

**THE ACULEATE WASPS AND BEES (HYMENOPTERA:
ACULEATA) OF THE AINSDALE-FORMBY SAND DUNES
ON THE LANCASHIRE COAST COMPARED WITH OTHER
NORTHERN SITES**

MICHAEL E. ARCHER

University College of Ripon & York St. John, York YO31 7EX, UK.

The main aims of this paper are, firstly, to give an account of the aculeate wasps and bees of the sand dunes of Ainsdale-Formby on the Lancashire coast, secondly, determine if the species list of the Ainsdale-Formby sand dunes is sufficiently complete to make comparisons with other sites, and thirdly, having shown the species list is sufficiently complete, to carry out comparisons at the community level with other north and north midland English sites.

The Ainsdale-Formby sand dunes are situated to the west of Ainsdale and Formby. Within the Ainsdale-Formby sand dunes the following sites have been sampled for aculeate wasps and bees: Birkdale Sandhills LNR (SD3013); Ainsdale Sandhills LNR (SD2912); Ainsdale Sand Dunes NNR (SD2911); National Trust Formby Point (SD2707); Lifeboat Road Formby Point (SD2706); Ravenmoels LNR (SD2706). These sites cover an area of about 940 ha, about 45% of the 2100 ha of the Sefton sand dunes (Atkinson & Houston, 1993).

The Ainsdale-Formby sand dunes consist of fore, yellow and grey dunes with wet and dry slacks and a small amount of salt marsh. Dune heath, shrubs (including seabuckthorn), pine and deciduous trees are also present. Many of the pines on the seaward side are dead and, with extensive bramble patches, provide aerial nesting sites for aculeates. The bordering habitats are urban.

SOURCES OF RECORDS

The earliest records are given by Gardiner (1907), probably produced by B. Cooke, from the latter part of the nineteenth century. Although detailed localities are not given, ten species of solitary wasps and five species of solitary bees are from the Ainsdale-Formby sand dunes. All these species have been found subsequently.

Records have been obtained from specimens at the museums of Liverpool, Leeds and Manchester. Records from Liverpool museum were supplied by T. Mawdsley and C. Clee. The records are from 20 collectors (1930-1988) of whom H. Britten (1930-1964), C. M. Jones (1950-1969) and C. O'Toole (1962-1969) are the most important. Other specimens were examined by me at the museums of Leeds (A. Norris) and University of Manchester (C. Johnson). Relatively few records (from five collectors, 1907-1951) were found at Leeds. At Manchester, records from eight collectors (1906-1959) were found. The most important were those of H. Britten (1921-1947). Most museum records were derived from the following sites: National Trust Formby Point; Ainsdale NNR; probably Ainsdale LNR; and a few records from Birkdale LNR.

Kenneth-Booker (no date) produced a list of 60 aculeate wasp and bee species recorded during 1976 at Ainsdale NNR. This list was extended by five species in a letter sent to G. R. Else during 1981. Another listing of 79 aculeate wasp and bee species, covering the years 1975-1980, was sent to me by W. Kenneth-Booker (*pers. comm.*, 1989). C. O'Toole sent a list of 73 aculeate wasp and bee species recorded from Ainsdale NNR (*pers. comm.*, 1988).

I visited the Ainsdale–Formby sand dunes on eleven days during 1983–1989. My visits were mainly to Ainsdale LNR, Ravenmoels LNR, Lifeboat Road Formby Point and National Trust Formby Point. I also have identified specimens collected by A. Godfrey from a visit to Ainsdale NNR during 1990.

In summary, 31 collectors have provided records from the Ainsdale–Formby sand dunes from 1906 until 1990, with a few records from the latter part of the nineteenth century. Most records were made from April until September with a few records from February, March and October.

Names and the ordering of species in Appendix 1 are according to Kloet & Hincks (1978). However, where there have been name changes since Kloet & Hincks the new species names are used but the old species are indicated in brackets.

SPECIES PRESENT

A total of 110 species (94 solitary and 16 social species) has been recorded (Appendix 1). Since 1970, 19 of these species have not been recorded (Appendix 1). Most of these 19 species probably are still present, but the following species, with appropriate reference in brackets, almost certainly will have been lost: *Ancistrocerus nigricornis* (Curtis) (Archer, 1988), *Oxybelus mandibularis* Dahlbom (Edwards, 1977), *Lasioglossum laevigatum* (Kirby) and *Coelioxys quadridentata* (L.) (Else, in prep.).

