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**A study of the dung-inhabiting
beetles of Priory Water NR**
(Coleoptera: Scarabaeidae, Hydrophilidae and
Histeridae)

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Aphodius prodromus

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Introduction

Dung beetles of the family Scarabaeidae play a prominent role in the decomposition of herbivore dung and so it is not surprising that a large number of studies have been undertaken on many aspects of their ecology. Examples of these studies include community structure and succession (Koskela & Hanski, 1977), resource partitioning (Hanski & Koskela, 1979), resource utilisation (Holter, 1982), life history traits (Gittings & Giller, 1997), resource quality and colonisation (Gittings & Giller, 1998), distribution and abundance in fragmented landscapes (Roselin & Koivunen, 2001) and competition (Finn & Gittings, 2003).

The Hydrophilidae and Histeridae have generally received less attention. Those species that feed on dung play only a minor role in its decomposition and are often found in other habitats, for example compost heaps and birds' nests (Ryndevich & Lundyslev, 2005), where some species, principally in the Sphaeridae and Histeridae are, at least in their larval stages, predators of other invertebrates (Sowig, 1997; Hansen, 1987). The work that has been done on this group includes studies on *Sphaeridium* species by Hanski (1980a) and Otronen & Hanski (1983) and on species of *Cercyon* and *Sphaeridium* by Prezewozny & Bajerlein (2010).

Records of dung inhabiting species for VC55 Scarabaeidae, Hydrophilidae and Histeridae are relatively few in comparison with other beetle families (Finch, 2015). No beetles associated with dung have previously been recorded at Priory Water NR. The aims of this study were to compile a species list for Priory Water, compare different methods of sampling, record seasonality, preference for dung type, habitat and spatial separation of species within dung piles.

Study site description

Priory Water comprises a complex of lakes of various sizes in abandoned gravel pits, separated by woodland and grassland habitats, in the flood plain of the River Wreake near Kirby Bellars (SK7118). The pits were acquired by the Leicestershire Wildfowls' Association in 1987 and managed by them as a reserve, principally for wildfowl. The reserve covers an area of 81 hectares, of which 32 are open water. For further information on the reserve see the Priory Water Wildfowl Project handbook (Shelton, 2007). The flood plain of the River Wreake lies to the north of the main body of the reserve from which it is fenced off from the main reserve. This area of the flood plain is grazed by sheep and cattle from spring to autumn. On the south side of the lake the reserve only extends to a few metres from the water's edge, the land beyond is owned by a farm and stables and is grazed daily by horses. For the purposes of this study this area was considered as part of the reserve.

Materials and Methods

Dung beetles were sampled from naturally occurring dung in different areas of grassland (direct searching), from experimental dung piles set up in woodland and grassland and by pitfall traps set in grassland. Direct searching was carried out primarily to obtain a species list for the site while the experimental dung piles and dung baited traps were used to obtain information on dung type and habitat preferences.

Direct searching

Naturally-occurring dung from sheep, cattle and horse were sampled for beetles in each month from February 2014 to February 2015. Samples of dung weighing approximately 500g were mixed in a bucket of water and beetles that floated to the surface were collected and preserved in tubes of 70% isopropyl alcohol. Koskela & Hanski (1977) found that this flotation method recovered more than 95% of beetles from a dung pat. As far as possible the dung sampled was more than two days old but younger than seven days. This period of time was chosen as Koskela & Hanski (*op cit.*) found that cattle droppings attracted maximum

numbers of *Aphodius* a few days after deposition. The age of the dung was judged by its softness and the degree of crust formation (Skidmore 1991). On a few occasions dung older than seven days was sampled.

Experimental dung piles

Fresh dung from horse and sheep was collected from a stable and a pasture respectively. The dung was divided into samples of 500-600g, stored in individual polythene bags and kept in a freezer at -15°C until put out into the field (see below). Freezing ensured that if any dung beetles had already colonised the dung before collection they would be killed; only live beetles were collected from the flotation method. For the investigation of spatial separation of beetles within dung piles (see below) fresh horse dung was collected from a stables in January 2014, divided up in to 500g samples and pressed in to foil containers (dimensions 18cm long x 9cm wide x 5cm deep) and frozen at -15°C.

Habitat preferences

In each month from June to September 2014 two 500g samples of sheep and/or horse dung, according to availability, were sited in shaded woodland (SK709185), open grassland (SK 710185) and an area of compacted granite chippings used as a car park (SK712183). To protect the samples from foraging birds they were covered with a mesh cage made from plastic coated chicken wire (hole size 3cm x 3cm) pegged to the ground. The samples were put out once a month and left in the field for seven days. At the end of this period beetles were recovered by flotation and preserved.

Spatial distribution of beetles within a dung pile

In March and again in April 2014 six of the horse dung samples frozen in foil containers as described above, were placed approximately 2m apart in open grassland and left for 7 days. Each sample was covered with 3cm hole size plastic coated chicken wire pegged to the ground to protect the samples from foraging birds. At the end of 7 days each sample was cut longitudinally in half with a serrated bread knife and each half put in a separate bucket of water. Beetles were recovered by flotation and preserved.

Dung-baited pitfall traps

Dung type preferences were investigated during the period August – October using three dung baited pitfall traps sited in grassland on the south shore of the main lake. Each trap comprised a 4 litre plastic bucket (21cm diameter) sunk up to its rim into the ground. The traps were covered with 4cm hole-size meshweld from which a fine mesh bag was suspended containing approximately 400g of dung. The meshweld was covered with 3cm hole size plastic coated chicken wire to prevent small rodents and amphibians falling in to the traps but still allowing access to dung beetles. The two layers of mesh were pinned to the ground with metal pegs. The mesh bag suspended over the bucket containing either sheep, cattle or horse dung. The three traps were placed in a line 2m apart and a preservative of 25% ethanediol with a few drops of detergent was added to each to a depth of 2cm. The traps were left for 7 days in each month after which the contents were collected and any beetles removed and preserved in labelled tubes of 70% isopropyl alcohol.

Sex and breeding condition

Aphodius species found in sufficient numbers (>10), by all sampling methods, were sexed by dissection. The breeding condition of females was assessed by the presence of chorionated eggs (Gittings & Giller, 1997).

Identification and statistical analysis

All beetles in Scarabaeidae, Hydrophilidae and Histeridae were identified to species with the aid of a dissecting microscope and keys by Jessop (1986), Duff (2012) and Foster *et al* (2014). Statistical analyses were carried out in either Excel or using online software <http://www.wessa.net/slr.wasp>.

Results

Twenty-six species of dung-inhabiting beetles in the families Scarabaeidae, Hydrophilidae and Histeridae were recorded at Priory Water NR from horse, sheep and cattle dung (Table 1).

Table 1: Species found in three herbivore dung types February 2014 – February 2015

Species	Horse dung	Sheep dung	Cattle dung
Scarabaeidae			
<i>Aphodius ater</i>	x	x	x
<i>Aphodius contaminatus</i>	x	x	x
<i>Aphodius fimetarius</i>	x	x	x
<i>Aphodius fossor</i>	x	x	x
<i>Aphodius haemorrhoidalis</i>		x	x
<i>Aphodius oblitteratus</i>	x	x	
<i>Aphodius prodromus</i>	x	x	
<i>Aphodius pusillus</i>			x
<i>Aphodius rufipes</i>	x	x	x
<i>Aphodius rufus</i>	x	x	x
<i>Aphodius sphacelatus</i>	x	x	x
<i>Aphodius sticticus</i>	x	x	
<i>Geotrupes stercorarius</i>	x		
Hydrophilidae			
<i>Cercyon haemorrhoidalis</i>	x	x	x
<i>Cercyon lateralis</i>	x	x	x
<i>Cercyon melanocephalus</i>	x	x	x
<i>Cercyon pygmaeus</i>		x	x
<i>Cercyon quisquilius</i>	x	x	x
<i>Cercyon unipunctata</i>	x		
<i>Cryptopleurum minutum</i>	x	x	x
<i>Cryptopleurum subtile</i>		x	
<i>Megasternum concinnum</i>	x	x	x
<i>Sphaeridium scarabaeoides</i>	x	x	x
<i>Sphaeridium lunatum</i>		x	x
<i>Sphaeridium marginatum</i>	x		x
Histeridae			
<i>Marginotus ventralis</i>		x	

The relative abundance of each species is shown in Figures 1 and 2. Twelve species of *Aphodius* were recorded among which *A. ater*, *A. contaminatus*, *A. prodromus*, *A. rufipes* and *A. sphacelatus* were numerically dominant (see below for seasonal occurrence). The only other Scarabaeidae recorded was *Geotrupes stercorarius*.

Among the Hydrophilidae there were six species of *Cercyon*, two *Cryptopleurum*, three *Sphaeridium* and *Megasternum concinnum*. The dominant species were *Cercyon haemorrhoidalis*, *C. melanocephalus* and *Sphaeridium scarabaeoides*. The only Histeridae recorded was *Marginotus ventralis*. Of the 26 species identified during the project two, *Cryptopleurum subtile* and *Sphaeridium marginatum*, were new records for VC55.

Seasonal activity

Most species showed fairly discrete periods of activity, exceptions being the hydrophilids *Cercyon haemorrhoidalis* and *C. melanocephalus*, which were recorded throughout most of the study period. The earliest species of *Aphodius* to appear were *A. sphacelatus* and *A. prodromus*, which were active from February to May or June and again in the autumn. Two other species, *C. pygmaeus* and *C. quisquilius*, also had bimodal activity periods, appearing in spring/summer and again in the autumn. The majority of species showed a single period of activity in spring/summer (*A. ater*) or summer/autumn (*Cryptopleurum minutum*) or autumn/winter (*A. contaminatus*, *A. oblitteratus*). Species occurring in low numbers are

included in the diagrams (e.g. *A. pusillus*, *A. haemorrhoidalis*, *C. subtile*) although the patterns displayed may not reflect their true activity periods (Figures 3 & 4).

