THE WASPS AND BEES (HYMENOPTERA: ACULEATA) OF THETFORD WARREN LODGE IN WATSONIAN WEST NORFOLK

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On the dry sandy Breckland heath of Thetford Warren Lodge, 91 species of aculeate wasps and bees have been found of which 18 are considered to be of national importance. Thetford Warren Lodge (TL 8484) is a property of English Heritage with its medieval game-keepers' or hunting lodge. The site is about 3km north-west of Thetford by the side of the B1107. The site is small, about 8.5 ha, with much bare stable sand and heather and lichen heath. Erosion of the sandy soil by cars has created small slopes and vertical cliffs which are used as nesting sites by the subterranean nesters. A small part of the site is covered by bracken which, perhaps, should be removed. The edges and banks of the site are rich in herbs which are important food sources for the aculeate wasps and bees. Small oaks provide sunning and mating sites. The site is surrounded by woodland with some bramble in the rides except on one side which abuts a golf course.

SAMPLING METHODS

Between 1983 and 2002, the author made 16 visits to the Thetford Warren Lodge distributed throughout the year as follows: April (1 visit), May (2), June (3), July (4), August (5) and September (1). During these approximately two to three hour visits all species of aculeate wasps and bees were recorded and usually collected with a hand net for identification. The walk around the study area was very similar on each visit. Except for one August visit, the weather during each visit was warm, often hot, and sunny so that conditions were suitable for the activity of aculeate adults. In the following account the nomenclature can be related to Kloet & Hincks (1978). An up-to-date checklist can be found on Bees, Wasps and Ants Recording Society (BWARS) web pages at http://www.bwars.com.

SPECIES PRESENT AND SEASONAL PROGRESSION OF SPECIES

A full list of recorded species is given in the Appendix. At the family and subfamily 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. Of the solitary wasps the Sphecidae is the dominant family in terms of the number of species and records although the Pompilidae are also well represented. Of the solitary bees the dominant subfamilies by number of species and records are the Halictinae followed by the Andreninae and Megachilinae. The solitary wasps were more frequent than solitary bees in terms of the number of species (ratio of wasps to bees 1 : 0.8) and records (ratio of wasps to bees 1 : 0.7).

The mean number of solitary species found per visit per month was: April 1 species; May 9 species (4, 14); June 17 species (19, 19, 14); July 19 species (15, 23, 15, 23); August 16 species (25, 10, 19, 18, 9) and September 9 species.

Table 2 shows the number of species recorded and when first recorded for each month. The most productive months for species of solitary wasps were June, July and August with June and July the most productive months for the first recording of species. Species that were most frequently recorded and can be regarded as the common resident species include: the caterpillar hunters *Ammophila sabulosa* and *Podalonia affinis* sometimes seen dragging their caterpillars across the bare sand; the spider-hunters *Episyron rufipes* and *Anoplius viaticus* with *E. rufipes* forming nesting aggregations in bare banks; the fly hunters *Crabro peltarius*, *Mellinus arvensis* and *Crossocerus wesmaeli*; the homopteran bug hunter *Mimesa equestris* which nests in small aggregations and the weevil hunter *Cerceris arenaria* flying to and from their nests in the bare sandy areas. All these solitary wasps are subterranean nesters.

The most productive months for species of solitary bees were June, July and August with from May until August, particularly July, being the most productive months for the first recording of species (Table 2). The common resident species included: the flower bee *Dasypoda hirtipes* foraging from tubular flowers; the sweat bees *Lasioglossum brevicorne* and *L. leucozonium* often found in yellow composite flowers; the cuckoo bee *Sphecodes pellucidus* with its host *Andrena barbilabris* which was much less frequent; *Colletes succinctus* collecting pollen from heather flowers with its cuckoo bee *Epeolus cruciger*; the leaf-cutter bee *Megachile willughbiella* with *D. hirtipes* at the same flowers and the cuckoo bee *Sphecodes puncticeps* whose host could have been any of the sweat bees *Lasioglossum brevicorne, L. punctatissimum* and *L. villosulum*. Again all these host bees are subterranean nesters except for *M. willughbiella* which was found nesting in holes in the upper part of the Lodge.

