

Aggregation in insect communities colonizing cattle-dung

R. Wall* and C.M. Lee

School of Biological Sciences, University of Bristol, Woodland Road,
Bristol, BS8 1UG, UK

Abstract

Ruminant dung is a highly ephemeral, patchily distributed resource, which is used by a diverse community of invertebrate species. In such environments, high levels of insect aggregation may be important in facilitating stability and coexistence across patchily distributed populations. The aim of the present work was to quantify the aggregation of the insects colonising cow-dung in cattle pasture in southwest England and to test the hypothesis that the dung-pat community assemblage observed was the result of stochastic colonization. This was examined using batches of ten standardised, 1.5 kg, artificial cow pats placed out in cattle pastures in each of 24 weeks between May and October in 2001. Pats were left exposed in the field for seven days before being brought back to the laboratory, where any insect colonizers were collected and identified. Individual pats contained, on average, only half the number of insect taxa present in an entire batch put out at any one time. All larval coleopteran taxa, 20 of the 22 adult coleopteran taxa and 22 of the 23 dipteran taxa, showed significant aggregation, with the abundance of most taxa within pats approximating a negative binomial distribution. A simulation analysis was used to show that the observed relative frequency of taxa within pats did not differ from that expected by chance if colonisation is a random binomial event in which each species colonises a pat independently of all other species. Aggregated populations, of even highly abundant insects, may be more susceptible to the deleterious effects of insecticidal contaminants in dung than if they were evenly distributed, if by chance they colonize a pat containing insecticidal residues from a recently treated animal.

Keywords: aggregation, Coleoptera, competition, cow dung, Diptera, dung-decomposition

(Accepted 19 September 2009)

Introduction

Amongst the most significant factors shaping an insect community are the spatial distribution and temporal stability of the habitat it occupies (Southwood, 1977). The occurrence of a habitat in ephemeral patches affects the dynamics of a community by preventing the complete mixing of individuals between patches (Sevenster, 1996),

which often results in uneven, or aggregated, distributions of individuals. Suitable resource patches may be sparsely distributed and the dispersal movements of individual inhabitants become important in shaping the community structure; the probability of colonisation may be determined by the dispersal and search ability of a species (Karieva, 1986). Where patches are frequent and close together, dispersal ability may be less important in shaping community structure.

In addition to dispersal, the probability of initial colonisation may be determined by factors such as the weather and habitat characteristics (Valiela, 1974); and, as a result, there may be pronounced stochastic variation in the

*Author for correspondence
Fax: 0 44 0117 3317 985
E-mail: richard.wall@bristol.ac.uk

mixture of species that find a given patch (Levin, 1974). Following colonisation, the subsequent species composition may depend more on survival, competitive ability and predation within the community, all of which may become increasingly important as time progresses (Beaver, 1977). Levels of predation and competition may be high and act as further mechanisms contributing coexistence and maintenance of high numbers of species (Hanski, 1981; Ives, 1991; Sevenster, 1996; Hartley & Shorrocks, 2002). As a result, the biological communities associated with patchy, ephemeral habitats are characterised by a large number of species, often with high dispersal ability, allowing colonisation of new habitat patches as they appear (Beaver, 1977; Chesson, 1986). Colonising species typically begin to inhabit a suitable habitat patch almost immediately. A strong succession of colonisation then often occurs, with specialised fauna arriving at new resource patches and giving way to more generalist species as the resource becomes incorporated into the surrounding environment (Hanski, 1987; Menendez & Gutierrez, 1999). Larger systems of patches may show relatively higher levels of community stability, emphasising the importance of scale in ecological studies (Hanski, 1987). Successional change in habitat patches alters their suitability to new colonisers so that, as new patches arise, old ones become hostile and development within a patch may become time-limited (Southwood, 1977).

Herbivore dung is a good example of such an ephemeral habitat, used by a large and diverse array of organisms. It is often highly abundant and can be relatively predictable in its occurrence compared with other patchily distributed resources, such as carrion, particularly where a large population of dung-producing vertebrates is present. Many insects, particularly among the Coleoptera and Diptera, exploit this valuable resource by feeding on dung throughout their larval stages (Strong, 1992). Understanding the assembly and structure of dung-colonizing invertebrate communities is important because the invertebrates that contribute to dung decomposition are vulnerable to a range of agricultural practices, especially the treatment of livestock with insecticides and anthelmintics (Floate, 1998; Floate *et al.*, 2005; Bang *et al.*, 2007). Following administration, these compounds may be metabolised only slowly in the body and pass largely unmodified into the faeces (Sommer, *et al.*, 1992; Strong & Wall, 1994; Floate, 1998). This exposes the larvae and adults of many dung-colonising insects to toxic residues (Sherratt *et al.*, 1998). Reductions in insect abundance are likely to be qualitative and ecological effects are likely to be subtle; hence, a precise understanding of the forces that structure the insect community in dung is required if the effects of insecticide residues are to be assessed or predicted.