SPECIES–AREA RELATIONSHIP

One of the problems in the study of any site is the difficulty of knowing when the species list is sufficiently complete so that comparisons with other sites may reasonably be carried out. One way to resolve this is the use of the species–area relationship, where the number of species and the area of 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 a site falls below the values of the other sites then this could indicate either many more species could be found at that site, or that the site consists of habitats which are particularly unfavourable for aculeate wasps and bees.

As an example of a favourable site where the species list is not sufficiently complete, Archer (1996c) found that the number of species of solitary aculeate wasps and bees from Sark fell well below the species–area relationship shown by the other Channel Islands. He suggested that about a further 35 species could be found on Sark to bring its number of species relative to its area to the level of species–area relationship of the other islands. I. C. Beavis (*pers. comm.*, 1997) has subsequently succeeded in finding 29 of the estimated 35 species on Sark.

Bog and closed woodland may be unfavourable habitats for aculeate wasps and bees and would be expected to have fewer species than the area of a site would indicate. For example, Askham Bog with an area of 49 ha should have about 71 species of solitary wasps and bees as calculated from the species–area relationship indicated in Fig. 1. Archer (1987) found that only 31 species have been recorded from this site, which is only about 44% of the number of species expected. Much of Askham Bog consists of bog and closed woodland.

The species–area relationship will be investigated with data from 18 sites from the north and north midlands of England (Table 1). Restriction of the comparison sites to north and north midlands sites is necessary because it is known that species–area

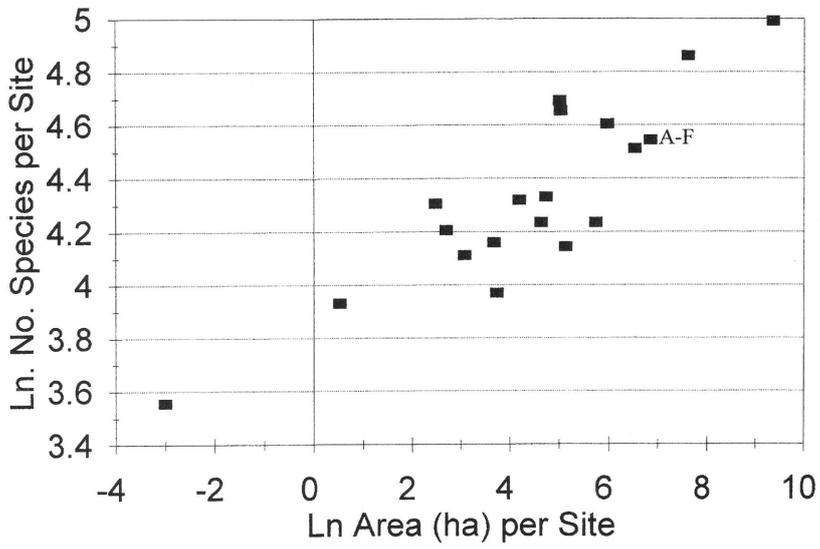


Fig. 1. A species–area relationship plot of 19 sites from the north and north midlands of England. A-F, Ainsdale–Formby sand dunes.

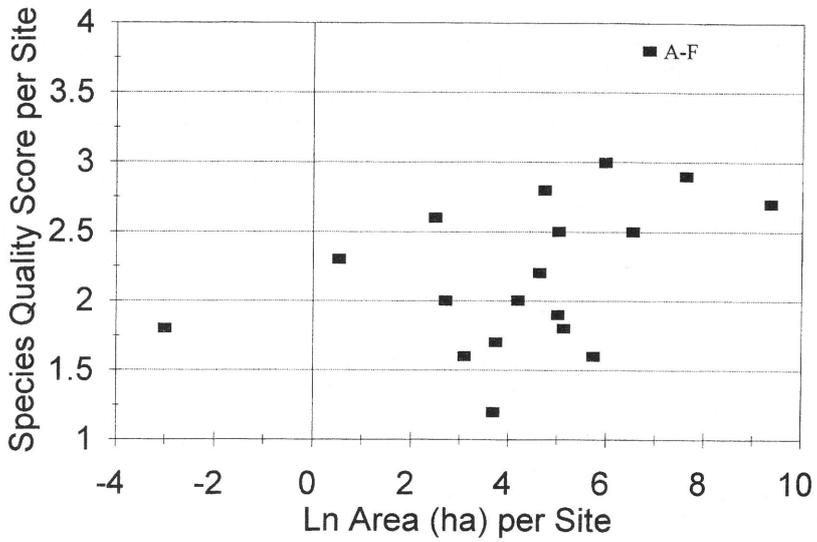


Fig. 2. A species quality score–area relationship plot of 19 sites from the north and north midlands of England. A-F, Ainsdale–Formby sand dunes.

