I), *Vespula rufa* (L.) (A,I), *V. germanica* (Fab.) (I), *V. vulgaris* (L.) (A,I).
- Sphecidae: *Astata boops* (Schrank) (A,I,RE), *Tachysphex pompiliformis* (Panzer) (A,I,U), *T. nitidus* (Spinola) (A,S), *Miscophus concolor* Dahlbom (A,I,RE), *Trypoxylon attenuatum* Smith (A,I,U), *T. clavicerum* Lepeletier (A,I,W), *T. figulus* (L.) (A,I,U), *T. medius* de Beaumont (A,I,U), *Crabro cribrarius* (L.) (A,U), *C. peltarius* (Schreber) (A,I,U), *C. scutellatus* (Scheven) (A,I,S), *Crossocerus elongatulus* (Vander Linden) (A,I,W), *C. ovalis* (Lepeletier & Brullé) (A,I,U), *C. pusillus* Lepeletier & Brullé (A,I,U), *C. tarsatus* (Shuckard) (I,U), *C. wesmaeli* (Vander Linden) (A,I,U), *C. cetratus* (Shuckard) (A,I,W), *C. megacephalus* (Rossius) (I,U), *C. nigritus* (Lepeletier & Brullé) (I,W), *C. walkeri* (Shuckard) (I,S), *C. podagricus* (Vander Linden) (A,I,U), *C. quadrimaculatus* (Fab.) (A,I,W), *Ectemnius borealis* (Zetterstedt) (A,I,VR), *E. dives* (Lepeletier & Brullé) (I,S), *E. cavifrons* (Thomson) (A,I,U), *E. lapidarius* (Panzer) (A,I,U), *E. ruficornis* (Zetterstedt) (A,I,W), *E. sexcinctus* (Fab.) (I,W), *E. continuus* (Fab.) (A,I,U), *E. cephalotes* (Olivier) (A,I,W), *E. lituratus* (Panzer) (A,I,RE), *Lindenius albilabris* (Fab.) (A,I,U), *L. panzeri* (Vander Linden) (A,I,RE), *Entomognathus brevis* (Vander Linden) (I,W), *Rhopalum clavipes* (L.) (I,U), *R. coarctatum* (Scopoli) (A,U), *Oxybelus mandibularis* Dahlbom (A,I,S), *O. unigumis* (L.) (A,I,U), *Psen dahlbomi* (Wesmael) (A,I,U), *P. unicolor* (Vander Linden) (I,R), *P. spooneri* (Richards) (I,VR), *P. bruxellensis* (Bondroit) (I,R), *P. equestris* (Fab.) (A,I,U), *P. lutarius* (Fab.) (A,I,W), *Psenulus pallipes* (Panzer) (A,I,W), *P. concolor* (Dahlbom) (I,W), *P. schencki* (Tournier) (A,I,R), *Spilomena troglodytes* (Vander Linden) (I,W), *Pemphredon lugubris* (Fab.) (A,I,U), *P. inornatus* Say (I,U), *P. lethifer* (Shuckard)

- (I,U), *P. morio* Vander Linden (I,S), *Diodontus insidiosus* Spooner (A,I,VR), *D. luperus* Shuckard (I,W), *D. minutus* (Fab.) (I,U), *Passaloecus corniger* Shuckard (A,I,W), *P. eremita* Kohl (A,I,W), *P. gracilis* (Curtis) (I,W), *P. singularis* Dahlbom (A,U), *Ammophila pubescens* Curtis (A,I,S), *A. sabulosa* (L.) (A,I,W), *Mellinus arvensis* (L.) (A,I,U), *Nysson spinosus* (Forster) (A,U), *N. trimaculatus* (Rossius) (A,S), *Gorytes quadrifasciatus* (Fab.) (A,I,W), *G. tumidus* (Panzer) (I,U), *Argogorytes mystaceus* (L.) (A,I,U), *Cerceris arenaria* (L.) (A,I,W), *C. ruficornis* (Fab.) (A,I,S), *C. rybyensis* (L.) (A,I,RE), *Philanthus triangulum* (Fab.) (A,I,W).
- Colletidae: *Colletes daviesanus* Smith (I,U), *C. fodiens* (Geoffroy in Fourcroy) (A,I,W), *C. similis* Schenck (A,I,W), *C. succinctus* (L.) (A,I,U), *Hylaeus communis* Nylander (A,I,W), *H. confusus* Nylander (A,I,U), *H. gibbus* Saunders (A,I,VR), *H. brevicornis* Nylander (A,I,W), *H. hyalinatus* Smith (A,W), *H. annularis* (Kirby) (A,RE).