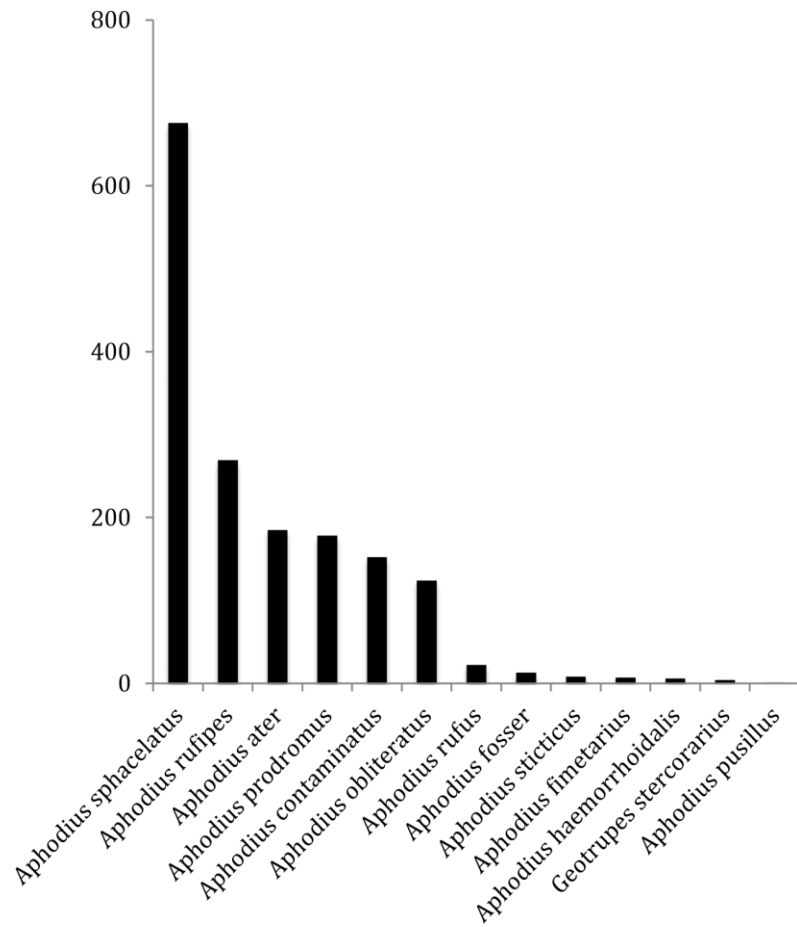


Figure 1. Scarabaeidae recorded at Priory Water NR

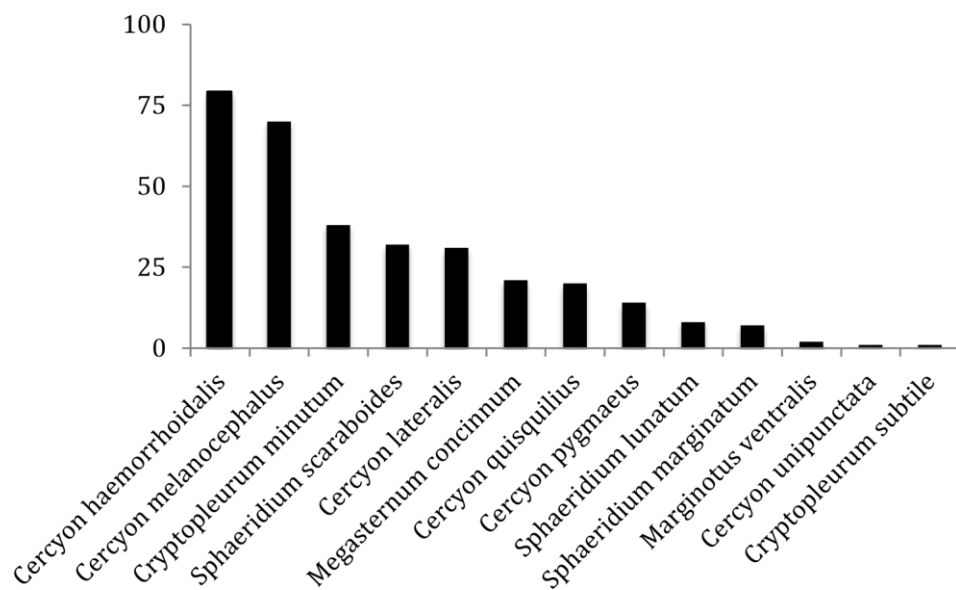


Figure 2. Hydrophilidae and Histeridae recorded at Priory Water NR

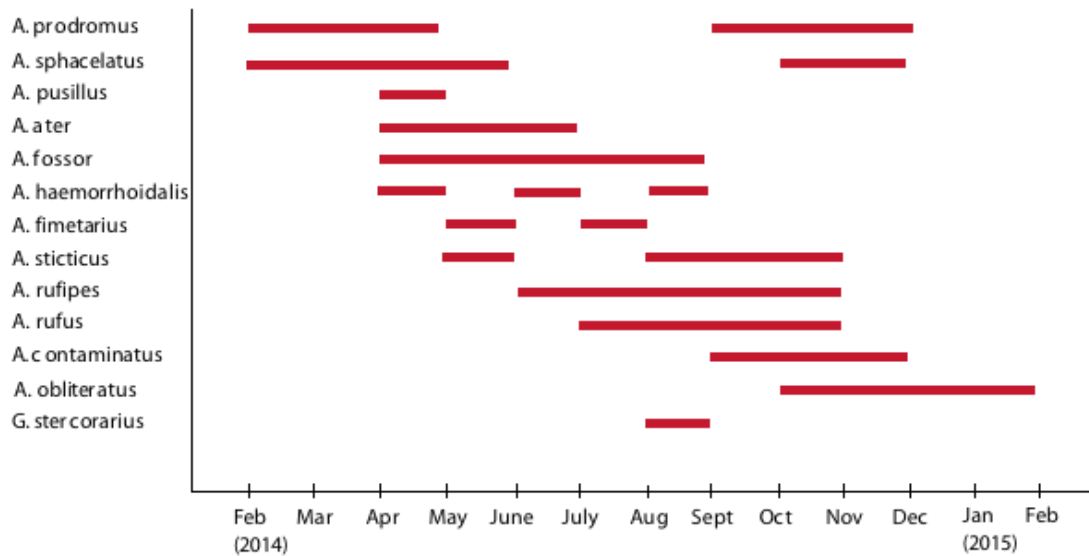


Figure 3: Seasonal activity patterns for Scarabaeidae



Figure 4: Seasonal activity patterns for Hydrophilidae and Histeridae

Sex ratios and sexual maturity in females

Sex ratios, based on numbers collected throughout the study period, were calculated for the eight most abundant species of *Aphodius* (Table 2). In all eight species there was a bias towards females but this was only significant for four species; *A. obliteratus*, *A. prodromus*, *A. rufipes* and *A. sphacelatus* ($\text{Chi}^2 P < 0.05$).

Table 2: Sex ratio of the most abundant species of Scarabaeidae

Species	Females	Males	Sex ratio
<i>Aphodius ater</i>	98	73	1.34 : 1 $\text{Ch}^2_1 = 3.65$ NS
<i>Aphodius contaminatus</i>	80	72	1.19 : 1 $\text{Ch}^2_1 = 0.42$ NS
<i>Aphodius fossor</i>	7	6	1.16 : 1 $\text{Ch}^2_1 = 0.076$ NS
<i>Aphodius obliteratus</i>	77	47	1.66 : 1 $\text{Ch}^2_1 = 7.25$ $P < 0.01$
<i>Aphodius prodromus</i>	115	63	1.82 : 1 $\text{Ch}^2_1 = 15.19$ $P < 0.01$
<i>Aphodius rufipes</i>	150	117	1.28 : 1 $\text{Ch}^2_1 = 4.07$ $P < 0.02$
<i>Aphodius rufus</i>	12	9	1.33 : 1 $\text{Ch}^2_1 = 0.42$ NS
<i>Aphodius sphacelatus</i>	398	273	1.45 : 1 $\text{Ch}^2_1 = 23.28$ $P < 0.01$

Among the other species tested *A. ater* only just missed significance while *A. contaminatus*, *A. rufus* and *A. fossor* were close to 1:1. Examination of the monthly sex ratios showed significant differences in favour of females, for *A. ater* (April) *A. sphacelatus* (February, March & October), *A. prodromus* (October) and *A. oblitteratus* (October). Significantly more males of *A. contaminatus* occurred in September but significantly more females in October (Table 3).

Table 3: Monthly sex ratios for the most abundant species of *Aphodius*

(Months where there were too few individuals for analysis are not included)

Species	Month	Females	Males	Sex ratio
<i>Aphodius ater</i>	April	43	24	1.79:1 $\text{Ch}^2_1 = 5.38$ $P < 0.05$
	May	28	19	1.47:1 $\text{Ch}^2_1 = 1.72$ NS
	June	26	27	0.96:1 $\text{Ch}^2_1 = 0.16$ NS
<i>Aphodius contaminatus</i>	September	15	28	0.53:1 $\text{Ch}^2_1 = 3.9$ $P < 0.05$
	October	61	41	1.48:1 $\text{Ch}^2_1 = 3.9$ $P < 0.05$
	November	3	3	1:1
<i>Aphodius oblitteratus</i>	October	55	34	1.61:1 $\text{Ch}^2_1 = 4.95$ $P < 0.01$
	November	21	13	1.61:1 $\text{Ch}^2_1 = 1.8$ NS
<i>Aphodius prodromus</i>	March	11	7	1.57:1 $\text{Ch}^2_1 = 0.88$ NS
	April	9	11	0.81:1 $\text{Ch}^2_1 = 0.2$ NS
	October	88	42	2.09:1 $\text{Ch}^2_1 = 16.2$ $P < 0.01$
<i>Aphodius rufipes</i>	July	8	2	4.00:1 $\text{Ch}^2_1 = 3.6$ NS
	August	95	82	1.15:1 $\text{Ch}^2_1 = 0.94$ NS
	September	36	32	1.12:1 $\text{Ch}^2_1 = 0.354$ NS
<i>Aphodius sphacelatus</i>	February	13	7	1.18:1 $\text{Ch}^2_1 = 10.2$ $P < 0.01$
	March	93	55	1.69:1 $\text{Ch}^2_1 = 9.6$ $P < 0.01$
	April	72	71	1.01:1
	May	15	17	0.88:1
	October	111	56	1.98:1 $\text{Ch}^2_1 = 18.58$ $P < 0.01$
	November	27	28	0.96:1

Female maturity

The number of females examined and the number of females with mature eggs are presented in Table 4. In most species examined mature eggs were present in 40–60% of females throughout their period of activity, although the percentage was higher in *A. oblitteratus* in which 68% and 73% of females were carrying eggs in October and November respectively. In the autumn-occurring species, *A. contaminatus*, *A. oblitteratus* and *A. sphacelatus*, no eggs were present in their final month of activity.

Table 4. Number of *Aphodius* females dissected in each month

(number carrying mature eggs given in brackets)

	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>A. ater</i>			43 (19)	29 (17)	26 (14)						
<i>A. contaminatus</i>								15 (4)	61 (23)	3 (1)	1
<i>A. oblitteratus</i>									55 (37)	21 (14)	1
<i>A. prodromus</i>	6 (2)	17 (5)	9 (4)	1					88 (33)		
<i>A. rufipes</i>					5 (2)	8 (2)	95 (36)	36 (11)	6 (3)		
<i>A. sphacelatus</i>	45 (13)	93 (20)	75 (27)	15 (4)					111 (15)	27 (11)	8

Baited dung traps

Thirteen species were recorded from the dung traps, mostly in low numbers. Only three species occurred in sufficient numbers to test for dung preference and of those *Aphodius contaminatus* and *Megasternum concinnum* showed a significant preference for horse dung ($P < 0.01$) and *Aphodius rufipes* for cattle dung ($P < 0.01$). The number of individuals in each species found in horse, cattle and sheep dung baited traps is given in Table 5.

