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Distribution and abundance of insects colonizing cattle dung in South West England

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Abstract
The succession of insects colonizing cow dung in south west England was examined over 2 years, using arrays of standardized 1.5 kg artificially constructed cow-dung pats in cattle pasture. The seasonal pattern of colonization was examined using batches of 10 pats each week for 24 weeks in 2001. Pats were left exposed in the field for 7 days, to allow colonization, and were then brought back to the laboratory to await insect emergence and identification. Overall seasonal changes in community structure were relatively gradual and subtle; Coleoptera were generally more abundant earlier and Diptera later in the season, and the number and order of species arrival broadly matched previous studies in similar habitats. The temporal pattern of colonization of individual pats was examined in six batches of 30 pats constructed in May, June, and August/September in 2002. Groups of five pats were recovered and brought back to the laboratory 1, 2, 4, 7, 14, or 21 days after construction. Overall, three broad, but statistically distinct, successional groups were identified, with the maximum number of colonizers present in pats that were 4–7 days old. The data contribute valuable information on the temporal distribution and abundance of dung-colonizing taxa in South West England, a clear local understanding of which is essential to allow the effects of agricultural practices which may damage dung invertebrate communities, such as livestock anthelmintic treatment, to be assessed.

Keywords: *Cattle, decomposers, decomposition, dung beetles, flies, pastureland*

Introduction

In cattle dung, from the time of deposition to its complete incorporation into the surrounding environment, the pat undergoes a series of rapid changes in its physical properties, mediated by both biotic and abiotic factors (Barth 1993; Barth et al. 1994). These changes alter the attractiveness of the pat to the diverse invertebrate dung-colonizing community and help to determine the range of species attracted to each dropping at any given time. In tropical areas the removal and burial of dung by scarabaeid beetles may result in the complete disappearance of the pat within a few hours, so that a structured community often may not have time to appear. In temperate regions, however, dung removal is slower and physical changes to the resources promote the formation of an

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ordered succession of inhabitants (Putman 1983). One of the most obvious such physical changes in wet dung, such as that of cattle, is the formation of the crust. Once formed, the crust creates a physical barrier to many insects, preventing them from entering the pat (Skidmore 1991) and blocking its odour (Hammer 1941). The activity of the invertebrates present also has direct effects on subsequent colonization and the speed and direction of this succession; as soon as they enter a dropping, colonizing insects begin to change it, mainly by their burrowing and tunnelling, altering its attractiveness to other species (Holter 1977, 1979; Stevenson and Dindal 1987a, 1987b). The pattern of succession may also change on a seasonal time-scale, again influenced by climate and phenology of individual species.

While understanding the dynamics of the insect dung community is of considerable fundamental ecological interest, it also has important practical application. The cycling of organic matter through herbivore dung into the soil plays an important role in helping to maintain pasture fertility and productivity in grazed pastureland ecosystems (Stevenson and Dindal 1987a; Lumaret and Kadiri 1995). The activity of the invertebrates that contribute to dung decomposition can, however, be disrupted by a range of agricultural practices, particularly the treatment of livestock with persistent antiparasitic anthelmintics, which may be excreted in the faeces (Floate 1998; Floate et al. 2005). Hence, understanding the patterns and processes of dung colonization and temporal changes in the dung-colonizing community may have an important role in helping to predict and, ultimately, reduce these impacts.

The aim of the present study, therefore, was to quantify the abundance and distribution of the insects colonizing cow dung in south west England over time. Although a number such studies have been undertaken previously (e.g. Holter 1977; Finn et al. 1998, 1999; Hutton and Giller 2003), it is possible that dung insect communities may be relatively site-specific, with variation in activity strongly determined by local differences in microclimate. Hence, the evaluation of local patterns of succession, which ultimately may support or modify regional models, is essential.

Materials and methods

The investigation was conducted during 2001 and 2002 in an area of permanent grassland pasture on a farm located approximately 20 km south-west of Bristol, UK. The area was at an altitude of 100 m above sea level and has a mean annual rainfall of 850 mm and a mean annual temperature of 11°C. The pastures used consisted of a network of fields, each of approximately 5–10 ha in area. These were grazed each summer by a dairy herd of about 250 Holstein-Friesian cows and a small number of sheep. During the winter the cows were kept indoors and fed on silage and feed concentrate. The majority of the cattle were let out to pasture in mid-May and were rotated between contiguous fields until mid-October, when they were brought back in for the winter. The cattle were milked twice daily, at approximately 07:00 and 16:00 h, and were not treated with anthelmintics while maintained in the milking herd. Dry (non-lactating) and pregnant animals were maintained separately from the main milking herd.

