Title	Variability in north temperate dung beetle assemblages at different spatial and temporal scales
Author(s)	Finn, John A.
Publication date	1998
Original citation	Finn, J. A. 1998. Variability in north temperate dung beetle assemblages at different spatial and temporal scales. PhD Thesis, University College Cork.
Type of publication	Doctoral thesis
Link to publisher's version	http://library.ucc.ie/record=b1284362~S0 Access to the full text of the published version may require a subscription.
Rights	**© 1998, John A. Finn** http://creativecommons.org/licenses/by-nc-nd/3.0/
Embargo information	No embargo required
Item downloaded from	http://hdl.handle.net/10468/1624

Variability in north temperate dung beetle assemblages at different spatial and temporal scales

by John A. Finn

Thesis submitted to the National University of Ireland in
candidature for the degree of Doctor of Philosophy

Department of Zoology and Animal Ecology,
National University Ireland, Cork.

Supervisor: Professor Paul S. Giller
Head of Department: Professor Máire Mulcahy

July 1998

Contents

Abstract

This study examined the spatial and temporal variability of dung beetle assemblages across a variety of scales e.g. from the between-pad scale (examining the effects of dung size and type) to larger spatial scales encompassing southern Ireland.

Dung beetle assemblage structure as sampled by dung pad cohort samples and dung-baited pitfall trapping were compared. Generally, the rank order of abundance of dung beetle species was significantly correlated between pitfall catches and cohort pad samples. Across different dung sizes, in both pitfall catches and cohort pad samples, the relative abundance of species was frequently significantly different, but the rank order of abundance of dung beetle species was usually significantly correlated. Considerable variations in pitfall catches at temporal scales of a few days appeared to be closely related to weather conditions and rotational grazing. However, despite considerable variation in absolute abundances between consecutive days of sampling, assemblage structure typically remained very similar.

The relationship between dung pad size and dung beetle colonisation was investigated. In field experiments in which pads of different sizes (0.25 L, 0.5 L, 1.0 L and 1.5 L) were artificially deposited, there was a positive relationship between pad size and both biomass and number of beetles colonising dung pads and pitfall traps. In addition, with one exception, the field experiments indicated a general positive relationship between dung pad size and biomass density (dung beetle biomass per unit dung volume). A laboratory experiment indicated that pat residence times of *A. rufipes* were significantly correlated with dung pad size. Investigation of naturally-deposited cow dung pads in the field also indicated that both larval numbers and densities were significantly correlated with dung pad size. These results were discussed in the context of theory related to aggregation and coexistence of species, and resource utilisation by organisms in ephemeral, patchy resources.

The colonisation by dung beetles of dung types from native herbivores (sheep, horse and cow) was investigated in field experiments. There were significant differences between the dung types in the chemical parameters measured, and there were significant differences in abundances of dung beetles colonising the dung types. Sheep dung was typically the preferred dung type. Data from these field experiments, and from published literature, indicated that dung beetle species can display dung type preferences, in terms of comparisons of both absolute and relative abundances. In addition, data from laboratory experiments indicated that both *Aphodius* larval production and pat residence times tended to be higher in those dung types which were preferred by adult *Aphodius* in the colonisation experiments.

Data from dung-baited pitfall trapping (from this and another study) at several sites (up to 180 km distant) and over a number of years (between 1991 and 1996) were used to investigate spatial and temporal variation in dung beetle assemblage structure and composition (*Aphodius, Sphaeridium* and *Geotrupes*) across a range of scales in southern Ireland. Species richness levels, species composition and rank order of abundances were very similar between the assemblages. The temporal variability between seasons within any year exceeded temporal variability between years. DCA ordinations indicated that there was a similar level of variability between assemblage structure from the between-field (~1 km) to regional (~180 km) spatial scales, and between year (6 years) temporal scales. At the biogeographical spatial scale, analysis of data from the literature indicated that there was considerable variability at this scale, largely due to species turnover.

Introduction

Introduction

Dung pads from large herbivores are examples of ephemeral, spatially delimited, patchily distributed resources and thus provide an experimental system with relative ease of replication and manipulation of samples. In addition, the discrete nature of dung facilitates extraction of the dung fauna without the arbitrariness in spatio-temporal extent of the sample which is often associated with other ecological sampling. Dung pads generally support large populations of invertebrates, as well as a considerable number of species and taxonomic groups. The majority of these invertebrates are beetles, particularly the Scarabaeidae, Hydrophilidae, Staphylinidae and Histeridae, and flies such as the Muscidae, Calliphoridae and Sarcophagidae (Hanski, 1991a, b).

The subfamily Scarabaeinae are more diverse and abundant in lower latitudes and are considered to be the true dung beetles, consisting of a number of functional groups based on different modes of sequestering dung (Doube, 1990). Scarabaeine dung beetles are notorious for their ability to completely remove large amounts of dung in short periods of time, giving rise to intense competitive interactions (Doube, Giller and Moola, 1988; Hanski and Cambefort, 1991ab)

In north temperate regions, assemblages of coprophagous beetles are dominated by *Aphodius* species (family Scarabaeidae) (Hanski, 1991b). However, the dung beetle community in northern Europe also regularly consists of a few species of *Geotrupes* (family Geotrupidae) in addition to *Sphaeridium* and *Cercyon* species (family Hydrophilidae). Unless otherwise indicated, I shall restrict further discussion to studies from north temperate coprophagous communities.

There are over 1000 *Aphodius* species found globally, and around 130 species in Europe (Balthasar, 1963), although only a fraction of this number are found at any one site. *Aphodius* species are typically endocoprid (the larvae living and feeding within the pad) and the adults are relatively small, the elytral length generally being less than 15 mm in length (over 40 mg dry weight). With the aid of highly developed antennae, they fly in search of suitable dung. Adults feed on the liquid content of dung, and, depending on the species, lay either single or clutches of eggs in the pad or at the pad/soil interface. Upon hatching, the larvae undergo three larval stages and a metamorphic pupal stage from which an adult emerges.

Geotrupes beetles are much larger than *Aphodius* species (around 300 mg dry weight). They are paracoprid (the larvae develop in brood masses of dung buried underneath the dung pad) and can bury substantial proportions of single pads. They are usually of relatively low abundance. *Sphaeridium* and *Cercyon* species are members of the largely aquatic Hydrophilidae which have become secondarily adapted to the dung environment. *Cercyon* species are no more than a few millimetres in length and because of their small contribution to biomass are not considered any further in this study, although they can occur in large abundances in dung samples. *Sphaeridium* species are approximately 8 mm in length (around 12 mg dry weight) and can occur in considerable abundances in pads. The adults are coprophagous, whereas the larvae are carnivorous within the pad.

Doube (1987) notes that most studies of dung beetle communities have been descriptive in nature and would fall into one of three categories. The first includes studies of species composition and successional processes for guilds. The second involves studies of the seasonal and habitat associations and behaviour of species from guilds, to which one could add studies on dung preference. The third category would include studies of the feeding and reproductive biology of coprophages. To these, I would add a fourth category which includes studies dealing with other ecological patterns/processes such as competition, aggregation, and predator/prey interactions. The following subsections provide a brief overview of the main themes in these four categories.

Studies of species composition and successional processes

Dung pads are considered to change rapidly in physical and chemical quality over time, and there have been a large number of studies documenting the successional changes in the corresponding composition of adult dung beetles over time (Mohr, 1943; Rainio, 1966; Kessler and Balsbaugh, 1972; Valiela, 1974; Wingo *et al.*, 1974; Hanski and Koskela, 1977; Koskela and Hanski, 1977; Denholm-Young, 1978, Hanski, 1980b; Holter, 1982; Desière, 1987; Yasuda, 1987a; Horgan, 1989; Gittings, 1994; Hirschberger and Bauer, 1994).

Seasonal and habitat associations of north temperate dung beetle communities.

Many studies have investigated seasonal patterns of occurrence (White, 1960; Rainio, 1966; Breymeyer, 1974; Wingo *et al.*, 1974; Hanski, 1980 a, d; Holter, 1982; Desière, 1983; De Graef and Desière, 1984; Yasuda, 1984; Yoshida and Katakura, 1985; Hirschberger and Bauer, 1994; Sowig and Wassmer, 1994; Palmer, 1995; Gittings and Giller, 1997). Generally, particular species tend to display consistent phenological patterns between studies, although Hanski (1980 c, d) has investigated between-field variation in species phenology. Studies on diel flight activity have also been published (Landin, 1967; Landin, 1968; Koskela, 1979). Studies on macrohabitat preferences (e.g. between pastures and forests) indicate that most *Aphodius* species can occur in different habitat types, but even amongst these species, preferences for one macrohabitat type over another do exist (Landin, 1961; Hanski and Koskela, 1977, 1979; Koskela and Hanski, 1977). Microhabitat preferences have been documented (Denholm-Young, 1978; Chisholm, 1978) and investigations on spatial distribution of dung beetles within dung pats have been caried out (Finnè and Desière, 1971; Holter, 1982; Desière, 1983). For example, Holter (1982) demonstrated that adult *Aphodius* species can show within-pad spatial preferences, in terms of whether they preferred the top, bottom or periperal regions of a pad. Desière (1983) found that at the scale of the dung pad, dung beetle species displayed preferences in occurrence between the pad and the underlying soil. However, data in Desière (1983) may have been confounded by the separation of the pad and underlying soil not occurring until after the samples had been transported to the laboratory.

Several studies have also looked at colonisation of, and preferences for, various dung types (Landin, 1961; Rainio, 1966; Kessler *et al.*, 1974; Breymeyer and Zachariev-Stoilova, 1975; Desière and Thome, 1977; Hanski and Kuusela, 1983; Heijerman, 1990) and in addition, Gittings and Giller (1998) have related chemical parameters of dung with colonisation preferences and species reproductive performance in different dung types. Colonisation and preferences for dung pads of different sizes have also been demonstrated (Landin, 1961; Olechowicz, 1974; Chisholm, 1978; Denholm-Young, 1978).

Studies of feeding and reproductive biology

Studies have investigated the role of diet in nutrition (Madle, 1934; Charpentier, 1968; Holter, 1974, 1975, 1977) and the subject has been reviewed by Hanski (1987). Other studies have detailed kleptoparasitism (Klemperer, 1980), and the effect of dung quality on reproduction (Gittings, 1994).

Other patterns and processes

Attempts to explain the high species richness of the coprophagous community in patches have contributed to developments in aggregation theory, and studies have examined the spatial cooccurrence of *Aphodius* species between pads (Chisholm, 1978; Holter, 1982; Hanski, 1986; Hirschberger, 1996). Such theories depend on the presence of competition, evidence of which has been relatively limited in *Aphodius* dung beetles. However, Landin (1961) demonstrated that at high densities of adults and larvae, interference competition for space can occur, and Chisholm (1978) investigated intra- and interspecific effects of different dung beetle densities on immigration and emigration rates. Holter (1982) demonstrated that an assemblage of adult *Aphodius* species utilised only a very small fraction (less than 1%) of the total energy in the dung pad, yet density-dependent oviposition has been demonstrated (Holter, 1979; Yasuda, 1987b, 1990). Recently, Hirschberger (1996) has demonstrated competition between the dung fly *Scatophaga stercoraria* and *A. ater*, as well as density-dependent intraspecific competition between larvae of *A. ater*.

Questions addressed in the present work

Until recently, dung beetle assemblages in Ireland have received very little attention (but see Gittings, 1994; Gittings *et al.*, 1994; Gittings and Giller, 1997, 1998). However, these and other studies of north temperate dung beetles have indicated relevant areas of research in which data is required, and I have attempted to direct my studies towards some of these areas. To date, many studies have been descriptive in nature and have lacked an experimental perspective to test directly certain hypotheses suggested by the observational data (but see above). Thus, few studies conclusively identify the role of natural variability in dung pads and associated factors in affecting assemblage dynamics. Examples of such variability may include changes in short-term weather conditions, movement of cattle herds, differences in dung pad size, between-pad differences in dung quality (within one dung type) and availability of different dung types. I have conducted a combination of field experiments to investigate in more detail the influence on dung beetle assemblages of dung pad type and size as sources of natural variability.

Gittings (1994) used pitfall trapping to intensively sample from two locations in southern Ireland. One of the locations had seven different sites, and trapping was conducted for three years (Gittings and Giller, 1997). I have analysed combined data from my own pitfall trapping and that from Gittings (1994), to examine and compare assemblages from five different locations in southern Ireland (Chapter 2). Data were available for more than one year at some of the sites, and this allowed for both temporal and spatial comparisons of assemblages. In an appendix to Chapter 2, more detailed information on individual species phenologies' and tibial wear is presented, along with assemblage characteristics and weather data. Gittings (1994) drew attention to the limitations of, and problems associated with, pitfall trapping, in comparison with cohort pad sampling. In Chapter 1, I present analyses of data from field experiments which compare the trapping efficiency of dung pad cohorts and dung-baited pitfall trapping, as well as data on the effects of short term weather fluctuations and cattle movements on dung beetle flight activity as measured by pitfall captures.

Comparing studies in the literature, there is a large variation in the dung sizes employed in various experiments, with only scant knowledge of the effects of differences in dung pad size on coprophage ecology (Landin, 1961; Olechowicz, 1974; Denholm-Young, 1978; Chisholm, 1978). In addition, variability in patch size is a potentially important dimension to patch theory which has been largely ignored (but see Sevenster, 1996; Sevenster and van Alphen, 1996). Chapter 3 reports on an assessment of variability in dung pad size in the field as well as field experiments conducted to investigate patterns of colonisation and development by dung beetle assemblages in relation to dung pad sizes.

Gittings (1994) stated that 'little is known about what aspects of dung quality affect dung beetle's ability to utilise the resource'. This is despite the changes in the availability and quality of the dung resource that has occurred across much of Europe as the intensification of agriculture dominated more of the landscape, and the suspected role of this agricultural intensification in extinctions of European dung beetle species (Väisänen and Rassi, 1990; Biström *et al.*, 1991; Hanski, 1991b). In addition, Lumaret *et al.* (1992) have shown distinct changes in a dung beetle assemblage when the available dung resource changed from that of sheep dung to cow dung. Gittings and Giller (1998) used CCA ordinations to relate chemical parameters of dung with colonisation preferences, which in turn were related to species reproductive performance in different dung types (Gittings, 1994). Dung types used in that study were largely derived from exotic herbivores from a nearby wildlife park. Chapter 4 describes how I employed dung from large mammalian herbivores traditionally found in most areas in northern Europe (cow, sheep and horse) to relate dung quality parameters and colonisation of the dung beetle species. I also compare colonisation by dung beetle species of cow dung of different quality, derived from cattle fed on different diets.

The role of scale in affecting the interpretation of observed patterns and processes is being increasingly recognised in many disciplines of ecology (Levin 1992; Giller and Doube; 1994; Nisbet *et al.*, 1997). The nature of the ecology of dung fauna makes it suitable to investigate the influence of scale on various community parameters in dung beetle assemblages. Chapter 5 presents a synthesis of some of the results from this study, which examines varibility in north temperate European dung beetle assemblage structure across a range of spatio-temporal scales, from the effects of weather at the between-day temporal scale, to the species turnover observed at biogeographical spatial scales.

Finally, some of the implications of the results of this study are discussed in a concluding chapter, focussing on how variability in pad size and dung quality may affect species coexistence, as well as on the importance of a consideration of sampling and scale in ecological investigations of coprophagous dung beetle assemblages.

References

Balthasar, V. (1963) Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region. Verlag der Tschekoslowakischen Akademie der Wissenschaften, Prag, 655 pages.

Biström, O., Silfverberg, H. and Rutanen, I. (1991) Abundance and distribution of coprophilous Histrini (Histeridae), *Onthophagus* and *Aphodius* (Scarabaeidae) in Finland (Coleoptera). *Entomologica Fennica*, **2**, 53-66.

Breymeyer, A. (1974) Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). XI. The role of coprophagous beetles (Coleoptera, Scarabaeidae) in the utilisation of sheep dung. *Ekologia Polska* **22**, 617-634.

Breymeyer, A. and Zacharieva-Stoilova, B. (1975) Scarabaeidae in two mountain pastures in Poland and Bulgaria. *Bulletin de l'Académie Polonaise des Sciences (Serie des sciences biologiques)*, **23**, 173-180.