SPECIES QUALITY

According to Shirt (1987) six Red Data Book species were recorded: *Podalonia affinis, Philanthus triangulum, Colletes marginatus, Halictus confusus, Lasioglossum brevicorne* and *Sphecodes reticulatus*. Falk (1991) introduced the Notable status (Na being higher than Nb) for species, a status that is lower than the Red Data Book status. He also (*op. cit.*) suggested that the status of *Colletes marginatus* and *Sphecodes reticulatus* should be downgraded to Notable (Na) status and the following nine species should have Notable status: *Oxybelus argentatus* (Na), *O. mandibularis* (Na), *Hedychridium cupreum* (Nb), *Arachnospila minutula* (Nb), *Evagetes dubius* (Nb), *Andrena humilis* (Nb), *Dasypoda hirtipes* (Nb), *Megachile dorsalis* (Nb) and *Nomada flavopicta* (Nb).

TABLE 1 — NUMBER OF WASP AND BEE SPECIES AND RECORDS FROM THETFORD WARREN LODGE

	Species	Records
Solitary wasps		
Chrysididae	5	9
Mutillidae	1	1
Pompilidae	10	39
Eumeninae	1	1
Sphecidae	27	111
Total solitary wasps	44	161
Solitary bees		
Colletinae	4	17
Andreninae	6	16
Halictinae	12	39
Melittinae	2	12
Megachilinae	6	14
Anthophorinae	4	11
Total solitary bees	34	109
Total solitary species	78	270
Social species		
Vespinae	3	
Apinae	10	
Total social species	13	
Total wasps and bees	91	

TABLE 2 — NUMBER OF SOLITARY SPECIES AND MONTHS WHEN SPECIES WERE FIRST RECORDED AT THETFORD WARREN LODGE

	Apr	May	Jun	Jul	Aug	Sep
Number of species						
Wasps	1	6	19	28	22	6
Bees	0	8	14	17	20	3
Number of species first recorded						
Wasps	1	5	16	14	7	1
Bees	0	8	7	12	7	0

TABLE 3 — ARCHER NATIONAL QUALITY SCORES OF SOLITARY SPECIES RECORDED FROM THETFORD WARREN LODGE

National status	Status value (A)	No. species (B)	Quality scores (A × B)
Universal	1	31	31
Widespread	2	25	50
Restricted	4	4	16
Scarce	8	15	120
Rare	16	2	32
Very rare	32	1	32
Total		78	281
Species Quality Score 281/78 = 3.6			

TABLE 4 — SPECIES QUALITY SCORES OF SOLITARY WASP AND BEE SPECIES FROM ENGLISH SANDY SITES

	Species quality score
Bagmoor Common, Surrey[1]	4.7
Ambersham Common, West Sussex[2]	4.5
Iping Common, West Sussex[2]	4.5
Elvedon Center Parc, Suffolk[3]	4.0
Rampart Field, Suffolk[4]	3.9
Santon Downham, Norfolk[3]	3.9
Roydon Common, Norfolk[5]	3.9
Thetford Warren Lodge, Norfolk	3.6
Hartlebury Common, Worcestershire[6]	3.4
Sherwood Forest, Nottinghamshire[7]	3.0
Devil's Spittleful, Worcestershire[8]	2.6
Strensall Common, Yorkshire[9]	2.5
Crow Wood, Yorkshire[10]	2.5
Blaxton Common, Yorkshire[11]	1.9
Messingham Sand Quarry, Lincolnshire[12]	1.9
Kirkby Moor, Lincolnshire[13]	1.9
Risby Warren, Lincolnshire[14]	1.8

[1] (Archer, 2000), [2] (Archer & Edwards, 2002), [3] (See acknowledgements), [4] (Archer, 2005), [5] (Archer, 2004a), [6] (Archer, 2002a), [7] (Archer, 1996), [8] (Archer, 2004b), [9] (Archer, 1988), [10] (Archer & Burn, 1995), [11] (Archer, 1995), [12] (Archer, 2003), [13] (Archer, 2001), [14] (Archer, 1994).