Batches of artificially constructed cow pats, formed from the fresh dung, were used to study degradation rates and the impact of early colonizing insect fauna on the subsequent colonization and pat breakdown. On days when dung was required, fresh dung from several cows was collected from the milking parlour during afternoon milking. This was thoroughly mixed to ensure uniform constituency and texture and used immediately. Using a hand-held spring balance, 1.5 kg of fresh dung was weighed out and circular pats, 4–5 cm deep with a diameter of approximately 19 cm, were produced using a polythene former. The former was removed once the pat had been created. Plastic netting (2 cm mesh) was placed under the pats to assist with their recovery; the netting was not considered likely to have affected invertebrate movement, given the size of the dung-colonizing species relative to the mesh width.

To study seasonal patterns of succession, in 2001 batches of 10 artificially constructed cow pats were placed out each week, between the 21 May and 29 October. Artificial pats were left exposed in the field for 1 week to allow colonization of invertebrates, following which they were retrieved. The more detailed colonization of individual pats was considered during three periods in 2002: May, July/August, and August/September, corresponding with early, mid- and late-season communities. During each period, two batches of 30 cow pats were placed out, then at 1, 2, 4, 7, 14, and 21 days after deposition, five randomly selected pats were retrieved from the field.

After collection each pat was returned to the laboratory, placed on to a thin layer of sawdust on a polythene sheet, and put in an individual fine-mesh bag to await the emergence of invertebrate colonizers. The mouth of the mesh bag was attached to a plastic collecting beaker and, as they emerged, insects were funnelled from the mesh bag into the beaker, where they quickly died. This funnel system helped to ensure that there was no recolonization of dung by newly emerged insects in the laboratory. Where possible, all insects collected were identified to species level. However, some groups could not be identified to this level and were considered as genera or family taxa.

Where median values are given, the interquartile range is also stated in parentheses. Mean values are stated plus or minus the standard error. Days are numbered throughout the season beginning on 1 May (day 1). Abundance data were $\log_{10}$ transformed and normality confirmed before inclusion in parametric statistical tests.

Results

From the 240 artificial cow pats placed in the field in 2001, a total of 145,454 insects were recovered over the season, with a median of 333 (188–795) individuals per pat. Overall, the composition of the community altered as the season progressed; in general the Diptera appeared significantly later in the season than the Coleoptera ($t_{(2),47}=3.33$, $P<0.01$; Figure 1). Many of the most abundant dipterous taxa, such as *Sylvicola punctata*, Chironomidae, *Polites lardaria*, *Scatophaga stercoraria*, *Chloromya formosa*, and *Sargus* spp. also showed more distinct peaks in abundance, compared to most of the Coleoptera, such as *Cercyon lateralis* and larvae of Oxytelinae, where relatively low levels of abundance continued over much longer periods (Figure 2). Apart from the very early appearance of *Aphodius fimitarius*, the other adult Coleoptera were found throughout June to August, with their peak abundance in July.

The 180 pats examined in 2002 were used initially to consider the overall changes in insect abundance with pat age. In 2002, as in 2001, the abundance of individual taxa changed little over the course of the season and the number of taxa present was not significantly different between the three time periods when pats were constructed. Hence, pats constructed at the three different times were pooled for subsequent analysis. For this the data were analysed initially using a Friedman non-parametric, two-way analysis of variance by ranks, including extension for more than one observation per cell, with χ_r^2 approximating to $\chi^2_{\alpha,5}$ (Marascuilo and McSweeney 1977; Zar 1996). Pat age was included as a fixed factor and each batch was included as a separate block with five replicates per cell.

