A SURVEY OF DUNG BEETLES (AND OTHER *COLEOPTERA*) ON LUNDY AND AN INVESTIGATION OF THE ANALYSIS OF BIRD PELLETS AS A BEETLE SURVEY TECHNIQUE

by

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ABSTRACT

Forty corvid pellets were collected on Lundy over a three day period in July 2017. The pellets were later dissected and beetle fragments were identified to species. A comparison was made between the numbers and species found in the pellets and those found alive or dead, in or around dung, over the same three days. Subsequently, our survey results were compared with the results of historical surveys.

Keywords: Lundy, Coleoptera, dung beetles, bird pellets, corvids

INTRODUCTION

To understand the nature of an ecosystem, the maximum amount of data on the type and nature of organisms present in a habitat must be collected. Beetles (Coleoptera) form a key part of all terrestrial ecosystems because they are such a functionally diverse group. However, apart from the large colourful ones which feed on flower heads, most beetles prefer to stay out of sight and are not easy to find. Insectivorous birds and mammals know where to find them, and their waste products often contain the hard indigestible parts of beetle exoskeletons. Mammals such as foxes and hedgehogs egest these in their faeces. Birds regurgitate insect remains from their crops in dry pellets. Analysis of both types of waste can be a rich source of information about the local beetle fauna.

Barn Owl (*Tyto alba*) pellets are reasonably well-studied by naturalists because they are comparatively large and easy to find, occurring below owl roosts inside dry buildings. In particular, it has become common practice to analyse the contents of Barn Owl pellets as a means of surveying the small mammal fauna of a locality.

Little Owl *(Athene noctua)* pellets can also be found at regular haunts, on fence posts and below nesting sites. A paper written in 1937 by Alice Hibbert-Ware contained details of an extensive long term analysis of Little Owl pellets (Hibbert-Ware, 1937). She showed that their diet consisted mainly of insects and hence that they were innocent of the charge of mass slaughter of young game birds. An analysis of Little Owl pellets from Gloucestershire that we carried out in 2017 provided data in line with Hibbert-Ware's findings (Crofts, 2017). These birds are large consumers of dung beetles, particularly of the larger species.

Despite these examples, Philip Miles pointed out over 60 years ago that there has been surprisingly little research into the insect content of bird pellets, describing it as a 'practically virgin field of investigation' (Miles, 1952). He would be even more surprised (and no doubt very disappointed) to discover that this is still true.

In fact, in their 2004 study of Hooded Crow (*Corvus corone cornix*) pellet content in the Lough Hyne area of County Cork, Ireland, Horgan and Berrow state that theirs is the first study 'to specifically address the occurrence of dung beetles in the diet of any crow species' (Horgan & Berrow, 2004). However, the focus of their study was the impact of the Crows' predation on the invertebrate assemblage living in the dung.

But Corvids (a group containing Rooks, Crows and Ravens) are opportunistic feeders, taking whatever they can find. So we believe that their pellets have the potential to yield valuable information about the nature of the broader local ecology.

Rook (*Corvus frugilegus*) pellets build up below rookeries so they are easy to locate in large quantities, but apart from the odd elytron of the weevil *Sitona lineatus*, they are rarely a good source of insect remains. However, we have recently found Rook pellets in Orkney containing three species of the smaller dung beetles (Aphodiini).

Carrion Crow (*Corvus corone corone*) and Raven (*Corvus corax*) pellets are bigger, denser and usually much richer in beetle remains, particularly of the larger dung beetles (Plate 1). On Lundy, Rooks are only rare migrants, but Crows and Ravens are always around, stalking through fields which contain sheep, Highland cattle or ponies, looking for the insects in dung. They are also fond of standing on the top of dry-stone walls, and hence this is where they produce many of their pellets (Plate 2). If the pellet falls into a crevice in the wall, it will be protected and its contents may remain intact, forming a time capsule of what beetles have been eaten.