Table 1. Grid references (G.R.), habitat characteristics*, cleptoparasitic loads (CL) and aerial nester frequencies (AF) of the solitary species, of 18 north and north midland English sites

Site name	G.R.	Habitat	CL		AF		Reference to Archer
			Wasps	Bees	Wasps	Bees	
Allerthorpe Common (pre-coniferized)	SE74	S	16.9	32.8	45.3	16.3	1989
Blaxton Common	SE60	S	15.0	26.5	43.1	13.9	1995
Burton Leonard Lime Quarries	SE36	Ca	16.7	25.8	68.0	13.0	1997
Charnwood Forest	SK41, SK51, SK50	S	18.1	27.0	71.2	22.2	1992b
Cave Wold	SE93	Ca	16.7	32.4	56.0	13.0	1997
Cornelian Bay	TA08	Cl	16.7	21.7	56.0	11.1	Unpub.
Crow Wood	SK69	S	16.9	28.9	20.4	9.4	1995
Duncombe Park	SE68	Ca	20.0	17.2	84.4	16.7	1993
Holmehouse Wood	SE04	Cl	10.3	31.6	53.8	7.7	Unpub.
Keswick Fitts	SE34	Si	22.2	30.0	67.9	21.4	Unpub.
Pompocali	SE34	S	20.0	36.6	20.0	8.0	1985
Risby Warren	SE91	S	17.2	29.4	12.5	8.3	1994
Sherwood Forest	SK66	S	17.6	25.0	47.6	19.4	1996e
Shipley Glen	SE13	S	15.6	34.9	56.6	7.1	1996d
Skipwith Common	SE63	S	13.2	35.5	42.4	30.0	1992a
Spurn Point	TA41	S	16.2	25.6	38.7	17.2	Unpub.
Strensall Common	SE65	S	18.0	35.0	41.5	8.0	1988
Swincarr Plantation	SE65	S	16.7	34.8	0.0	6.7	1984

*S sandy, Ca calcareous, Cl clay, Si silty.

relationship varies with latitude (Archer & Burn, 1995, Archer, 1996c). The species-area relationships are based on the species of solitary wasps and bees.

The species-area relationship of the 19 sites, including the Ainsdale-Formby sand dunes, is shown in Fig. 1. The dot for the Ainsdale-Formby sand dunes falls within the range of the 18 sites, and so the species list from the Ainsdale-Formby sand dunes can be considered sufficiently complete to make valid comparisons with other sites.

The correlation coefficient of the species-area relationship of the 19 sites indicates a highly significant linear relationship ($r=0.88$, $p<0.001$) with 77% 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 = $3.84 + 0.11 \cdot \ln$ area (ha). Two other statistics from this regression equation are: 1. the number of species of solitary aculeate wasps and bees expected to be found on one ha is 47 (anti- \ln 3.84) and, 2. to double the number of solitary species of aculeate wasps and bees the area would need to be increased about 475-fold (2 raised to the power of $1/0.11$).

Possible reasons why the number of species should increase with increase in area are discussed by Archer & Burn (1995).

The 19 sites used for Fig. 1 are mainly sandy sites but also include calcareous sites: Burton Leonard Lime Quarries and Cave Wold, Duncombe Park; clay sites: Holmehouse Wood and Cornelian Bay; and silty river margin sites; Keswick Fitts (Table 1). Clearly the traditional belief that sandy sites have a higher species richness than non-sandy sites is not upheld. Probably what is more important is for a site to

have the particular resources needed by aculeate species. Morris (1997) gave a list of such resources: bare, dry and friable soil in sunny situations for subterranean nesters; dead plant stems or dead wood in sunny situations for aerial nesters; and ruderal plant communities and particular flower species as a source of pollen for oligolectic bees. To this list may be added other specific nesting sites, such as snail shells, rock surfaces in sunny situations, crevices in walls or other bare surfaces; specific nest building materials needed by some species, e.g. resin, cottony down of leaves, petals, clay; specific types of prey for the larvae of species of solitary wasps; and sources of nectar, either floral or extra-floral. It is possible for non-sandy, as well as sandy sites to contain these resources.