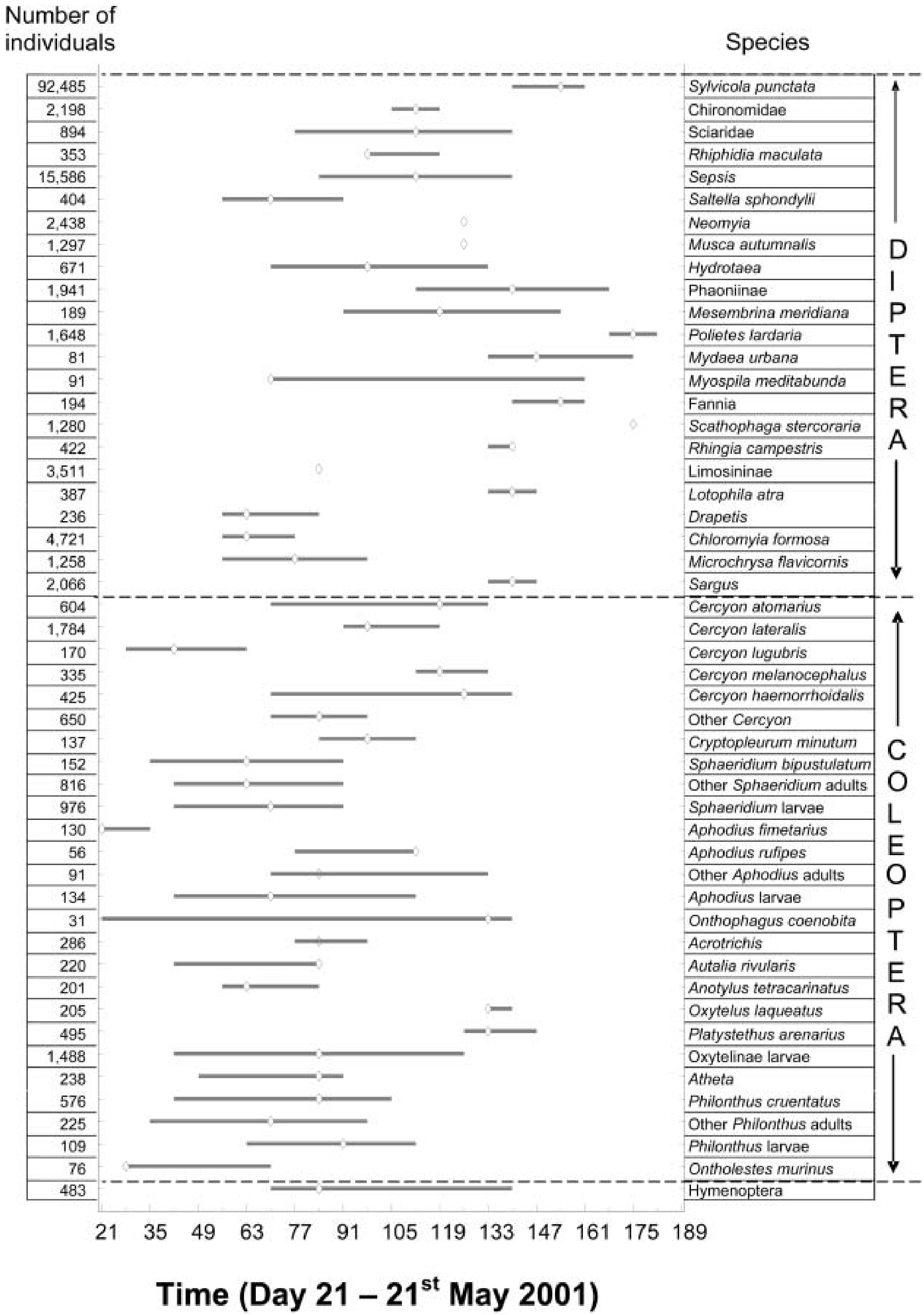

Figure 1. The median seasonal occurrences (and inter-quartile ranges), and total number recovered for the insect taxa from artificial cow pats placed out between May and November 2001. Day 1 is 1 May.