Plate 1: Some pellets are more obviously 'beetley' than others. The size of this one suggests it comes from a Raven. © Bob Cowley



Plate 2: This wall by the sheep field is a favourite of the Crows, which makes it a good place to look for their pellets. © Bob Cowley

We were originally alerted to Lundy's potential as a site for bird pellet research by reading an online version of Alan Rowland's 2014 paper in the *Journal of the Lundy Field Society* (Rowland, 2014). He had had the vertebrate content of various pellets analysed by Alasdair Love, but the insect content was not fully considered. When we contacted him, he sent some remaining pellets collected on Lundy in 2012 for us to investigate. Subsequently, we were put in touch with Steve Kett from Middlesex University, who supplied us with some additional pellets collected on Lundy in 2015. All of the pellets which we received from them (selected because of their 'beetley' surface) appeared to be from Crow and Raven.

As a result of these investigations, we decided to plan our own expedition, and this paper deals with the analysis of bird pellets we collected over three days on Lundy in July 2017.

One purpose of our current study was to see whether the contents of the pellets, specifically the dung beetle remains, were a true reflection of the occurrence of the live dung beetles currently in the dung pats. If this could be shown, then past and future analysis of corvid pellets could be used as a method for gathering a lot of data on the beetle fauna of Lundy (and subsequently, elsewhere). It sidesteps the problems of collection of live material from an SSSI. Photography of live specimens in the field is fraught with problems if the beetle is tiny, covered in dung and very similar to related species. Even under a powerful microscope, the crucial details may be impossible to see in a live, moving specimen. Corvid pellets can be collected in quantity throughout the year, stored and then analysed to provide a window into annual changes in beetle populations on the island.

METHOD

The method of collecting data was straightforward. We covered as much of the island as we could on foot in the time available.

On arrival on Thursday 6 July 2017, we completed a circuit through the sheep pasture in the south-west of the island. On Friday 7 July, we followed the main track to the northern tip of the island, returning along a western coastal route. On Saturday 8 July, we explored in detail the dry-stone walls around the sheep pasture to the north-east of the village, and then followed the paths through the wooded area to the east of the island.

Any live beetles on the ground or on the heads of flowers were noted and photographed if necessary. Any dead beetles or parts of beetles were collected (Plate 3). The dung of Highland cattle, ponies and sheep were examined for the presence of live dung beetles (Plate 4). These were identified, photographed if necessary, and their numbers noted (Plate 5). Dry stone walls and the surfaces of single large stone blocks were searched for pellets or pellet remains (Plate 6); these were bagged separately along with their grid reference (Plate 7).

Once back in Oxford, Linda Losito undertook the pellet analysis. Each pellet was soaked in a mixture of disinfectant and washing-up liquid and then broken apart under a microscope. Any beetle fragments were sorted out from the stones, plant material, and other debris. Fragments of bone, snail shells, seeds and larval forms were also removed for potential identification.

The beetle fragments ranged in size from whole heads and complete large elytra (wing cases) to tiny pieces a few millimetres long. These had to be cleared of adhering debris. Any hollow structure (like a weevil thorax) has to be emptied out because it might contain a beetle head or pieces of elytra. Legs are fairly robust and often survive the crushing process in a bird's crop, but they are not very useful, except to give some estimation of numbers. Sometimes, very distinctive legs, like those of *Typhaeus typheous*, are present without any other remains.

Rarely, fragments of an unusual beetle may appear in two different pellets, and separate fragments of elytra can be matched to form a complete whole. One must conclude that the two pellets were produced by the same bird. Hence the contents of pellets from the same place should always be checked against each other to aid difficult identifications.

On the other hand, a pellet will occasionally contain a virtually perfect uncrushed specimen, complete with intact legs and antennae. The insect is likely to be from the top of the food mass when it is ejected from a full crop. This tends to occur with smaller beetles, which may be eaten in large numbers.

Once isolated and cleaned, each beetle fragment was dried, carded and stored (Plate 8). It then had to be identified. Unfortunately, identification keys are designed for use with whole specimens. They may refer to features present on the abdomen when all that you have are the head and elytra. Identification can only be achieved by comparison with a named specimen. This was facilitated by owning a large personal collection, as well as having regular access to the world-class collections in the Oxford University Natural History Museum. Even so, weevils present a particular problem. Bird crops are full of tiny stones which have a very abrasive effect, rubbing off most of the diagnostic scales, but careful searching will usually reveal a few scales left around the edges of the thorax.