The aim of the present work, therefore, was to examine the distribution of the insects colonising cattle dung, to uncover patterns within and between taxa in the degree of aggregation and to use these data to consider mechanisms by which such aggregated assemblages may be produced.

Materials and methods

Artificial, 1.5 kg cow pats, created from fresh dairy-cattle dung, were used to study populations of dung insects. Ten fresh pats were placed out each week in an area of permanent cattle pasture, with 24 batches placed out between the 21st May and 29th October 2001. Batches of pats were placed in a linear array, with at least 1 m between each pat.

Pats were left exposed for seven days, following which they were retrieved and returned to the laboratory where colonizing insects were collected and identified. More complete details of the methods used and a species list with seasonal abundance patterns are given in Lee & Wall (2006).

Aggregation analysis

Aggregation analysis was undertaken for all species or taxa identified and quantified as the index of dispersion (I_D), calculated as the variance multiplied by the number of pats minus one, divided by the mean number of individuals per pat (Southwood, 1977). To explore the nature of any aggregation in more detail, further analysis was then undertaken for the larvae of six taxa of dung colonizing Diptera: *Sepsis* spp., *Chloromyia formosa* (Scopoli), *Mesembrina meridiana* Linnaeus, *Hydrotaea* spp., *Scatophaga stercoraria* (Linnaeus) and *Musca autumnalis* DeGeer; and four taxa of Coleoptera: two genera of larvae (*Aphodius* spp. and *Sphaeridium* spp.) and two species of adult beetle, *Aphodius fimetarius* (Linnaeus) and *Cercyon lateralis* (Marsham). These taxa were selected on the basis of their significance in the dung colonizing community and the fact that they represented a range of availability and abundance characteristics (Lee & Wall, 2006). For these ten taxa, normal, Poisson, logarithmic and negative exponential models were fitted to the frequency distribution of the number of each taxon per pat by maximum likelihood estimation (Statgraphics, Centurion XV, Herndon, Virginia). Chi-square analysis was used to compare the observed and expected best-fit frequency distributions. Where a negative-binomial distribution was fitted and considered to give a good fit to the data, the coefficient of aggregation, k , was also determined. This is an inverse measure of the degree of 'clumping' of the population within patches. Low levels of k indicate a high degree of aggregation.

Modelling the distribution of taxa

Using all the invertebrate taxa identified from the pats, simulations were performed (Excel, Poptools, Microsoft), based on the assumption that colonization is a random binomial event in which each species colonises a pat independently of all other species. For this, for each taxon the probability of colonization, P , is given by the proportion of pats that were seen to be colonised by that taxon in any one week. Monte Carlo simulations were then carried out, in which a randomised binomial outcome with probability P is generated in over 1000 iterations for each of the taxa recorded. The simulation gives an estimate of the frequency distribution of taxa that would be expected in each batch of ten pats, in each week examined, if colonisation occurs at random and independently of other taxa. The simulation was repeated for weeks one, ten and 20, to give a representation of the range of relative abundances seen over the summer field season. The predictions were then pooled and compared to the observed numbers of taxa identified in these three weeks; the observed and expected numbers were compared by χ^2 analysis.

Results

In total, 145,454 insects were collected from the 240 artificial cow pats, with a median of 333 (188–795)

Table 1. The total number of each of ten selected taxa collected from artificial cow pats placed out in cattle pasture in southwest England between May and November 2001 and the index of dispersion (I_D). Also, the best fit model which describes the frequency distribution of the numbers of this taxon per pat, the negative binomial index of aggregation, k , and the output values of chi-squared analysis resulting from the statistical comparison of the observed distribution against the distribution fitted.