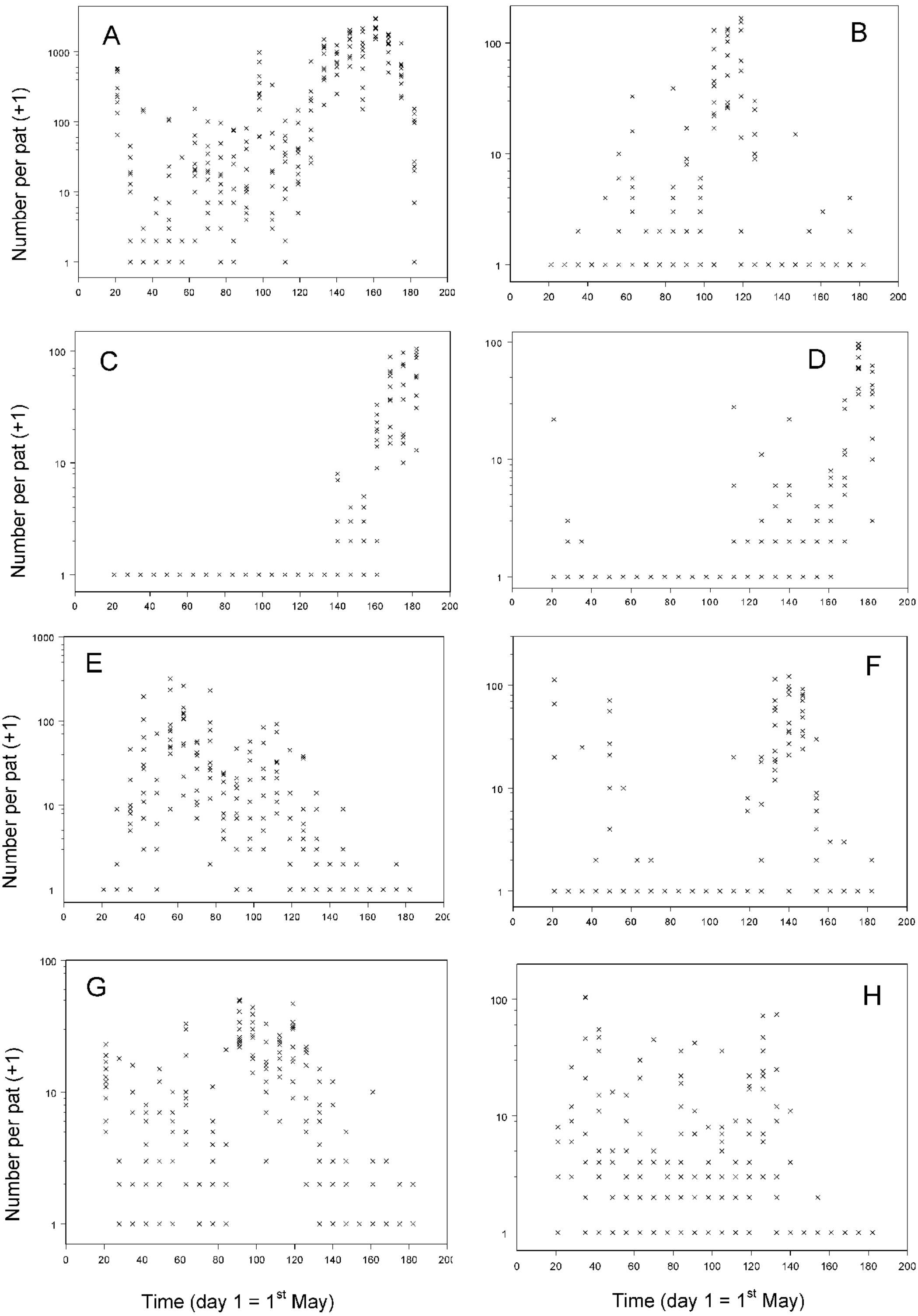

Figure 2. The numbers of various taxa recovered from individual artificial cow pats placed out between May and November 2001; day 1 is 1 May. (A) *Sylvicola punctata*; (B) Chironimidae; (C) *Polites lardaria*; (D) *Scatophaga stercoraria*; (E) *Chloromyia formosa*; (F) *Sargus* spp.; (G) *Cercyon lateralis*; (H) Oxytelinae larvae.

This analysis showed that the total numbers of insects present varied significantly with pat age ($\chi_r^2=60.4$, $P<0.001$); the median number of insects per pat appeared to peak in pats exposed for 4–7 days, although there was considerable variation between batches. Twenty-one-day-old pats contained significantly fewer insects than all other ages, while greater numbers were recovered from 4-day-old pats than those aged both 2 and 14 days. Seven-day-old pats also contained more insects than those aged 2 days. Within this overall pattern there were also major differences in the patterns of colonization of the different insect groups. The numbers of adult Coleoptera were high over the first 4 days and then declined, whereas the number of Diptera were low initially, peaked in 7-day-old pats, and then also declined (Figure 3). In contrast, the peak abundance of larval Coleoptera was observed in 14-day-old pats (Figure 3).