SPECIES QUALITY

Information about the status and quality scoring (Archer, 1996a) of aculeate wasps and bees is given in Shirt (1987), Falk (1991), and Archer (1996b, 1997a, 1997b, 1998a). Archer's national statuses (Appendix 2) will be used since these statuses use the new information from the *Newsletters* of the Bees, Wasps and Ants Recording Society (BWARS) and consider all species, not just the RDB and nationally scarce species. Caution must be exercised in the use of quality scoring since the status of a species is not fixed and needs to be kept under constant review.

The very rare, rare and scarce species are the high quality species. Seventeen high quality species have been recorded from the Ainsdale-Formby sand dunes, although only 14 species have been recorded from 1970 onwards (Appendix 1).

Each solitary species can be given a status value, so that a quality score for the Ainsdale-Formby sand dunes can be calculated (Table 2). Dividing the quality score by the number of species gives the species quality score. The species quality score for both All Records and 1970 Records Onwards is the same (3.8, Table 2).

How does this species quality score compare with those from the other 18 sites?

SPECIES QUALITY SCORE-AREA RELATIONSHIPS

A plot of species quality scores versus the area (in natural logarithms) for the 19 sites from the north and north midlands of England, including the Ainsdale-Formby sand dunes, is shown in Fig. 2. The correlation coefficient is not significant ($r = 0.45$, $p > 0.05$), and only 20% of the variation of species quality scores between sites is

Table 2. The Archer national quality scores of the species of solitary wasps and bees recorded from the Ainsdale-Formby sand dunes, for All Records (AR) and 1970 Onwards Records (OR) (Species quality score 3.8 for All Records and 1970 Onwards Records)

Status	Status Value (A)	No. species (B)		Quality Scores (A*B)	
		AR	OR	AR	OR
Universal	1	51	44	51	44
Widespread	2	25	19	50	38
Restricted	4	1	0	4	0
Scarce	8	8	6	64	48
Rare	16	6	6	96	96
Very Rare	32	3	2	96	64
Total		94	77	361	290

explained by the variation in the area of sites. These observations would seem to indicate that species quality scores are relatively independent of site area. Nevertheless, within the geographical area of the north and north midlands of England, the species quality score for the Ainsdale-Formby sand dunes is the highest yet recorded (Fig. 2). The reason for this high score, at present, is unknown.

CLEPTOPARASITIC LOAD

The cleptoparasitic load (CL) is the percentage of aculeate species that are cleptoparasites (or parasitoids) on other host aculeates. Wcislo (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 synchronized in their life-history characteristics. From a review of the literature Wcislo (1987) found the CLs in Europe for bees varied between 16% and 33%, a range of 17%.

The CLs for the solitary bees from north and north midlands sites vary between 22% and 37% (Table 1) (except for Duncombe Park), a range of 15%. The range of values of CL for the English sites is similar to the wider European sites (Wcislo, 1987). The low CL for Duncombe Park is due to the loss of all *Sphecodes* species from this site (Archer, 1993). The CL for the solitary species of bees from the Ainsdale-Formby sand dunes (Table 3) falls within this range.

Wcislo (1987) gives no CL values for wasps. However, for the north and north midland sites, CL values for the solitary wasps have been found to vary between 10% and 22% (Table 1). The narrow range of this variation indicates that the argument Wcislo (1987) developed for the bees also applies to the solitary wasps. The CL for the solitary species of wasps from the Ainsdale-Formby sand dunes (Table 3) falls within this range.

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.

AERIAL NESTER FREQUENCY

The aerial nester frequency (AF) is the percentage of host aculeate species that have aerial nest sites. Aerial nesters used old beetle burrows in dead wood, central stem cavities, e.g. bramble, old snail shells, or crevices in cob walls, 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.