Chisholm, M.D. (1978) Some Aspects of Competition Between Insects Inhabiting Cow dung. Unpublished PhD thesis, University of Bristol.

De Graef, F. and Desière, M. (1984) Écologie des coléoptères coprophiles en prairie permanente pâturée. *Bulletin de la Société Royale des Sciences de Liège*, **53**, 158-172.

Desière, M. (1983) Écologie des coléoptères coprophiles en prairie permanente pâturée. I. Caractéristiques des populations de coléoptères adultes coprophiles. Phénologie et dynamique saisonniére. *Bulletin d'Écologie*, **14**, 99-117.

Desière, M. (1987) Écologie des coléoptères coprophiles en prairie permanente pâturée. II. Les brigades de coléoptères adultes coprophiles. *Bulletin d'Écologie,* **18**, 13-21.

Desière, M. and Thome, J.P. (1977) Variations qualitatives et quantitatives de quelques populations de coléoptères coprophiles associés aux excréments de 3 types d'herbivores. *Revue d'Écologie et de Biologie du Sol,* **14**, 583-591.

Denholm-Young, P. (1978) Studies of Decomposing Cattle Dung and its Associated Fauna. Unpublished DPhil thesis, University of Oxford.

Doube, B. (1987) Spatial and temporal organization in communities associated with dung pads and carcasses. *Organisation of communities: past and present.* (ed. by J.H.R. Gee and P.S. Giller), pp 255-280. Oxford: Blackwell Scientific Publications.

Doube, B.M., Giller, P.S. and Moola, F. (1988) Dung burial strategies in some South African coprine and onitine dung beetles (Scarabaeidae, Scarabaeinae). *Ecological Entomology*, **13**, 251-261.

Doube, B.M. (1990) A functional classification for analysis of the structure of dung beetle assemblages. *Ecological Entomology,* **15**, 371-383.

Finné, D. and Desière, M. (1971) Étude synécologique des bouses de Bovidés. I. - Évolution estivale de la biomasse des Coléoptères en fonction du vieillissement des bouses. *Revue d'Écologie et de Biologie du Sol,* **8**, 409-417.

Gittings, T. (1994) The community ecology of *Aphodius* dung beetles. Unpublished PhD thesis, National University of Ireland.

Gittings, T., Giller, P.S. and Stakelum, G. (1994) Dung decomposition in contrasting temperate pastures in relation to dung beetle and earthworm activity. *Pedobiologia,* **38**, 455-474.

Gittings, T. and Giller, P.S. (1997) Life history traits and resource utilisation in an assemblage of north temperate *Aphodius* dung beetles (Coleoptera: Scarabaeidae). *Ecography*, **20**, 55-66.

Gittings, T. and Giller, P.S. (1998) Resource quality and the colonisation and succession of coprophagous dung beetles. *Ecography* (in press).

Giller, P.S. and Doube, B.M. (1994) Spatial and temporal co-occurrence of competitors in Southern African dung beetle communities. *Journal of Animal Ecology,* **63**, 629-643.

Hanski, I. (1980a) The community of coprophagous beetles (Coleoptera, Scarabaeidae and Hydrophilidae) in northern Europe. *Annales Entomologici Fennici,* **6**, 57-73.

Hanski, I. (1980b) Patterns of beetle succession in droppings. *Annales Zoologici Fennici,* **17**, 17-25.

Hanski, I. (1980c) Spatial patterns and movements in coprophagous dung beetles. *Oikos,* **34**, 293-310.

Hanski, I. (1980d) Spatial variation in the timing of the seasonal occurrence in coprophagous dung beetles. *Oikos,* **34**, 311-321.

Hanski, I. (1986) Individual behaviour, population dynamics and community structure of *Aphodius* (Scarabaeidae) in Europe. *Acta Œcologica, Œcologia Generalis,* **7**, 171-187.

Hanski, I. (1987) Nutritional ecology of dung- and carrion-feeding insects. Nutritional Ecology of Insects, Mites, and Spiders (ed. by F. Slansky, Jr. and J.G. Rodriguez), pp. 837-884, Wiley, New York.

Hanski, I. (1991a) The dung insect community. Dung Beetle Ecology (ed. by I. Hanski and Y. Cambefort), pp. 5-21, Princeton University Press.

Hanski, I. (1991b) North temperate dung beetles. Dung Beetle Ecology (ed. by I. Hanski and Y. Cambefort), pp. 75-96, Princeton University Press.

Hanski, I. and Koskela, H. (1977) Niche relations among dung-inhabiting beetles. *Oecologia (Berlin),* **28**, 203-231.

Hanski, I. and Koskela, H. (1979) Resource partitioning in six guilds of dung-inhabiting beetles (Coleoptera). *Annales Entomologici Fennici,* **45**, 1-12.

Hanski, I. and Kuusela, S. (1983) Dung beetle communities in the Åland archipelago. *Acta Entomologica Fennica,* **42**, 36-42.

Hanski, I. and Cambefort, Y. (1991a) Resource partitioning. Dung Beetle Ecology (ed. by I. Hanski and Y. Cambefort), pp. 330-349, Princeton University Press.

Hanski, I. and Cambefort, Y. (1991b) Species richness. Dung Beetle Ecology (ed. by I. Hanski and Y. Cambefort), pp. 350-371, Princeton University Press.

Heijerman, T. (1990) Seasonal changes in the relative abundance of some dung beetles in the faeces of the wild boar and mufflon (Coleoptera, Scarabaeoidea). *Entomologische Berichten (Amsterdam)*, **50**, 81-86.

Hirschberger, P. (1996) Spatial distribution and resource utilisation in the dung beetle *Aphodius ater*. PhD dissertation. University of Kiel.

Hirschberger, P. and Bauer, T. (1994) The coprophagous insect fauna in sheep dung and its influence on dung disappearance. *Pedobiologia*, **38**, 375-384.

Holter, P. (1974) Food utilization of dung-eating *Aphodius* larvae (Scarabaeidae). *Oikos*, **25**, 71-79.

Holter, P. (1975) Energy budget of a natural population of *Aphodius rufipes* larvae (Scarabaeidae). *Oikos*, **26**, 177-186.

Holter, P. (1977) An experiment on dung removal by *Aphodius* larvae (Scarabaeidae) and earthworms. *Oikos*, **28**, 130-136.

Holter, P. (1979) Abundance and reproductive strategy of the dung beetle *Aphodius rufipes* (L.) (Scarabaeidae). *Ecological Entomology*, **4**, 317-326.

Holter, P. (1982) Resource utilisation and local coexistence in a guild of scarabaeid dung beetles (*Aphodius* spp.). *Oikos*, **39**, 213-227.

Horgan, F.G. (1989) Dung beetle (Scarabaeoidae, Hydrophilidae, Coleoptera) assemblages at Fota Island Wildlife Park, Republic of Ireland. Unpublished BSc thesis, Department of Zoology, University College Cork.

Kessler, H. and Balsbaugh Jr., E.U. (1972) Succession of adult Coleoptera in bovine manure in East Central South Dakota. *Annals of the Entomological Society of America*, **65**, 1333-1336.

Kessler, H., Balsbaugh Jr., E.U. and McDaniel, B. (1974) Faunistic comparison of adult Coleoptera recovered from cattle and sheep manure in east-central South Dakota. *Entomological News*, **85**, 67-71.

Klemperer, H.G. (1980) Kleptoparasitism behaviour of *Aphodius rufipes* (L.) larvae in nests of *Geotrupes spiniger* Marsh. (Coleoptera, Scarabaeidae). *Ecological Entomology*, **5**, 143-151.

Koskela, H. (1979) Patterns of diel flight activity in dung-inhabiting beetles: an ecological analysis. *Oikos*, **33**, 419-439.

Koskela, H. and Hanski, I. (1977) Structure and succession in a beetle community inhabiting cow dung. *Annales Zoologici Fennici*, **14**, 204-223.

Landin, B.-O. (1961) Ecological studies on dung beetles. *Opuscula Entomologica (Supplementum)*, **19**, 1-228.

Landin, B.-O. (1968) The diel flight activity of dung-beetles (Coleoptera Scarabaeidae). *Opuscula Entomologica (Supplementum)*, **32**, 1-172.

Landin, J.P. (1967) On the relationship between the microclimate in cow droppings and some species of *Sphaeridium* (Col. Hydrophilidae). *Opuscula Entomologica*, **33**, 207-213.

Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **63**, 1943-1967.

Lumaret, J.P., Kadiri, N. and Bertrand, M. (1992) Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology*, **29**, 349-356.

Madle, H. (1934) Zur Kenntnis der Morphologie, Okologie und Physiologie von *Aphodius rufipes* Lin. und einigen verwandten Arten. *Zoologische Jahrbucher Abteilung für Anatomie und Ontogenie der Tiere*, **58**, 303-396

Mohr, C.O. (1943) Cattle droppings as ecological units. *Ecological Monographs*, **13**, 275-309.

Nisbet, R.M., Diehl, S., Wilson, W.G., Cooper, S.D., Donalson, D.D. and Kratz, K. (1997) Primary productivity gradients and short-term population dynamics in open systems. *Ecological Monographs*, (in press).

Olechowicz, E. (1974) Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). X. Sheep dung and the fauna colonizing it. *Ekologia Polska*, **22**, 589-616.

Palmer, M. (1995) Testing for seasonal displacement in a dung beetle guild. *Ecography*, **18**, 173-177.

Raino, M. (1966) Abundance and phenology of some coprophagous beetles in different kinds of dung. *Annales Zoologici Fennici*, **3**, 88-98.

Sevenster, J.G. (1996) Aggregation and coexistence. I. Theory and analysis. *Journal of Animal Ecology*, **65**, 297-307.

Sevenster, J.G .and van Alphen, J.J.M. (1996) Aggregation and Coexistence. II. A neotropical *Drosophila* community. *Journal of Animal Ecology*, **65**, 308 - 324.

Sowig, P. and Wassmer, T. (1994) Resource partitioning in coprophagous beetles from sheep dung: Phenology and microhabitat preferences. *Zool. Jb. Syst.* **121**, 171-192.

Väissänen, R. and Rassi, P. (1990) Abundance and distribution of *Geotrupes spiniger* in Finland (Coleoptera, Scarabaeidae). *Entomologica Fennica*, **1**, 107-111.

Valiela, I. (1974) Composition, food webs and population limitation in dung arthropod communities during invasion and succession. *The American Midland Naturalist*, **92**, 370-385.

White, E. (1960) The natural history of some species of *Aphodius* (Col., Scarabaeidae) in the northern Pennines. *Entomologists' Monthly Magazine*, **96**, 25-30.

Wingo, C.W., Thomas, G.D., Clark, G.N. and Morgan, C.E. (1974) Succession and abundance of insects in pasture manure: relationship to face fly survival. *Annals of the Entomological Society of America*, **67**, 386-390.

Yasuda, H. (1984) [Seasonal changes in the number and species of scarabaeid dung beetles in the middle part of Japan]. *Japanese Journal of Applied Entomology and Zoology*, **28**, 217-222. (In Japanese).

Yasuda, H. (1987a) Differences in temporal utilization patterns of dung pats among three scarabaeid dung beetles. *Researches on Population Ecology*, **29**, 167-177.

Yasuda, H. (1987b) Reproductive properties of two sympatric dung beetles, *Aphodius haroldianus* and *A. elegans* (Coleoptera: Scarabaeidae). *Researches on Population Ecology*, **29**, 179-187.

Yasuda, H. (1990) Effect of population density on reproduction of two sympatric dung beetle species, *Aphodius haroldianus* and *A. elegans* (Coleoptera: Scarabaeidae). *Researches on Population Ecology*, **32**, 99-111.

Yoshida, N. and Katakura, H. (1985) Life-cycles of *Aphodius* dung beetles (Scarabaeidae, Coleoptera) in Sapporo, northern Japan. *Environmental Science Hokkaido*, **68**, 1-7.

Chapter 1

An Investigation of some Factors Affecting the Sampling of Dung Beetle Assemblages

Chapter 1

An Investigation of some Factors Affecting the Sampling of Dung Beetle Assemblages

Abstract

1. The description of dung beetle assemblage structure was compared between dung pad cohort samples and dung-baited pitfall trap samples. Data from different dung types and sizes were employed.

2. The rank order of abundance of dung beetle species was usually significantly correlated between pitfall catches and cohort pad samples. The relative abundance of *Sphaeridium* was typically significantly lower in pitfall catches than in pad samples.

3. Although the relative abundance of species was frequently significantly different across different dung sizes, the rank order of abundance of dung beetle species was usually significantly correlated between different dung sizes, in both pitfall catches and cohort pad samples.

4. Variations in pitfall catches appeared to be closely related to weather conditions and rotational grazing at temporal scales of a few days.

5. Dung-baited pitfall trapping would appear to be an unreliable method for providing detailed descriptions of absolute and relative abundance of species. Pitfall trapping is probably most reliable for use in investigations of species richness and community composition, seasonal patterns of occurrence and the rank order of species.

Introduction

A variety of methods have been employed to sample dung beetles, including dung-baited pitfall trapping (Hanski, 1980ab; Lumaret and Kirk, 1987; Heijerman, 1990; Lumaret *et al.*, 1992; Gittings, 1994), cohort pad sampling (Hanski and Koskela, 1977; Holter, 1982; Desière, 1983; Yasuda, 1984; Gittings, 1994; Hirschberger and Bauer, 1994), baited suction sampling (Koskela, 1979) and quadrat pad sampling (White, 1960), as well as other non-quantitative methods such as light trapping (Koskela, 1979).

Of these methods, dung-baited pitfall trapping and cohort pad sampling are the most widely used. Dung-baited pitfall trapping allows quantitative data on dung beetle flight activity to be collected, and provides a pooled catch over a sampling period of known duration. The method samples over a successional range which is related to the ageing of the bait, and samples may be retrieved and processed relatively quickly. However, pitfall trap baits may not age in precisely the same manner as dung pads, the possibility of emigration (an important process in actual dung pads) is excluded and pitfall data is therefore not very useful for obtaining data on density values of beetles per pad.

Cohort pad sampling typically involves the use of replicated, standardised dung pads, a proportion of which are sampled at a number of known intervals after deposition. The method is relatively time-consuming; a range of successional ages must be sampled as on any day of sampling only those beetles present in the pad are sampled, and one must extract beetles from the pads. In successional studies, cohort pad sampling is susceptible to problems due to double-counting, which will occur when pat residence times of species are greater than the duration between sampling occasions (and see below). However, the use of cohort pad samples allows sampling of beetles that only colonise and remain in the pad, incorporating the effects of interactions and the balance between immigration and emigration. Cohort pad sampling also allows the determination of actual density values of beetles in pads.

Gittings (1994) made the point that, with the exception of Doube and Giller (1990), 'little consideration has been given to the adequacy of pitfall trapping in describing and comparing dung beetle assemblages.' Gittings (1994) provides one of the few investigations of the efficiency of dung baited pitfall trapping in northern European dung beetles and this present study explores the problem further. To have confidence in descriptions of assemblage structure, two important caveats should be considered (Gittings, 1994); is the method equally effective at sampling all relevant species and is there a reasonably constant relationship between captures and the population being sampled?

In pitfall trapping, the use of a dung bait which attracts insects may largely exclude those problems associated with the passive sampling otherwise involved in pitfall trapping (e.g. Topping and Sunderland, 1992), provided all species are equally attracted. Interspecific differences in behaviour within arthropod groups have been shown to affect the efficiency of pitfall traps (Halsall and Wratten, 1988) and it is possible that interspecific differences may affect the efficiency of pitfall trapping of dung beetles. For example, in comparisons of captures from pitfall traps and cohort pad samples, Gittings (1994) demonstrated that *Sphaeridium* spp were consistently found with lower relative abundances in the former, which was possibly due to a behavioural difference. Dung beetle flight activity has previously been shown to be affected by rainfall and temperature, and a model presented in Gittings (1994) also suggests that dung beetle flight activity may be affected by successional parameters and dung pad availability. In addition, the literature reveals that there have been a wide variety of dung sizes employed between studies (cf. Holter, 1982; Peck and Forsyth, 1982; Kohlman and Sanchez Colon, 1984; Peck and Howden, 1984; Gittings, 1994; Hirschberger, 1994; see Chapter 3).