To consider these patterns in more detail, the successional mean occurrence (SMO) was calculated for each taxon (Hanski 1980). This represents the mean age of dung in which individuals of particular taxon were present (in days), taking into account the unequal time periods between samples.

$$\text{Successional mean occurrence} = \frac{\sum_{i=1}^{n} p_i(t_i - t_{i-1})t_i}{\sum_{i=1}^{n} p_i(t_i - t_{i-1})} \tag{1}$$

where p_i is the number of individuals collected from pats of age t_i days and n is the number of sampling days along the succession. All 180 pats were combined to give a single overall successional mean occurrence value for each species (Table I).

Cluster analysis, using a nearest neighbour (single linkage) method, indicates that the successional mean occurrence values measured can be divided into three groups, which have significantly different mean successional values ($F=195.9$, $P<0.001$). Group I insects began to arrive as soon as the pat was produced, reaching a maximum during the first five

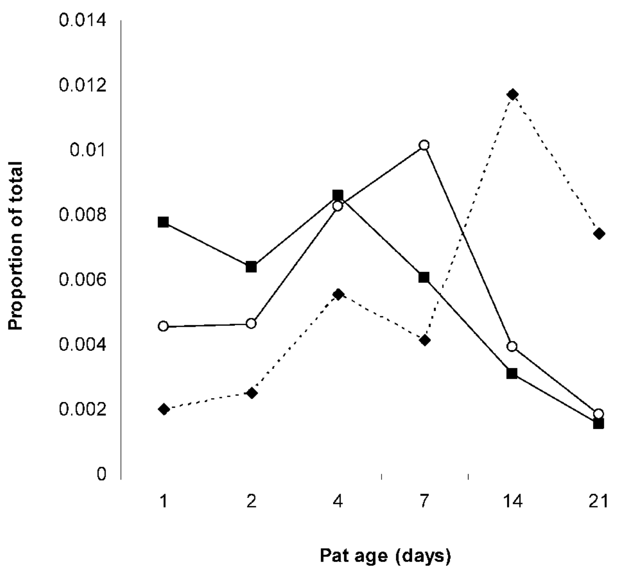

Figure 3. The proportion of the total number of adult Coleoptera (solid squares, solid line), adult Diptera (open circles, solid line), and larval Coleoptera (diamonds, dashed line) insects collected from pats of different ages.

Table I. The number of individuals in various taxa from recovered artificial cow pats placed out in the field in 2002. The successional mean occurrence (SMO) mean age (days) of the pat when individuals in each taxon were present, is used to classify taxa into three distinct successional groups.

	Number	SMO
Group I		
Aphodius luridus	10	1.2
Aphodius equestris	55	2.1
Aphodius rufipes	521	2.4
Aphodius prodromus	59	2.4
Musca autumnalis	229	2.6
Sphaeridium scarabaeoides	132	2.7
Aphodius rufus	97	2.9
Anthomyiidae	111	3.1
Aphodius sphacelatus	12	3.6
Mydaea urbana	21	3.8
Morellia simplex	144	4.1
Scathophaga stercoraria	9,564	4.4
Aphodius haemorrhoidalis	146	4.5
Aphodius erraticus	89	4.5
Myospila meditabunda	547	4.7
Neomyia species	2,990	4.6
Sphaeroceridae	180	4.6
Sphaeridium lunatum	477	5.0
Cercyon haemorrhoidalis	318	5.1
Haematobia stimulans	31	5.2
Sphaeridium bipustulatum	76	5.3
Sepsis species	11,512	6.2
Aphodius ater	28	6.7
Cercyon quisquilus	20	6.8
Cercyon melanocephalus	288	7.0
Group II		
Fannia species	200	8.0
Phaoniinae	1,198	8.1
Cercyon terminatus	51	8.2
Mesembrina meridiana	71	8.2
Cercyon atomarius	494	8.6
Hymenoptera	184	8.7
Oxytelinae (larvae)	115	8.9
Cercyon lateralis	619	9.0
Cercyon pygmaeus	34	9.0
Cryptopleurum minutum	141	9.9
Staphylinidae (other than *Philonthus* species)	140	10.0
Hydrotaea species	407	10.4
Philonthus species (adults)	247	10.7
Chloromyia formosa	2,418	11.0
Cercyon lugubris	69	11.2
Chironomidae	2,531	11.4
Microchrysa flavicornis	130	11.9
Group III		
Aphodius fossor	59	13.3
Sylvicola punctata	7,605	14.3
Aphodius fimetarius	286	14.5
Sargus species	8	14.8
Aphodius species (larvae)	913	16.0
Sciaridae	509	16.1
Philonthus species (larvae)	95	16.6
Rhiphidia maculata	34	18.3