Table 3. The relative frequency of the cleptoparasitic (or parasitoid) species among the species of solitary wasps and bees recorded from Ainsdale-Formby sand dunes

	No. hosts (H)	No. cleptoparasites (C)	Cleptoparasitic Load CL = 100*C/(H + C)
Solitary wasps*	45	8	15.1
Solitary bees	30	10	25.0

**Cleptes nitidulus* excluded as not a parasitoid of an aculeate.

Table 4. The nesting habits of the host species of solitary wasps and bees recorded from Ainsdale-Formby sand dunes

	No. aerial nesters (A)	No. subterranean nesters (S)	Aerial nester frequency $AF = 100 * A / (A + S)$
Solitary wasps	18	27	40.0
Solitary bees	7	23	23.3

The AFs for the solitary wasps from the north and north midlands sites vary between 0% and 84%, and for the solitary bees between 7% and 22% (Table 1). For the Ainsdale-Formby sand dunes the AF for the solitary wasps falls into the middle of the range of the English sites, but for the solitary bees the range is extended slightly upwards (Table 4). The Ainsdale-Formby sand dunes are relatively richer in aerial-nesting solitary bees. An investigation of why this should be so remains to be done.

The AF for the solitary wasps is higher than the AF for the solitary bees (Table 4). Why should this be so?

Archer (1990) found that the summer abundance of solitary wasps was more sensitive to summer weather conditions than solitary bees. Solitary wasp abundance was positively related to higher mean temperature and hours of sunshine and decreases in rainfall. Lomholdt (1975) showed that aerial nester frequency increased with increasing latitude for the solitary wasps (Sphecidae, 28% in France and 79% in northern Norway) along a decreasing warmth gradient. Perhaps the species of solitary wasps in order to take advantage of any warmth tend to have aerial nesting sites, since such sites are likely to warm up earlier in the day and stay warmer for a longer period of time than subterranean nesters? No investigation of this hypothesis has taken place.

SUMMARY

In comparison with the other sites from the north and north midlands the community of species of solitary wasps and bees from the Ainsdale-Formby sand dunes:

- Has the expected number of species for the area of the site, and so can properly be compared with the other sites.
- Has a higher species quality score than the other sites.
- Has similar cleptoparasitic load to those of other sites as predicted by Weislo (1987).
- Has an average aerial nester frequency (AF) for the solitary wasps and a higher AF for the solitary bees.

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APPENDIX 1

A list of the aculeate Hymenoptera recorded from the Ainsdale-Formby sand dunes. V=very rare, R=rare, S=Scarce, RE=Restricted, W=Widespread, U=Universal species—see Appendix 2 for definitions. *Species not recorded from 1970 onwards.

- Chrysididae—*Omalus auratus* (L.) (W), *Hedychridium ardens* (Latreille in Coquebert) (U), *H. cupreum* (Dahlbom) (= *integrum*) (S), *C. ignita* (L.) (U), *C. impressa* Schenck (U)*, *Cleptes nitidulus* (Fab.) (R).
- Mutillidae—*Myrmosa atra* Panzer (W)*.
- Pompilidae—*Priocnemis parvula* Dahlbom (U), *Pompilus cinereus* (Fab.) (U), *Arachnospila anceps* (Wesmael) (U), *A. trivialis* (Dahlbom) (W), *A. wesmaeli* (Thomson) (R), *Evagetes crassicornis* (Shuckard) (U), *Anoplius nigerrimus* (Scopoli) (U), *A. infuscatus* (Vander Linden) (W), *Episyron rufipes* (L.) (W), *Ceropales maculata* (Fab.) (R).
- Eumenidae—*Ancistrocerus nigricornis* (Curtis) (W)*, *A. parietinus* (L.) (U), *A. parietum* (L.) (U), *A. scoticus* (Curtis) (U)*, *Symmorphus bifascatus* (L.) (= *mutinensis*) (U).
- Vespididae—*Dolichovespula sylvestris* (Scopoli), *Vespula rufa* (L.), *V. germanica* (Fab.), *V. vulgaris* (L.).
- Sphecidae—*Astata pinguis* (Dahlbom) (U), *Tachysphex pompiliformis* (Panzer) (U), *T. nitidus* (Vander Linden) (= *unicolor*) (S), *Crabro cribrarius* (L.) (U), *C. peltarius* (Schreber) (U), *Crossocerus tarsatus* (Shuckard) (U), *C. wesmaeli* (Vander Linden) (U), *C. annulipes* (Lepeletier & Brullé) (U), *C. megacephalus* (Rossius) (U), *C. quadrimaculatus* (Fab.) (W), *Ectemnius lapidarius* (Panzer) (U), *E. continuus* (Fab.) (U), *Oxybelus argentatus* Curtis (S)*, *O. mandibularis* Dahlbom (S)*, *O. uniglumis* (L.) (U), *Psen littoralis* (Bondroit) (V), *P. bruxellensis* (Bondroit) (R), *P. equestris* (Fab.) (U), *Spilomena troglodytes* (Vander Linden) (W)*, *Pemphredon lugubris* (Fab.) (U), *P. inornatus* Say (U), *P. lethifer* (Shuckard) (U), *P. morio* Vander Linden (S), *Diodontus minutus* (Fab.) (U), *D. tristis* (Vander Linden) (W), *Passaloecus corniger* Shuckard (W), *P. gracilis* (Curtis) (W)*, *P. insignis* (Vander Linden) (W), *Ammophila sabulosa* (L.) (W), *Podalonia affinis* (Kirby) (R), *P. hirsuta* (Scopoli) (S), *Mellinus arvensis* (L.) (U).

