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The wasps and bees (Hymenoptera: Aculeata) of the river bank at Beningbrough and Keswick Fitts in Watsonian Yorkshire

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Aculeate wasps and bees require open terrestrial habitats, particularly as nesting sites. The open landscape that we now know is largely a result of human activity. The habitats originally used by the aculeate wasps and bees were coastal and inland sand dunes and dynamic floodplains (Klemm, 1996). River banks were kept open either through the erosion of winter floods or by the deposition of gravels, sands and silts. The river banks at Beningbrough (SE5257, VC62) on the river Ouse and at Keswick Fitts (SE3446, VC64) on the river Wharfe can be seen as modern examples of such river action.

The curving river at Beningbrough has created vertical bare banks, up to about three metres high by erosion, and, mainly through silt deposition, sloping open areas. The bare banks have attracted subterranean nesting species such as *Colletes daviesanus*, *Halictus rubicundus* and *Argogorytes fargei* in small and large aggregations. A herb flora has also developed providing nectar and pollen besides the prey needed by the wasp species. Tansy is particularly attractive to *C. daviesanus*. Wood detritus, boundary walls and wooden fences of properties, tree stumps and overhanging dead tree branches provide sites for the aerial nesting species. From time to time cattle have been allowed to graze the river bank which has also helped to keep the habitat open, although grazing can destroy the herb flora.

The curving river at Keswick Fitts has had a similar effect to that at Beningbrough, although the depositions have mainly been of shingle and sand. From the southern river bank the deposition areas extend for several metres and willow carr has developed. Also on this deposition area is Carthick Wood which is an open wood with much standing dead wood and a rich herb flora.

The aims of this paper are to describe the aculeate wasp and bee fauna of the two sites, to show the importance of the two sites in the context of Watsonian Yorkshire, to calculate the cleptoparasitic loads and aerial nesting frequencies and to use non-parametric statistical procedures to estimate potential species diversity.

Methods

The northern bank of the river Ouse at Beningbrough was visited on 19 occasions during three time periods: 1970–1974, 1985–1987 and 1995–1999. During 16 of these visits, which usually lasted about two hours, all species of aculeate wasps and bees were recorded and usually collected with a hand net for identification. The 16 visits were distributed through the year as follows: March (one visit), April (2), May (4), June (2), July (3), August (3), September (1). The linear strip of land visited is about 0.063 ha.

The southern bank of the river Wharfe at Keswick Fitts was visited on 18 occasions between 1987 and 1996 distributed through the year as follows: April (2 visits), May (4), June (4), July (4), August (3), September (1). All species of aculeate wasps and bees were recorded during these visits which usually lasted about three hours or longer. The area of land visited is about 12 ha. In addition records are available from A. Godfrey's one visit (13 July 1996) when four species of aculeate wasps and bees were recorded, and subsequently identified by the author.

In the following account, scientific names are according to Kloet & Hincks (1978).

Species present

A full list of the species recorded is given below. At the family level, Table 1 shows the taxonomic distribution of species and records. A record represents a specimen differing in one of the following three variables: name, sex and day of visit. The solitary wasp family Sphecidae is particularly well represented, as is the Chrysididae by the number of records. Among the solitary bee families the Andrenidae, Halictidae and Anthophoridae are particularly well represented.

Table 1. The number of species and records of aculeate wasps and bees from Beningbrough and Keswick Fitts (KesFit).

	No. species		No. records	
	Beningbrough	KesFit	Beningbrough	KesFit
Solitary wasps				
Chrysididae	3	6	8	22
Mutillidae	1	0	1	0
Sapygidae	0	1	0	1
Pompilidae	3	1	6	3
Eumenidae	5	4	8	7
Sphecidae	14	27	33	91
Total solitary wasps	26	39	56	124
Solitary bees				
Colletidae	2	3	12	6
Andrenidae	7	15	34	52
Halictidae	12	10	33	48
Megachilidae	1	2	1	4
Anthophoridae	5	10	12	30
Total solitary bees	27	40	92	140
Total solitary wasps and bees	53	79	148	264
Social wasps and bees				
Vespidae	4	5		
Apidae	11	8		
Total social wasps and bees	15	13		
Total wasps and bees	68	92		