days, following which numbers declined gradually as the pat aged. Group II species were present only in low numbers during the first 2 days following deposition, increased rapidly to peak in pats aged between 8 and 11 days and returned to very low numbers by the time the pats had reached 21 days old. Insects belonging to group III were much less numerous overall; they occurred mostly in the oldest pats (14 and 21 days old), with very few being recovered from pats aged less than 14 days.

Discussion

The ecology of the invertebrate dung community has received particular attention in recent years. This focus has been associated with the widespread use of anthelmintics, particularly macrocyclic lactones (Floate et al. 2005). These are broad-spectrum drugs which are toxic at low doses to a wide variety of organisms, including many nematode, mite, and insect species. They have been available since the early 1980s and are widely used in animal husbandry to control a range of ectoparasites and endoparasites. Macrocyclic lactones are degraded slowly and several of these compounds, particularly the avermectins, have been shown to pass through cattle largely unmodified following administration both orally and through injection, ending up in their faeces over several days following administration (Sommer et al. 1992). This exposes the larvae and adults of many insects of both pest and non-pest species to avermectin residues.

The presence of avermectins in faeces has been seen as beneficial, because several important pest flies could potentially be controlled using these pesticides (Strong and Brown 1987). However, a range of studies have shown that the decomposition of cow pats containing ivermectin may be retarded and that this is linked to the absence of dung-degrading insects (particularly beetles) in the faeces of treated animals (Wall and Strong 1987; Madsen et al. 1990, Sommer et al. 1992; Strong and Wall 1994; Floate 1998; Floate et al. 2005). This has led to a variety of studies into the specific effects of pesticide residues on non-pest dung species. Both lethal and non-lethal effects have been studied in several species including the yellow dung fly, *S. stercoraria* (Strong and James 1992, 1993), *N. cornicina* (Gover and Strong 1995a, 1995b), *Onthophagus taurus* Schreber (Wardhaugh et al. 2001), *Euoniticellus intermedius* (Lumaret et al. 1993), and *Onitis alexis* (Krüger and Scholtz 1997). Concern has been expressed over the long-term impacts of the use of these chemicals on the dung insect community and its environment together with the potential secondary effects on agriculture, such as increased pasture fouling, caused by reduced dung degradation.

However, most previous studies are restricted either to single species/pesticide combinations or the general effects of a compound on dung pat colonization and decomposition. The result of anthelmintic application on the structure of the dung invertebrate community and its precise functional consequences have not been studied in detail, perhaps partly because the structure of the healthy dung community is highly variable and still little understood. It has been suggested (Herd et al. 1993) that future work should focus on the main functional groups of the dung community in order to gain a more thorough understanding of the implications of continued pesticide use, but a better understanding of the nature of such functional groups and their importance within the community is needed before this can happen.

To contribute to such an understanding, the present study has considered the general seasonal patterns and shorter-term changes in colonizer succession with pat age in south west England. Although an important component of the dung invertebrate community in the later stages of pat decomposition (Holter 1977, 1979), interestingly no earthworms were recovered from the artificially constructed pats and earthworm abundance was therefore not considered in the present study.

The occurrence of almost all taxa were well spread throughout the summer with relatively gradual seasonal changes in the insect taxa present over the course of the summer observed. However, Diptera were generally significantly more abundant later in the summer and, in many cases, showed more distinct peaks in abundance than most of the Coleoptera, which for the most part were present consistently throughout June, July, and August. It is generally unclear why this should be the case, although it is possible that very early spring peaks, particularly for some Diptera such as *S. stercoraria*, may have been missed as, in that year, the study could not be started before 21 May due to the outbreak of foot and mouth disease in the UK. Many of the Diptera also undergo several generations in a season and this may result in a gradual build-up in numbers resulting in later peaks than the larger dung beetles, which often have only one or two generations in a year (Hanski and Koskela 1977; Hanski 1980; Holter 1982; Otronen and Hanski 1983).