Table 5: Species found in dung baited pit fall traps over the period August – October 2014

Species	Horse dung	Sheep dung	Cattle dung	Chi ²
Scarabaeidae				
<i>Aphodius contaminatus</i>	17	6	0	11.73 $P < 0.01$
<i>Aphodius prodromus</i>	1	2	0	
<i>Aphodius rufipes</i>	63	47	90	14.1 $P < 0.01$
<i>Aphodius rufus</i>	0	0	1	
<i>Aphodius sphaelatus</i>	3	1	1	
<i>Aphodius sticticus</i>	4	1	0	
<i>Geotrupes stercorarius</i>	1	0	0	
Hydrophilidae				
<i>Cercyon haemorrhoidalis</i>	1	2	3	
<i>Cercyon lateralis</i>	6	3	0	
<i>Cercyon melanocephalus</i>	3	0	1	
<i>Cercyon pygmaeus</i>	0	1	1	
<i>Megasternum concinnum</i>	11	4	1	6.0 $P < 0.01$
<i>Sphaeridium scaraboides</i>	1	0	1	

Experimental dung piles

Ten species of *Aphodius* were recorded in experimental dung piles but only five were found in sufficient numbers to provide data on dung preference (Table 6). *A. obliterated*, *A. prodromus* and *A. sphaelatus* showed a significant preference for horse dung (chi-squared, $P < 0.01$) while *A. ater* and *A. rufipes* showed a significant preference for sheep dung (chi-squared, $P < 0.01$). The only species to show a strong association with habitat was *A. obliterated*, which occurred only in woodland (chi-squared, $P < 0.01$).

Table 6: Species found in experimental dung piles

Species	Horse	Sheep	Chi ²	Species	Horse	Sheep	Chi ²
Scarabaeidae				Hydrophilidae			
<i>Aphodius ater</i>	4	49	38.2	<i>Cercyon haemorrhoidalis</i>	11	26	6.1
<i>Aphodius contaminatus</i>	5	0	-	<i>Cercyon lateralis</i>	0	12	-
<i>Aphodius fimetarius</i>	0	1	-	<i>Cercyon melanocephalus</i>	4	6	-
<i>Aphodius fossor</i>	0	2	-	<i>Cercyon pygmaeus</i>	0	2	-
<i>Aphodius haemorrhoidalis</i>	0	4	-	<i>Cryptopleurum minutum</i>	4	30	19.9
<i>Aphodius obliterated</i>	96	0	96	<i>Cryptopleurum subtile</i>	0	1	-
<i>Aphodius prodromus</i>	22	0	22	<i>Megasternum concinnum</i>	0	2	-
<i>Aphodius pusillus</i>	0	1	-	<i>Sphaeridium scaraboides</i>	0	3	-
<i>Aphodius rufipes</i>	5	22	10.7	<i>Sphaeridium marginatum</i>	1	0	-
<i>Aphodius rufus</i>	3	7	-				
<i>Aphodius sphaelatus</i>	99	1	88.4				
<i>Aphodius sticticus</i>	2	2	-				
<i>Geotrupes stercorarius</i>	0	1	-				

Eight species of Hydrophilidae and one Histeridae were found in the experimental piles, three in numbers sufficient to test for dung preference (Table 6). *C. haemorrhoidalis*, *C. lateralis*, and *Cryptopleurum minutum* all showed a significant preference for sheep dung (chi-squared, $P < 0.01$).

Spatial distribution of beetles within dung piles

In the spatial distribution trials only *A. sphaelatus* and *A. prodromus* colonised the experimental horse dung piles at a very low densities. *A. sphaelatus* was the more

abundant of the two species and showed a clear preference for the lower portion (2.5cm) of the dung pile (upper mean = 1.2, lower mean = 5.25). A Wilcoxon matched pairs test confirmed that there were significantly more individuals in the lower portion of the dung than the upper ($W=15$ $P=0.071$). *A. prodromus*, although fewer in number, also showed a preference for the lower portion of the dung but too few individuals were present for any statistical comparison.

Comparison of collecting methods

All species of *Aphodius* in this study were found by directly searching naturally occurring dung piles. All species were also found in either the experimental dung piles or dung baited traps with the exception of *A. pusillus*, which was recorded only once in naturally occurring cattle dung. *Geotrupes stercorarius* was found by all three methods.

In the Hydrophilidae all species of *Cercyon*, *Megasternum*, *Sphaeridium* and one of *Cryptopleurum*, were found by direct searching naturally-occurring dung piles. All species were also found in either experimental piles or dung-baited traps except *C. quesquilius*, *C. unipunctatum* and *S. lunulatum* which were not found in either. *Cryptopleurum minutum* and *S. marginatum* were not taken in dung baited traps. The single specimen of *Cryptopleurum subtile* was found in an experimental pile. The histerid *M. ventralis* was found only by direct searching of naturally-occurring dung and in experimental piles. Details for each species caught using the three methods in this study are given in Table 7.

Table 7: Species found by the three methods of collecting used at Priory Water

(N/A= trap not operating during the species period of activity)

Species	Direct searching	Experimental dung piles	Dung baited traps
Scarabaeidae			
<i>Aphodius ater</i>	x	x	N /A
<i>Aphodius contaminatus</i>	x	x	x
<i>Aphodius fimetarius</i>	x	x	
<i>Aphodius fossor</i>	x	x	
<i>Aphodius haemorrhoidalis</i>	x		N /A
<i>Aphodius obliteratedus</i>	x	x	
<i>Aphodius prodromus</i>	x	x	x
<i>Aphodius pusillus</i>	x		N/A
<i>Aphodius rufipes</i>	x	x	x
<i>Aphodius rufus</i>	x	x	x
<i>Aphodius sphaelatus</i>	x	x	x
<i>Aphodius sticticus</i>	x	x	x
<i>Geotrupes stercorarius</i>	x	x	x
Hydrophilidae			
<i>Cercyon haemorrhoidalis</i>	x	x	x
<i>Cercyon lateralis</i>	x	x	x
<i>Cercyon melanocephalus</i>	x	x	x
<i>Cercyon pygmaeus</i>	x	x	x
<i>Cercyon quisquilius</i>	x		
<i>Cercyon unipunctatus</i>	x		
<i>Cryptopleurum minutum</i>	x	x	
<i>Cryptopleurum subtile</i>		x	
<i>Megasternum concinnum</i>	x	x	x
<i>Sphaeridium scaraboides</i>	x	x	x
<i>Sphaeridium lunatum</i>	x		
<i>Sphaeridium marginatum</i>	x	x	
Histeridae			
<i>Marginotus ventralis</i>	x	x	

Discussion

The majority of the twenty six species of Scarabaeidae, Hydrophilidae and Histeridae recorded at Priory Water NR in this study are fairly common in VC55 and Nationally (Appendix 1).

The seasonal activity patterns of the *Aphodius* species found in this study agree with those given by Jessop (1986), and Gittings & Giller (1997) working in the SW Ireland. Broadly speaking, the occurrence of common species found in this study can be grouped into the following categories; spring and autumn (*A. sphacelatus* and *A. prodromus*), late spring and early summer (*A. ater* and *A. fossor*), mid to late summer (*A. rufus* and *A. rufipes*) and autumn (*A. contaminatus* and *A. obliteratus*). Our observations on the number of females carrying eggs in the above species showed that for most of their period of activity females are carrying mature eggs, which agrees with the findings of Gittings & Giller (1997). Among the less common species found *Aphodius sticticus* occurred in April and May and from July to October, agreeing with Jessop (1986), *A. fimetarius* appeared to have two activity periods as found by Gittings & Giller (1997) and *A. haemhorroidalis* displayed a rather punctuated activity pattern being found in April, June and August, but in all cases too few individuals were found for any firm conclusions to be made. A single specimen of *A. pusillus* was found in May. It is worth noting that *Aphodius fimetarius* was considered by all coleopterists to be a widespread and abundant species not only in Britain but across the Holarctic until 2001 when Wilson (2001) discovered, in a chromosomal study of the Scarabaeidae, that *A. fimetarius* comprised two cryptic species, *A. fimetarius* and *A. pedellus*, with completely different karyotypes. Miraldo *et al* (2014) used three different complimentary methods (karyotypes, DNA sequencing & morphological characters) to distinguish between the two species. Using morphological differences between the two species given by Miraldo *et al* (*opp. cit*) it was concluded that only *A. fimetarius* occurred in this study. To date there is only one record for *A. pedellus* from VC55 (Finch, 2015).

The coprophagous hydrophilids found at Priory Water NR are recorded nationally as being present throughout the year, often with peaks in late spring or summer (Foster *et al*, 2014). They are a dominant feature of dung beetle communities and being multivoltine most species are likely to be found throughout the year (Hanski & Koskela, 1977). The species found in this study display a variety of seasonal patterns, the commonest (e.g. *C. haemhorroidalis* and *C. melanocephalus*) occurring throughout the year and the less common found more sporadically. *Cryptopleurum subtile*, a species originally described from Japan was first recorded in England in 1958. Since that time it has been recorded in a number of counties in England, including Northamptonshire and Warwickshire, and also in Scotland, Wales and Northern Ireland (Foster *et al*, 2014). The Priory record was the first for this species in VC55. Also a first for VC55, *Sphaeridium marginatum* was only recognized in 1989 as being distinct from the very similar *S. bipustulatum* (not recorded at Priory). Based on present records it should be considered Nationally Scarce, occurring in fewer than 100 hectads in England and Wales, but this may be due to under-recording.

Of the three species of *Sphaeridium* found *S. scaraboides* was the most abundant and was found in each month from April to October. *S. lunatum* and *S. marginatum* were found less frequently although the period of activity recorded nationally for both species is March to September.

Cercyon larvae are predators of small dipteran larvae and so the developmental patterns of their prey may, to some extent, determine when the adults are found. There is some evidence that *Cercyon* sp. and *Sphaeridium* sp. larvae compete for fly larvae in dung with peaks in abundance of one corresponding with troughs in the other (Prezewozny & Bajerlein, 2010). We found no evidence of this at the densities encountered in this study.