Colletidae—*Colletes fodiens* (Geoffroy in Fourcroy) (W), *C. marginatus* Smith (S), *C. similis* Schenck (W)*, *C. succinctus* (L.) (U)*, *C. cunicularis* (L.) (V), *Hylaeus communis* Nylander (W), *H. brevicornis* Nylander (W), *H. hyalinatus* Smith (W)*.

Andrenidae—*Andrena clarkella* (Kirby) (U)*, *A. fulva* (Müller in Allioni) (U), *A. scotica* Perkins (U), *A. nigroaenea* (Kirby) (U), *A. denticulata* (Kirby) (U), *A. haemorrhua* (Fab.) (U)*, *A. barbilabris* (Kirby) (U).

Halictidae—*Halictus rubicundus* (Christ) (U), *Lasioglossum laevigatum* (Kirby) (RE)*, *L. albipes* (Fab.) (U), *L. calceatum* (Scopoli) (U)*, *L. nitidiusculum* (Kirby) (U), *L. punctatissimum* (Schenck) (W), *L. villosulum* (Kirby) (U), *Sphecodes ferruginatus* von Hagens (S), *S. geoffrellus* (Kirby) (= *fasciatus*) (U), *S. pellucidus* Smith (U).

Megachilidae—*Stelis ornatula* (Klug) (R), *Osmia caerulescens* (L.) (W), *O. leaiana* (Kirby) (W), *O. aurulenta* (Panzer) (W), *Hoplitis claviventris* (Thomson) (W), *Megachile centuncularis* (L.) (U)*, *M. willughbiella* (Kirby) (U), *M. circumcincta* (Kirby) (U), *C. maritima* (Kirby) (W), *Coelioxys quadridentata* (L.) (V)*, *C. elongata* Lepeletier (U).

Anthophoridae—*Nomada marshalli* (Kirby) (U), *N. rufipes* Fab. (U), *Epeolus cruciger* (Panzer) (W), *E. variegatus* (L.) (U).

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

APPENDIX 2

The national statuses of species of solitary aculeate wasps and bees according to Archer, for England, Wales and Scotland, but excluding Ireland and the Channel Islands.

Very rare—Species found in 1–15 10 km squares, 1970 onwards.

Rare—Species found in 16–30 10 km squares, 1970 onwards.

Scarce—Species found in 31–70 10 km squares, 1970 onwards.

Restricted, Widespread and Universal species are found in more than 70 km squares, 1970 onwards.

Restricted—Species only found in the Institute of Terrestrial Ecology (I.T.E) Land Classification groups 1 and 2 (Pienkowski *et al.*, 1996) (Southern England, South-West and Southern Coasts). Roughly this is about half of England.

Widespread—Species found in I.T.E. Land Classification groups 3 and 4 (Midland Lowlands and Central Coasts) besides groups 1 and 2. Roughly this is about three-quarters of England, lowland Wales and south-west Scotland. Northumbria is excluded.

Strictly these definitions of restricted and widespread species are for southern restricted and widespread species. In practice northern restricted and widespread species can occur.

Universal—Species found throughout England, Wales and more extensively in Scotland, including further I.T.E. Land Classification groups 5 and 6 (Low Moorlands and Northern Uplands), but particularly groups 7 and 8 (Northern Lowlands and North-western Seaboard).

It is hoped that the statuses above, with those of Shirt (1987) and Falk (1991), and the IUCN statuses (IUCN Species Survival Commission 1994, Ball 1996) will be harmonized in the near future.