The model of Gittings (1994) indicated that beetle captures in both pitfall traps and cohort pad samples would be inversely related to the number of available dung pads. A field example of the situation where the number of dung pads changes over time occurs in the case of rotational grazing, which involves cattle being rotated through a series of pastures over a period of up to 20-30 days. Therefore, in any one pasture of the rotational grazing regime, fresh dung will be available for only a few days each month and it may be that beetle populations, and early successional ones in particular, will follow cattle movements through the rotation. Thus, this will cause short term variability in abundances (from pitfall traps or cohort pad samples) in any one field, despite there not necessarily being any change in the actual population size of the beetles. Here, I present data from an experiment investigating the effect of rotational grazing (and, thus, changing dung availability) on pitfall captures.

I am not aware of any study which compares sampling efficiency across a range of dung sizes, and data from field experiments (Chapter 3) were used to assess how the use of different dung sizes in both pitfall and cohort pad sampling affects assemblage structure. Field experiments were also used to provide further data (particularly on *Sphaeridium* spp.) that suggested that dung beetle flight activity is affected by rainfall and temperature, as well as being affected by dung pad availability in a rotational

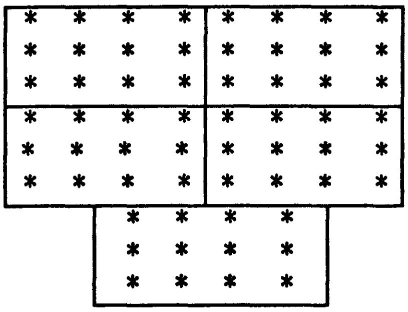


Fig. 1. Example of the stratified randomised design used in the field experiments. There were five blocks and each block consisted of a grid of replicate standardised dung pads and pitfall trap baits (both represented by asterisks) of the various dung types/sizes, with each row of dung pads/pitfall traps a similar interval (5m) apart.

grazing regime. The objectives of the present study were, therefore, to compare dung beetle assemblage structure as sampled by cohort pad sampling and dung baited pitfall trapping. The influence of dung size on sampling dung beetles was investigated through comparisons of dung beetle assemblage structure across different dung sizes, using both cohort pad samples and pitfall trapping. In addition, pitfall trapping was used to explore the effects on dung beetle captures of short-term variability in weather conditions, and rotational grazing.

Methods

Comparison of pitfall trap and dung pad samples from dung of different types and sizes.

Field experiments investigating patterns of dung beetle colonisation on dung of different types and sizes were used to provide data for comparisons between pitfall trap and cohort pad sampling. The underlying design of these experiments consisted of replicate standardised dung pads and pitfall trap baits of the various dung types/sizes, placed in a grid of replicate randomised blocks (n = 5) with each row and each dung pad/pitfall trap a similar interval (5m) apart. There were five blocks, each with a single pitfall trap baited with each dung type/size and a number of dung pads of each dung type/size. The pitfall trap design was based on that of Tyndale-Biscoe *et al.* (1981); for further details see Gittings (1994). Baits consisted of dung of a known size wrapped in one thickness of muslin. 5% chloral hydrate was used as a preservative in the pitfall traps. Pitfall traps were baited at the start of the experiment with the same dung (and sizes) used to form pads. Dung types used in experimetns C1-C3 were cow, horse and sheep dung, and two types of horse dung were used in experiment C1. Experiments S1-S3 used cow dung. When the contents of the pitfall traps were collected, the baits were not changed; thus, these pitfall traps provide a measure of dung beetle immigration to aging dung of different types or sizes ("findability"). Experiments C1-C3 employed pads of one litre (L) volume and diameter 16 cm. Pad sizes in experiments S1-S3 were composed of 0.25, 0.5, 1.0 or 1.5 L of fresh homogenised dung and deposited in plastic formers of 8, 12, 16 and 22 cm diameter, respectively. On each sampling day, one pitfall trap dung pad of each type/size was emptied and one dung pad of each type/size and the underlying soil were sampled from each block. Dung pad samples were immediately transported to the laboratory and stored at 4 °C before using Tullgren funnels to extract beetles from both the dung pat sample and underlying soil. Deposition and collection of the pads and pitfall trap contents were conducted between 09.00 and 13.30. Field experiments were carried out at Fota, County Cork, in southern Ireland.

Comparisons of the species composition of the pitfall captures and the cohort pad samples were conducted after pooling the captures of each species across the sampling days. The rank order of abundance of species was compared between the sum totals of the pitfall and pad data using Spearman's rank correlation analysis. χ^2 analysis was used to compare the relative abundance of the component species of both the *Aphodius* and *Sphaeridium* taxocenes, as well as to compare the relative abundance of the total number of *Aphodius* and *Sphaeridium* individuals. In addition to looking at the effect of sampling type (pitfall or cohort pad sampling) on species composition, I similarly compared the effect of dung size on species composition of dung beetles. The analyses were conducted seperately for data from pitfall traps and cohort pad samples.

Flight activity, weather conditions and rotational grazing

The relation between dung beetle flight activity, weather conditions and the influence of rotational grazing on dung availability was investigated by conducting intensive pitfall trapping during a short period of 10-15 days. There were three experiments in which the dung beetle assemblage was sampled over a period of up to 17 days, employing dung-baited pitfall traps. As part of experiment C2 (19 June to 29 June), an additional set of flight activity pitfall traps (n = 5) was employed. Every 48 hours, the contents of the pitfall traps were collected, and the pitfall traps rebaited with fresh dung. Experiment CT was similarly conducted from 3 July to 20 July. Contents of the pitfall traps were collected after a period of 48 hours and the pitfall traps rebaited with fresh dung at the time of collection.

Experiment BF commenced on 1 August and finished on 9 August and involved a set of pitfall traps located in each of three different pastures which were no less than 300 m apart. Contents of pitfall traps were collected every 24 hours, and the old baits replaced with fresh ones. One herd of 25-30 cattle were present within at least 50 m of pitfall trapping site 1 from 3 days before the experiment until day 5. On day 6, the herd moved into the field containing site 3, and then moved into the adjacent field on day 8. Another smaller herd of about 15 cattle was also present in the rotational grazing regime at Fota at this time. This second herd was located in those pastures between the road and wildlife park (Fig. 3) until day 6. On day 7, this herd moved into the pasture containing site 2 and moved into the adjacent pasture on day 8. For clarity, I have indicated in Fig. 2 (c) the periods during which cattle were present in, or immediately adjacent to, a field containing pitfall traps.

In each of the three experiments, there were five replicate traps (five replicate traps per site in experiment BF), with each replicate located at 5m intervals along a transect. Weather data were available from a nearby weather station at Cork County Airport. Abundances of dung beetles over the duration of the experiments were compared with weather data and, in experiment BF, with the location of cattle herds.

Results

Comparison of pad and pitfall sampling.

Results of the comparisons of rank order of abundances of species and relative abundance of species are presented in Table 1. In experiments C1-C3, and S1- S3, the rank order of abundance of species in pad and pitfall samples of different dung types and sizes were typically significantly and positively correlated (18 out of 24 comparisons). Experiment S3, however, was anomalous as the rank order of abundance of species in pad and pitfall samples was not significantly correlated in any of the four dung sizes (see Discussion). In 21 out of the overall 24 comparisons, the relative abundance of *Sphaeridium* was significantly lower in captures from pitfall traps than in captures from pad samples. The relative abundance of the component species of the *Sphaeridium* taxocene was significantly, or nearly significantly, different in 10 out of 22 comparisons between the two sampling types. The relative abundance of the *Aphodius* species was significantly different in 22 out of 24 comparisons.

Table 2 presents the results of comparisons of assemblage structure between different dung sizes. Within both the pitfall and pad sampling data, significant differences were frequently found in the relative abundance of the constituent species within both the *Aphodius* and *Sphaeridium* taxocenes. Correlations of rank abundance of the species in pads of different sizes were almost always significant, and correlation coefficients were usually higher in the pitfall trap data than in data from cohort pad samples.

Table 1. Comparison of assemblage structure in cohort pad samples and dung baited pitfall traps in experiments C1 - C3 and S1 - S3. Data represent the sum of five replicates on each of a number of sampling days. χ^2 analysis was used to compare the relative abundance of component species of both the *Aphodius* and *Sphaeridium* taxocenes, as well as to compare the relative abundance of the total number of *Aphodius* and *Sphaeridium* individuals. Species rank order of abundances are compared by Spearman rank correlation. There were two types of horse dung used in experiment C1; horse (imp) was collected from improved pastures, whereas horse (rgh) was collected from rough pastures (see Chapter 4). Significances of the values are indicated as follows: ^{ns} $p > 0.1$; † $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

(**a**) Experiment C1: May 1996

	sheep		horse (imp)		cow		horse (rough)	
	pat	pit	pat	pit	pat	pit	pat	pit
A. ater	51	49	2	8	6	18	1	3
A. depressus	75	111	1	68	35	52	0	1
A. erraticus	10	34	0	38	20	64	1	0
A. fimetarius	4	0	0	0	2	0	8	7
A. fossor	37	9	7	0	11	1	0	3
A. prodromus	653	904	703	1861	248	594	27	71
A. rufipes	10	46	1	7	1	8	0	2
A. sphacelatus	2	5	24	64	0	4	0	2
Total *Aphodius*	842	1158	738	2046	323	741	37	89
S. bipustulatum	1	0	0	0	0	0	0	0
S. lunatum	323	156	42	27	261	31	1	1
S. scarabaeoides	192	71	205	48	274	21	0	1
Total *Sphaeridium*	516	227	247	75	535	52	1	2
r_s	0.945**		0.561†		0.724*		0.518^{ns}	
χ^2:								
Aphodius	57.5***		57.5***		35.6***		10.1ns	
Sphaeridium	2.9ns		12.3***		2.2ns		0.75ns	
Aphodius vs *Sphaeridium*	162.1***		336***		560***		0.02ns	

(**b**) Experiment C2: June 1996

dung type	sheep		cow		horse		sheep	
size	1.0		1.0		1.0		0.25	
	pat	pit	pat	pit	pat	pit	pat	pit
A. ater	399	293	68	60	45	108	178	132
A. depressus	101	81	22	47	12	15	26	28
A. erraticus	8	24	2	22	0	4	10	3
A. fimetarius	50	16	18	2	22	15	9	2
A. fossor	180	94	32	4	73	40	17	16
A. granarius	0	0	0	1	0	0	0	0
A. prodromus	4	2	7	16	0	1	2	1
A. rufipes	65	39	24	8	2	18	4	6
Total *Aphodius*	807	549	173	160	154	201	246	188
S. bipustulatum	2	1	1	0	1	0	1	0
S. lunatum	238	98	47	41	27	10	40	21
S. scarabaeoides	60	7	132	166	31	19	13	4
Total *Sphaeridium*	300	106	180	207	59	29	54	25
r_s	0.952**		0.745**		0.855**		0.915**	
χ^2:								
Aphodius	30.1***		72.9***		49.7***		8.3^{ns}	
Sphaeridium	10.2**		3.4^{ns}		1.7^{ns}		1.2^{ns}	
Aphodius vs *Sphaeridium*	27.7***		2.1^{ns}		15.8***		3.75†	

(c) Experiment C3: August 1996

dung type	sheep		cow		horse		sheep	
size	1.0		1.0		1.0		0.25	
	pat	pit	pat	pit	pat	pit	pat	pit
A. ater	0	1	2	1	0	0	2	0
A. depressus	71	56	11	19	2	0	22	17
A. erraticus	28	27	1	5	0	1	2	6
A. fimetarius	49	13	30	20	17	1	19	2
A. fossor	4	3	11	5	0	3	0	0
A. rufipes	296	438	69	243	18	12	32	52
A. rufus	84	34	28	21	1	0	4	4
Total *Aphodius*	532	572	152	314	38	17	81	81
G. spiniger	1	0	1	0	0	0	0	0
S. bipustulatum	7	2	1	1	0	0	0	0
S. lunatum	2264	1042	197	233	5	0	217	69
S. scarabaeoides	403	190	120	38	3	0	27	12
Total *Sphaeridium*	2674	1234	318	272	8	0	244	81
r_s	0.955**		0.912**		0.238^{ns}		0.92**	
χ^2:								
Aphodius	71.1***		58.1***		16.86**		23.2***	
Sphaeridium	0.43^{ns}		42.7***		-		0.81^{ns}	
Aphodius vs *Sphaeridium*	152.9***		47.7***		3.38†		30.6***	

(d) Experiment S1: August 1995

dung size	0.25		0.5		1.0		1.5	
	pat	pit	pat	pit	pat	pit	pat	pit
A. depressus	1	0	5.25	0	3	0	1	4
A. erraticus	0	0	0	0	1	0	0	0
A. fimetarius	7	0	21.75	3.75	33	11.75	44	13
A. rufipes	9	21	50.75	96.25	143	249.5	334	497
A. rufus	0	0	1.25	0	18	4.75	23	14
Total *Aphodius*	17	21	79	100	198	266	402	528
G. spiniger	0	1	0	0	0	1	5	4
S. bipustulatum	0	0	0	0	4	0	4	0
S. lunatum	11	10	55.75	18.75	249	107.5	275	144
S. scarabaeoides	17	11	64.75	46.25	243	142.5	193	208
Total *Sphaeridium*	28	21	120.5	65	492	250	468	352
r_s	0.73*		0.88**		0.81*		0.92**	
χ^2:								
Aphodius	12.5**		30.2***		40.9***		36.4***	
Sphaeridium	0.34^{ns}		5.1*		5.8†		28.7***	
Aphodius vs *Sphaeridium*	1.32^{ns}		16.1***		65.1***		33.4***	

Two replicates (from different sizes) were accidentally destroyed in experiment S1. In the above presentation, average abundances on the day on which the replicates were missing (n=4) were multiplied by five and rounded to the nearest integar for analyses.