Plate 3: Many beetle fragments were found by thorough searching of tracks and bare places. © Bob Cowley





Plate 4: Although other techniques are available, getting hands-on with the dung maximises our chances of locating and identifying dung beetles, while causing them minimum disturbance. © Bob Cowley

Plate 5: After removing this beetle from the dung, we put it in a collecting tube where it was photographed and identified as *Agrilinus ater*. It was returned to the same dung in less than a minute. (Note the use of a Lundy map as background!) © Bob Cowley





Plate 6: A typical corvid pellet, in a typical location. This one is probably from a Raven. © Bob Cowley

Plate 7: Every pellet and specimen was bagged or photographed, and listed (with its grid reference) on our daily log sheet. © Linda Losito





Plate 8: Many of the beetle fragments extracted from the pellets for identification were less than 2mm long. © Bob Cowley

It must always be understood that this method of analysis can only provide information about what is there. Absence in the pellet is not proof of absence in the diet. For instance, one might expect that soft bodied or very small organisms leave no trace, and beetles with particularly robust exoskeletons like scarabs and weevils may be over-represented in the pellets. However, this does not appear to be the case as some pellets contained very large numbers of fairly fragile but intact elytra of Elateridae (click-beetles). Having said that, it is improbable that corvids would bother with anything much smaller than a weevil, so pellets would not be a good tool for investigating the presence of very small beetles such as Latridiidae.

RESULTS AND DISCUSSION

Table 1 shows the range of species found either live in dung, on the ground (dead or alive), or as fragmentary remains identified in pellets. The nomenclature used accords with the most recent edition of the Checklist of Beetles of the British Isles (Duff, 2018).

You can see from Table 1 that there was a broad correspondence between the range of beetle species found in our pellets and those found by direct inspection of the ground and animal dung. However, our pellet analysis revealed the presence of 33 species, compared to a total of only 18 species observed directly in the wild. More particularly, the pellet analysis revealed the presence of 20 species not found by other means, while missing only five that were. This suggests that the pellet sampling process was actually more thorough than directly surveying the ground and dung.

The 33 species found in the pellets are representatives of just 10 families which is quite a limited spread, given that there are 102 families of Coleoptera. It is a similar list to those found in our analysis of the 2012 and 2015 samples; they had contained 26 species from eight families, but the overall content was very similar. All of the beetles are of a type likely to be found at ground level. Weevils are plant feeders but tend to throw themselves to the ground when disturbed. Chrysomelids and other large plant-eating beetles may be under-represented. This is just what you would expect to find in the pellets of ground-feeding corvids.

The pellets contained six species of dung beetle and five of the same species were also found as live or recently dead specimens whilst surveying the island. The sixth species *Melinopterus sphacelatus* avoids the months of July and August, and is replaced by other Aphodiini species. We have previously found it in one of the June 2015 pellets. Its presence in ten of the samples we collected suggests that these were older pellets, which was confirmed by their hard, dry nature and mite infestations. Comparison with previous pellets shows the expected change in Aphodiini species due to seasonal change. There were no *Acrossus rufipes* or *Agrilinus ater* in the pellets from 2012 and 2015.

Three types of dung (pony, sheep and Highland cattle) were present in large quantities on Lundy. During our three day visit, we investigated samples from all over the island. None were very productive in terms of live dung beetles present when compared to similar places on the mainland. The largest numbers found at one site were 18 *Agrilinus ater* in sheep droppings and eight *Acrossus rufipes* in cattle pats. A lot of dung was completely devoid of dung beetles. This may reflect the presence of anthelmintics such as Ivermectin which are frequently fed to domestic animals as a prophylactic against internal parasites.

Table 1: Coleoptera species found during our survey either living in dung, elsewher	e
on the ground (alive or dead), or identified from remains found in corvid pellets	