TABLE 5 — NON-PARAMETRIC ESTIMATES OF SPECIES RICHNESS AT THETFORD WARREN LODGE

	Chao estimate	Jackknife estimate
All species		
No. species recorded	78	78
No. species estimated	106	104
95% confidence limits	82–130	91–118
% estimated species recorded	73.6	75.0

TABLE 6 — RELATIVE FREQUENCY OF THE CLEPTOPARASITIC (OR PARASITOID) SPECIES AMONG THE SOLITARY SPECIES RECORDED FROM THETFORD WARREN LODGE

	No. hosts (H)	No. cleptoparasites (C)	Cleptoparasitic Load CL = 100 × C/(H+C)
Solitary wasps	36	8	18.2%
Solitary bees	23	11	32.4%

TABLE 7 — NESTING HABITS OF THE SOLITARY SPECIES FROM THETFORD WARREN LODGE

	No. aerial nesters (A)	No. subterranean nesters (S)	Aerial Nester Frequency AF = 100 × A/(A+S)
Solitary wasps	7	29	19.4%
Solitary bees	4	19	17.4%

Recent work carried out by BWARS indicates that further changes are necessary. To take account of these changes, Archer (1999, 2002b) developed a national quality scoring system of high and low quality species. High quality species have a scarce (= Nb), rare (= Na) or very rare (= RDB) status while low quality species have a universal, widespread or restricted status. These Archer statuses for each species are given in the appendix. The one major change in status is that *Philanthus triangulum* changes its very rare high quality status to a widespread low quality status. This change in status reflects its relatively recent increase in range. By giving each of the 78 species of solitary wasps and bees an Archer national status a national quality score of 281 can be calculated (Table 3) with a national species quality score of 3.6 (281 divided by the 78 solitary species). How then does the SQS of Thetford Warren Lodge compare with other inland sandy sites in England? Archer (1999) showed that although quality scores are influenced by the area of sites the SQSs are relatively independent of site areas so SQSs can be used to compare sites without regard to site areas.

Table 4 shows some SQSs from the best inland sandy sites from south-east England (Surrey, West Sussex), Midlands (Worcestershire, Nottinghamshire), East Anglia (Norfolk, Suffolk), Yorkshire and Lincolnshire. The SQS for Thetford Warren Lodge is similar to the SQSs of the other four East Anglia sites. The five East Anglian sites have values intermediate between SQSs from the Midlands and south-east England. Thetford Warren Lodge can be considered amongst the best inland sandy sites for solitary wasps and bees in England.

ESTIMATING THE POTENTENTIAL 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 the site, but as yet unrecorded. Recent advances in non-parametric statistical procedures offer a way of addressing this problem. Chao (in Colwell & Coddington, 1994) and Heltshe & Forrester (1983) describe 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 recorded in one (singletons) or two (doubletons) samples. The Jackknife estimate of Heltshe & Forrester is based only on singletons. Because some aculeate species are only active in the spring or summer it is advisable that sampling is distributed throughout the months of adult activity. The software to carry out these statistical procedures was provided by Pisces Conservation Ltd.