A list of the aculeate wasps and bees (Hymenoptera) recorded from Beningbrough (B) and Keswick Fitts (K)

Yorkshire regional status – Common (C), Frequent (F), Occasional (O), Rare (RR). National status – Universal (U), Widespread (W), Scarce (S), Rare (RN), Very rare (VR). Nature Conservancy Council status – Notable a (Na), Notable b (Nb), Red Data Book 3 (RDB3).

CHRYSIDIDAE: *Omalus auratus* (L.) (K,F,W), *Chrysis angustula* Schenck (B,K,C,W), *C. ignita* (L.) (K,C,U), *C. impressa* Schenck (B,K,C,U), *C. rutiliventris* Abeille de Perrin (K,O,U), *Trichrysis cyanea* (L.) (B,K,C,U).

MUTILLIDAE: *Myrmosa atra* Panzer (B,C,W).

SAPYGIDAE: *Sapyga clavicornis* (L.) (K,O,S,Nb).

POMPILIDAE: *Dipogon subintermedius* (Magretti) (= *nitidus*) (B,K,F,U), *Priocnemis exaltata* (Fb.) (B,F,U), *P. perturbator* (Harris) (B,F,U).

EUMENIDAE: *Ancistrocerus gazella* (Panzer) (B,C,W), *A. parietinus* (L.) (B,K,C,U), *A. parietum* (L.) (B,K,C,U), *A. trifasciatus* (Müller) (B,K,C,U), *Symmorphus bifasciatus* (L.) (= *mutinensis*) (B,K,F,U).

VESPIDAE: *Dolichovespula norwegica* (F.) (K), *D. sylvestris* (Scopoli) (B,K), *Vespula rufa* (L.) (B,K), *V. germanica* (F.) (B,K), *V. vulgaris* (L.) (B,K).

SPHECIDAE: *Trypoxylon attenuatum* Smith (K,C,U), *T. clavicerum* Lepeletier (K,F,W), *T. figulus* (L.) (B,K,C,U), *Crabro cribrarius* (L.) (K,C,U), *C. peltarius* (Schreber) (B,F,U), *Crossocerus cetratus* (Shuckard) (B,K,F,W), *C. dimidiatus* (F.) (K,C,U), *C. elongatulus* (Vander Linden) (K,C,W), *C. megacephalus* (Rossius) (K,C,U), *C. podagricus* (Vander Linden) (B,K,F,U), *C. pusillus* Lepeletier & Brullé (= *varus*) (K,C,U), *C. quadrimaculatus* (F.) (B,K,C,W), *C. tarsatus* (Shuckard) (B,K,C,U), *C. walkeri* (Shuckard) (K,RR,S,Nb), *Ectemnius cavifrons* (Thomson) (K,C,U), *E. cephalotes* (Olivier) (K,F,W), *E. continuus* (F.) (K,C,U), *Lindenius albilabris* (F.) (K,C,U), *Rhopalum coarctatus* (Scopoli) (K,F,U), *Oxybelus uniglumis* (L.) (B,F,U), *Psenulus pallipes* (Panzer) (K,F,W), *Pemphredon inornatus* Say (K,C,U), *P. lugubris* (F.) (K,C,U), *P. morio* Vander Linden (B,RR,S,Nb), *Diodontus minutus* (F.) (B,O,U), *D. tristis* (Vander Linden) (B,F,W), *Passaloecus corniger* Shuckard (B,K,O,W), *P. gracilis* (Curtis) (K,O,W), *Mellinus arvensis* (L.) (B,K,C,U), *Nysson spinosus* (Forster) (K,F,U), *Argogorytes fargei* (Shuckard) (B,K,RR,RN,Na), *A. mystaceus* (L.) (B,K,C,U).