(e) Experiment S2: May 1996

dung size	0.25		0.5		1.0		1.5	
	pat	pit	pat	pit	pat	pit	pat	pit
A. ater	9	87	27	158	46	254	30	355
A. depressus	17	11	14	58	43	101	68	184
A. erraticus	1	2	1	3	3	10	7	17
A. fimetarius	1	1	3	1	1	0	5	0
A. fossor	1	1	10	12	35	23	64	32
A. prodromus	791	2077	1020	4075	3270	6247	3709	9572
A. sphacelatus	12	29	12	34	17	72	20	65
Total *Aphodius*	832	2208	1087	4341	3415	6707	3903	10225
S. bipustulatum	1	0	0	0	1	1	4	1
S. lunatum	71	21	120	111	307	169	672	257
S. scarabaeoides	38	10	22	35	137	65	297	69
Total *Sphaeridium*	110	31	142	146	445	235	973	327
r_s	0.81**		0.95**		0.909**		0.864**	
χ^2:								
Aphodius	32.5***		20.9***		77.6***		163.4***	
Sphaeridium	0.36^{ns}		3.26†		0.91^{ns}		10.9**	
Aphodius vs *Sphaeridium*	165.8***		138.9***		278.9***		1227***	

(f) Experiment S3: July 1996

dung size	0.25		0.5		1.0		1.5	
	pat	pit	pat	pit	pat	pit	pat	pit
A. ater	2	38	12	78	26	129	19	146
A. depressus	6	7	14	9	26	9	23	35
A. erraticus	3	0	2	1	1	1	1	1
A. fimetarius	0	0	1	0	5	2	7	10
A. fossor	2	8	1	17	11	40	23	34
A. rufipes	0	3	0	12	14	31	14	40
A. rufus	0	0	0	1	6	1	6	0
Total *Aphodius*	13	56	30	118	89	213	93	266
S. bipustulatum	0	0	0	0	2	0	2	0
S. lunatum	14	1	27	2	145	4	228	40
S. scarabaeoides	13	0	63	0	274	0	450	2
Total *Sphaeridium*	27	1	90	2	421	4	680	42
r_s	0.26^{ns}		0.07^{ns}		0.28^{ns}		0.54^{ns}	
χ^2:								
Aphodius	24.8***		39.78***		64.4***		49.5***	
Sphaeridium	0.9^{ns}		-		7.5*		64.5***	
Aphodius vs *Sphaeridium*	49.5***		136.5***		408.3***		548***	

Table 2. Comparison of assemblage structure between dung samples of different sizes, with separate analyses for cohort pad samples and dung baited pitfall traps. Data represent the sum of five replicates on each sampling day. See Table 1 for original data. Species frequencies are compared using χ^2 tests; species rank order of abundances are compared by Spearman rank correlation. In some experiments, the number of *Aphodius* species included in the analysis is indicated where some species had to be excluded due to violation of the assumptions of the χ^2 test. In experiments S1-S3, the number of significant pairwise correlations between all four dung sizes is indicated. Significances of p-values are indicated as follows: ^{ns} $p > 0.1$; † $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Expt.			Pads	Pitfall traps
S 1	χ^2:	*Aphodius* (n=2)	25.6***	3.2^{ns}
		Sphaeridium	11.6**	4.5^{ns}
		Aphodius vs *Sphaeridium*	49.9***	4.5^{ns}
	Correlation: r_s		6 out of 6	6 out of 6
S 2	χ^2:	*Aphodius*	56.1***	44.2***
		Sphaeridium	15.8**	4.4^{ns}
		Aphodius vs *Sphaeridium*	146.7***	24.3**
	Correlation: r_s		6 out of 6	6 out of 6
S 3	χ^2:	*Aphodius* (n=5)	20.3** (3 sizes)	30.5**
		Sphaeridium	4.8^{ns}	-
		Aphodius vs *Sphaeridium*	25.5***	37.5***
	Correlation: r_s		5 out of 6	6 out of 6
C2	χ^2:	*Aphodius*	67.4***	22.4**
		Sphaeridium	0.53^{ns}	2.27^{ns}
		Aphodius vs *Sphaeridium*	10.38**	2.48^{ns}
	Correlation: r_s		0.867**	0.900**
C3	χ^2:	*Aphodius* (n=5)	32.4***	10.5*
		Sphaeridium	2.9†	0.02^{ns}
		Aphodius vs *Sphaeridium*	14.3***	22.5***
	Correlation: r_s		0.883**	0.958**

Flight activity

Weather conditions and the mean abundance of the dominant dung beetle groups and species in each of the three experiments are presented in Fig. 2. In experiment BF, only the mean values of the totals of *Sphaeridium* and *Aphodius* individuals captured at each of the three sites are presented. All three experiments were numerically dominated by *Sphaeridium* spp.

In experiment C2, the most obvious extreme in weather conditions was the rainfall on day 7, which coincided with a marked decrease in flight activity of both *S. lunatum* and *S. scarabaeoides*. There was no marked decrease in the flight activity of *Aphodius* individuals on day 7, but overall low captures of *Aphodius* probably did not facilitate between-day comparisons.

In experiment CT, days 1-4 were the only days during which rainfall occurred. Temperatures were relatively low on days 1-4 (averaging 11- 13 °C), and showed an overall increase to about 18°C on day 12. After a slight drop on day 13, temperatures remained at an average of about 15°C. Mean numbers of pitfall captures of *Aphodius* were relatively low, and differed little over the duration of the experiment. Note that captures of *A. rufipes* were lowest on day 3, which coincided with the sampling interval when night-time temperatures were lowest and rainfall occurred. There was no general trend of an increase in either *Aphodius* or *Sphaeridium* with the increase in temperature over days 4-12. Note that neither the drastic increase in abundance of *Sphaeridium* on day 12 nor the decrease in numbers of *Sphaeridium* and *Aphodius* on day 13 coincided with a change in weather conditions. Note, however, that a herd of cattle in a rotational grazing regime were moving through fields adjacent to the pitfall traps on days 9-14 (see below).

Fig. 2. Comparisons of dung beetle pitfall captures with weather conditions [Fig. 1 (a-c)] and cattle movements [Fig. 1 (c)]. For experiments C2, CT and BF (a, b, and c, respectively) the top graph shows daily mean temperature and rainfall during the experiment. The other graphs show the mean number of pitfall captures (± s.e., n = 5) of total *Aphodius* and *Sphaeridium*, and of the most common of the species within these taxocenes. For clarity, some of the lines are horizontally displaced. Note that in Fig. 1 (c) the middle graph indicates the time period during which a herd of cattle were in, or immediately adjacent to, a field containing pitfall traps.

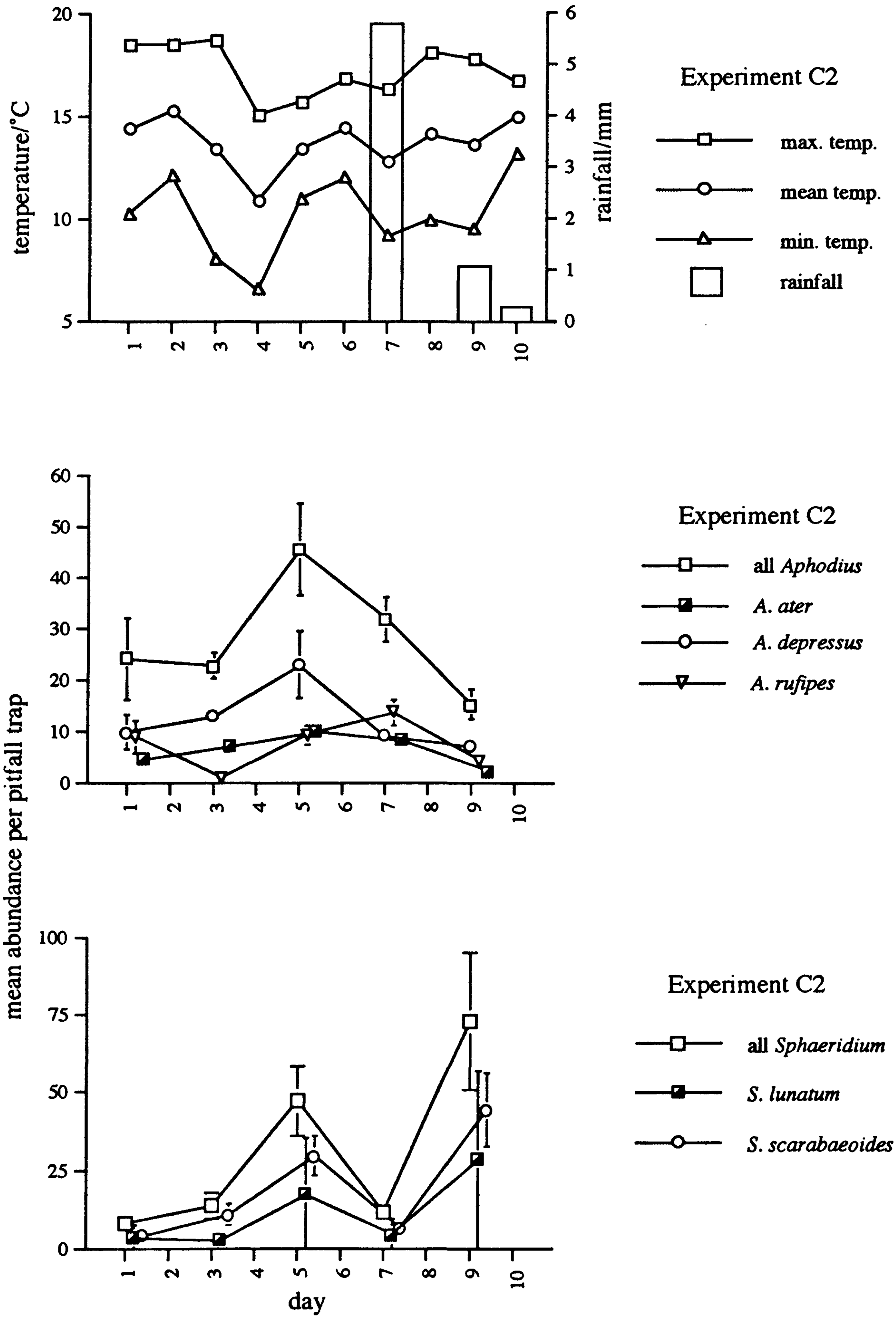


Fig. 2 (b)

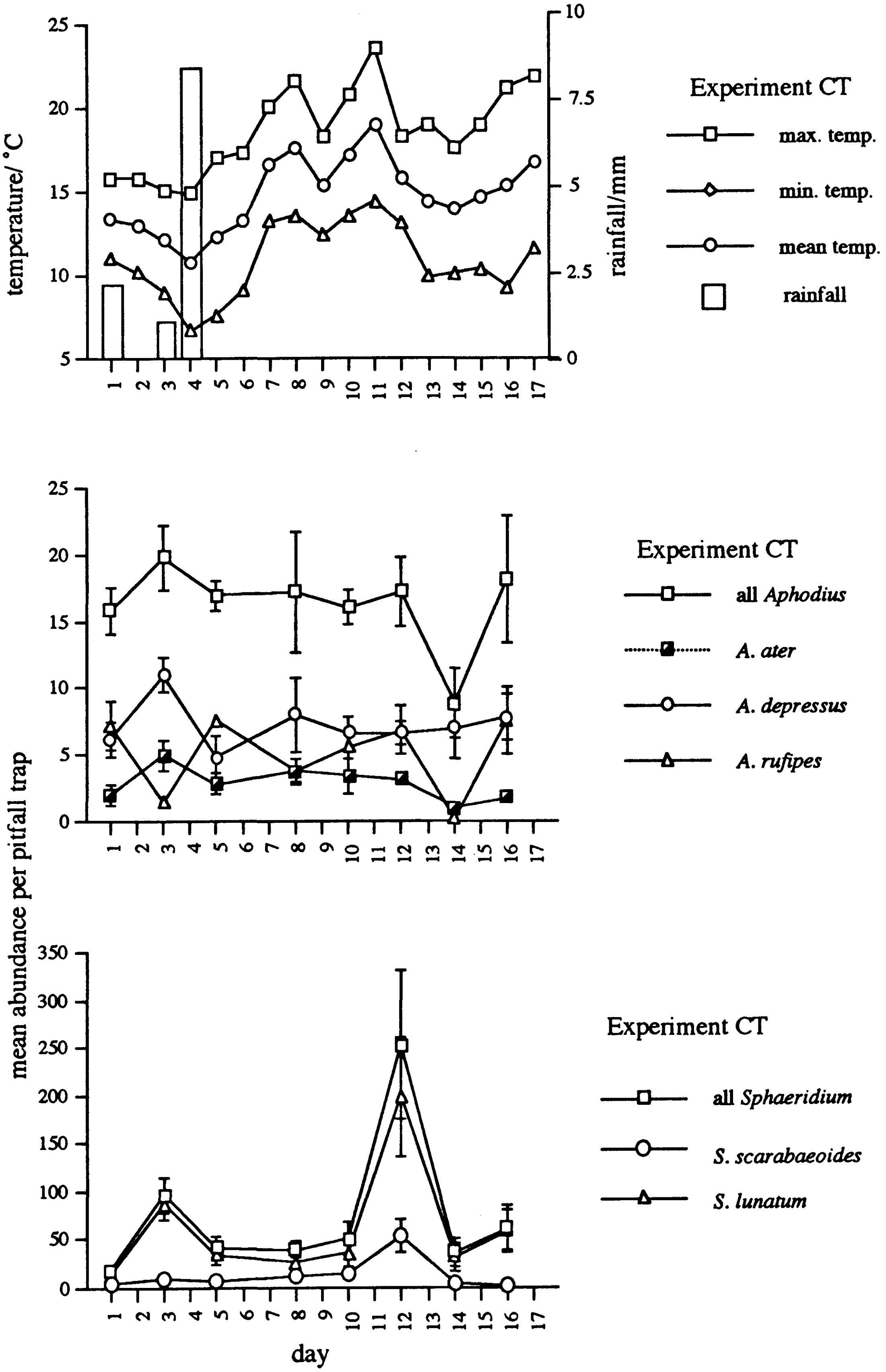
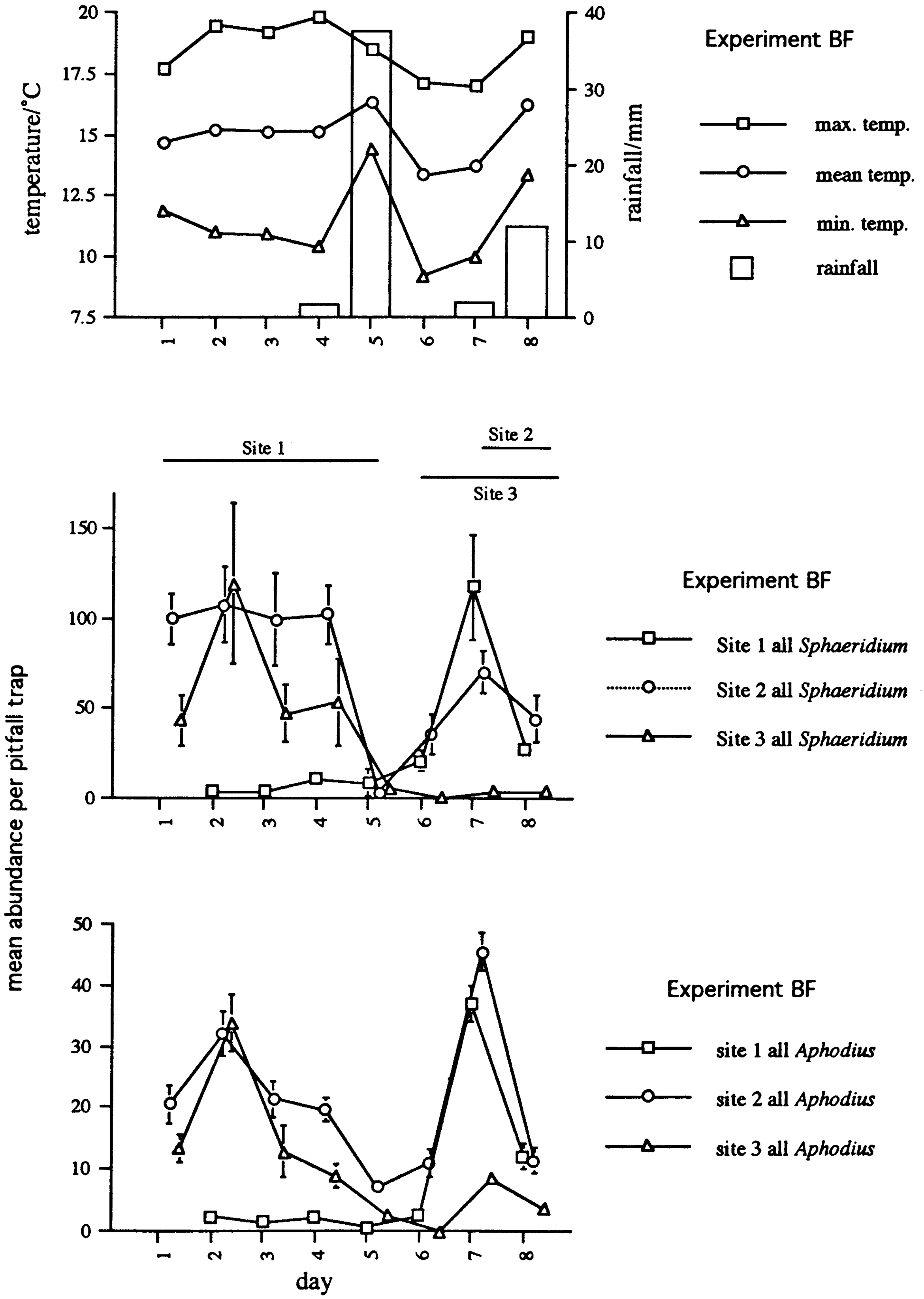

temperature/ °C
25
20
15
10
5
rainfall/mm
10
7.5
5
2.5
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Experiment CT
max. temp.
min. temp.
mean temp.
rainfall
mean abundance per pitfall trap
25
20
15
10
5
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Experiment CT
all *Aphodius*
A. ater
A. depressus
A. rufipes
350
300
250
200
150
100
50
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
day
Experiment CT
all *Sphaeridium*
S. scarabaeoides
S. lunatum

Fig. 2 (c). Note that the middle graph indicates the time period during which a herd of cattle were in, or immediately adjacent to, a field containing pitfall traps.