- Andrenidae: *Andrena clarkella* (Kirby) (A,I,U), *A. fucata* Smith (A,U), *A. helyola* (L.) (A,W), *A. praecox* (Scopoli) (A,I,W), *A. synadelpha* Perkins (A,W), *A. varians* (Rossius) (A,S), *A. scotica* Perkins (A,U), *A. trimmerana* (Kirby) (A,S), *A. bicolor* Fab. (A,I,U), *A. angustior* (Kirby) (A,I,W), *A. pubescens* Olivier (A,I,W), *A. thoracica* (Fab.) (A,W), *A. denticulata* (Kirby) (A,I,U), *A. fuscipes* (Kirby) (A,I,U), *A. haemorrhoea* (Fab.) (A,I,U), *A. bimaculata* (Kirby) (A,I,S), *A. dorsata* (Panzer) (A,I,RE), *A. florea* Fab. (A,I,VR), *A. tarsata* Nylander (A,W), *A. coitana* (Kirby) (A,I,W), *A. argentata* Smith (A,I,R), *A. barbilabris* (Kirby) (A,I,U), *A. labiata* Fab. (A,R), *A. falsifica* Perkins (A,R), *A. minutula* (Kirby) (A,I,U), *A. saundersella* Perkins (A,I,U), *A. subopaca* Nylander (A,I,U), *A. congruens* Schmiedeknecht (I,R), *A. dorsata* (Kirby) (A,I,W), *A. ovatula* (Kirby) (A,I,W), *A. wilkella* (Kirby) (A,I,U), *Panurgus calcaratus* (Scopoli) (A,I,RE), *P. banksianus* (Kirby) (A,I,W).
- Halictidae: *Halictus rubicundus* (Christ) (A,I,U), *H. confusus* Smith (A,I,VR), *H. tumulorum* (L.) (A,I,U), *Lasioglossum lativentre* (Schenck) (I,W), *L. leucozonium* (Schränk) (A,I,W), *L. prasinum* (Smith) (A,I,RE), *L. zonulus* (Smith) (A,I,RE), *L. albipes* (Fab.) (A,I,U), *L. calceatum* (Scopoli) (A,I,U), *L. fulvicorne* (Kirby) (A,I,W), *L. malachurus* (Kirby) (A,S), *L. minutissimum* (A,I,W), *L. nitidiusculum* (Kirby) (I,U), *L. parvulum* (Schenck) (A,I,W), *L. punctatissimum* (Schenck) (A,I,W), *L. villosulum* (Kirby) (A,I,U), *L. leucopum* (Kirby) (A,I,U), *L. morio* (Fab.) (A,I,W), *Sphecodes crassus* Thomson (A,I,S), *S. ephippius* (L.) (A,I,W), *S. geoffrellus* (Kirby) (A,I,U), *S. gibbus* (L.) (A,I,W), *S. longulus* von Hagens (A,R), *S. monilicornis* (Kirby) (A,I,U), *S. pellucidus* Smith (A,I,W), *S. puncticeps* Thomson (A,W), *S. reticulatus* Thomson (I,R).
- Melittidae: *Melitta leporina* (Panzer) (I,W), *M. tricineta* Kirby (I,S).
- Megachilidae: *Anthidium manicatum* (L.) (A,I,W), *Stelis ornatula* (Klug) (A,R), *Heriades truncorum* (L.) (A,I,VR), *Osmia rufa* (L.) (A,U), *O. caerulescens* (L.) (A,I,W), *O. leaiana* (Kirby) (A,W), *O. bicolor* (Schränk) (A,S), *Hoplitis claviventris* (Thomson) (A,I,W), *Megachile centuncularis* (L.) (A,I,U), *M. ligniseca* (Kirby) (A,I,W), *M. versicolor* Smith (A,I,U), *M. willughbiella* (Kirby) (A,I,U), *M. circumcincta* (Kirby) (A,U), *M. maritima* (Kirby) (A,I,W), *Coelioxys elongata* Lepeletier (I,U), *C. inermis* (Kirby) (I,W), *C. rufescens* Lepeletier & Serville (A,I,W).
- Anthophoridae: *Nomada baccata* Smith (A,R), *N. fabriciana* (L.) (A,I,U), *N. flava* Panzer (A,I,W), *N. flavoguttata* (Kirby) (A,I,U), *N. fulvicornis* Fab. (A,VR), *N. goodeniana* (Kirby) (A,I,U), *N. leucophthalma* (Kirby) (A,I,W), *N. marshamella* (Kirby) (A,I,U), *N. rufipes* Fab. (A,I,U), *N. striata* Fab. (A,W), *Epeolus cruciger* (Panzer) (A,I,W), *E. variegatus* (L.) (I,U), *Anthophora furcata* (Panzer) (A,I,W), *A. bimaculata* (Panzer) (A,I,RE).
- Xylocopidae: *Ceratina cyanea* (Kirby) (A,I,R).
- Apidae: *Bombus lucorum* (L.) (A,I), *B. terrestris* (L.) (A,I), *B. lapidarius* (L.) (A,I), *B. jonellus* (Kirby) (A,I), *B. pratorum* (L.) (A,I), *B. hortorum* (L.) (A,I), *B. pascuorum* (Scopoli) (A,I), *Psithyrus bohemicus* (Seidl) (A), *P. campestris* (Panzer) (A,I), *P. sylvestris* (Lepeletier) (A), *P. vestalis* (Geoffroy in Fourcroy) (A,I).