COLLETIDAE: *Colletes daviesanus* Smith (B,F,U), *Hylaeus communis* Nylander (B,K,F,W), *H. confusus* Nylander (K,O,U), *H. hyalinatus* Smith (K,O,W).

ANDRENIDAE: *Andrena barbilabris* (Kirby) (B,K,C,U), *A. bicolor* F. (K,C,U), *A. chrysosceles* (Kirby) (B,K,C,W), *A. cineraria* (L.) (K,C,W), *A. clarkella* (Kirby) (K,C,U), *A. fucata* Smith (K,C,U), *A. fulva* (Müller in Allioni) (B,K,C,U), *A. fuscipes* (Kirby) (K,F,U), *A. haemorrhoa* (F.) (B,K,C,U), *A. helvola* (L.) (K,O,W), *A. nigriceps* (Kirby) (K,O,S,Nb), *A. nigroaenea* (Kirby) (B,C,U), *A. ruficrus* Nylander (K,O,RN,RBD3), *A. saundersella* Perkins (B,K,C,U), *A. scotica* Perkins (B,K,C,U), *A. wilkella* (Kirby) (K,C,U).

HALICTIDAE: *Halictus rubicundus* (Christ) (B,K,C,U), *H. tumulorum* (L.) (B,K,F,U), *Lasioglossum albipes* (F.) (K,C,U), *L. calceatum* (Scopoli) (B,K,C,U), *L. nitidiusculum* (Kirby) (B,K,O,U), *L. rufitarse* (Zetterstedt) (B,K,C,W), *L. villosulum* (Kirby) (B,F,U), *L. cupromicans* (Pérez) (B,K,C,W), *L. smeathmanellum* (Kirby) (B,F,U), *Sphecodes geoffrellus* (Kirby) (= *fasciatus*) (B,K,C,U), *S. gibbus* (L.) (B,K,F,W), *S. monilicornis* (Kirby) (B,K,F,U), *S. pellucidus* Smith (B,F,W).

MEGACHILIDAE: *Chelostoma florisomne* (L.) (K,O,W), *Osmia rufa* (L.) (B,K,C,U).

ANTHOPHORIDAE: *Nomada fabriciana* (L.) (B,K,C,U), *N. flavoguttata* (Kirby) (B,K,F,U), *N. goodeniana* (Kirby) (B,K,C,U), *N. lathburiana* (Kirby) (K,F,W,RBD3), *N. leucophthalma* (Kirby) (K,F,W), *N. marshamella* (Kirby) (B,K,C,U), *N. panzeri* Lepeletier (K,C,U), *N. ruficornis* (L.) (K,C,U), *N. striata* F. (K,F,W), *Anthophora furcata* (Panzer) (B,K,O,W).

APIDAE: *Bombus lucorum* (L.) (B,K), *B. terrestris* (L.) (B,K), *B. lapidarius* (L.) (B,K), *B. pratorum* (L.) (B,K), *B. hortorum* (L.) (B,K), *B. pascuorum* (Scopoli) (B,K), *Psithyrus bohemicus* (Seidl) (B,K), *P. campestris* (Panzer) (B), *P. sylvestris* Lepeletier (B), *P. vestalis* (Geoffroy in Fourcroy) (B), *Apis mellifera* L. (B,K).

The recorded number of solitary species from Keswick Fitts is of a magnitude expected from its area in terms of species-area relationship for northern and north Midlands sites of England (Archer, 1995), but that for Beningbrough is larger, being of a magnitude more typical of south-eastern England (Archer, unpublished). Two hypotheses can be suggested to explain the increased species richness of Beningbrough. Firstly, species that are nesting outside the study area are flying into the study area for resources which are less available in the surrounding agricultural land. Secondly, species may be using the river as a dispersal pathway and are recorded as they pass through the study area. Because the number of species is so related to the area of Keswick Fitts, the community characteristics of the solitary species of wasps and bees can be compared with other northern and north Midlands sites of England. Such a comparison for Beningbrough would be less valid.