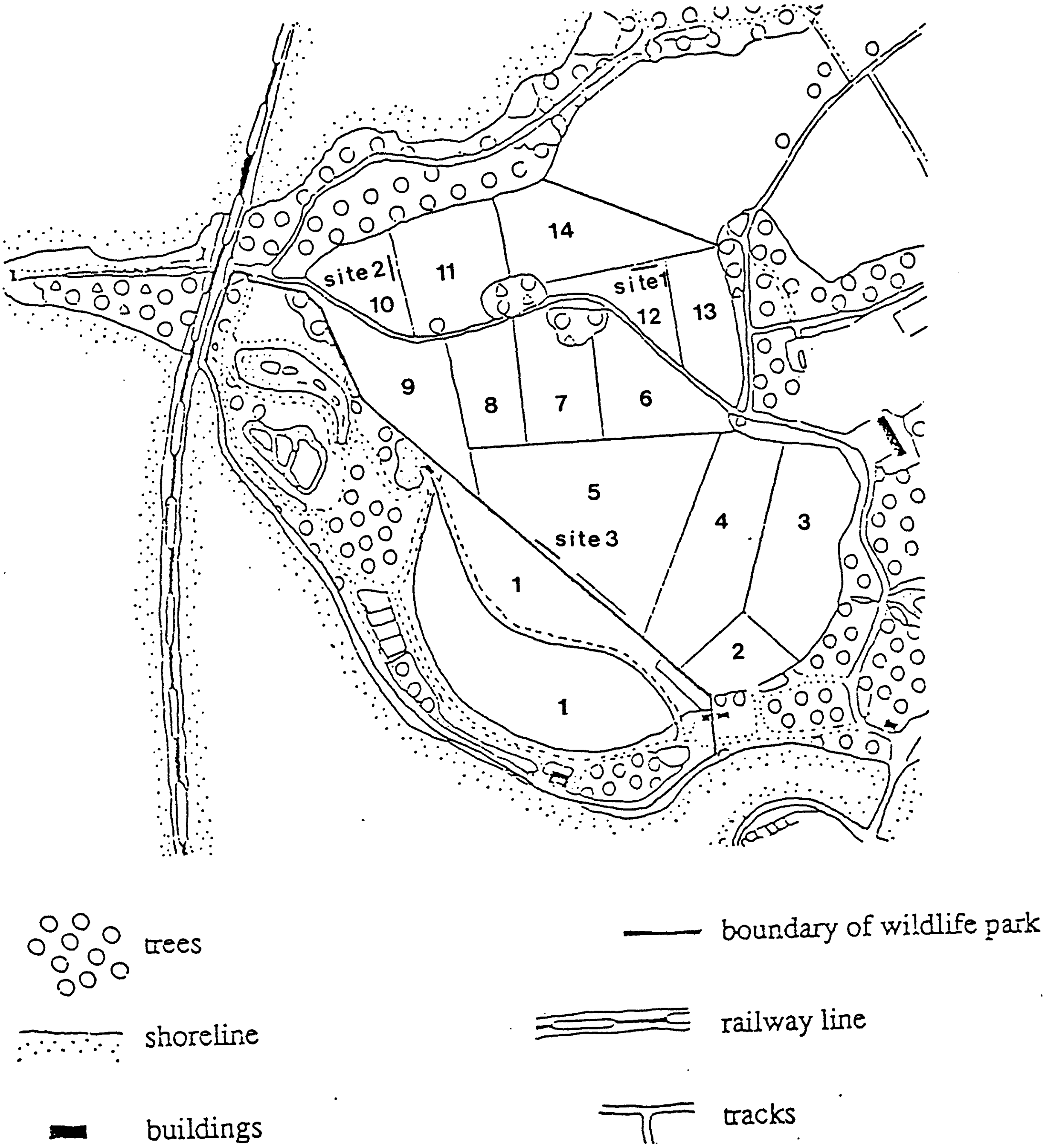


Fig. 3. The location of study pastures at Fota Island (from Gittings, 1994). Pasture 1 is permanently grazed by a variety of exotic herbivores. Pastures 2-14 are rotationally grazed cattle pastures. Sites 1-3 indicate the location of the flight activity pitfall traps.

Table 3. Location of cattle herds in pastures (indicated by numbers) during the rotational grazing regime at Fota over the duration of experiment BF. Pasture numbers correspond with those in Fig. 3.

Day	Herd 1	Herd 2
1	12	6
2	12	6
3	12	7
4	12	7
5	12	8
6	5	9
7	5	10
8	4	11

Experiment BF compared the flight activity of dung beetles in three different pastures (Sites 1-3, Fig. 2). Table 3 indicates the location of the two herds of cattle during the eight days of experiment BF. In contrast to experiments C2 and CT, there were large differences between days in the number individuals captured at any site. Mean temperatures varied little until day 6 and then decreased by about 2.5 °C before increasing again by about 2.5°C over days 7 and 8. There was some light rainfall on days 4 and 7, moderate rainfall on day 8 and heavy rainfall on day 5. In association with rainfall on days 5 and 8, pitfall captures on days 5 and 8 decreased markedly in those sites which had high captures on the previous day [Fig. 2 (c)]. At site 1, mean pitfall captures of all beetles were very low (< 10 beetles per trap) during the period when cattle were present. During the same period, weather conditions on days 1-4 were conducive to beetle activity, and the other sites had mean pitfall captures of over 100 individuals [Fig. 2 (c)]. Pitfall captures at site 3 were almost negligible in the presence of cattle on days 6, 7 and 8. At site 2, the presence of the second (smaller) herd of cattle did not seem to have any appreciable effect on pitfall captures [Fig. 2 (c)].

Discussion

Comparisons of assemblage structure

Looking at the comparisons of assemblage structure between trapping methods, the rank order of abundance in cohort pad samples and pitfall traps were usually correlated (18 out of 20 comparisons, excluding the apparently anomalous results from experiment S3). Nevertheless, χ^2 analyses generally demonstrated that species' relative frequencies between the two methods were significantly different. There was a marked lower relative frequency of *Sphaeridium* species in the pitfall catches than in the cohort pad samples, which is in agreement with Gittings (1994). Hydrophilid species may locate dung pads visually (Schwind, 1991), and it may be that the wrapping of the dung bait in muslin alters some visual cues that *Sphaeridium* beetles use to locate dung. In both pitfall trapping and cohort pad sampling, the rank order of abundance of species between dung samples of different sizes was typically highly correlated. However, significant differences in the relative frequencies of species often occurred, and occurred more often between cohort pad samples of different sizes, compared to pitfall trapping with baits of different sizes.

The interpretation of these comparisons of assemblage structure is possibly confounded when sample sizes of species are low. This was particularly so in experiment S3, when there were low abundances of *Aphodius* species. In such a situation, small changes ($n \approx 10$) in the captures of species could drastically alter the rank order of abundance. Krebs (1989) suggests that correlation coefficients are most suitable in low diversity assemblages with 'reasonably large' sample sizes.

χ^2 analysis of species frequencies may have to be interpreted with caution. The significance of a difference in species frequencies (χ^2 analysis) between pitfall traps and pads may be unreliable when one has low sample sizes of species, e.g. some comparisons between 0.25 L pitfall trap and pad samples. In addition, in some instances where there were large sample sizes, χ^2 analysis of species frequencies gave statistically significant differences, even though the relative abundances (e.g. based on percentages) of species were very similar. This was particularly so when the total abundance of captured beetles was very large, and the captures were dominated by one or two species, e.g. experiments S2 and C1. Thus, it appears that a more robust analytical method is needed that overcomes these problems using χ^2 analysis, and yet is more sensitive to changes in species frequencies than correlation of rank abundances.

Gittings (1994) provides a thorough discussion on the limitations of dung-baited pitfall trapping. His model (see above) considers factors affecting the number of beetles collected from a pitfall trap over a sampling interval or collected from a single cohort of pad samples. Assumptions of the model include that sampling occurs throughout the entire successional period, beetles are evenly distributed across suitable dung ages, pitfall traps are equally efficient at catching all beetles, cohort pad samples are collected daily and a negligible proportion of the overall beetle population is sampled. A number of parameters are defined as follows:

n= number of fresh dung pads deposited per day
t_i = pat residence time (PRT) of population on day i
t'_i = PRT of beetles colonising dung pads on day i
d_i= successional duration of colonisation (SDC) of population on day i
D = SDC of population over sampling period
p_i = total population on day i

Thus, according to this model, on each day p_i/t_i beetles are flying, and d_i*n pads are available for colonisation. Gittings (1994) produced the following predictive equations for pitfall captures:

$$\text{total pitfall captures on day i } (PC_i) \quad = \quad (p_i/t_i)/(d_i*n)$$

$$\text{total pitfall captures (PC)} \quad = \sum_{i=1}^{D}(PC_i) \quad = \sum_{i=1}^{D}(p_i/(t_i*d_i*n)$$

The number of beetles collected from cohort pad samples (CP) is:

$$CP \quad = \quad \text{number colonising pad * pad residence time}$$

$$CP \quad = \sum_{i=1}^{D}(PC_i*t'_i) \quad = \sum_{i=1}^{D}((p_i*t'_i)/(t_i*d_i*n))$$

Most importantly, the model indicates that differences in pat residence times of beetles will affect the relationship between pitfall captures of beetles and the actual size of the beetle population. Pat residence times may be affected by adverse weather conditions (Landin, 1968; Gittings, 1994), as well as the suitability of the dung pad, either due to variation in dung quality (Gittings and Giller, 1998) and/or dung pad size (Chapter 3). Interspecific differences in the response of dung beetles to weather conditions (e.g. Landin, 1968; Gittings, 1994) may produce further interspecific variation in the relation between weather conditions and flight activity and, hence, pitfall captures. In addition, the model indicates that both pitfall and cohort pad captures will be expected to be inversely related to dung availability. Using the framework provided by this model, the role of weather and dung pad availability in affecting dung beetle sampling is considered further.

Weather conditions and pitfall captures

Previous studies have generally investigated relationships between the initiation of flight by dung beetles and various weather parameters (eg Landin, 1967; Landin, 1968 and Koskela, 1979). The approach employed here differs in allowing one to monitor the effects of day-to-day changes in weather conditions on the sampled dung beetle population. From pitfall trapping in the field, Gittings (1994) provided convincing evidence that *Aphodius* dung beetle flight activity is reduced by both rainfall and lower temperatures. Laboratory experiments in Gittings (1994) also confirmed that pat residence times of *A. rufus* and *A. rufipes* were greater at colder temperatures. In the present study, data in a series of short-term experiments suggest that rainfall affects dung beetle flight activity, particularly *Sphaeridium*, but the data did not provide clear evidence that dung beetle flight activity is affected by temperature. The present study has not considered the influence of other weather conditions, such as wind speed, awind direction, humidity levels etc.

Dung pad availability

The above model predicts that both pitfall and cohort pad captures are expected to be inversely related to dung availability. There are very few studies which examine the effect of resource density in ephemeral patches. However, in a study investigating mycophagous diptera, Heard (1998) found an increase in larval aggregation (as opposed to abundance) when inter-patch spacing in grids increased from 5 to 200 cm. Heard considered this was attributed to increased aggregation of ovipositing females or, more likely, to increased clutch sizes of ovipositing females. Likewise, in a field experiment, Gittings (1994) constructed two adjacent grids of pitfall traps; one grid had pitfall traps spaced 1.55 m apart, whereas the other grid had pitfall traps spaced 5 m apart. Average captures of *A. rufipes* were significantly higher in the grid in which pitfall traps were located 5 m apart.

One can exploit agricultural rotational grazing regimes as larger scale natural experiments in which dung pad availability (resource density) is varied. Rotational grazing will be expected to cause short term variability in beetle captures (from either pitfall traps or cohort pad samples) in any one field, despite there being no change in the actual population size. Apart from one example (see Chapter 1, Gittings, 1994), I am aware of no other published studies with empirical data in support of this scenario. The data presented in [Fig. 2 (c)] indicate that pitfall captures can be quickly affected by the presence of cattle, with abundances dropping to very low levels over a period of

1 or 2 days (in the case of site 3, heavy rainfall confounds the interpretation). In addition, when cattle moved from site 1 to a pasture about 400m away, beetle abundances recovered to high levels over a period of about 2 days. Also, note that the presence of the smaller herd of cattle at a distance of about 200m from site 2 over days 3-4 had no apparent effect on pitfall captures at that site. These results suggest that changes in dung availability due to rotational grazing can result in severe fluctuations in pitfall captures of dung beetles at relatively small spatial and temporal scales.

In summary, it appears that dung-baited pitfall trapping is more appropriate for some research objectives than others. For example, it will usually provide a reliable representation of species richness and seasonal patterns of occurrence, as well as the rank order of abundance of species. However, pitfall trapping does not give accurate estimates of density per pad, and hence cannot provide much information on species interactions, density-dependent processes or immigration/emigration dynamics. Gittings and Giller (1998) conducted tibial wear age-grading of *Aphodius* species from pitfall captures, and this revealed life history details such as the emergence and senescence of different generations of multivoltine species. Pitfall trapping may be an acceptable compromise (which must often occur) between scientific exactitude and logistical considerations/time constraints. Nevertheless, it is important to be aware that dung beetle flight activity and hence pitfall captures are strongly related to weather conditions and that this confounding factor may be exaggerated when extended portions of a sampling period undergo contrasting weather conditions. In addition, at emporal scales of several days, rotational grazing may influence pitfall captures of dung beetles, presumably without any change occurring in actual abundances of beetle populations.

References

Desière, M. (1983) Écologie des coléoptères coprophiles en prairie permanente pâturée. 1.-Caractéristiques des populations de Coléoptères adultes coprophiles. Phénologie et dynamique saisonnière. *Bulletin d'Écologie*, **14**, 99-117.

Doube, B.M. and Giller, P.S. (1990) A comparison of two types of trap for sampling dung beetle populations (Coleoptera: Scarabaeidae). *Bulletin of Entomological Research*, **80**, 250-263.

Finn, J., Gittings, T. and Giller, P.S. (1998) *Aphodius* dung beetle assemblage stability at different temporal and spatial scales. *Applied Soil Ecology*, In press.

Gittings, T. (1994) The Community Ecology of *Aphodius* Dung Beetles. Unpublished PhD thesis, National University of Ireland.

Gittings, T. and Giller, P.S. (1997) Life history traits and resource utilisation in an assemblage of north temperate *Aphodius* dung beetles (Coleoptera, Scarabaeidea). *Ecography*, **20**, 55-66.

Gittings, T. and Giller, P.S. (1998) Resource quality and the colonisation and succession of coprophagous dung beetles. *Ecography*, In press.

Halsall, N.B and Wratten, S.D. (1988) The efficiency of pitfall trapping for polyphagous predatory Carabidae. *Ecological Entomology*, **13**, 293-299.

Hanski, I. (1980a) The community of coprophagous beetles (Coleoptera, Scarabaeidae and Hydrophilidae) in northern Europe. *Annales Entomologici Fennici*, **46**, 57-73.

Hanski, I. (1980b) Spatial patterns and movements in coprophagous beetles. *Oikos*, **34**, 293-310.

Hanski, I. and Koskela, H. (1977) Niche relations among dung-inhabiting beetles. *Oecologia* (Berl.), **28**, 203-231.

Heard, S.B. (1998) Resource density and larval aggregation in mushroom-breeding flies. *Oikos*, **81**, 187-195.

Heijerman, T. (1990) Seasonal changes in the relative abundances of some dung beetle species in faeces of the wild boar and mufflon (Coleoptera: Scarabaeoidae). *Ent. Ber., Amst.*, **50** (**7**), 81-86.

Hirschberger, P. and Bauer, T. (1994) The coprophagous insect fauna and its influence on dung disappearance. *Pedobiologia*, **38**, 375-384.

Holter, P. (1982) Resource utilisation and local coexistence in a guild of scarabaeid dung beetles (*Aphodius* spp.). *Oikos*, **39**, 213-227.

Koskela, H. (1979) Patterns of diel flight activity in dung-inhabiting beetles: An ecological analysis. *Oikos*, **33**, 419-439.