Clear patterns in colonization were also observed as pats aged and three relatively distinct clusters of insect colonizers were identified with significantly different mean successional occurrences. These groups agree broadly with the microseral stages identified by Mohr (1943). The greatest number of species and individuals were found during the early and middle stages of succession, in dung aged between 4 and 7 days. By this time, a substantial crust has often formed and this may prevent further invasion. It is also notable that at around the end of the first week, the bacteria on which several of the insects feed reach their peak numbers (Barth et al. 1994). In general, specialist coprophages were found earlier in the succession and remained for shorter periods of time than the more generalist saprophagous species and predators.

The Coleoptera in the first group of colonizers consisted of the majority of *Aphodius* species, all three *Sphaeridium* species, and the small hydrophilid species, *Cercyon haemorrhoidalis* and last in this group, *Cercyon quisquilus* and *Cercyon melanocephalus*. *Sphaeridium scarabaeoides* appeared to colonize much earlier than the slightly larger *S. lunatum* and the much smaller species, *S. bipustulatum*, a pattern supported in other studies (Mohr 1943; Hanski 1980; Otronen and Hanski 1983; Gittings and Giller 1998). It is possible that this difference represents a mechanism facilitating the coexistence of these three otherwise very similar, potentially competing species (Otronen and Hanski 1983). Of the remaining hydrophilid species encountered (all of which are small coprophagous beetles), all occurred later than the larger *Sphaeridium* species and were placed into successional group II, with peak numbers generally found in pats between days 7 and 11. The order of occurrence of *Cercyon* species shown here is consistent with previous results (Hanski 1980).

The first wave of colonizing Diptera included the Muscidae, Anthomyiidae, Sepsidae, and *S. stercoraria*, and their numbers generally remained high in pats up to 7 days old, while numbers of Coleoptera declined more steeply.

The third successional stage to be observed was marked by the appearance of the coprophagous larvae of the *Aphodius* beetles and the predatory *Philonthus* larvae. The *Philonthus* larvae are large, mobile predators, which, like the adults, may not be restricted to the dung pat and it is unclear how important the pat is as a part of their niche space (Hanski and Koskela 1977). *Aphodius* larvae, on the other hand, are large, slow-moving coprophages, restricted to the dung pat and the soil below for the whole of their development, which may last until the pat has completely disintegrated. Perhaps surprisingly, they often did not appear until several days after the adults of many species had left the pat. There are several possible explanations for this delay. Firstly, as the larvae could not be identified to species level, it is possible that all of the larvae encountered belonged to the species with late-successional adults, *A. fimetarius* and *A. fossor*, that were still present in the pat when the larvae appeared, although this seems unlikely. *Aphodius* species employ two different strategies when laying their eggs. Early successional species oviposit in the soil underneath or around the pat, while later species generally oviposit directly into the dung (Gittings and Giller 1998; Menéndez and Gutiérrez 1999). In soil-ovipositing species, larvae would not have been detected until they had hatched out and migrated into the pat. Since *A. rufipes* eggs are known to take 5 days to hatch (Holter 1979) this could be well after the adults have emigrated. In several dung-ovipositing species it has been shown previously that mature females remain in the pat significantly longer than males and immature females (Hanski 1980; Hirschberger 1998) and it is therefore possible that even in these species oviposition occurs after most adult beetles have left the pat. It has been suggested that competition might become important to *Aphodius* larvae in older pats (Holter 1979, 1982; Gittings and Giller 1998; Hirschberger 1998).

In conclusion, the insect community present in the artificially constructed cow pats, particularly amongst the Coleoptera, changed relatively gradually and predictably over time during the summer months and over the 2 years of the study. While more marked changes in colonization did occur in response to the age of the pat, again this pattern was consistent between pats present at different times of the spring/summer season. The number and order of species arrival observed here broadly match previous studies undertaken in similar north temperate European habitats (e.g. Holter 1977; Finn et al 1998, 1999; Hutton and Giller 2003), supporting the conclusion that robust regional patterns in succession exist.

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