The species of *Aphodius* and *Cercyon* found at Priory Water each comprise an assemblage of species which exploit the same environmental resource in a similar way and therefore can

be described as a guild, as outlined by Root (1967). However, as the larvae of *A. sphacelatus* and *A. prodromus* are saprophagous, Gittings & Giller (1997) have suggested they should be classified as a separate guild and Holter (1982) separates species within a guild into groups of 'generalists' and 'specialists' depending on where in the dung pat they were found; the generalists occurring throughout the pat and the specialists in particular sections. Based on experimental evidence specialist species of *Aphodius* have been divided into 'top specialists', 'bottom specialists' and 'peripheral specialists'. According to Holter's classification (Holter *opp. cit.*) the *Aphodius* found at Priory Water fall into the following categories: generalists - *A. fossor*, *A. fimetarius*, *A. rufus*; bottom specialists - *A. rufipes*, *A. pusillus* and peripheral specialists - *A. contaminatus*, *A. ater*, *A. prodromus*. In this study information was obtained only for *A. prodromus* and *A. sphacelatus* both of which occurred almost exclusively in the bottom half of pats (no distinction was made between peripheral and internal sections).

Hanski (1986) considered that local assemblages of *Aphodius* should be split into 'core species' (locally abundant), and 'satellite species' (locally rare). The majority of species found at Priory were reasonably abundant and so could be considered core species. *Aphodius pusillus*, *A. haemhorroidalis*, *A. sticticus* and *A. fimetarius* are all possible satellite species as they occurred in low numbers during the study period (under 10 in each case), although *A. fimetarius* tends to occur in older dung (see below) and may have been undersampled. It has been shown by Roselin (2000) that smaller species such as *A. pusillus* have short, under 1km, dispersal flights which may contribute to their rarity at sites where suitable dung is only sporadically available, which is probably the case at Priory. Similar constraints may apply to the other rarer species e.g. *A. haemhorroidalis* and *C. subtilis*.

The composition of assemblages has been reported to be influenced by dung type. For example, Lamaret *et al* (1992) found significant changes in community structure at a site where the resource changed from sheep to cow. In this study many of the core species were found in all three dung types examined, exceptions being *A. obliteratedus* and *A. prodromus* which were absent from cattle dung and *A. fossor* which was absent from horse. However, dung-baited traps showed that some species, although coming to all three types of dung, showed a significant preference for one type, i.e. *A. contaminatus* and *Megasternum concinnum* for horse dung and *A. rufipes* for cattle dung. Although *A. ater* was out of season when the dung-baited traps were in operation, data from the rest of the study suggest it has a strong affinity for sheep dung. Landin (1961) states that dung beetles use their olfactory senses to locate dung pats, the findability of a dung pat depending on its odour dispersion (Gittings & Giller, 1998) which would be influenced by how quickly a crust formed and environmental factors operating at the time (Thome & Desiere, 1979 in Gittings & Giller, 1998). In this study although *A. rufipes* showed a significant preference for cattle dung there was a good number of individuals in the other two treatments. For this species cattle dung may hold its attraction for longer. Although *A. contaminatus* and *M. concinnum* were both significantly more abundant in horse dung they too were present, albeit in low numbers, in the other two treatments.

Dung quality and age have also been shown to be instrumental in determining species present. As dung ages it undergoes physical and chemical changes (Denholm-Young, 1978 in Gittings & Giller, 1998). A number of researchers e.g. Holter (1982), Gittings & Giller (1998) have shown that dung beetle assemblages changed in a succession with dung ageing. Early successional beetles (1-5 days) comprised *A. rufipes*, *A. sphacelatus*, *A. prodromus*, *Sphaeridium lunatum*, *S. scaraboides* and *Cercyon* species. Mid-successional (6-10 days) comprised *A. ater* and *A. rufus* and late-successional (10-25 days) *A. fimetarius* and *A. fossor*. The majority of dung samples examined, both naturally occurring and experimental, were not greater than 7 days old, therefore early to mid-successional species dominate. It is noteworthy that most of the specimens of *A. fimetarius* and *A. fossor* were found in the few older (>7 days) dung samples examined. Hanski (1980b) found that most individuals of *C. haemhorroidalis*, *C. melanocephalus* and *C. pygmaeus* arrived at a dung pat within two

days. *Cercyon lateralis* had a slower rate of arrival but was within the 7 day period of dung samples examined in this study. No data on arrival rates was given for the other *Cercyon* species found in this study.

Due to the mechanisms of meiosis and to natural selection there is a tendency towards the production of an equal number of males and females. However, many species of insect often exhibit skewed sex ratios (for example Charnov *et al*, 1981). Hanski (1986), found in a study of the population and community structure of *Aphodius* in Europe, that the sex ratio was female-biased. In an earlier study Hanski (1980c) showed that *Aphodius* females move longer distances and more frequently than males concluding that this may lead to female-biased samples. However, Roslin (2000) in a study of the movements of dung beetles found no difference between *Aphodius* males and females. In this study we found four species had significantly more females than males when the monthly totals were combined but when the individual monthly sex ratios were examined a more variable picture emerged. Several species had significantly more females than males in the months when they first emerged but the ratio tended to even up towards the end of their period of activity. A different pattern was shown by *A. contaminatus*, which had significantly more males than females in September when it first emerged, but had significantly more females in October (see Tables 2 & 3). Our results, with the exception of those for *A. contaminatus*, support the findings of Hanski (1980c), although the reason for the greater dispersal rates in females after emergence is far from clear.

Of the three methods used to sample dung beetles, examination of naturally occurring dung was the only one that recorded the full species list, possibly because greater quantities of dung, of all the grazing species, were sampled using this method. Although recording fewer species in this study, experimental piles have the advantage over naturally occurring dung of samples based on equal quantities of dung of known age that can be placed in different habitats. This method has been used in a number of other studies (e.g. Gittings & Giller, 1998). We first discovered *A. obiteratus* in an experimental pile placed in woodland (a habitat that is not grazed at Priory Water NR), which prompted further searches of naturally occurring dung in shady habitats (i.e. the edges of fields shaded by woodland) where the species was also found. The fact that fewer species were recorded using this method may have been due to the relatively short period the dung was left in the field (7 days). Dung traps were also effective in providing quantitative data and this method has been widely employed in many studies of dung beetle communities (for example Gittings & Giller, 1997). We used dung traps at only one location but they could be used in different habitats. Dung traps have the advantage over experimental dung piles in that their catches can be removed frequently over a period of time and the bag containing the dung put back to attract mid- and late- successional species. However, Lobo *et al* (1998) found that at least 15 traps are necessary to collect 95% of species present at a site. In this study three traps over a period of three months collected 56% of potentially available species.

Hanski (1986) pointed out that dung beetle assemblages can change over a short period of time and any change in dung availability will affect assemblages at a local level. At Priory Water NR no livestock have been grazed on the Wreake flood plain since autumn 2014 until the present time (June 2015). For larger core species this may not have a significant effect since horse dung is always available on the south shore and sheep generally on the north side of the Wreake, but for smaller satellite species such as *A. pusillus* and *A. haemhorroidalis* such discontinuity may result in local extinction. To study the effects of dung availability on the dung beetle community would involve a much longer term sampling programme.

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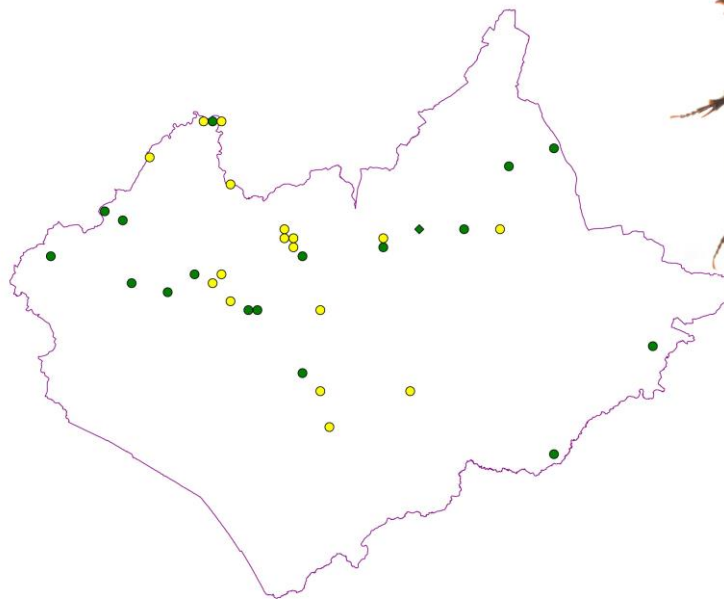
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Appendix: VC55 records of dung beetles found at Priory Water NR

Yellow circles show pre-1990 site records and filled circles (green) show post-1989 site records. All maps are based on data from Finch (2015). Priory Water NR is shown by a filled (green) diamond.

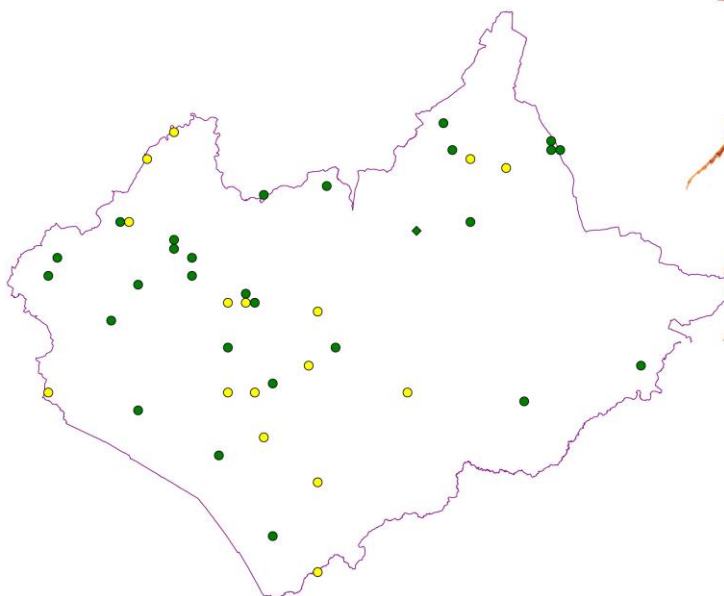
The number of VC55 site records quoted for each species refers only to those since 1989.

Habitat and distribution notes are from Jessop (1986), Duff (2012) and Foster et al. (2014).