	Total	I_D	Distribution fitted	k	χ^2	d.o.f.	P
Diptera							
<i>Sepsis</i> spp.	15,586	17,461	Negative binomial	0.15	88.9	80	0.23
<i>Chloromyia formosa</i>	4721	1628	Negative binomial	0.13	32.8	40	0.78
<i>Mesembrina meridiana</i>	189	269	Poisson		4.87	3	0.18
<i>Hydrotaea</i> spp.,	671	11,594	Negative binomial	0.28	17.4	14	0.22
<i>Scathophaga stercoraria</i>	1280	24,559	Negative binomial	0.11	27.5	20	0.12
<i>Musca autumnalis</i>	1297	6374	Negative binomial	0.06	10.7	12	0.56
Coleoptera							
<i>Cercyon lateralis</i>	230	3372	Negative binomial	0.2	46.1	27	<0.01
<i>Aphodius fimetarius</i>	140	805	Negative binomial	0.18	16.8	5	<0.01
<i>Aphodius</i> (larvae)	120	1929	Negative binomial	0.09	10.2	5	0.07
<i>Sphaeridium</i> (larvae)	170	1318	Negative binomial	0.29	26.0	18	0.1

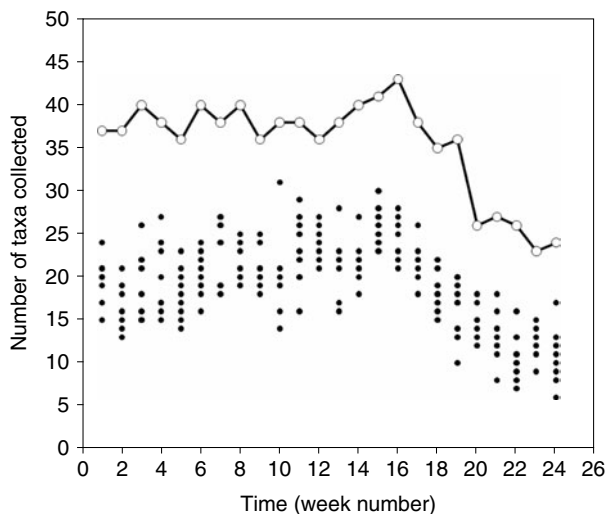


Fig. 1. The total number of taxa recorded from each batch of ten artificial cow pats (○) and the number of taxa recorded from each individual artificial cow pat (●) placed out in cattle pastures between May and November 2001. Weeks are numbered throughout the season beginning on May 1st (week one).

individuals per pat in 52 different taxa. The number of taxa present in each batch of ten pats varied as the season progressed (fig. 1). Batches placed out during the early summer consistently contained 35–40 taxa, rising to a peak of 43 in pats placed out in week 15 (3rd September) and then falling sharply towards the end of the study (fig. 1). The last five batches, placed out during October, contained the fewest taxa (no more than 27 in all cases). However, individual pats contained on average only half the taxa present in the entire batch, although the overall pattern closely followed that measured in total (fig. 1). The lowest number of taxa in a single pat was 6, (week 24) and the greatest number was 31 (week 12). Negligible numbers of earthworms were found in any of the pats.

Aggregation analysis

Twenty-two of the 23 dipteran taxa showed significantly aggregated distributions between pats, the one exception being *M. meridiana*, the distribution of which was not significantly different from a Poisson model (table 1). Although present throughout the study, *M. meridiana* only occurred in low abundance within individual pats (fig. 2). For the other dipteran taxa subjected to detailed analysis, the frequency distribution of individuals between pats was not significantly different from a negative binomial model (fig. 2).

All of the four larval coleopteran taxa and twenty of the 22 adult coleopteran taxa were significantly aggregated. The distributions of the remaining two taxa, the scarabaeid dung beetles *O. coenobita* and *A. fimetarius*, were not significantly different from random, as indicated by the index of dispersion. Of the four taxa selected for more detailed analysis, the distributions of the two genera of coleopteran larvae were not significantly different from a negative binomial model (table 1, fig 3). In contrast, the distributions of the two species of adult beetle, *A. fimetarius* and *C. lateralis*, were significantly more over-dispersed than expected from the negative binomial (fig. 3); but the latter distribution was nevertheless a closer description of these data than a Poisson model, both frequency distributions giving low values for the fitted coefficient of aggregation, k (table 1).