Krebs, C.J. (1989) *Ecological Methodology*. HarperCollins, New York.

Landin, B.-O. (1968) The diel flight activity of dung beetles (Coleoptera Scarabaeidae). *Opuscula Entomologica (Supplementum)*, **32**, 1-172.

Landin, J.P. (1967) On the relationship between the microclimate in cow droppings and some species of Sphaeridium (Col. Hydrophilidae). *Opuscula Entomologica*, **33**, 207-212.

Lumaret, J.P. and Kirk, A.A. (1987) Ecology of dung beetles in French mediterranean region (Coleoptera: Scarabaeinae). *Acta Zoologica mexicana (ns)*, **24**, 1-55.

Lumaret, J.P., Kadiri, N. and Bertrand, M. (1992) Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology*, **29**, 349-356.

Schwind, R. (1991) Polarization vision in water insects and insects living on a moist substrate. Journal of Comparative Physiology A, **169**, 531-540.

Topping, C.J. and Sunderland, K.D. (1992) Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of Applied Ecology*, **29**, 485-491.

Tyndale-Biscoe, M., Wallace, M.M.H. and Walker, J.M. (1981) An ecological study of an Australian dung beetle, *Onthophagus granulatus* Boheman (Coleoptera: Scarabaeidae), using physiological age-grading techniques. *Bulletin of Entomological Research*, **71**, 137-152.

White, E. (1960) The natural history of some species of *Aphodius* (Col., Scarabaeidae) in the northern Pennines. *Entomologist's Monthly Magazine*, **96**, 25-30.

Yasuda, H. (1984) [Seasonal changes in the number and species of scarabaeid dung beetles in the middle part of Japan]. *Japanese Journal of Applied Entomology and Zoology*, **28**, 217-222. (In Japanese).

Chapter 2

Spatial and temporal variation in species composition of dung beetle assemblages in southern Ireland

John A. Finn, Tom Gittings and Paul S. Giller
Department of Zoology and Animal Ecology, University College Cork, Ireland

Accepted by Ecological Entomology, June 1998

Chapter 2

Spatial and temporal variation in species composition of dung beetle assemblages in southern Ireland

Abstract. 1. This study attempts to identify the main community characteristics that contribute to variability in dung beetle assemblage composition and structure across a range of spatial and temporal scales.

2. Dung beetle assemblages (*Aphodius*, *Sphaeridium*, and *Geotrupes* species) were monitored by dung-baited pitfall trapping at 10-day intervals during the seasonally active period at eleven sites in southern Ireland. Three of the sites were monitored over at least 2 years between 1991 and 1996.

3. Whilst the species composition of the above taxonomic groups was comparable among sites and years, relative abundances of component species varied considerably. Detrended Correspondence Analysis ordinations indicated a similar level of variability in dung beetle assemblage structure among years, and among sites ~ 1 km - 180 km apart.

4. Processes that may contribute to spatio-temporal variability in dung beetle assemblages are discussed, and strategies for future research are suggested.

Key words. *Aphodius*, assemblage composition, dung beetle, scarabaeoidea, spatial and temporal variability.

Introduction

One of the ultimate aims of community ecology is to understand the processes that regulate the composition, structure, and, ultimately, diversity of communities. Such an aspiration, however, is dependent to a great extent on an adequate knowledge of the variation in the abundance and distribution of the species assemblages of a particular community in space and time. It also depends on the ability to delimit the community itself and the spatial scale on which population dynamics are controlled. Dung beetle communities offer a very tractable study system, given their clearly defined boundaries, restricted temporal activity period, delimited resource supply and well studied taxonomy.

North European temperate coprophagous dung beetle assemblages are typically dominated by *Aphodius* species, complemented by some *Geotrupes* species, members of the Hydrophilidae (*Sphaeridium* and *Cercyon* species) and a few genera of Staphylinidae in the subfamily Oxytelinae. *Aphodius* dung beetles are typically small to medium sized (4-20 mm elytral length) beetles, more commonly known as *dwellers*, that lay their eggs within (or under) the dung pad. *Geotrupes* spp. are larger (~30 mm elytral length) beetles of the *tunneller* functional group, sequestering dung in nests beneath the dung pad. The adults are fluid feeders, whereas the larvae feed on dung fibres. The *Sphaeridium* species, *S. lunatum* and *S. scarabaeoides*, are approximately 10 mm in elytral length. The adults are dung-feeders, whereas the larvae are predatory within the dung pad. *Cercyon* species are much smaller ($\leq$ 1.5 mm elytral length) and are not considered here.

Studies of north European dung beetle assemblages have concentrated largely on the colonisation and succession of *Aphodius* beetles in dung pads, habitat preferences and seasonal activity patterns (for a review, see Hanski, 1991). Understandably, most of these studies are set on small spatial and temporal scales, as is necessitated by intensive fieldwork associated either with monitoring programmes or reductionist experimentation. For example, many studies are confined to a single plot or field and are conducted for sufficient time to sample adequately the succession of beetles colonising dung (10-30 days). They can suffer from a lack of replication within seasons, among seasons, and among years, as well as lacking replication in space. Similarly, studies at several sites that incorporate a measure of variation on a spatial scale are often temporally restricted or lacking in temporal replication.

Dung-baited pitfall trapping was conducted at 10-day intervals during the active season to monitor the composition and structure of dung beetle assemblages in open pastures at a range of sites over a number of years in southern Ireland. This study provides a comprehensive data set on dung beetle assemblage composition, in terms of the temporal and spatial range considered (up to 6 years and ~180 km), whilst still maintaining a relatively high degree of temporal resolution (10 day intervals). In addition, data is provided on dung beetle assemblages at scales of study which are acknowleged to be lacking (Hanski, 1986; Doube, 1987). Utilising this approach, the study attempts to identify the main community characteristics that contribute to variability in dung beetle assemblage composition and structure at the above spatial and temporal meso-scales. Suggestions are offered on how future research strategies for dung beetle research may be designed to improve and overcome problems in the interpretation of community patterns and processes that are associated with spatial and temporal variation in assemblage structure.

Methods

Sampling sites

Dung baited pitfall trapping was conducted at a range of sites in S. Ireland from 1991 and 1996 (Fig. 1). Seven sites were sampled at Fermoy, Co. Cork in 1991; two lowland (40-50 m a.s.l.) within-farm pairs (0.6 km apart) at Moorepark (MA/MB) and Ballyderown (BA/BB), (approximately 2 km apart); and three upland (190-230 m a.s.l.) sites, Coolnakilla (C), Flagstaff (F) and the privately-owned Hawes (H). C and H were 1 km apart and approximately 14 km from F. The upland and lowland sites were 6-11 km apart. Sampling at Fota Island, Co. Cork (50 km from Fermoy) was carried out during 1991, 1992, 1995 and 1996 (F91, F92, F95 and F96; 10 m a.s.l.) and at a site near Killarney in 1995 and 1996 (K95 and K96; 75 m a.s.l). Three other sites were sampled similarly in 1996; near Carrigaline, Co. Cork (C96; 75 m a.s.l.), Moorepark near Fermoy, Co. Cork (MP96), and Johnstown Castle, Co. Wexford (W96; 45 m a.s.l.). The site MP96 was located on the same farm as sites MA and MB. The two most distant sites, Killarney and Wexford, were approximately 180 km apart. See Fig. 1 for relative locations and distances among other sites.

There are a number of habitats at Fota including woodland copses, a wildlife park and cattle pastures, the latter being grazed rotationally by one or two herds of cattle. The soils of Fota wildlife park and adjacent pastures are glacial tills and gravels (Kiely *et al.*, 1984). The Killarney site was located in pastures where low numbers of sheep (n ≤ 15) and cattle (n ≤ 10) were grazing. The site in Carrigaline was on a gleyed clay loam soil, and was grazed by about 15 cattle. The Ballyderown, Moorepark, and Wexford sites were Teagasc agricultural research stations which are managed intensively in a rotational grazing regime with several herds of cattle. The Wexford site was located on a complex of soil types. The Fermoy lowland plots had

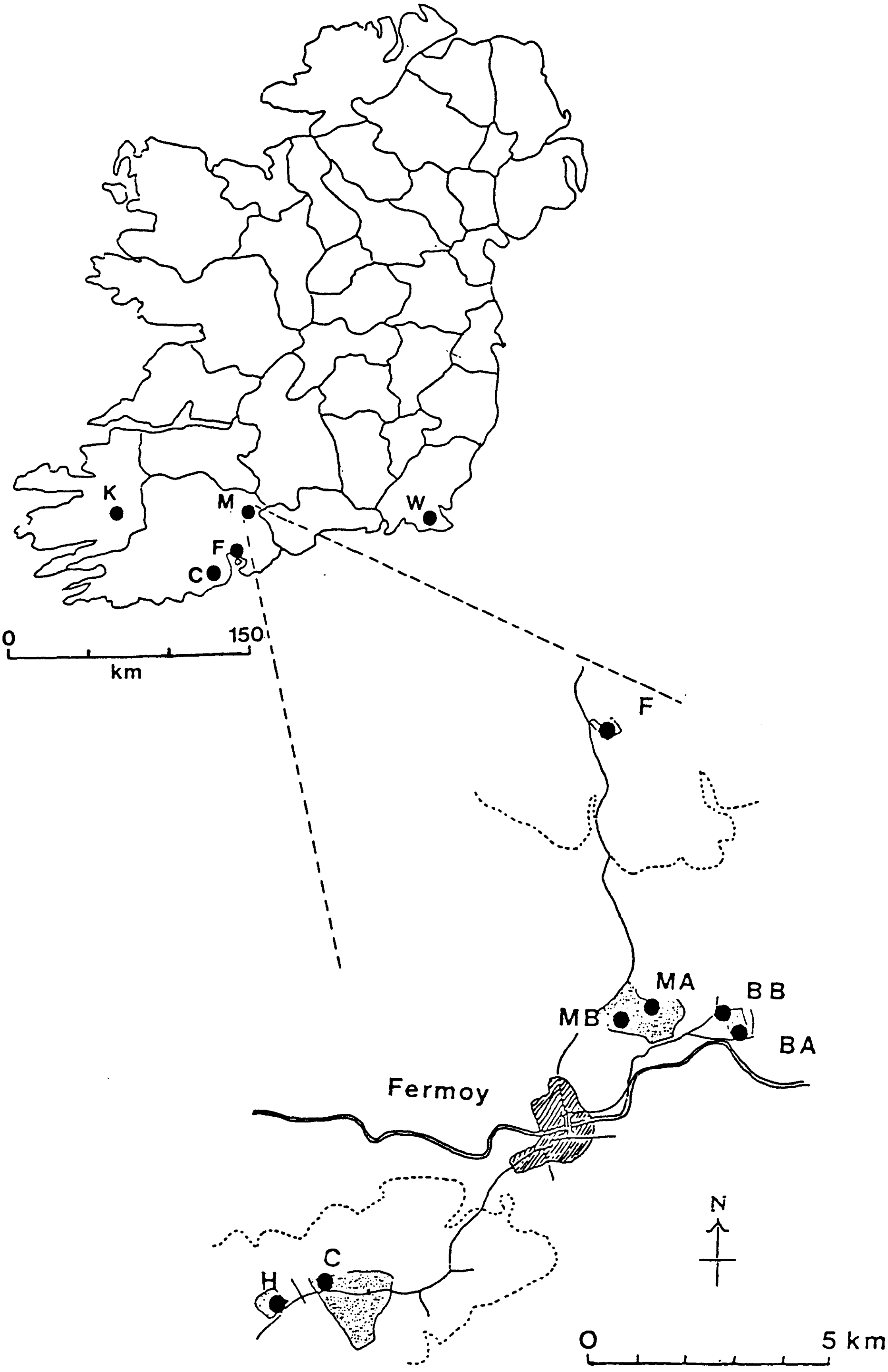


Fig. 1. Map of Ireland indicating the distances between the regionally separated sites. The lower map is a magnified representation of the sites near Fermoy. The regional sites are Killarney (K), Carrigaline (C), Fota (F), Moorepark (M) and Wexford (W). See text for details of other sites.

acid brown earth soils, the upland plots had stony loam soils. The Fermoy upland plots were cattle-grazed, and adjoined extensive areas of sheep-grazed pastures.

Pitfall traps were located in open pastures at all sites. While several sites had woodlands in close proximity, none of these woodlands had large mammals grazing in them. All sites were surrounded by a wider landscape of intensively grazed pastures. During any year of sampling, pitfall traps remained in fixed positions at all but two sites; at Moorepark, the pitfall traps were relocated in 1996 due to interference by cattle and proximity to a road (see below), and the traps in the Killarney site were not more than 50 m apart between the two years. At all sites, pitfall trapping covered at least the period extending from mid-April to mid-October.

Trapping methods

The pitfall trap design was based on that of Tyndale-Biscoe *et al.* (1981). A set of traps consisted of five replicate traps per site, each replicate located at 5 m intervals along a transect. Trapping at Fota and at the Fermoy sites in 1991 consisted of two sets of traps, one set of traps being baited 10 days after the other. The contents were collected every 10 days and baits replaced with fresh dung baits after 20 days. At all other sites, one set of traps was used, which had the contents collected and the dung baits replaced every 10 days as far as was practicable. Generally, heavy rainfall or logistical problems delayed rebaiting of the pitfall traps by only 1-3 days. At each site, 1 l of fresh homogenised cow dung was employed for baits. Baits were usually wrapped in one thickness of muslin, although two thicknesses were used occasionally, depending on the consistency of the dung. Five per cent chloral hydrate was used as preservative in the pitfall traps.

Data Analysis

To compare assemblages and constituent species, the variation among sites and years was described by parameters that include species richness, seasonal and subannual changes in assemblage biomass, composition and diversity, and analyses of assemblage variability.

All individuals captured were identified and counted. *Aphodius* species were divided into non-breeding and breeding groups. The non-breeding group included immature and mature beetles of species with exclusively saprophagous larvae (*A. prodromus* (Brahm) and *A. sphacelatus* (Panz.)) and the immature f_2 generations of dung-breeding species. Calculations of biomass are based on dry weights of species (Gittings, 1994). For calculation of total catches of f_1 and f_2 generations in *Aphodius* species in which these generations overlapped, individuals caught during the overlap period were assigned to one of the two generations on the basis of their tibial wear (Gittings & Giller, 1997).

The problems involved in the interpretation of pitfall trapping data (see Discussion) complicate the extent and type of analysis that is appropriate (see Gittings & Giller, 1997; Finn *et al.*, 1998). Therefore, four periods (spring, early and late summer, and autumn) were identified during which *Aphodius* species composition was relatively constant, and between which distinct breaks in species composition may be identified. The definition of these periods was generally conservative so as to exclude transitional periods. The start of the spring period was set by the availability of data from Fermoy, where trapping started on 19 April 1991. The break between spring and early summer was identified by the end of large abundances of *A. prodromus*/*A. sphacelatus*. The end of the early summer period was identified by the earliest dates when very large numbers of *A. rufipes* (L.)/*A. rufus* (Moll) occurred, or when all early summer species (*A. ater* (De Geer), *A. depressus* (Kugel.), *A. erraticus* (L.)) disappeared in a majority of the data sets. The start of the late summer period was recognised as the latest date when large numbers of *A. rufipes* first appeared in any of the data sets. The end of the late summer period was identified by the earliest date when large numbers of *A. prodromus* appeared, or large numbers of *A. rufipes* disappeared, in any of the data sets. The autumn period began when *A. rufipes* was virtually absent and large numbers of *A. prodromus* or *A. sphacelatus* were present. The time periods were therefore identified as follows (dates indicate when pitfall traps were initially baited): spring - *c.* 20 April - *c.* 20 May (4 trapping intervals; 3 only in Moorepark 1996); early summer - *c.* 30 May - *c.* 8 July (5 trapping intervals; 3 only in Killarney 1995); late summer - *c.* 28 July - *c.* 6 September (5 trapping intervals; 3 only in Wexford 1996); autumn - *c.* 28 September - *c.* 5 November (4 trapping intervals; 3 only in Fota, 1992, Wexford 1996, Carrigaline 1996, and Moorepark 1996).