Seasonal progression of species

For Keswick Fitts, June, July and August were the best months for recording species of solitary wasps with June and July the most productive months for new species (Table 2). April, May and June were the best months for recording species and new species of solitary bees (Table 2). The species most evident were the aerial-nesting species from Carthick Wood including *Trypoxylon clavicerum*, *T. figulus* and *Crossocerus cetratus* with the males flying between the upstanding dead wood looking for the females and the females flying to and from their nests in the dead wood. The parasites of these species, e.g. *Chrysis angustula* and *Trichrysis cyanea*, were also observed flying between the dead wood. Of the subterranean nesters the most evident species were the sphecid wasp *Argogorytes fargei* around its nesting sites on the bare vertical river banks, and the solitary bees with their cleptoparasites: *Colletes daviesanus* (its cleptoparasite *Epeolus variegatus* (L.) was not found), *Andrena haemorrhoa* (with *Nomada ruficornis*), *A.*

Table 2. The number of species and additional species of solitary wasps and bees recorded per month at Beningbrough and Keswick Fitts.

	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.
No. species							
Beningbrough							
Solitary wasps	0	0	1	8	13	14	4
Solitary bees	1	7	11	10	11	9	6
Keswick Fitts							
Solitary wasps	–	0	1	21	29	17	8
Solitary bees	–	14	25	20	8	8	5
No. additional species							
Beningbrough							
Solitary wasps	0	0	1	8	10	6	1
Solitary bees	1	6	6	3	5	5	1
Keswick Fitts							
Solitary wasps	–	0	1	20	14	3	1
Solitary bees	–	14	14	9	1	1	1

chrysosceles (*Nomada fabriciana*), *Halictus rubicundus* (*Sphecodes gibbus* and *S. monilicornis*), *Lasioglossum calceatum* (*S. monilicornis*) and *L. nitidiusculum* (*S. fasciatus*).

For Beningbrough, July and August were the best months for recording species of solitary wasps with June, July and August the best months for recording species new to the area (Table 2). May, June and July were the best months for recording species of solitary bees and April through to August for additional species (Table 2). The good months for recording new species of solitary wasps during August and new bees during July and August is unusual compared with past experience. Some of these new species could be those visiting the site for resources or flying through on their dispersal flights as hypothesized above. The species most evident are all subterranean nesters in the bare river bank: *Andrena haemorrhoa* (its cleptoparasite *Nomada ruficornis* has not yet been found), *Andrena barbilabris* (*Sphecodes pellucidus*), *A. chrysosceles* (*Nomada fabriciana*), *Halictus rubicundus* (*S. gibbus* and *S. monilicornis*) and *Lasioglossum nitidiusculum* (*S. fasciatus*).

Estimating the potential number of solitary wasp and bee species

Keswick Fitts

Although sufficient solitary species have been recorded from Keswick Fitts to carry out comparisons with other Yorkshire sites, the problem of how many more species are present on the site, but as yet unrecorded, remains. Recent advances in non-parametric statistical procedures offer some hope 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 observed 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 these statistical procedures was provided by Pisces Conservation Ltd.

The statistical procedure was run 18 times and the resulting estimates of species richness are given in Fig. 1. In practice the software selects 1, 2, etc. samples at random from the 18 samples, each time calculating an estimate of species richness. With a small number of samples the estimates are erratic, but as more samples are selected the estimates stabilise giving confidence in the estimates. Since 18 estimates are calculated for each sample size selected, the error, or confidence limits, at each sample size can also be calculated. The estimated species richness is 109 (84–134 species at 95% confidence limits), so that 72% (79 observed species × 100 divided by 109 estimated species) of the species estimated have been found.

Another non-parametric statistical estimator is the first order jackknife procedure (Heltshe & Forrester, 1983) which was performed with the software of Pisces Conservation Ltd. This jackknife procedure gave a species richness estimate of 106 (97–115 species at 95% confidence limits), so that 75% of the species estimated have been found.