Modelling the distribution of taxa

Given the observation that the distribution of most taxa between pats can be adequately modelled by a negative binomial distribution, a Monte Carlo simulation was undertaken based on the assumption that colonization is a random binomial event in which each species colonises a pat independently of all other species, the probability of which, P , can be estimated from the proportion of pats seen to be colonised by each taxon in any one week. This analysis shows that if insects colonised pats at random, independently of the presence of other taxa, the observed frequency distribution of taxa should follow an approximately normal distribution (fig. 4). The frequency distribution of observed taxa in weeks one, ten and 20 was similar in shape (fig. 4) and was not significantly different from that expected by

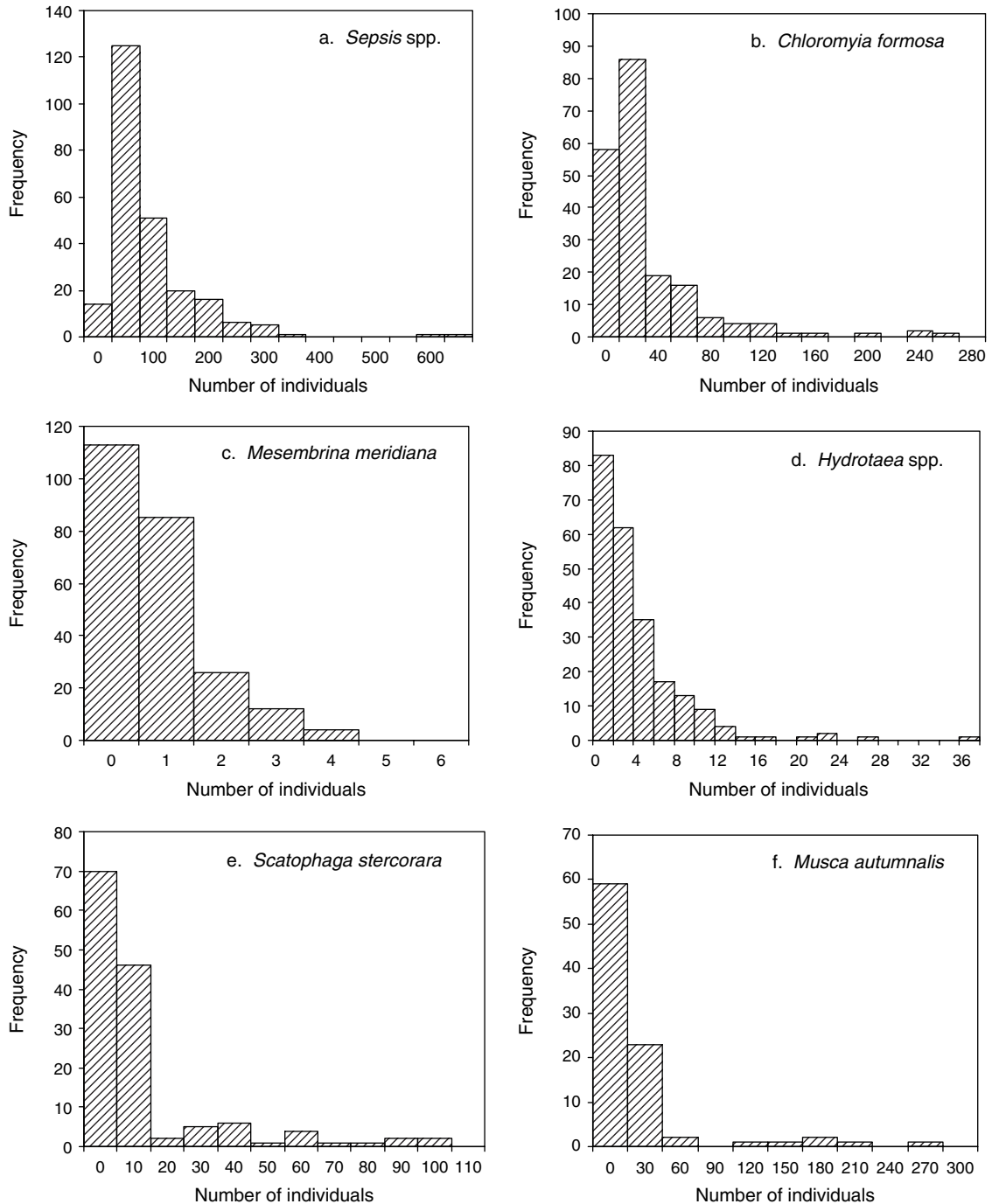


Fig. 2. The frequency distributions of numbers per pat, of six species or genera of dung-breeding Diptera collected from artificial cow pats placed out in cattle pastures between May and November 2001. a, *Sepsis* spp.; b, *Chloromyia formosa*; c, *Mesembrina meridiana*; d, *Hydrotaea* spp.; e, *Scatophaga stercoraria*; f, *Musca autumnalis*.

chance (Kolmogorov-Smirnov, two-tailed test, $K-S=1.26$, $P=0.09$).