The two statistical procedures were run with the samples, or visits. In practice the software takes 1, 2, etc. samples at random, each time calculating a mean estimate of species richness. The procedures were

repeated 50 times. With a small number of samples the estimates are erratic, but as more samples are selected these may stabilise, giving confidence in them. The estimates for the two procedures are given in figs 1 and 2. The estimates of species richness with 95% confidence limits after 16 samples are given in Table 5. The estimates are beginning to stabilise (figs 1 & 2) and the estimates of the two procedures are similar to each other (Table 5). These estimates indicate that at least about 104–106 species could be present at Thetford Warren Lodge of which 74%–75% have been recorded.

SPECIES-AREA RELATIONSHIP

Another problem in the study of any site is the difficulty of knowing when the species list is sufficiently complete to enable reasonable comparison with other sites. The list of solitary species from Thetford Warren Lodge can be considered reasonably complete from the species-richness analysis. It is possible, therefore to compare the species-area relationship for Thetford Warren Lodge with other sandy sites from south-east England. Fig 3 shows a species-area plot for solitary species from 27 inland sandy sites from south-east England including Thetford Warren Lodge. The species-area dot for Thetford Warren Lodge falls within the range of the other sites. Thus Thetford Warren Lodge has the expected number of solitary species for its area. Since the sites of south-east England represent the best aculeate sites in the U.K. for species richness, Thetford Warren Lodge again can be regarded as among the best aculeate sites in the U.K.

The correlation coefficient of the species-area plot of the 27 sites indicates a highly significant positive linear relationship ($r = 0.90$, $p < 0.001$) with 80% of the variation of the number of species between sites explained by the variation in the area of the sites. The species-area equation is: ln number of species = $4.19 + (0.1641 \times \ln \text{area (ha.)})$. Two other statistics from the regression equation are: the mean number of species of solitary wasps and bees expected from the best sites on one hectare is 66 species (anti-log 4.19) and, in order to double the number of solitary species of wasps and bees the mean area would need to be increased about 68-fold (2 raised to the power of 1/0.1641).

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 parasite rates are higher in temperate regions as host populations are more synchronized in their life-history characteristics. This finding probably does not hold for desert climates where the occurrence of rainfall would tend to synchronize life-history characteristics.

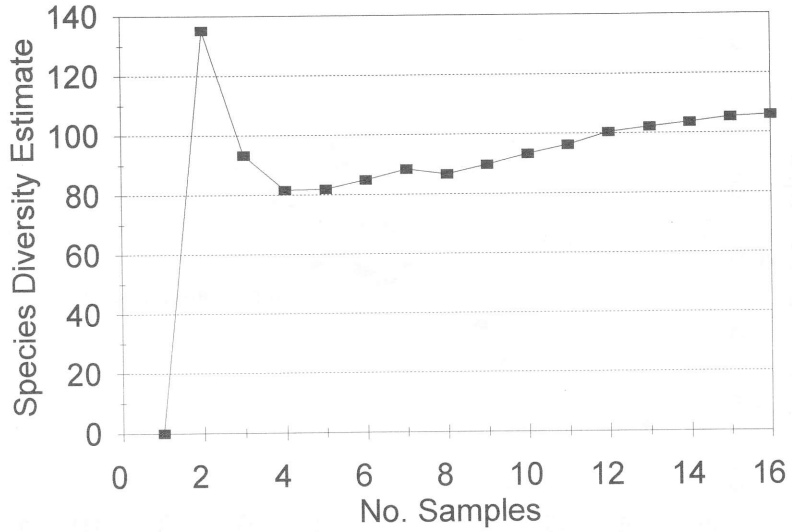

Fig. 1. — Chao estimate of species diversity for all species recorded from Thetford Warren Lodge