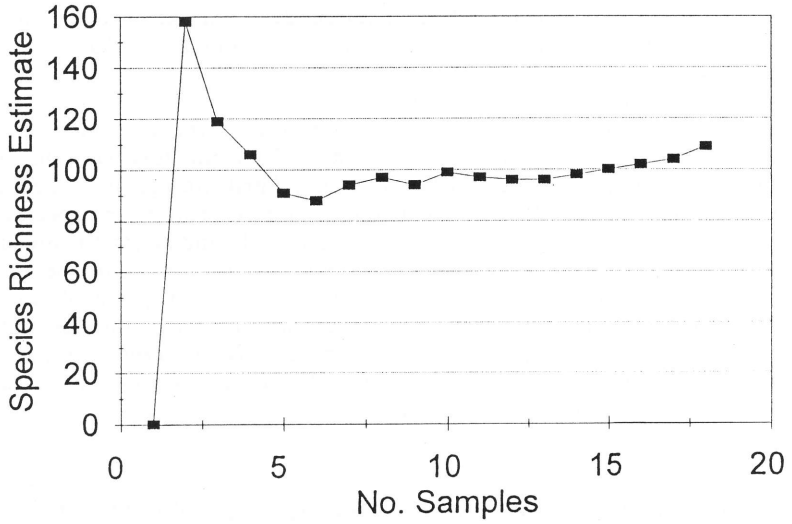

Fig. 1. The Chao presence/absence estimate of species richness for Keswick Fitts.

Since the Chao and jackknife estimates are of similar value and the estimates on Fig. 1, although still slightly increasing, are relatively stable, confidence may be placed in these estimates.

The Chao estimate has been calculated for several of the author's study sites in the north and north Midlands sites of England. The number of solitary species of aculeate wasps and bees found by the author at these sites expressed as a percentage of the Chao estimate is given in Table 3. The percentages vary from

Table 3. The observed number of solitary species of aculeate wasps and bees as a percentage of the Chao presence/absence estimate of species richness at sites in the north and north midlands of England.

Site	Percentage
Messingham Sand Quarry, North Lincs.	71
Saltfleetby-Theddlethorpe NNR, Lincs.	75
Pompocali, West Yorks.	76
Skipwith Common, North Yorks.	77
Blaxton Common, South Yorks.	78
Sherwood Forest, Notts.	78
Strensall Common, North Yorks.	80
Allerthorpe Common, East Riding Yorks.	81
Cave Wold, East Riding Yorks.	81
Duncombe Park, North Yorks.	81
Risby Warren, North Lincs.	87
Burton Leonard Lime Quarries, North Yorks.	88
Shipley Glen, West Yorks.	88
Gibraltar Point, Lincs.	90
Holmehouse Wood, nr Keighley, West Yorks.	91

71% to 91%. Based on these data it has arbitrarily been decided that when the percentage reaches 70% sufficient samples have been taken from a site to have confidence in the species richness estimates.

Beningbrough

From the species-area relationship investigation for Beningbrough and the hypotheses developed to explain the relationship it may be predicted that species richness estimates would be far greater than the observed number of species of solitary wasps and bees. The Chao presence/absence estimate of species richness is 92 (57–127 species at 95% confidence limits) so that only 58% of the estimated species have been found. The first order jackknife estimate is 76 species (63–89 species at 95% confidence limits) so that 70% of the estimated species have been found. The lack of agreement between the two estimates does not give confidence in these estimates and indicates that further samples need to be taken. From the study of the seasonal progression of species probably these additional samples should be taken during July and August.

Quality assessment of the solitary species

According to Shirt (1987) and Falk (1991) Beningbrough has two species of national importance (*Pemphredon morio* and *Argogorytes fargei*) and Keswick Fitts six species of national importance (*Sapyga clavicornis*, *Crossocerus walkeri*, *Argogorytes fargei*, *Andrena nigriceps*, *A. ruficrus* and *Nomada lathburiana*). In a Watsonian Yorkshire context, each site also has two species with a rare status: Beningbrough (*Pemphredon morio* and *Argogorytes fargei*) and Keswick Fitts (*Crossocerus walkeri* and *Argogorytes fargei*) (Archer, 1998). Current work being carried out by members of the Bees, Wasps and Ants Recording Society indicates that the status of *Nomada lathburiana* will need to be down-graded and lose its national status.