Discussion

In a resource-limited, patchy environment, unless insects develop strategies for avoidance, high levels of competition

and predation might be expected to lead to exclusion and low levels of diversity. However, stability and coexistence may be facilitated by aggregation, particularly where colonisers are small relative to resource patches and cannot monopolise a single patch (Atkinson & Shorrocks, 1984; Shorrocks, *et al.*, 1984; Hanski & Cambefort, 1991; Ives, 1991; Heard & Remer, 1997; Woodcock *et al.*, 2002). Contagious

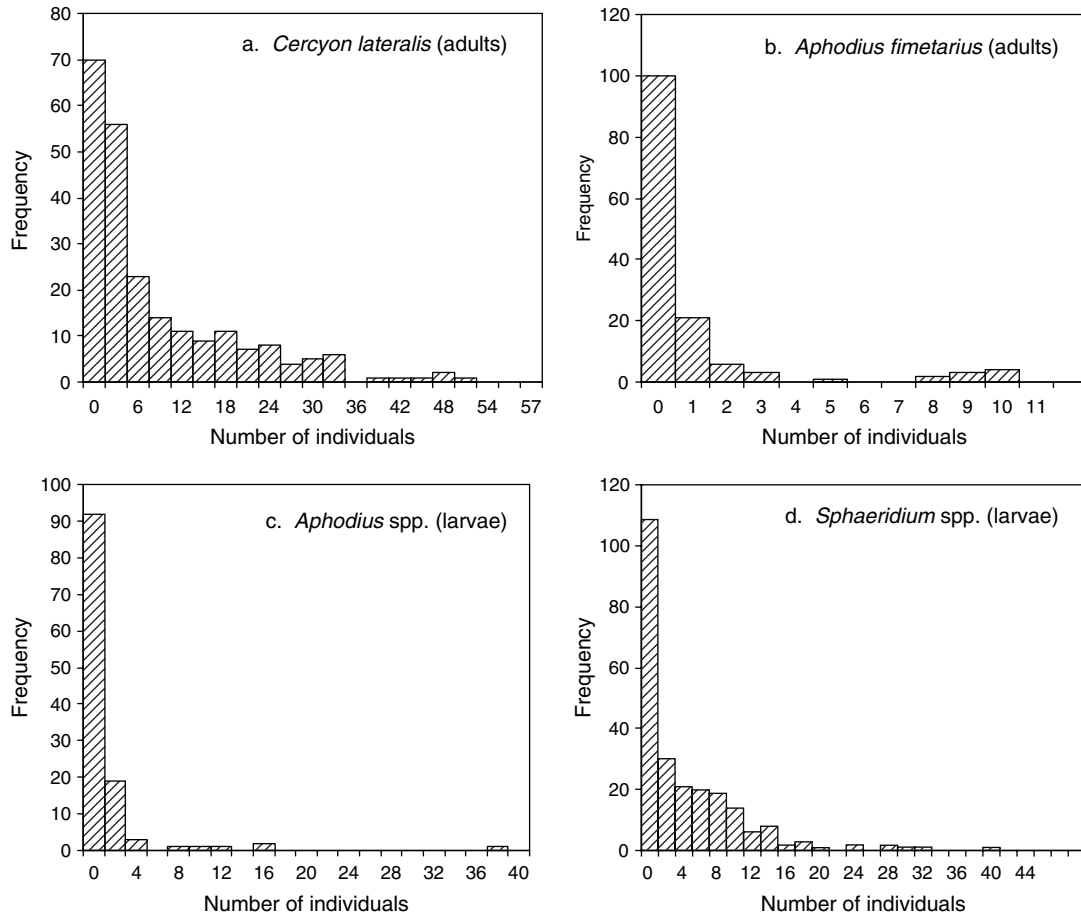


Fig. 3. The frequency distributions of numbers per pat, of four species or genera of dung-breeding Coleoptera collected from artificial cow pats placed out in cattle pastures between May and November 2001. A, adults of *Cercyon lateralis*; b, adults of *Aphodius fimetarius*; c, larvae of *Aphodius* spp.; d, larvae of *Sphaeridium* spp.