Aphodius ater

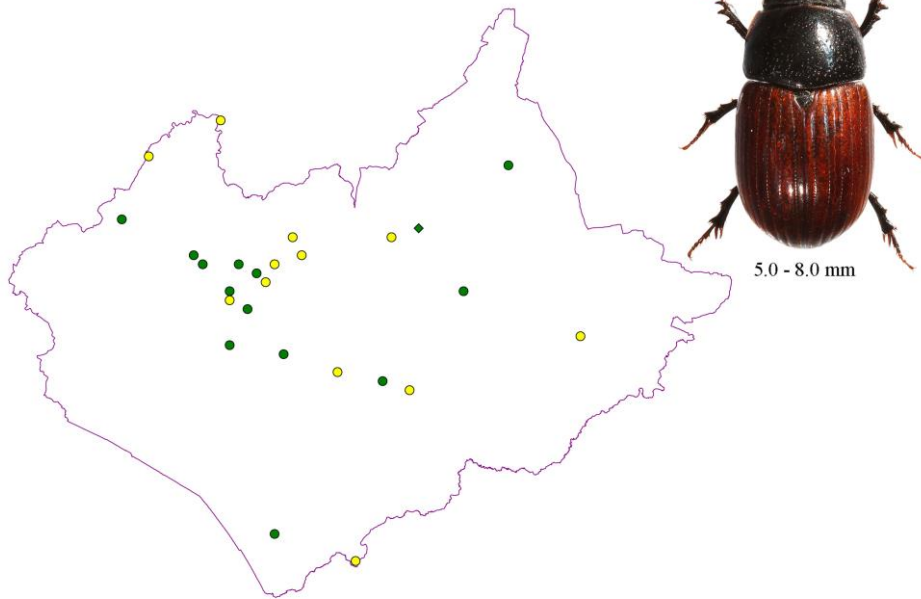
4.0 - 6.0 mm

Common and widespread in England, Wales and Scotland in various types of dung and decaying vegetable matter from March – October. There are 19 sites for VC55.

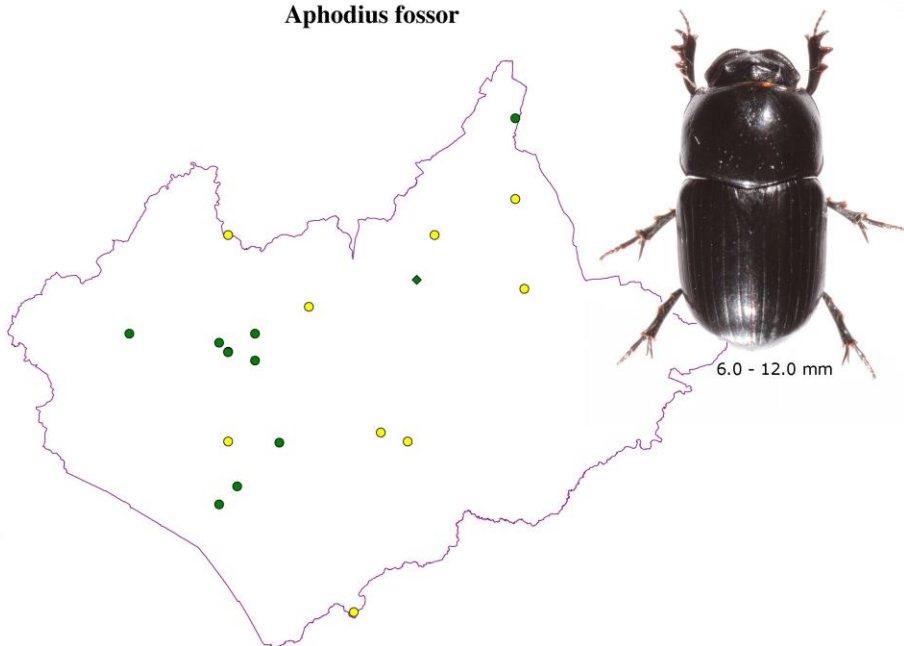
Aphodius contaminatus

5.0 - 7.0 mm

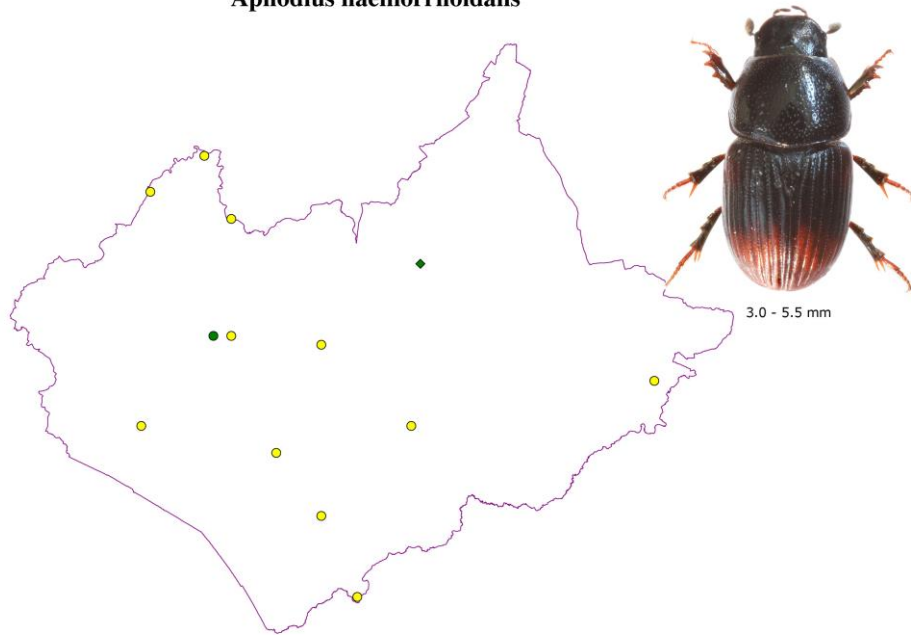
Common in England, Wales and Scotland in various types of dung especially horse. An autumn species. There are 28 sites in VC55.

Aphodius fimetarius

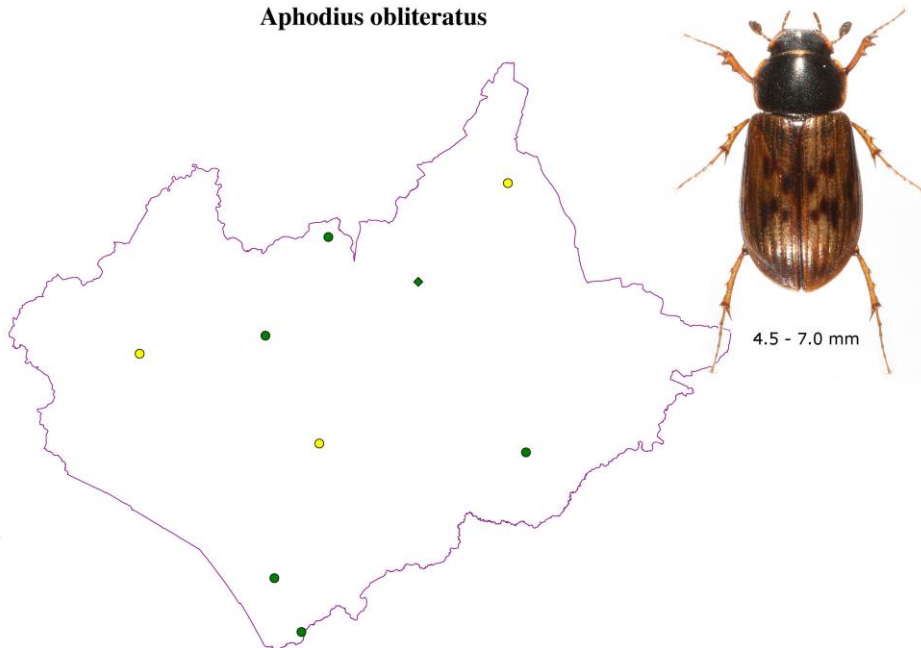
Common throughout Great Britain in various types of dung and decaying vegetable material from February – October. There are 14 sites for VC55.

Aphodius fossor

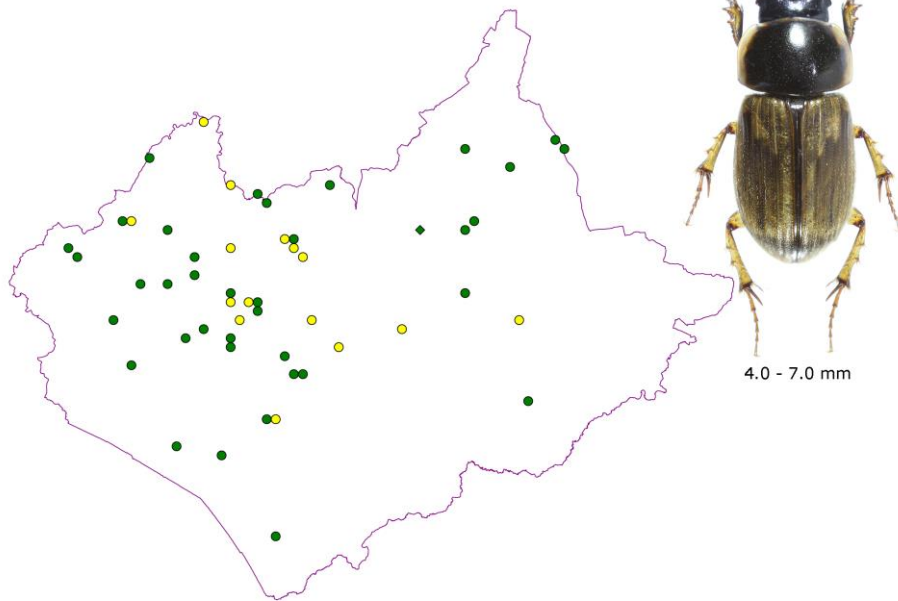
Common in most of England and Wales, less common in northern Britain and Scotland, usually found in cattle dung March – October. There are 10 sites for VC55.

Aphodius haemorrhoidalis

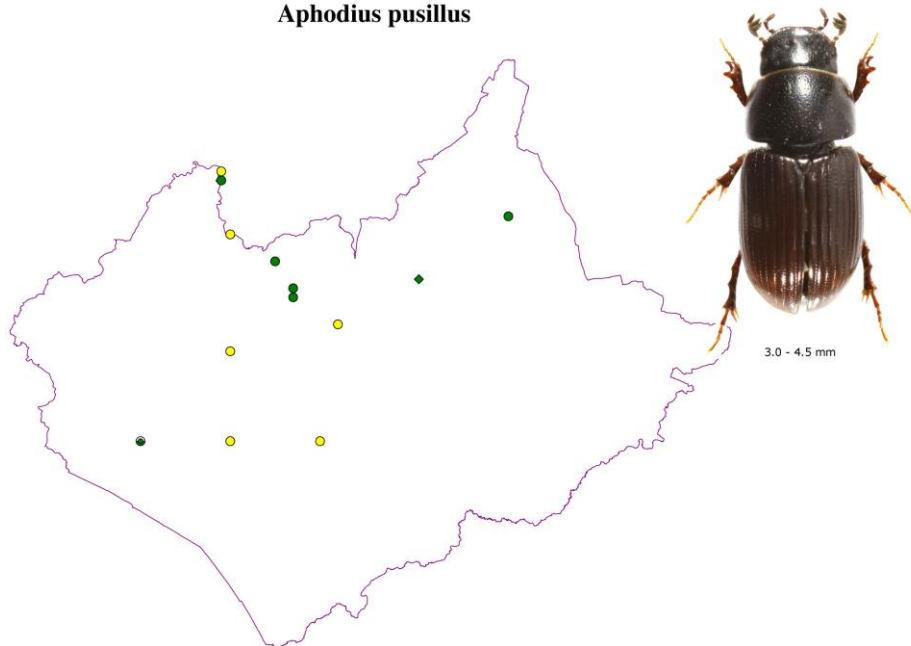
Common in England and Wales becoming less common in the north, absent from Scotland. Found in various types of dung April – August. There are 2 sites for VC55.