FAMILY	SPECIES	DUNG	GROUND	PELLET
CARABIDAE	Carabus granulatus L.		Y	Y
	Carabus nemoralis Mull.		Y	
	Poecilus versicolor (Sturm)			Y
	Pterostichus niger (Schaller)		Y	Y
	Pterostichus melanarius (Ill.)		Y	Y
	Abax parallelepipedus (Pill. & Mitt.)			Y
	Calathus fuscipes (Gze.)		Y	
	Harpalus rufipes (De Geer)			Y
HYDROPHILIDAE	Sphaeridium bipustulatum F.	Y		
HISTERIDAE	Margarinotus striola (Sahl.)			Y
LEIODIDAE	Ptomaphagus subvillosus (Goeze)			Y
SILPHIDAE	Thanatophilus rugosus (L.)			Y
	Phosphuga atrata (L.)		Y	Y
	Silpha tristis Ill.		Y	Y
	Nicrophorus investigator Zetters.		Y	Y
STAPHYLINIDAE	Ocypus olens (Mull.)			Y
	Philonthus marginatus (Mull.)			Y
	Philonthus decorus (Grave.)			Y
GEOTRUPIDAE	Typhaeus typhoeus (L.)		Y	Y
	Anoplotrupes stercorosus (Scriba)	Y	Y	Y
	Geotrupes stercorarius (L.)		Y	Y
SCARABAEIDAE	Acrossus rufipes (L.)	Y		Y
	Agrilinus ater (De Geer)	Y		Y
	Melinopterus sphacelatus (Panzer)			Y
	Cetonia aurata (L.)		Y	Y
BYRRHIDAE	Byrrhus pilula (L.)			Y
ELATERIDAE	Agrypnus murinus (L.)			Y
	Agriotes lineatus (L.)			Y
	Agriotes obscurus (L.)			Y
	Agriotes sputator (L.)			Y
	Athous haemorrhoidalis (F.)			Y
CANTHARIDAE	Rhagonycha fulva (Scop.)		Y	
TENEBRIONIDAE	Cteniopus sulphureus (L.)		Y	
CURCULIONIDAE	Rhinoncus pericarpius (L.)			Y
	Otiorhynchus sulcatus (F.)		Y	Y
	Sitona obsoletus (Gmelin)			Y
	Sitona waterhousei Walton			Y
	Brachypera zoilus (Scop.)			Y

The larger dung beetles, *Typhaeus*, *Geotrupes* and *Anoplotrupes* are more likely to be in tunnels under the dung itself so are less likely to be found without serious digging. One *Anoplotrupes* was found in dung, but mostly they were found walking along the edge of paths (Plate 9).

Plate 9: *Anoplotrupes* stercorosus is the dung beetle you are most likely to see on the footpaths of Lundy. © Bob Cowley



One hydrophilid species, *Sphaeridium bipustulatum*, was present in Highland cattle dung in some numbers but was not present in any pellet. In fact, although we have found this and other *Sphaeridium* species on the mainland in dung many times, we have only ever found one in a pellet, which could either reflect their ability to move fast and evade predation, or possible rejection by birds.

Pellets seem to give a better indication of the numbers of large dung beetles than could be obtained by searching for live specimens. When present in pellets, they can be in large numbers, especially considering the size of the pellet. In pellets from this study, two contained evidence of nine *Anoplotrupes*. In one of the 2015 pellets there were 22 *Anoplotrupes*, eight *Typhaeus* and one *Geotrupes* as well as other large beetles. One 2012 pellet was composed almost entirely of *Anoplotrupes* remains.

The collection and examination of pellets has provided insight into both the range and number of dung beetle species on the island and it seems to correlate with the beetles actually present during a specific time window.

In the 1970s, Martin Brendell compiled a comprehensive list of Lundy's Coleoptera from all known records, going back over some 130 years (Brendell, 1976). Of the 16 Geotrupidae and Scarabaeidae on his list, we found seven in pellets and four in dung. Ten Aphodiini species have been found on the island in the past and the six which we did not find could potentially have been around in June and July. They tend to be in smaller populations, so their absence from the samples may be chance or due to a population decline as is happening elsewhere.

The Rose Chafer (*Cetonia aurata*), while a scarab, is associated with flowers not dung, but ground feeding birds would find the adult in large numbers when it emerges from the ground in the spring. In some of the 2012 pellets it was very abundant, making up almost 100% of one pellet. *Anoplotrupes* and *Cetonia* are major components of the corvid diet along with ground beetles.

Although Geotrupidae and Scarabaeidae were the original focus of our study, once we had analysed the fragments from our pellets, we found two other families were particularly well represented.

Silphidae are associated with dead matter. There are six silphids on Brendell's list, of which our pellets produced four. *Phosphuga atrata* and *Silpha tristis* were found in over a third of the samples but in small numbers, presumably because they do not have mass emergences like the geotrupids and scarabs. *Nicrophorus investigator* is a beetle which lives in and around the small corpses which it buries. A carrion-feeding bird is ideally placed to find such specimens. So one might be surprised that it was not found in any of the 2012 and 2015 pellets. But then, although *Nicrophorus investigator* was found by Brendell himself in 1972, his is the only Lundy record between Wollaston in 1845 and our own.