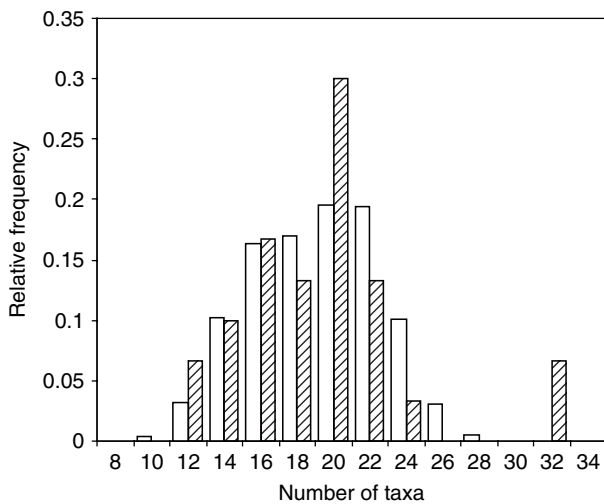


Fig. 4. The relative frequency of taxa observed in groups of ten artificial cow pats (hatched bars) placed out in cattle pastures in weeks one, ten and 20 between May and November 2001 and the relative frequency expected in the same weeks from a random binomial colonisation model (open bars).

distributions have been identified in the insects colonising a range of patchy environments, such as fruit (Atkinson & Shorrocks, 1984; Rosewell *et al.*, 1990), mushrooms (Heard, 1998) and carrion (Beaver, 1977; Ives, 1991).

In the present study, the dung-colonising community identified was characterised by a wide diversity of species that varied as the season progressed, as has been observed in previous studies (Hammer, 1941; Mohr, 1943; Laurence, 1954; Valiela, 1974). The total number of taxa present per batch was greater than 35 for much of the study period, rising to a peak of 43 during early September following which it declined sharply through the autumn to the end of the study. Other studies have found that species richness among dung beetles in southern Ireland was highest during the early summer. Finn *et al.* (1999) and Hanski (1980) observed the maximum species diversity of *Aphodius* species during May and June in Oxfordshire. However, notably here, individual pats contained only approximately half the number of taxa present in the entire batch. The majority of dipteran and coleopteran taxa showed significant aggregation which appeared broadly binomial in distribution; and, based on this observation, a Monte Carlo simulation, which generated an expected distribution frequency if colonization occurred at random, was not different from that observed.

This result supports the proposal that colonization and assembly of the dung-inhabiting community observed is a stochastic event.

In a study of Diptera breeding in fallen fruit, Atkinson & Shorrocks (1984) found that the distributions of only two out of 34 species examined were not significantly aggregated. One of these two species was a muscid belonging to the Phaoniinae. The authors suggested that the lack of contagion in this species may be due to cannibalism, or a mechanism to prevent it, since the larvae of Phaoniinae are generally predacious. Notably, of the Diptera considered here, *M. meridiana* is considered predatory and was the one taxon that was not significantly aggregated.

Since most insect larvae cannot disperse from the dung, their distribution between pats would be expected to be strongly determined by the levels of mortality within the pat and the oviposition behaviour of adults (Beaver, 1977). Females of most insects deposit their eggs in clutches, and clutch size is a fundamental aspect of the life-history of both the adult female and offspring (Godfray & Parker, 1992; Withers *et al.*, 1997). Different habitat patch types influence the range of strategies that are successful according to the average patch quality and the distance between individual patches (Beaver, 1977; Hanski, 1987; Withers, *et al.*, 1997; Thiel & Hoffmeister, 2004). Accordingly, species breeding in rarer, less predictable but high quality habitat patches should typically deposit their eggs in large clutches, while smaller clutch sizes are expected where patches are more frequent and predictable or of lower quality (Godfray *et al.*, 1991; Heard, 1998). Adult mortality is also an important factor, as it will influence the average number of patches that are encountered in a female's lifetime (Skinner, 1985; Withers *et al.*, 1997).

Several carrion-breeding blowflies of the genera *Lucilia* and *Calliphora* produce clutches of between 200 or more eggs (Ives, 1991; Wall, 1993), resulting in high levels of aggregation and considerable risk of exceeding the carrying-capacity of a carcass, often leading to severe competition (Holter, 1979; Ives, 1991). Most dung-breeding Diptera oviposit in much smaller clutches than carrion-breeding species, rarely exceeding 70 eggs and often considerably fewer (Wall *et al.*, 2008). Dung is a more predictable and abundant resource than carrion, and so dung-breeding species can expect to encounter a greater number of available oviposition sites in their lifetime. The abundance of predatory flies, such as *S. stercoraria*, around fresh cow pats may also influence the clutch size of other dung-breeding Diptera, since an increased risk of predation during oviposition favours reduced clutch sizes (Skinner, 1985). However, such comparisons must be treated with caution because of the variety of other ecological variables that differ between the two groups, many of which may contribute to differences in clutch size (Godfray *et al.*, 1991).