Aphodius obliteratus

A somewhat local species in various types of dung especially horse dung in wooded areas in England and southern Scotland. There are 5 sites for VC55.

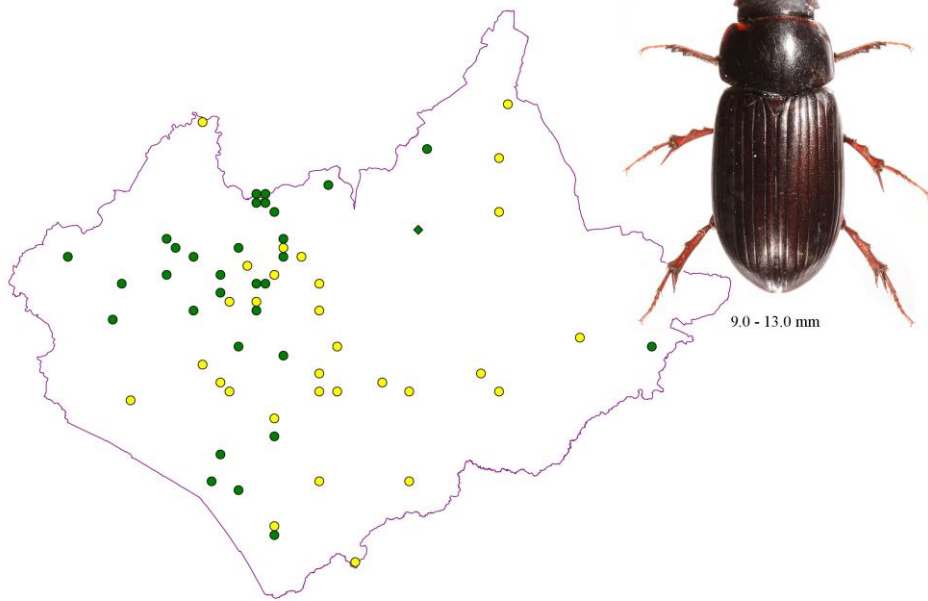
Aphodius prodromus

Common in England, wales and Scotland in various types of dung and decomposing vegetable matter in spring and autumn. There are 38 sites for VC55.

Aphodius pusillus

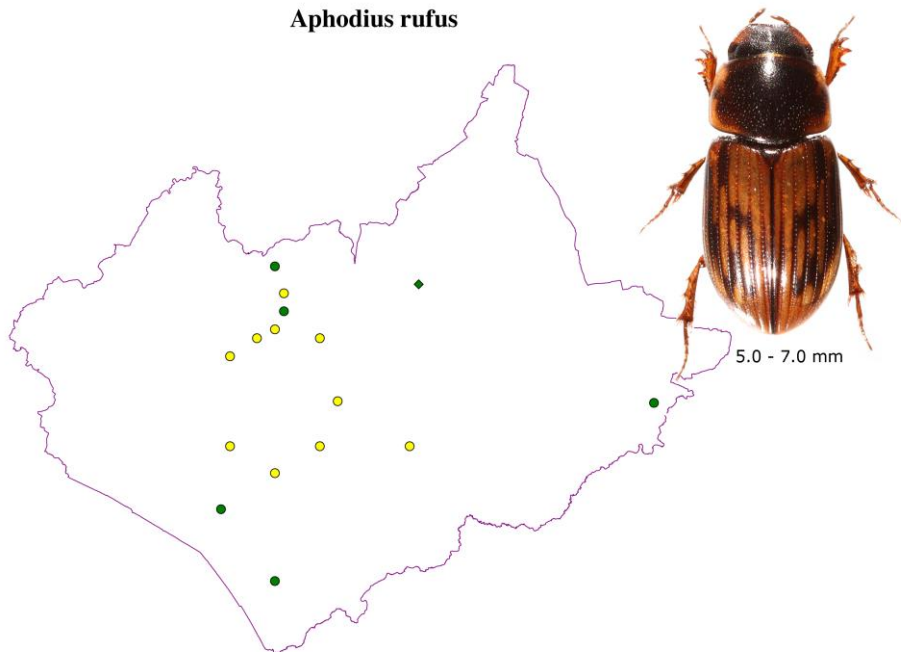
Local in England, Wales and Scotland in various types of dung and decaying vegetable matter from March – July. There are 7 sites for VC55.

Aphodius rufipes

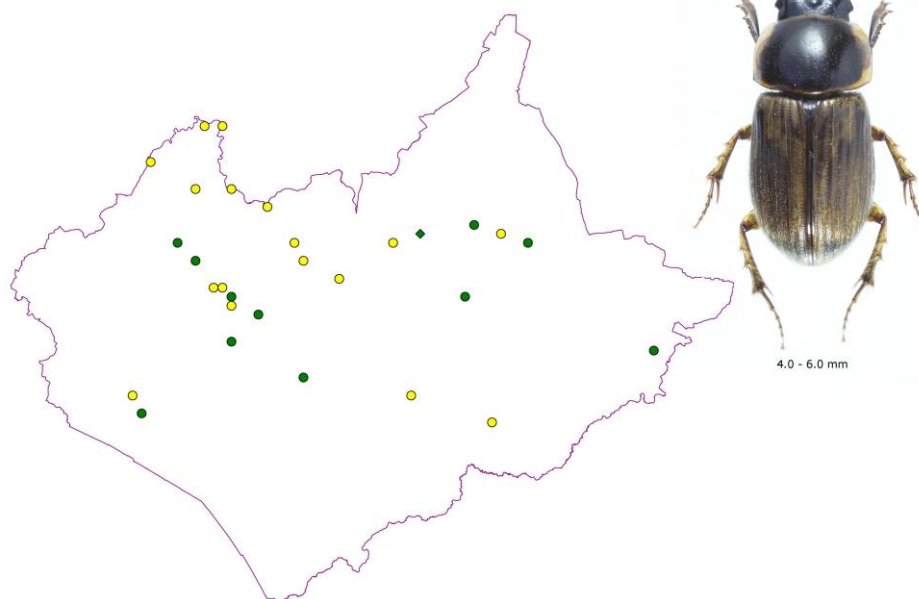


Common throughout Great Britain in large herbivore dung from March – October. There are 32 sites for VC55.

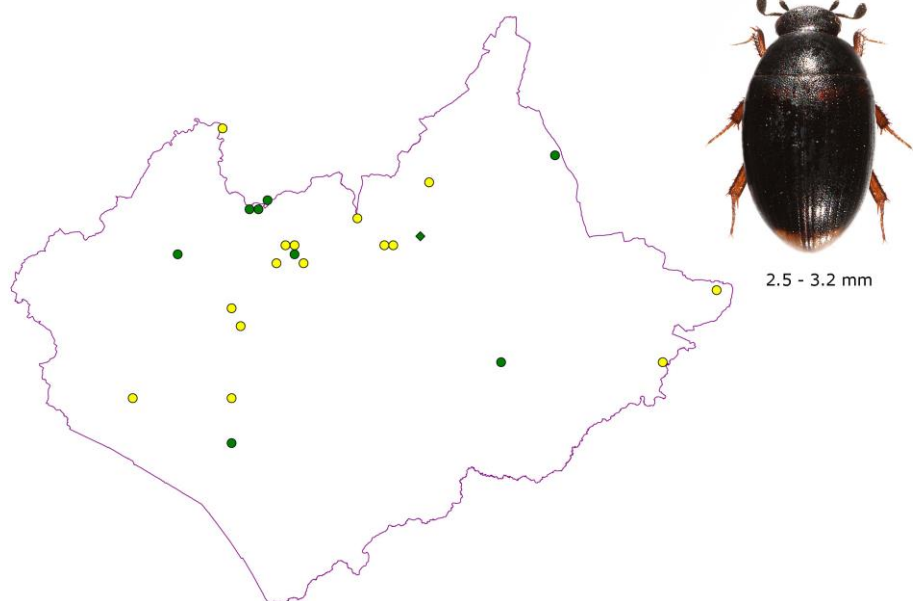
Aphodius rufus



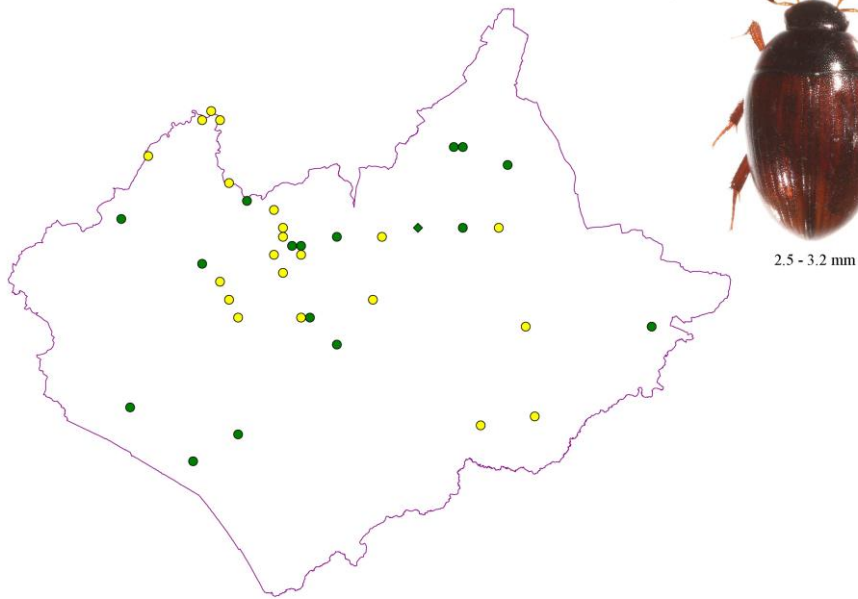
Common in England, Wales and Scotland in various types of dung from July to October. There are 6 sites for VC55.