By giving each of the 53 solitary species from Beningbrough and the 79 solitary species from Keswick Fitts a regional status (Archer, 1993) gives Beningbrough a regional quality score of 113 and a species quality score of 2.1 (113/53) and Keswick Fitts a regional quality score of 216 and a species quality score of 2.7 (216/79) (Table 4). Within Watsonian Yorkshire the species quality score for Beningbrough puts it on a par with Holmehouse Wood, near Keighley

Table 4. The regional status scheme for the solitary species of wasps and bees recorded at Beningbrough (BH) and Keswick Fitts (KF).

Status	Status value (A)	No. species BH(B)	No. species KF(B)	Quality score BH(AxB)	Quality score KF(AxB)
Common	1	29	46	29	46
Frequent	2	18	19	36	38
Occasional	4	4	9	16	36
Rare	8	0	0	0	0
Nationally scarce	16	2	4	32	64
Nationally rare	32	0	1	0	32
Total		53	79	113	216

Table 5. The Archer National Status Scheme for the solitary species of wasps and bees recorded at Beningbrough (BH) and Keswick Fitts (KF).

Status	Status value (A)	No. species BH(B)	No. species KF(B)	Quality score BH(AxB)	Quality score KF(AxB)
Universal	1	37	51	37	51
Widespread	2	14	23	28	46
Restricted	4	0	0	0	0
Scarce	8	1	3	8	24
Rare	16	1	1	16	16
Very rare	32	0	1	0	32
Total		53	79	89	169

(2.0), Swincarr Plantation (2.1) and Skipwith Common (2.2). Keswick Fitts may be grouped with Shipley Glen (2.4), Pompocali (2.7) and Duncombe Park (2.7).

Using a national status for each solitary species gives Beningbrough a national quality score of 89 and a species quality of 1.7 (89/53) and Keswick Fitts a quality score of 199 and a species quality score of 2.1 (169/79) (Table 5) (Archer, 1995). In these provisional calculations *Nomada lathburiana* is given a widespread status. Within Watsonian Yorkshire the species quality score for Beningbrough groups it with Burton Leonard Lime Quarries (1.6), Skipwith Common (1.6) and Swincarr Plantation (1.8). Keswick Fitts may be grouped with Shipley Glen (2.0) and Duncombe Park (2.2).

Since more samples need to be taken from Beningbrough the regional and national quality scores for this site should be increased when these additional samples are taken.

National quality and species quality scores have also been calculated for the 18 visits to Keswick Fitts from April until September (Table 6). Table 6 also shows the overall quality and species quality score. Quality scores are likely to be greatly influenced by recording effort, but species quality scores should largely correct for variation in recording effort (Ball, 1992; Foster, 1996). Although recording effort was more or less constant for each visit, the percentage variation of daily scores (783%) is greater than that for species quality scores (390%). The greater percentage variation of the quality scores is a consequence of the variation in the number of species recorded on each visit (varied between 4–23 species, % variation 575%) and the presence of high quality species. High quality species are those species that have a very rare, rare or restricted status. The high quality species (with the exception of *Argogorytes fargei*) were each only found in one sample and their presence relative to the number of species observed can greatly increase the quality score, e.g. 4 May 1987 and 10 August 1990. Thus species quality scores can correct, like variation in recording effort, for the variation in the number of species recorded.

Can a species quality score from one or two visits to a site be used to give a relatively good prediction of the overall species quality score for the site? Of the 18 visits only two fall within 10% of the overall species quality score, i.e. 1.9–2.3, with 12 visits falling below this range and four visits above this range. As such it is unlikely that one or two visits would give a relatively good prediction of the

Table 6. The Archer National Daily Quality Scores of the solitary species of wasps and bees recorded from Keswick Fitts.