The abundance data for each of these time periods were obtained by summing the mean number of captured beetles per trapping interval across the time period. To examine the relative assemblage similarity across the various sites and years, a detrended correspondence analysis (DCA) was conducted on log transformed abundance data from each of the first three time periods of the annual assemblage, and rare species were down-weighted. In addition, another DCA analysis of the data sets was conducted that excluded species of *Sphaeridium* and *Geotrupes*.

Simpson's index was used to assess diversity as this gives less weight to rare species. The *Aphodius* species were the only sizeable group of ecologically similar species and diversity was calculated for this group only. Generally, there were both low abundances and numbers of species in the autumn period, so the autumn period was not included in the graphs of taxonomic group composition, *Sphaeridium* composition, or in the DCA analyses.

Results

Species richness

A total of 13 *Aphodius* species, 3 *Sphaeridium,* and 1 *Geotrupes* species was found in the data sets. Of the *Aphodius* species, only single specimens of *A. contaminatus* (Herbst) and *A. lapponum* Gyllen were recorded, while *A. merdarius* (Fabr.) was always rare and *A. granarius* (L.) was generally rare. Most *Aphodius* species occurred at most sites; eight species were shared among all sixteen data sets. At Fota, eleven species of *Aphodius* were captured in 1991, ten in 1992, and nine in both 1995 and 1996. Eight species were found in Killarney in 1995, and seven in 1996. The lowland sites at Moorepark yielded ten or eleven species, while eight or nine species were found at the upland sites. A total of nine species was found at Carrigaline and ten species at Wexford. *Sphaeridium lunatum* Fabr. and *S. scarabaeoides* (L.) were the commonest *Sphaeridium* species found, whereas *S. bipustulatum* Fabr. was rare and was found only at Fota. *Sphaeridium bipustulatum* was not distinguished from *S. marginatum* Fabr. (Van Berge Henegouwen, 1989). *Geotrupes spiniger* (Marsh.) was the only non-aphodid scarabaeid to be captured and was found at all sites.

Seasonal changes in biomass

Seasonal patterns of the changes in biomass of the breeding and non-breeding *Aphodius*, *Sphaeridium,* and *Geotrupes* taxonomic groups are clearly illustrated from the Fota data (Fig. 2). Generally, biomass of breeding *Aphodius* peaked in late summer, mostly due to high numbers of *A. rufipes.* Biomass of other breeding *Aphodius* species contributed relatively little in the late summer period. Non-breeding *Aphodius* biomass usually peaked in spring and autumn, due to the activity of *A. prodromus* and *A. sphacelatus.*

Although *G. spiniger* is by far the largest of the dung beetles found in Ireland, it only rarely occurred in sufficient numbers to contribute considerably to overall biomass in those trapping intervals in which it occurred e.g. Fota, late summer 1991; Wexford, late summer 1996. Usually, *Sphaeridium* species did not contribute a lot to the overall biomass. However, at Fota in 1996, there were persistent and exceptionally high abundances of *Sphaeridium* species in mid summer. A summary of the total annual biomass of the taxonomic groups captured is presented in Table 1. Note that, in Table 1, although the number of samples varied somewhat between sites and years,

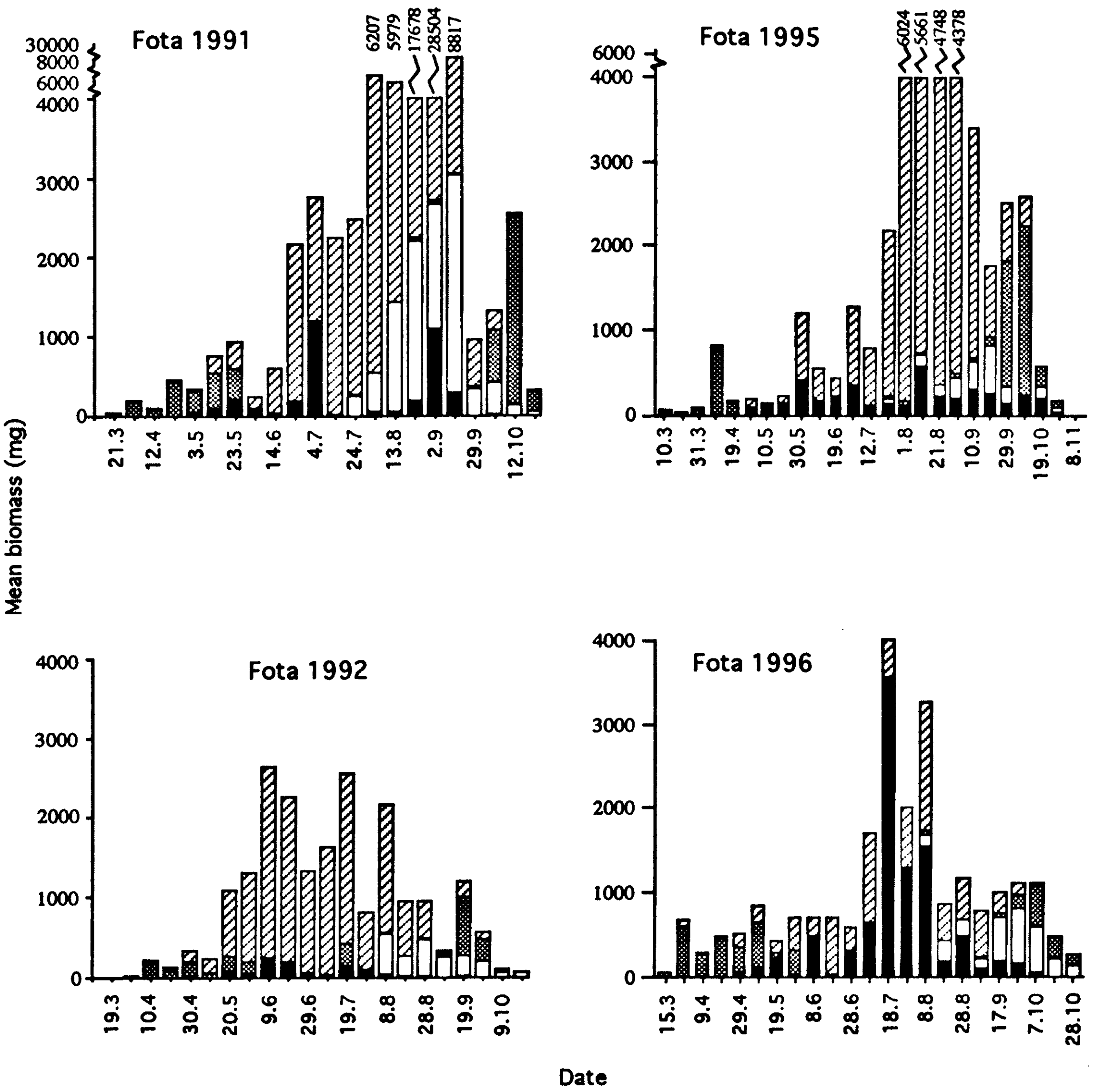


Fig. 2. Seasonal changes in dung beetle biomass captured in baited pitfall traps at Fota in 1991-1992 and 1995-1996. Key to taxonomic groups: breeding *Aphodius* ▨, non-breeding *Aphodius* ▩, *Geotrupes* ☐, *Sphaeridium* ■.

Table 1. Total annual biomass (g dry weight) of dung beetle taxonomic groups captured at several sites and in different years in southern Ireland. Totals represent the sum of the average biomass per sampling interval. The seasonal duration of sampling and number of sampling events are indicated. *Aphodius* species are divided into breeding and non-breeding *Aphodius* (see text).

Sites	Duration of sampling	Number of samples (*n*)	Breeding *Aphodius*	Non-breeding *Aphodius*	*Geotrupes*	*Sphaeridium*	Total
Fota 1991	23/4 - 21/11	22	336.90	26.42	48.47	18.21	429.99
Fota 1992	20/3 - 20/10	22	77.82	12.45	10.41	4.84	105.53
Fota 1995	10/3 - 8/11	25	154.41	25.54	9.43	19.12	208.5
Fota 1996	25/3 - 6/11	23	38.63	19.77	13.66	47.47	119.54
Killarney 1995	26/3 - 9/9	14	48.48	1.13	0.00	0.65	50.26
Killarney 1996	16/4 - 24/10	19	103.72	4.17	0.33	4.75	112.97
Moorepark 1996	12/4 - 8/11	20	14.99	12.08	7.16	3.70	37.929
Carrigaline 1996	1/4 - 8/11	23	98.43	12.42	2.28	16.62	129.75
Wexford 1996	26/4 - 24/10	15	44.26	5.26	12.36	2.53	64.414
Ballyderown A	19/4 - 15/11	22	132.00	12.15	9.43	8.53	162.11
Ballyderown B	19/4 - 15/11	22	92.60	10.98	9.43	0.54	113.56
Moorepark A	19/4 - 15/11	22	84.78	4.80	9.76	1.24	100.58
Moorepark B	19/4 - 15/11	22	203.63	9.52	9.76	2.59	225.51
Coolnakilla	19/4 - 15/11	22	83.22	1.86	0.98	2.24	88.292
Flagstaff	19/4 - 15/11	22	102.06	1.72	0.98	2.83	107.59
Hawes	19/4 - 15/11	22	186.46	6.63	4.23	4.46	201.78

additional samples were derived from the beginning or end of the sampling season when dung beetle biomass was typically quite low.

Sub-annual patterns of assemblage composition

There was no obvious pattern in diversity between the spring and early summer periods, but diversity was generally lowest in the late summer and autumn periods (Table 2). This is to be expected given the dominance of *A. rufipes* and *A. prodromus/sphacelatus* in the catch during the latter periods, respectively. Species richness was typically highest in the early summer, intermediate in spring and late summer, and lowest in the autumn. During all periods, most sites possessed a majority of the species present in the regional pool (Table 2). It is possible that comparisons of species richness may be biased by the different sample sizes among sites. However, within the spring, early summer, and late summer time periods, correlations of sample size and species richness across the data sets were not significant.

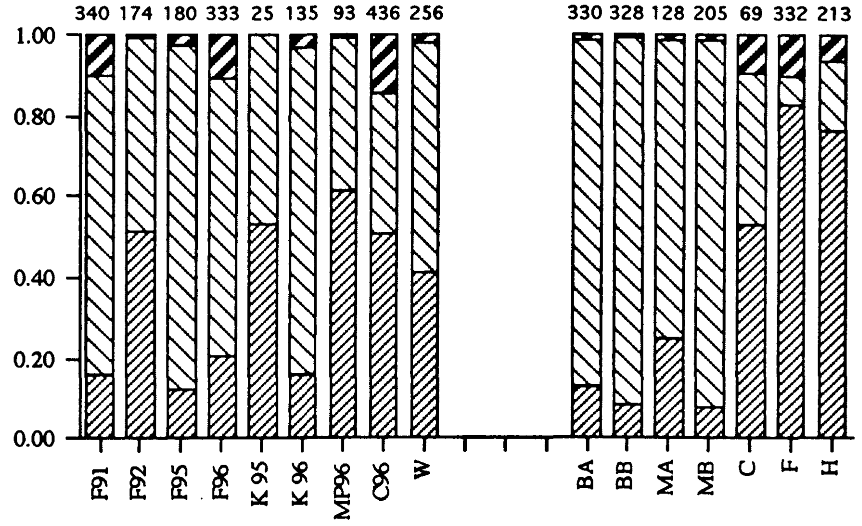
The *Aphodius* genus was numerically dominant in the assemblage throughout the year (Fig. 3). Non-breeding *Aphodius* species (mostly *A. prodromus* and *A. sphacelatus*) contributed considerably to the assemblage in spring and autumn. Generally, fewer individuals of the f_2 generation of any species were captured, but the relative contribution of the f_1 and f_2 generations of both *A. sphacelatus* and *A. prodromus* differed from year to year as well as from site to site within any one year. The greatest abundances of *Sphaeridium*, though not necessarily their greatest proportional contribution to the assemblage, were in the summer periods. The Fota 1996 data set displayed a remarkably high proportion of *Sphaeridium* in the late summer period. *Geotrupes spiniger* was found in low abundances in the late summer/autumn periods only.

The percentage contribution of each species to the total *Aphodius* abundance in the four identified periods is presented in Fig. 4. In the spring period, distinct differences occurred both among years and among sites. Generally, *A. prodromus* was the most abundant species, however, in 1996 *A. sphacelatus* was most abundant in the Killarney and Wexford data sets. *Aphodius granarius* was most abundant in Moorepark in this time period in 1996. High relative abundances of *A. ater* and *A. depressus* occurred in the upland Fermoy sites. In the early summer period, *A. rufipes* was often the most abundant species, followed by *A. ater* and *A. depressus*. *Aphodius granarius* was rare, apart from being abundant in Moorepark in 1996, and occurring in small numbers in the Fota 1991, Fota 1992 and Wexford 1996 data sets. The Wexford early summer data set was comparatively unusual in being dominated by *A. ater*. In late summer, *Aphodius rufipes* dominated all sites, contributing more than 80% of the

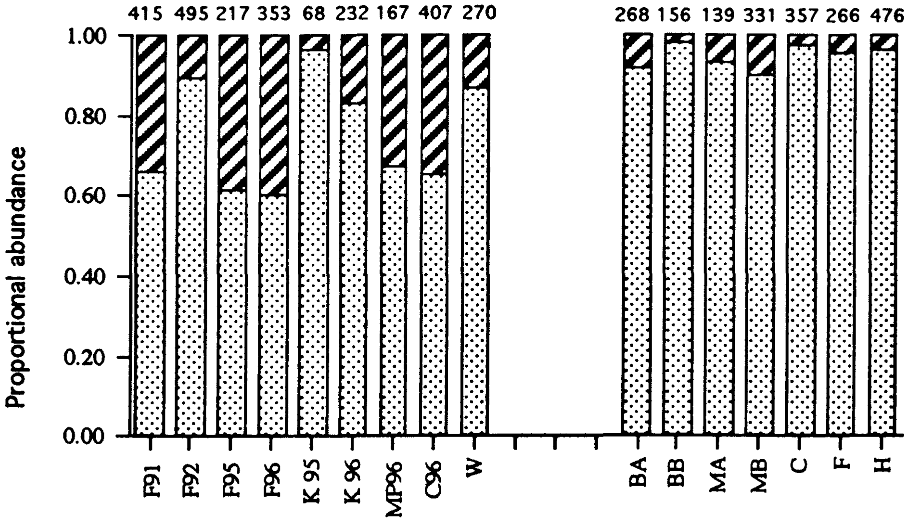
Table 2. Characteristics of *Aphodius* assemblages at several sites and in different years in southern Ireland. In each time period, columns indicate the sum (*n*) of the mean number of beetles trapped in the trapping intervals, Simpson's index of diversity and the number of *Aphodius* species captured. The last row indicates the number of species found across all the sites in each time period.