Aphodius sphacelatus

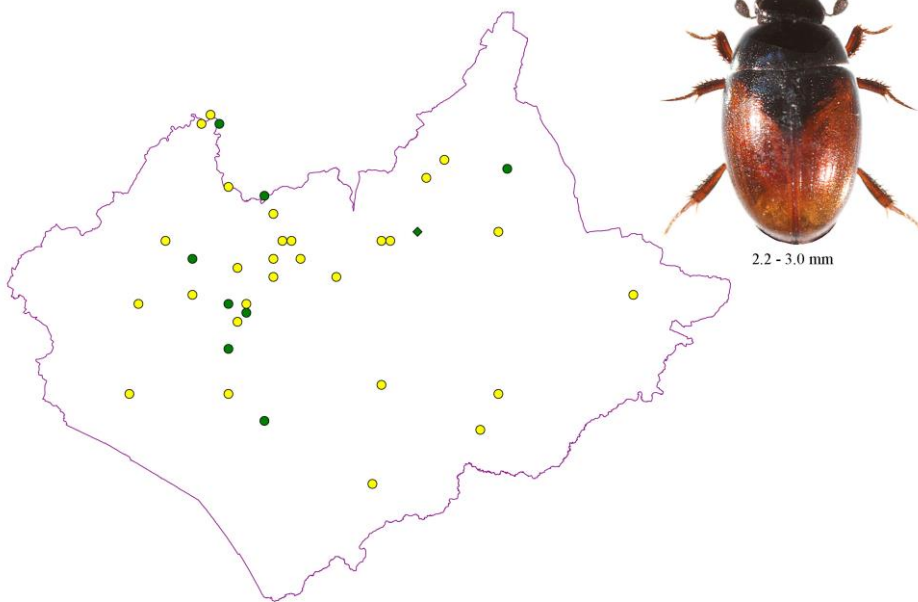
Common in England Wales and Scotland in various types of dung in spring and autumn. There are 12 sites for VC55.

Cercyon haemorrhoidalis

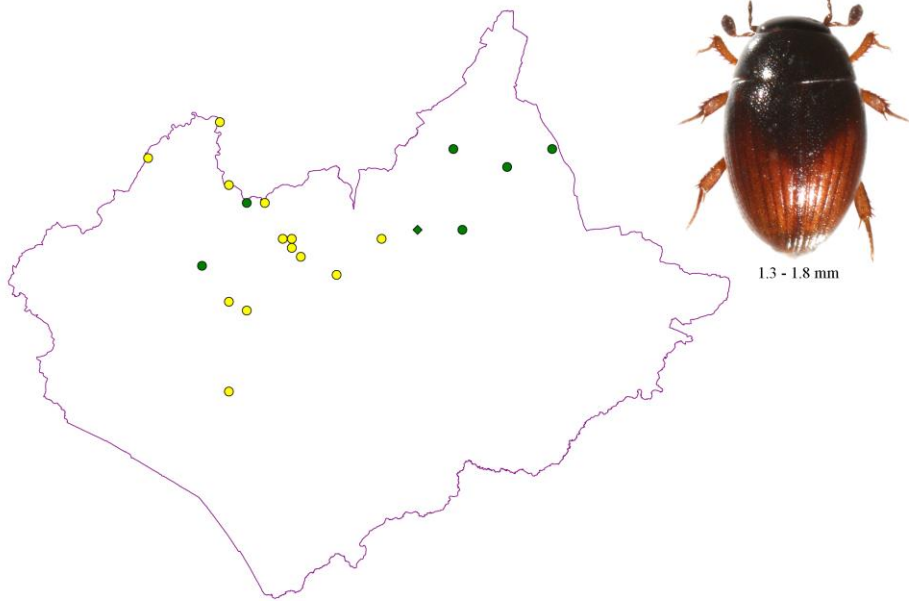
Common throughout the year in lowland Britain in dung and rotting organic matter. There are 9 sites for VC55.

Cercyon lateralis

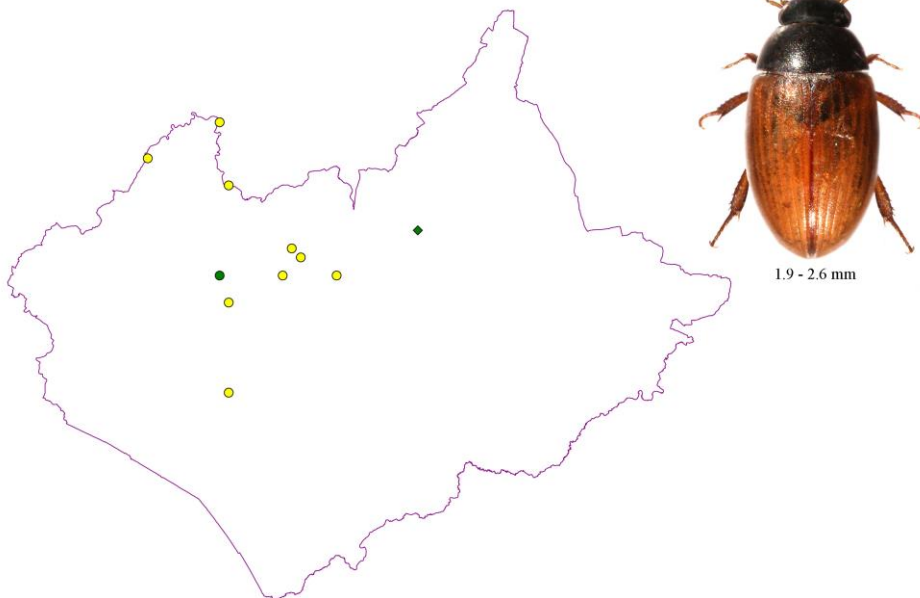
Found throughout the year, except December, across lowland Britain in dung and rotting organic matter and bird's nests. There are 17 sites for VC55.

Cercyon melanocephalus

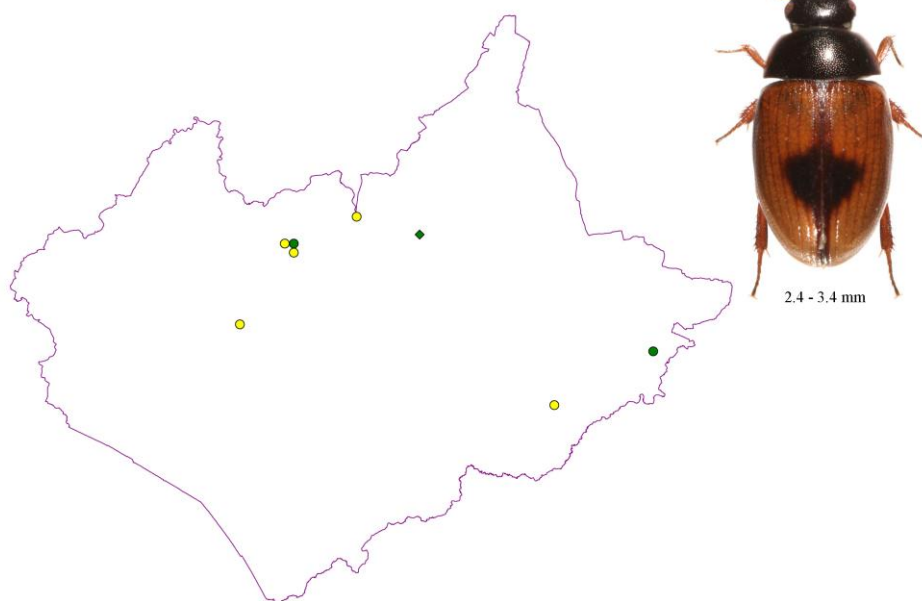
Found in dung throughout the year over much of Britain. There are 9 sites for VC55.

Cercyon pygmaeus

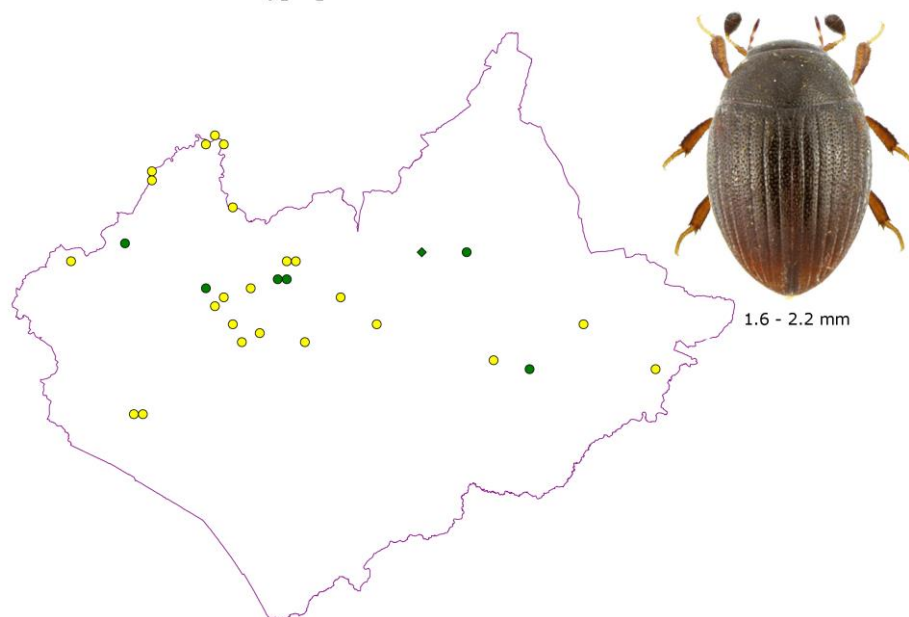
Found throughout the year, except March, in dung and rotting organic matter over much of Britain north to northern Scotland. There are 7 sites for VC55.

Cercyon quisquilius

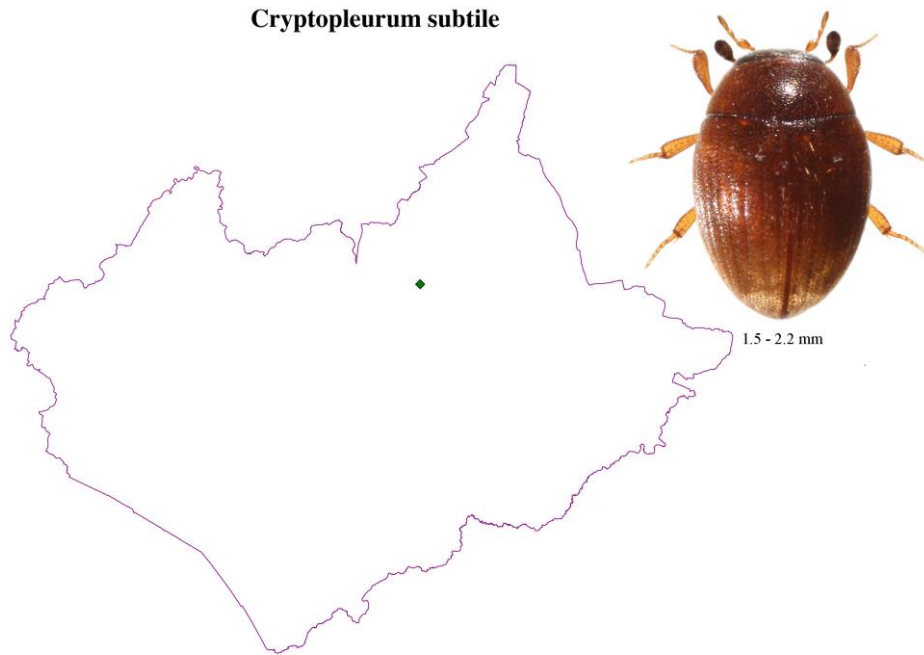
Found throughout the year, except February, in cow and horse dung across much of Britain. There are 2 sites for VC55.