Other causes of aggregation may also exist. For example, Hammer (1941) found that *H. irritans* adults aggregate on certain cows, so that their visits to individual pats may also be non-random and Blanckenhorn *et al.* (1999) showed that *S. stercoraria* adults were regularly distributed between pats, while *Sepsis cynipsea* were not. Hence, there may be a wide variety of additional factors, associated with mating behaviour, predation, or the density-dependent distribution of clutches, which determine the degree of aggregation observed and the resultant community structure. Little is known about whether patch sampling is employed by some

colonizing species to assess local insect abundance prior to oviposition, or whether patch density (as opposed to pat abundance *sensu stricto*) will influence aggregation.

Overall, the results of this study demonstrate the aggregation of individuals within resource patches and the stochastic colonization and assemblage of the dung-inhabiting community. In terms of practical implications, the highly aggregated distributions highlight the possibility that the populations of even highly abundant insects will be more susceptible to the deleterious effects of insecticidal residues in dung than if they were evenly distributed, if by chance they colonize a pat containing chemical residues from a recently treated animal.

Acknowledgements

We would like to thank Mr John Keedwell for permission to use his farm, the University of Bristol for financial support to CL and Dr Eric Morgan for statistical advice.

References

- Atkinson, W.D. & Shorrocks, B. (1984) Aggregation of larval Diptera of discrete and ephemeral breeding sites: the implications for coexistence. *American Naturalist* **124**, 336–351.
- Bang, H.S., Lee, J.H., Na, Y.E. & Wall, R. (2007) Reproduction of the dung beetle *Copris tripartitus* in the dung of cattle treated topically with high cis-cypermethrin and chlorpyrifos. *Applied Soil Ecology* **35**, 546–552.
- Beaver, R.A. (1977) Non-equilibrium 'island' communities: Diptera breeding in dead snails. *Journal of Animal Ecology* **46**, 783–798.
- Blanckenhorn, W.U., Morf, C. & Reuter, M. (1999) Are dung flies ideal-free distributed at their oviposition and mating site? *Behaviour* **137**, 233–248.
- Chesson, P.L. (1986) Environmental variation and the coexistence of species. pp. 240–256 in Diamond, J. & Case, E.J. (Eds) *Community Ecology*. New York, USA, Harper and Row.
- Finn, J.A., Gittings, T. & Giller, P.S. (1999) Spatial and temporal variation in species composition of dung beetle assemblages in southern Ireland. *Ecological Entomology* **24**, 24–36.
- Floate, K.D. (1998) Off-target effects of ivermectin on insects and on dung degradation in southern Alberta, Canada. *Bulletin of Entomological Research* **88**, 25–35.
- Floate, K.D., Wardhaugh, K.G., Boxall, A.B.A. & Sherratt, T.N. (2005) Faecal residues of veterinary pharmaceuticals: non-target effects in the pasture environment. *Annual Review of Entomology* **50**, 153–179.
- Godfray, H.C.J. & Parker, G.A. (1992) Sibling competition, parent-offspring conflict and clutch size. *Animal Behaviour* **43**, 473–490.
- Godfray, H.C.J., Partridge, L. & Harvey, P.H. (1991) Clutch size. *Annual Review of Ecology and Systematics* **22**, 409–429.
- Hammer, O. (1941) Biological and ecological investigations on flies associated with pasturing cattle and their excrement. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* **105**, 141–393.
- Hanski, I. (1980) Spatial variation on the turning of the seasonal occurrence in coprophagous beetles. *Oikos* **34**, 311–321
- Hanski, I. (1981) Coexistence of competitors in patchy environment with and without predation. *Oikos* **37**, 306–312.