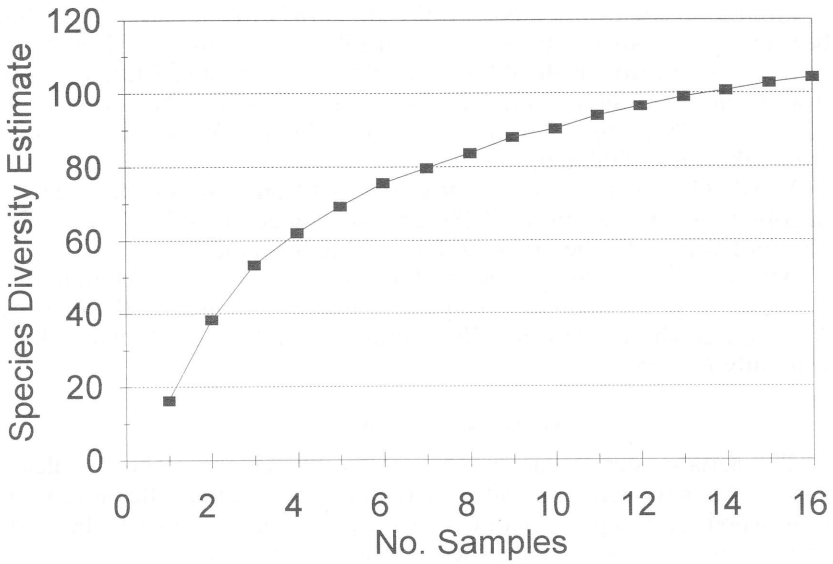

Fig. 2. — Jackknife estimate of species diversity for all species recorded from Thetford Warren Lodge

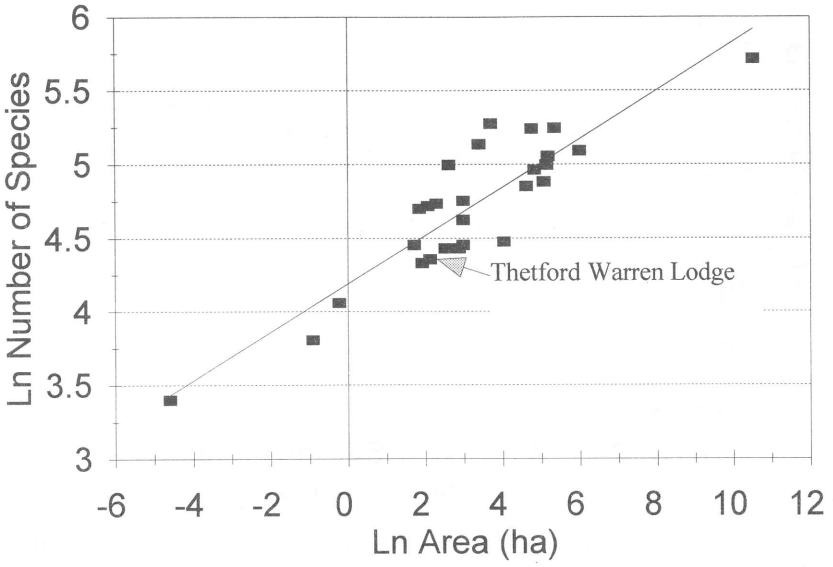

Fig. 3. — A species-area plot based on the solitary wasp and bee species from 27 inland sandy sites in south-east England including Thetford Warren Lodge

From a review of the literature Wcislo (1987) found that the CLs for bees in Europe varied between 16% and 33%, a range of 17%. Therefore, CLs for sites in Britain should have similar values. From 27 English sites from Cumbria to Sussex, the CLs for species of solitary bees vary from 22.4 %–40.0% (range 17.6%). The CL for Thetford Warren Lodge falls within this range (Table 6).

Wcislo (1987) gives no CLs for wasps, but from English sites the CLs of solitary wasps vary from 10.3%–25.0%, a range of 14.7%. The CL for Thetford Warren Lodge (Table 6) falls within this range.

All the social wasp species are host species, as are the bumble bee species, except for *Bombus bohemicus* whose host is usually *B. lucorum*, *B. sylvestris* whose host is usually *B. pratorum* and *B. vestalis* whose host is usually *B. terrestris*.