Cercyon unipunctatus

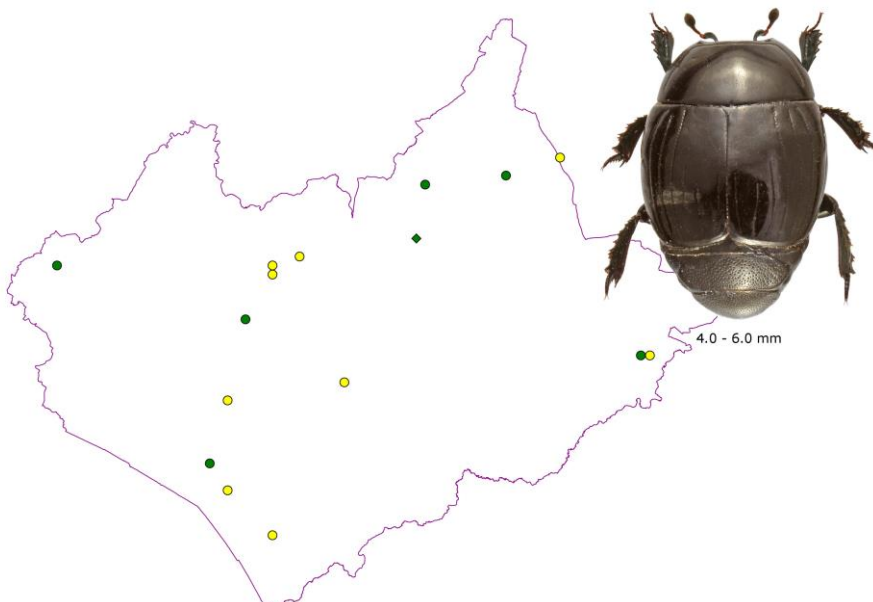
Found over much of England from February to November in rotting vegetable matter, horse dung and occasionally bird's nests. There are 3 sites for VC55.

Cryptopleurum minutum

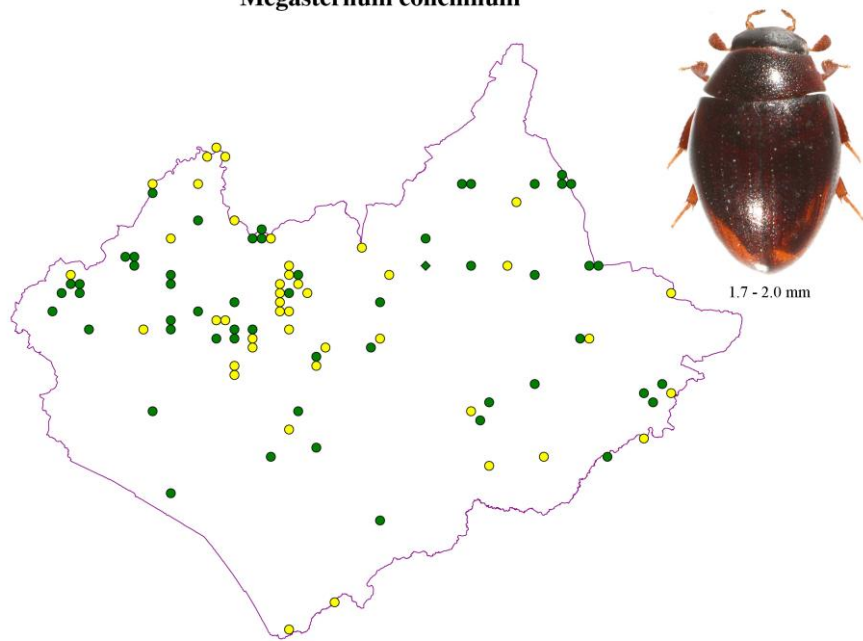
Widely distributed across Britain throughout the year in rotting material. There are 7 sites for VC55.

Cryptopleurum subtile

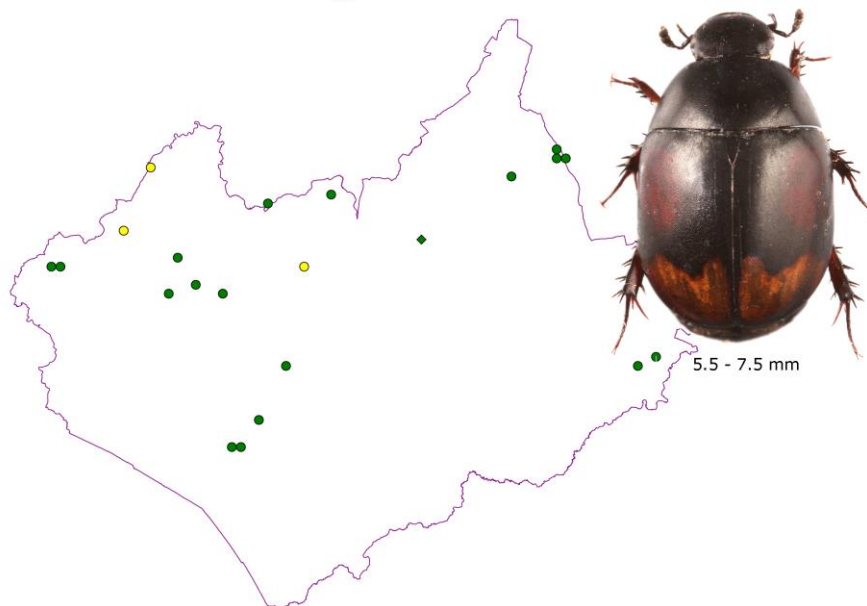
A species originally described from Japan first recorded in England in 1958. Since has been recorded in a number of English counties including Northamptonshire and Warwickshire, and also in Scotland, Wales and Northern Ireland (Foster *et al* 2014). Recorded in April, May and from July to January. There is only one site for VC55.

Margarinotus ventralis

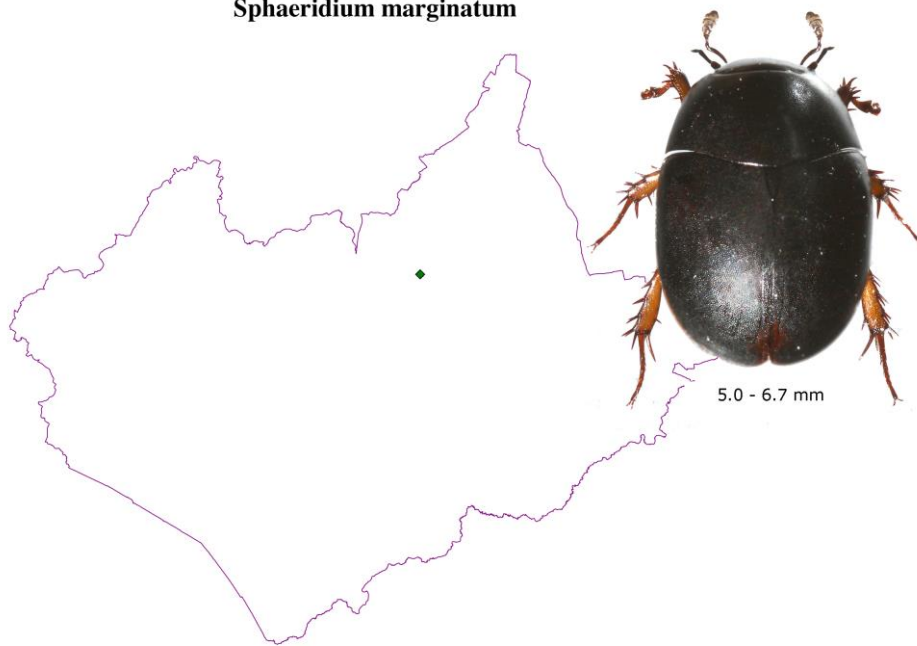
There are 20 records for VC55. Found in sheep dung at Priory, but known to occur in decaying vegetation and carrion as well as dung. Widespread over much of England and Wales, local in Scotland (Duff, 2012). There are 7 sites for VC55.

Megasternum concinnum

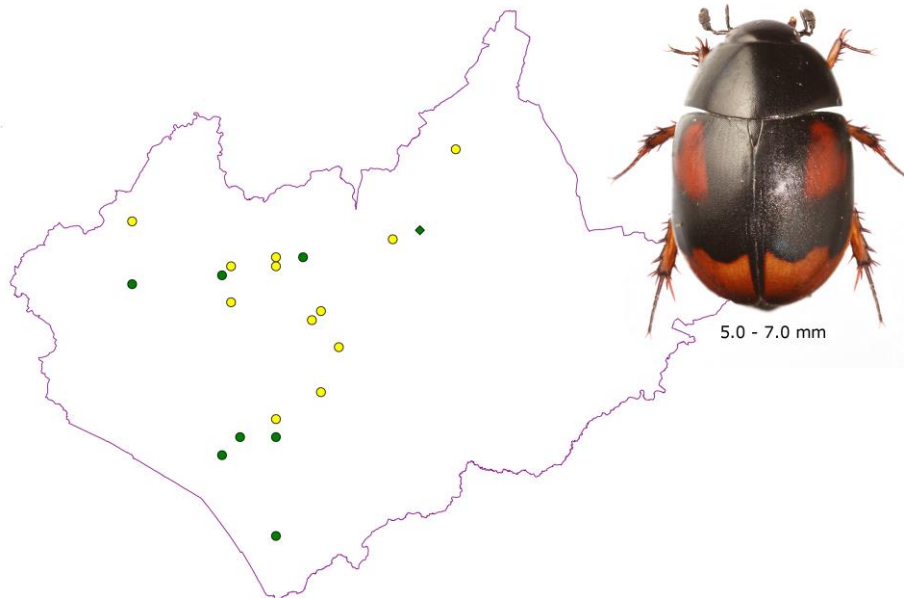
Widespread in Britain throughout the year in decaying vegetable matter and sheep dung. There are 54 sites for VC55.

Sphaeridium lunatum

Found throughout Britain in various types of dung it is commoner than *S. scaraboides* in the English Midlands (Foster *et al* 2014). There are 19 sites for VC55.

Sphaeridium marginatum

Only recognized in 1989 as being distinct from the very similar *S. bipustulatum* (not recorded at Priory). Based on present records it should be considered Nationally Scarce, occurring in fewer than 100 hectads in England and Wales, but this may be due to under-recording. There is 1 site for VC55.

Sphaeridium scarabaeoides

Recorded throughout Britain in various types of dung being the commonest species of *Sphaeridium*. Found throughout the year (Foster *et al* 2014). There are 8 sites for VC55.

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