Date	No. species	Quality score	Species quality score
24 April 1988	11	14	1.3
29 April 1990	7	9	1.3
4 May 1987	12	47	3.9
14 May 1988	14	18	1.3
23 May 1993	12	14	1.2
30 May 1987	5	6	1.2
6 June 1987	10	15	1.5
13 June 1987	13	18	1.4
15 June 1989	23	44	1.9
25 June 1988	13	41	3.2
4 July 1989	16	39	2.4
5 July 1993	18	40	2.2
25 July 1987	7	7	1.0
27 July 1992	16	24	1.5
10 August 1987	4	13	3.3
18 August 1990	10	12	1.2
28 August 1993	16	23	1.4
14 September 1996	13	17	1.3
Overall	79	169	2.1

overall species quality score unless the visits were during the second half of June and first half of July (Table 6).

An analysis for Beningbrough has not been carried out because, as indicated above, further samples need to be taken. However, it will be interesting to observe whether the species quality score does or does not change when further samples are taken.

Cleptoparasitic load

The cleptoparasitic load (CL) is the percentage of aculeate species that are cleptoparasitic (or parasitoids) on other host aculeates. According to Wcislo (1987) the amount of parasitic behaviour among the aculeate Hymenoptera correlates with geographical latitude, being higher in the temperate regions compared with the tropical regions. As such, CLs for sites in Britain should have similar values. The CLs for the solitary wasps and bees are given in Table 7.

Table 7. The relative frequency of the cleptoparasitic species among the solitary wasps and bees at Beningbrough and Keswick Fitts.

	No. hosts (H)	No. cleptoparasites (C)	Cleptoparasitic load CL = 100 x C/(H+C)
Solitary wasps			
Beningbrough	22	4	15.4
Keswick Fitts	31	8	20.5
Solitary bees			
Beningbrough	19	8	29.6
Keswick Fitts	28	12	30.0

Table 8. The nesting habits of the host species of solitary wasps and bees recorded from Beningbrough and Keswick Fitts.

	No. aerial nesters (A)	No. subterranean nesters (S)	Aerial nester frequency AF = 100 x A/(A+S)
Solitary wasps			
Beningbrough	11	11	50.0
Keswick Fitts	22	9	71.0
Solitary bees			
Beningbrough	3	16	15.8
Keswick Fitts	6	22	21.4

In Watsonian Yorkshire the CLs for species of solitary wasps vary from 10.3%–20.0% (range 9.7%). The CL for Beningbrough occurs within this range while that of Keswick Fitts slightly extends the range to 10.2%. In Watsonian Yorkshire the CLs for species of solitary bees vary from 25.8%–36.6% (range 10.8%). The CLs for Beningbrough and Keswick Fitts fall within this range.

Aerial nester frequency

The aerial nester frequency (AF) is the percentage of host aculeate species that use aerial nest sites. The AFs for the solitary wasps and bees are given in Table 8. In Watsonian Yorkshire the AFs for solitary wasps vary widely from 0.0%–84.4%. The AF for the British species of solitary wasps is 46.2%. As such, the AF for Beningbrough is about average but the AF for Keswick Fitts is high owing to the plentiful dead wood of Carthick Wood. In Watsonian Yorkshire the AFs for solitary bees again vary widely from 6.7%–30.8%. The AF for the British species of solitary bees is 17.9%. As such, the AFs for Beningbrough and Keswick are about average and the plentiful dead wood at Keswick Fitts has not encouraged the presence of more species of aerial-nesting solitary bees.

Summary

In comparison with other sites from Watsonian Yorkshire the community of species of solitary wasps and bees from Beningbrough and Keswick Fitts show:

1. Beningbrough is a good site with one nationally high quality species and two Yorkshire rare species and Keswick Fitts is a very good site with five nationally high quality species and two Yorkshire rare species.
2. Keswick Fitts has the expected number of solitary species for the area of the site, and can properly be compared with other sites. Beningbrough probably only represents part of a natural unit and further samples are needed to extend the species list.
3. Both sites have similar cleptoparasitic loads to those of other Watsonian Yorkshire sites, as predicted by Wcislo (1987).
4. Keswick Fitts is particularly rich in aerial-nesting solitary wasps.

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