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 plant stem cavities (e.g. bramble), old snail shells, or crevices in 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, or sometimes holes and crevices are used after being altered.

The AFs for the solitary species are given in Table 7. The AFs for all the British species of solitary wasps is 46.2% and for solitary bees is 17.9%. The AFs for the solitary wasp species is much lower than the national AF while the AFs for the solitary bee species is similar to the national AF. The low AF for the solitary wasp species emphasizes the importance of bare sandy areas as nesting sites.

Social wasp species and bumble bees are usually subterranean nesters, although the nest of *Bombus pratorum* has been found in aerial situations such as old bird nests.

SUMMARY

Thetford Warren Lodge:

1. has 91 recorded species of aculeate wasps and bees, of which 18 species are of national importance;
2. has a potential estimate of at least 104–106 solitary species that could be found;
3. has the number of solitary species expected for its area;
4. has a species quality score that might be expected of the best inland sandy sites in East Anglia;
5. has solitary wasp and bee cleptoparasitic loads similar to other sites as predicted by Wcislo (1987); and
6. has a low aerial nester frequency for the solitary wasps indicating the importance of the bare sandy areas as nesting sites.

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APPENDIX – LIST OF RECORDED SPECIES

Archer National Statuses: VR = Very rare, Ra = Rare, S = Scarce, Re = Restricted, W = Widespread, U = Universal.

CHRYSIDIDAE: *Elampus panzeri* (Fab.) (W), *Hedychridium ardens* (Latreille *in* Coquebert) (U), *H. cupreum* (Dahlbom) (S), *Chrysis impressa* Schenck (U), *Trichrysis cyanea* (L.) (W).

MUTILLIDAE: *Myrmosa atra* Panzer (W).

POMPILIDAE: *Priocnemis parvula* Dahlbom (U), *P. pusilla* Schiødte (W), *Pompilus cinereus* (Fab.) (U), *Episyron rufipes* (L.) (W), *Anoplius viaticus* (L.) (S), *Arachnospila anceps* (Wesmael) (U), *A. trivalis* (Dahlbom) (W), *A. minutula* (Dahlbom) (S), *Evagetes crassicornis* (Shuckard) (U), *E. dubius* (Vander Linden) (Ra).

EUMENINAE: *Ancistrocerus nigricornis* (Curtis) (W).