Another notable result from our pellet analysis was the number of Elateridae (clickbeetles) species which were found to be present. We had observed no click-beetles during our time on Lundy, and yet our pellets yielded five species out of the 14 on Brendell's list.

Looking more closely at the four families discussed above, Table 2 compares the species found by our current pellet survey with all those listed by Brendell.

As you can see, from our pellet survey alone, we succeeded in finding four out of the six Silphidae on Brendell's list, three out of four Geotrupidae, four out of 12 Scarabaeidae, and five out of 14 Elateridae (for a total of 16 out of 36 species).

But there is an additional column in Table 2, which one could argue offers an even more relevant and impressive comparison. This middle column restricts our attention to only those species on Brendell's list that have been recorded more than once in the last 100 years. After all, any species that has been recorded once or less in the last 100 years is certainly very rare, and may by now be locally extinct (always assuming that one can rely on the accurate identification of such a rare specimen).

Comparing the results of our pellet survey against this arguably more representative list, you can see that we recorded four of four Silphidae, three of three Geotrupidae, four of seven Scarabaeidae, and five of 10 Elateridae (for a total of 16 out of 24 species).

CONCLUSIONS

Despite having only a small amount of time in the field (about 20 hours), we have been able to add considerably more data records for the Coleoptera of Lundy. But of course, this could only be achieved by subsequently spending a disproportionately large amount of time analysing our collected beetle fragments under a microscope.

All our records have been added to the Biological Records Centre's online database iRecord, and so are freely accessible to anyone who may be interested. More specifically, anyone with a particular interest in the natural history of Lundy is encouraged to explore our data through the Lundy Sightings Group section of the iRecord site.

If you do so, looking at all recorders of flora and fauna, you will see that Linda Losito is now second only to Alan Rowland in the overall number of Lundy records submitted, and third in the number of distinct species recorded. In terms of Coleoptera, we have increased the number of records by 969%, our 281 new records raising the total from 29 to 310.

Table 2: Comparison of Silphidae, Geotrupidae, Scarabaeidae, and Elateridaeappearing on Brendell's list of all beetles recorded during 129 years on Lundy (1844-1972) with those detected by our analysis of the corvid pellets we collected during threedays in July 2017. The middle column shows those species on Brendell's list that havebeen recorded more than once in the last 100 years

FAMILY	SPECIES	BRENDELL	>1/100 YEAR?	PELLET SURVEY
SILPHIDAE	Thanatophilus rugosus (L.)	Y	Y	Y
	Aclypea opaca (L.)	Y		
	Phosphuga atrata (L.)	Y	Y	Y
	Silpha tristis Ill.	Y	Y	Y
	Nicrophorus humator (Gled.)	Y	Y	
	Nicrophorus investigator Zetters.	Y		Y
GEOTRUPIDAE	Typhaeus typhoeus (L.)	Y	Y	Y
	Anoplotrupes stercorosus (Scriba)	Y	Y	Y
	Geotrupes mutator (Marsh.)	Y		
	Geotrupes stercorarius (L.)	Y	Y	Y
SCARABAEIDAE	Acrossus depressus (Kugel.)	Y	Y	
	Acrossus luridus (F.)	Y		
	Acrossus rufipes (L.)	Y	Y	Y
	Agrilinus ater (De Geer)	Y	Y	Y
	Aphodius fimetarius (L.)	Y	Y	
	Colobopterus erraticus (L.)	Y		
	Esymus pusillus (Hbst.)	Y		
	Melinopterus sphacelatus (Panzer)	Y	Y	Y
	Rhodaphodius foetens (F.)	Y		
	Teuchestes fossor (L.)	Y	Y	
	Serica brunnea (L.)	Y		
	Cetonia aurata (L.)	Y	Y	Y
ELATERIDAE	Agrypnus murinus (L.)	Y	Y	Y
	Agriotes acuminatus (Steph.)	Y	Y	
	Agriotes lineatus (L.)	Y	Y	Y
	Agriotes obscurus (L.)	Y	Y	Y
	Agriotes pallidulus (Ill.)	Y	Y	
	Agriotes sputator (L.)	Y		Y
	Dalopius marginatus (L.)	Y	Y	
	Adrastus pallens (F.)	Y		
	Melanotus villosus (Geoff. in Four.)	Y		
	Athous haemorrhoidalis (F.)	Y	Y	Y
	Athous vittatus (F.)	Y		
	Prosternon tessellatum (L.)	Y	Y	
	Selatosomus aeneus (L.)	Y	Y	
	Cardiophorus vestigialis Erich.	Y	Y	

In addition, this study has contributed 135 new records to the Dung Beetle UK Mapping Project (DUMP) and 155 new records to the National Recording Scheme for Scarabaeoidea.