- Hanski, I. (1987) Colonization of ephemeral habitats. pp. 155–185 in Gray, A.J., Crawley, M.J. & Edwards, P.J. (Eds) *Colonization, Succession and Stability*. Oxford, UK, Blackwell.
- Hanski, I. & Cambefort, Y. (1991) *Dung Beetle Ecology*. Princeton, New Jersey, USA, Princeton University Press.
- Hartley, S. & Shorrocks, B. (2002) A general framework for the aggregation model of coexistence. *Journal of Animal Ecology* **71**, 651–662.
- Heard, S.B. (1998) Resource patch density and larval aggregation in mushroom breeding flies. *Oikos* **81**, 187–195.
- Heard, S.B. & Remer L.C. (1997) Clutch-size behaviour and coexistence in ephemeral-patch competition models. *The American Naturalist* **150**, 744–770.
- Holter, P. (1979) Abundance and reproductive strategy of the dung beetle *Aphodius rufipes*. *Ecological Entomology* **4**, 317–326.
- Ives, A.R. (1991) Aggregation and coexistence in a carrion fly community. *Ecological Monographs* **61**, 75–94.
- Karieva, P. (1986) Patchiness, dispersal, and species interactions: consequences for communities of herbivorous insects. pp. 192–206 in Diamond, J. & Case, E.J. (Eds) *Community Ecology*. New York, USA, Harper and Row.
- Laurence, B.R. (1954) The larval inhabitants of cow pats. *Journal of Animal Ecology* **23**, 234–260.
- Lee, C.M. & Wall, R. (2006) Distribution and abundance of insects colonizing cattle dung. *Journal of Natural History* **40**, 1167–1177.
- Levin, S.A. (1974) Dispersion and population interaction. *American Naturalist* **108**, 207–228.
- Menendez, R. & Gutierrez, D. (1999) Heterotrophic succession within dung-inhabiting beetle communities in northern Spain. *Acta Oecologia* **20**, 527–535.
- Mohr, C.O. (1943) Cattle droppings as ecological units. *Ecological Monographs* **13**, 275–298.
- Ridsdill-Smith, T.J. (1988) Survival and reproduction of *Musca vetustissima* Walker (Diptera: Muscidae) and a scarabaeine dung beetle in dung of cattle treated with Avermectin B1. *Journal of the Australian Entomological Society* **27**, 175–178.
- Rosewell, J., Shorrocks, B. & Edwards, K. (1990) Competition on a divided and ephemeral resource – testing the assumptions.1. Aggregation. *Journal of Animal Ecology* **59**, 977–1001.
- Sevenster, J.G. (1996) Aggregation and coexistence. I. Theory and analysis. *Journal of Animal Ecology* **65**, 297–307.
- Sherratt, T.N., Macdougall, A.D., Wratten, S.D. & Forbes, A.B. (1998) Models to assist the evaluation of the impact of avermectins on dung insect populations. *Ecological Modelling* **110**, 165–173.
- Shorrocks, B., Rosewell, J., Edwards, K. & Atkinson, W. (1984) Interspecific competition is not a major organizing force in many insect communities. *Nature* **310**, 310–312.
- Skinner, S.W. (1985) Clutch size as an optimal foraging problem for insects. *Behavioural Ecology and Sociobiology* **17**, 231–238.
- Sommer, C., Steffansen, B., Overgaard Nielsen, B., Gronvold, J., Vagn Jensen, K.-M., Brochner Jespersen, J., Springborg, J. & Nansen, P. (1992) Ivermectin excreted in cattle dung after subcutaneous injection or pour-on treatment: concentrations and impact on dung fauna. *Bulletin of Entomological Research* **82**, 257–264.
- Southwood, T.R.E. (1977) Habitat, the template for ecological strategies? *Journal of Animal Ecology* **46**, 337–365.
- Strong, L. (1992) Avermectins: a review of their impact on insects of cattle dung. *Bulletin of Entomological Research* **82**, 256–274.
- Strong, L. & Wall, R. (1994) Effects of ivermectin and moxidectin on the insects of cattle dung. *Bulletin of Entomological Research* **84**, 403–409.
- Thiel, A. & Hoffmeister, T.S. (2004) Knowing your habitat: linking patch encounter rate and patch exploitation in parasitoids. *Behavioral Ecology* **15**, 419–425.
- Valiela, I. (1974) Competition, food webs and population limitation in dung arthropod communities during invasion and succession. *American Midland Naturalist* **92**, 370–385.
- Wall, R. (1993) The reproductive output of the blowfly *Lucilia sericata*. *Journal of Insect Physiology* **39**, 743–750.
- Wall, R., Anderson, E. & Lee, C.L. (2008) Seasonal abundance and reproductive output of the dungflies, *Neomyia cornicina* and *N. viridescens*. *Bulletin of Entomological Research* **98**, 397–403.
- Withers, T.M., Madie, C. & Harris, M.O. (1997) The influence of clutch size on survival and reproductive potential of hessian fly. *Entomologia Experimentalis et Applicata* **83**, 205–212.
- Woodcock, B.A., Watt, A.D. & Leather, S.R. (2002) Aggregation, habitat quality and coexistence: a case study on carrion fly communities in slug cadavers. *Journal of Animal Ecology* **71**, 131–140.