VESPINAE: *Vespa crabro* L., *Vespula rufa* (L.), *Paravespula vulgaris* (L.).
SPHECIDAE: *Astata boops* (Schrank) (Re), *Dryudella pinguis* (Dahlbom) (U), *Tachysphex pompiliformis* (Panzer) (U), *T. nitidus* (Spinola) (S), *Crabro cribrarius* (L.) (U), *C. peltarius* (Schreber) (U), *Crossocerus pusillus* Lepeletier & Brullé (U), *C. wesmaeli* (Vander Linden) (U), *C. cetratus* (Shuckard) (W), *C. megacephalus* (Rossi) (U), *C. quadrimaculatus* (Fab.) (W), *Ectemnius cavifrons* (Thomson) (U), *E. lituratus* (Panzer) (Re), *Lindenius albilabris* (Fab.) (U), *L. panzeri* (Vander Linden) (Re), *Oxybelus argentatus* Curtis (S), *O. mandibularis* Dahlbom (S), *O. uniglumis* (L.) (U), *Mimesa equestris* (Fab.) (U), *M. lutaria* (Wesmael) (W), *Pemphredon lugubris* (Fab.) (U), *Passaloecus corniger* Shuckard (W), *Ammophila sabulosa* (L.) (W), *Podalonia affinis* (Kirby) (Ra), *Mellinus arvensis* (L.) (U), *Cerceris arenaria* (L.) (W), *Philanthus triangulum* (Fab.) (W).
COLLETINAE: *Colletes fodiens* (Geoffroy *in* Fourcroy) (W), *C. marginatus* Smith (S), *C. succinctus* (L.) (U), *Hylaeus communis* Nylander (W).
ANDRENINAE: *Andrena scotica* (Perkins) (U), *A. bicolor* Fab. (U), *A. fuscipes* (Kirby) (U), *A. barbilabris* (Kirby) (U), *A. humilis* Imhoff (S), *A. dorsata* (Kirby) (W).
HALICTINAE: *Halictus confusus* Smith (VR), *Lasioglossum leucozonium* (Schrank) (W), *L. albipes* (Fab.) (U), *L. brevicorne* (Schenck) (S), *L punctatissimum* (Schenck) (W), *L. villosulum* (Kirby) (U), *Sphecodes geoffrellus* (Kirby) (U), *S. gibbus* (L.) (W), *S. monilicornis* (Kirby) (U), *S. pellucidus* Smith (W), *S. puncticeps* Thomson (W), *S. reticulatus* Thomson (S).
MELITTINAE: *Melitta haemorrhoidalis* (Fab.) (S), *Dasypoda hirtipes* (Fab.) (S).
MEGACHILINAE: *Hoplitis spinulosa* (Kirby) (Re), *Megachile versicolor* Smith (U), *M. dorsalis* Pérez (S), *M. willughbiella* (Kirby) (U), *M. maritima* (Kirby) (W), *Coelioxys concoidea* (Illiger) (S).
ANTHOPHORINAE: *Nomada flavopicta* (Kirby) (S), *N. rufipes* Fab. (U), *Epeolus cruciger* (Panzer) (W), *E. variegatus* (L.) (W).
APINAE: *Bombus lucorum* (L.), *B. terrestris* (L.), *B. hortorum* (L.), *B. lapidarius* (L.), *B. pratorum* (L.), *B. pascuorum* (Scopoli), *B. bohemicus* (Seidl), *B. sylvestris* (Lepeletier), *B. vestalis* (Geoffroy *in* Fourcroy), *Apis mellifera* L.

Solitary aculeate wasps and bees (Hym.) recorded from the Isle of Portland (Dorset) during early July 2006. — I visited the following sites: West Cliff (SY 6872) (WC) on the 1st and 2nd, Church Op Cove (SY 6970) (COC) on the 4th and Portland Bill (SY 6768) (PB) on the 1st. The following 27 species were found: *Chrysis ruddii* Shuckard (PB), *Odynerus melanocephalus* (Gmelin *in* L.) (WC), *Euodynerus quadrifasciatus* (Fab.) (WC), *Ancistrocerus gazella* (Panzer) (COC), *A. oviventris* (Wesmael) (WC), *Trypoxylon medium* de Beaumont (WC), *Crossocerus elongatulus* (Vander Linden) (WC, COC, PB), *Pemphredon inornata* Say (WC), *Cerceris rybyensis* (L.) (COC, PB), *Hylaeus annularis* (Kirby) (COC), *H. brevicornis* Nylander (COC), *H. hyalinatus* Smith (WC), *Andrena nigroaenea* (Kirby) (WC), *A. semilaevis* Pérez (COC), *A. nitidiusculum* Schenck (PB), *Halictus tumulorum* (L.) (COC), *Lasioglossum leucozonium* (Schrank) (WC), *L. puncticolle* (Morawitz) (WC), *L. smeathmanellum* (Kirby) (COC), *L. villosulum* (Kirby) (WC, PB), *Sphecodes geoffrellus* (Kirby) (WC), *Osmia aurulenta* (Panzer) (WC), *O. caerulescens* (L.) (WC), *O. leaiana* (Kirby) (COC), *Hoplitis spinulosa* (Kirby) (WC, COC), *Megachile willughbiella* (Kirby) (WC), *Coelioxys concoidea* (Illiger) (PB). — Dr. MICHAEL ARCHER, 17 Elmfield Terrace, York, YO31 1EH, U.K. *January 10th*, 2007.