According to Brendell's list, only 16 different species of Geotrupidae and Scarabaeidae were recorded on Lundy in 129 years. Set against this, it is encouraging that we were able to find seven of those species in only 20 hours of field work. But as noted in the discussion of Table 2 above, restricting our attention to only those species on Brendell's list that have been recorded more than once in the last 100 years gives an arguably more enlightening comparison. By that measure, our pellet survey succeeded in finding seven of the 10 species from these two families.

But in addition, our pellet survey turned out to be very successful at finding Silphidae and Elateridae. We recorded four Silphidae compared with the four species on Brendell's list that have been recorded more than once in the last 100 years, and five out of 10 Elateridae.

One can also interrogate the iRecord database to get a good idea of how common a species is in the UK (by looking at the total number of records of that species on the database). Applying that metric to the 16 species of Geotrupidae and Scarabaeidae on Brendell's list, it is interesting to note that the nine species that we failed to find have each been recorded fewer than 90 times nationally, so may be considered comparatively rare. On the other hand, we succeeded in finding all seven of the more commonly occurring species on his list. One might hope that this implies that there has been no great change to the range of dung beetle species present on Lundy.

However, of course this tells us nothing about any possible change of population numbers of each species. The amount of (unoccupied) dung observed on the surface of the pasture certainly suggests the numbers of dung beetles are not adequate to their task.

By simultaneously collecting bird pellets and surveying beetles on the ground and in dung, we sought to investigate whether bird pellet analysis could be a useful technique for the survey of Coleoptera.

Our results clearly indicate that it is - at least for certain birds and certain beetles. Specifically, we believe the pellets of Crows and Ravens could be very useful for the study of ground-living beetles.

Looking specifically at the dung beetle families, Geotrupidae and Scarabaeidae, Table 1 shows that only three species were found in dung and only four were found on the ground. Given that there was one species in common, the two techniques together found a total of six species. However, the pellet analysis succeeded in finding not only all these six species, but an additional one, *Melinopterus sphacelatus*, making a total of seven (Plate 10).

The presence of this additional species is particularly interesting, as it illustrates both a strength and a potential weakness of the pellet analysis technique. The typical season for *Melinopterus sphacelatus* comes to an end during June. So at the time of our visit to Lundy in early July, one would not have expected to find surviving individuals. It is likely that the pellets containing these specimens had been regurgitated some weeks before our visit.

This illustrates that pellets act as time capsules of the species active at the time they are deposited. So the only way to get reliable data of when each species is present is to inspect the same locations on a regular basis, and collect all the pellets you find on each visit. Only by doing this, can you be reasonably confident of the date of deposit of each pellet.



Plate 10: A line-up of the dung beetle species we found on Lundy. (Although *Cetonia aurata* is also classified as a scarab, the adult beetle is not found in dung.) © Bob Cowley

With this caveat, we believe that the analysis of bird pellets does indeed have the potential to be a very useful additional technique for the study of Coleoptera.

More specifically, we conclude that the analysis of Crow and Raven pellets could have exceptional value in the study of Silphidae, Geotrupidae, Scarabaeidae and Elateridae.

Crows and Ravens consume a large number of ground-living beetles, and both birds produce fairly large and cohesive pellets in fairly predictable locations. This means that their pellets are comparatively easy to collect, which could provide new opportunities for surveying.

For example, since the fieldwork of collecting pellets can be undertaken by a nonspecialist, pellets could be collected from a variety of sites on a regular monthly or weekly basis by somebody living nearby. The pellets could then be dispatched by post to a specialist coleopterist for analysis, allowing one to efficiently monitor the pattern of changes of beetle species month by month (or indeed, year by year).

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Steve Kett (of Middlesex University) was equally generous in donating a number of pellets from his archive for further analysis.

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