Sites	Spring			Early summer			Late summer			Autumn		
	n	Diversity	Species richness	*n*	Diversity	Species richness	*n*	Diversity	Species richness	*n*	Diversity	Species richness
Fota 1991	340	1.70	10	415	1.81	9	2359	1.35	7	531	1.10	5
Fota 1992	174	3.39	9	495	3.01	10	151	1.26	7	79	1.75	6
Fota 1995	180	1.47	7	217	3.52	9	849	1.09	7	649	1.23	5
Fota 1996	333	1.97	8	353	4.64	9	493	1.52	8	151	1.19	5
Killarney 1995	25	4.28	7	68	3.23	8	296	1.20	5	-	-	-
Killarney 1996	135	1.72	6	232	3.29	7	594	1.15	7	13	2.95	5
Moorepark 1996	93	2.59	5	167	4.65	8	75	1.39	8	231	1.34	6
Carrigaline 1996	436	3.21	6	407	3.67	7	441	1.20	9	23	1.83	4
Wexford 1996	256	3.17	8	270	2.40	10	231	1.45	7	68	1.75	5
Ballyderown A	330	1.73	9	268	1.86	9	751	1.29	7	10	1.08	2
Ballyderown B	328	1.84	9	156	1.73	9	440	1.23	7	22	1.06	2
Moorepark A	128	2.12	10	139	2.24	8	442	1.20	8	23	1.07	2
Moorepark B	205	2.14	8	331	1.53	8	1031	1.11	8	74	1.10	2
Coolnakilla	69	5.02	7	357	2.69	8	258	1.31	6	3	1.90	2
Flagstaff	332	1.96	8	266	3.11	6	494	1.36	6	10	1.41	5
Hawes	213	3.43	7	476	2.88	8	946	1.32	7	3	2.09	4
Total			10			11			9			6

(a) Spring



(b) Early summer



(c) Late summer

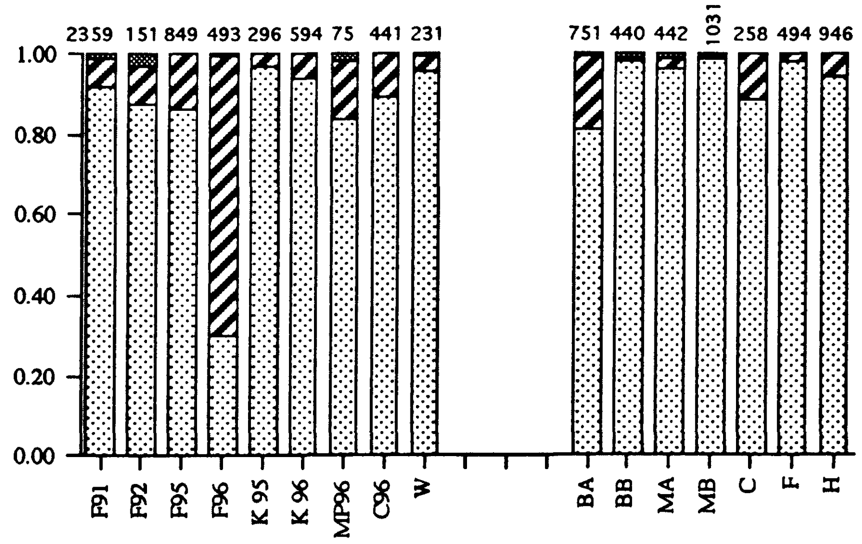
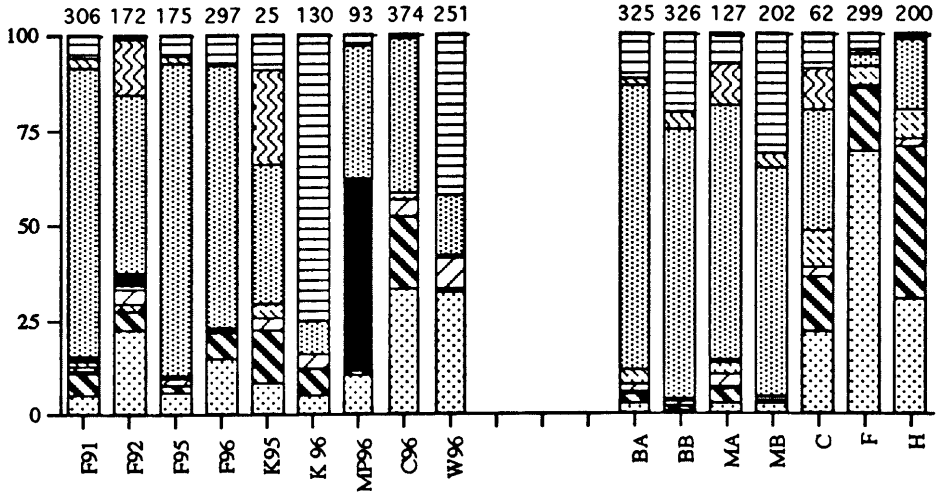


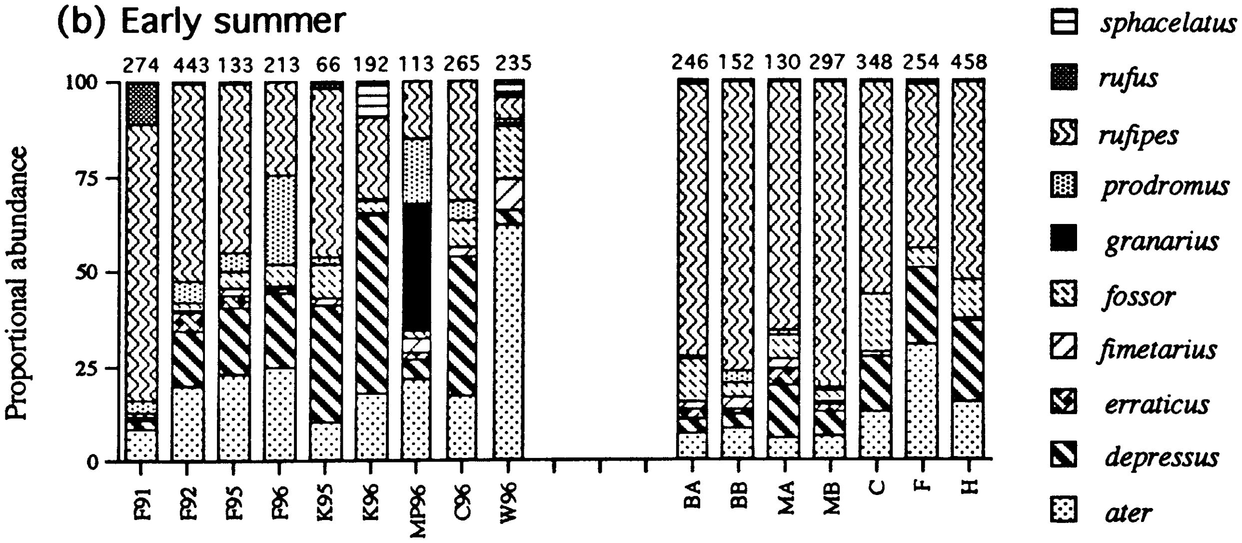
Fig. 3. Proportional contribution of abundances of *Aphodius, Sphaeridium* and *Geotrupes* taxocenes in the spring, early summer and late summer periods. Breeding (▨) and non-breeding (▧) *Aphodius* are indicated separately in the spring period, that being the only period where appreciable differences occurred between the two. Key to taxonomic groups: *Aphodius* (░), *Sphaeridium* (▨), and *Geotrupes* (■).

Fig. 4. Proportional contribution of abundances of *Aphodius* species in the spring (a), early summer (b), late summer (c) and autumn time (e) periods. Also indicated is the proportional contribution of *Aphodius* species to the late summer period with the exclusion of the dominant *A. rufipes* (d). Numbers above columns indicate the sum of the mean numbers of beetles in each trapping interval.

(a) Spring



(b) Early summer



(c) Late summer

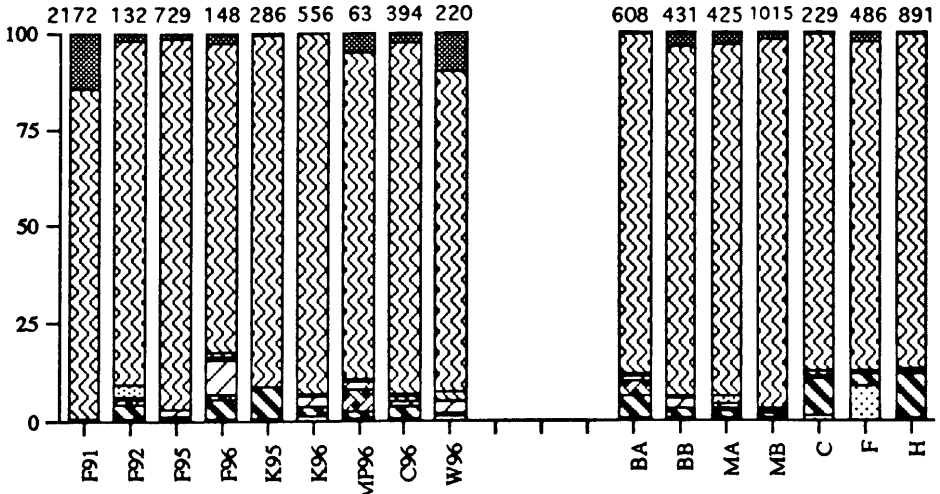
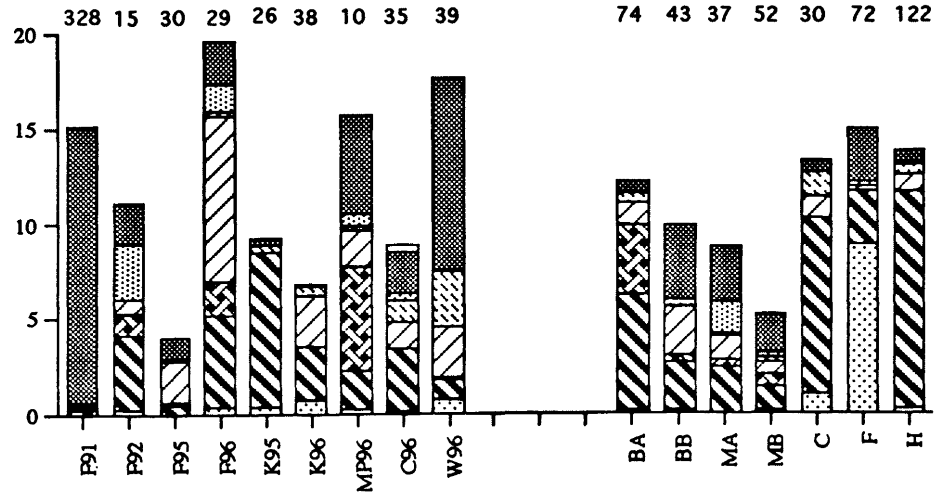
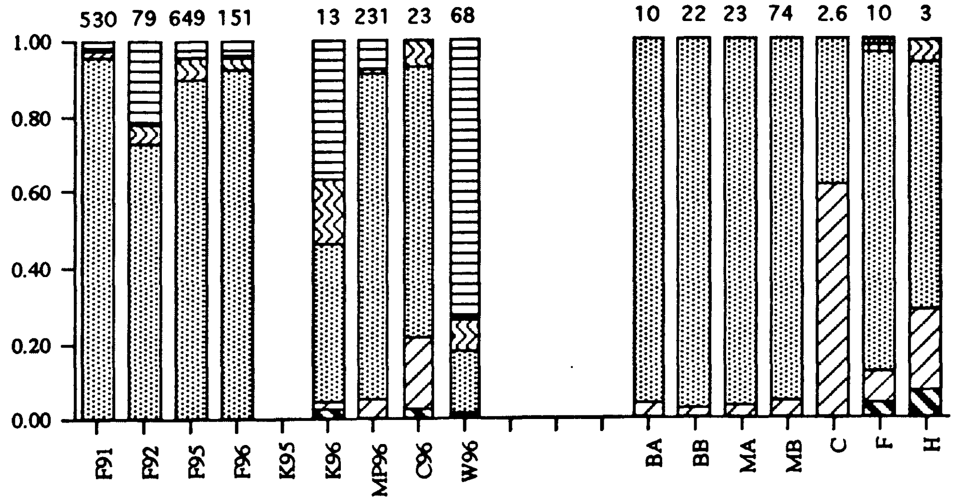


Fig. 4- contd.

(d) Late summer- without *A. rufipes*



(e) Autumn



abundances. Considerable differences in the relative abundances of the remaining late summer species amongst sites can be seen when the *A. rufipes* data are removed (Fig. 4d). However, most of these species were either immatures from f_2 generations or species at the beginning or end of their flight period, and this explains a lot of the variation. The differences in *A. rufus* are more notable as this is its main flight period. The autumn period is typically dominated by *A. prodromus* and/or *A. sphacelatus.*

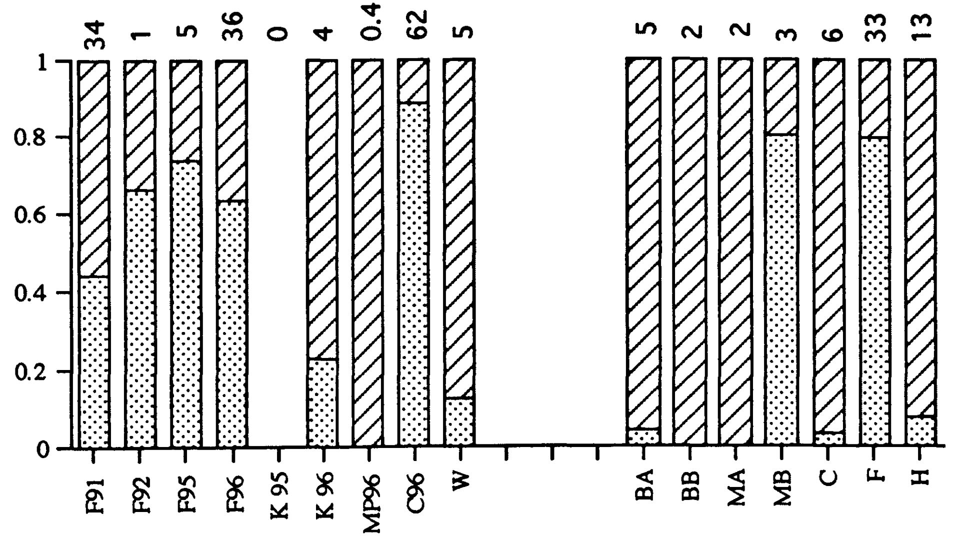
The relative abundances of the two main *Sphaeridium* species, *S. lunatum* and *S. scarabaeoides,* were variable and the rare *S. bipustulatum* was captured in pitfall traps in the late summer period only (Fig. 5), although high numbers of *S bipustulatum* were recorded in other samples taken from Fota in June 1992 (Gittings, 1994). Generally, data sets had comparable relative abundances of *Sphaeridium* species among time periods. However, at Fota, *S. lunatum* was usually dominant in the three time periods across the 4 years of sampling. *Sphaeridium lunatum* was conspicuously dominant at C96, where it accounted for approximately 90% of the abundances in all time periods, while at MP96, W96 and some of the Fermoy sites, *S. scarabaeoides* was dominant.

In summary, species composition across the data sets was fairly consistent within any time period, as were the changes among time periods. Within time periods, the relative contributions of the three taxonomic groups appeared to vary most in the spring period, although there was an unusually high proportion of *Sphaeridium* species in the late summer of F96 (Fig. 3). The greatest variability in assemblage structure appeared to be derived from differences in the relative abundances of the component species of the *Aphodius* and *Sphaeridium* genera (cf. Figs 3, 4, and 5). The following section deals more specifically with the examples of among-year changes in the dung beetle assemblage.

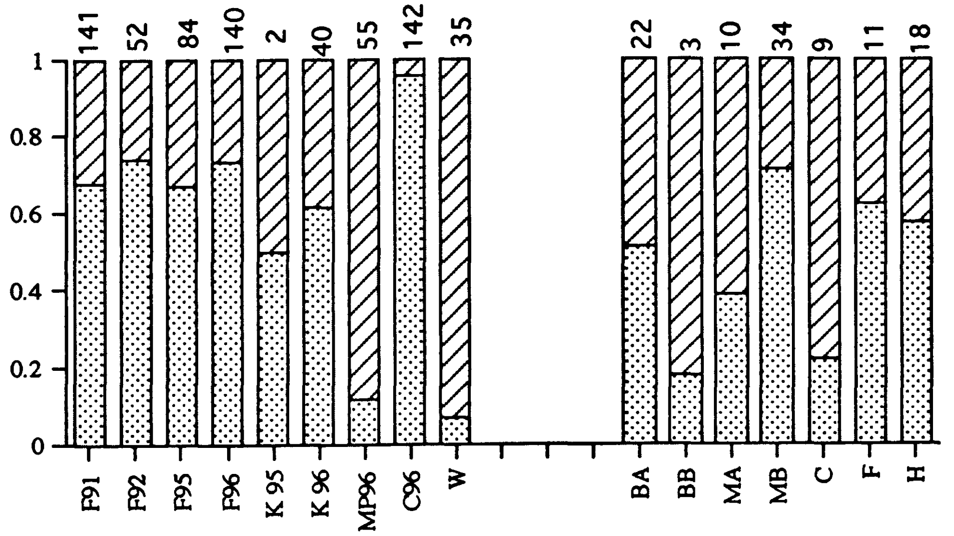
Inter-annual comparisons

Assemblage comparisons among years were available from comparisons of data from Moorepark (1991 and 1996), Fota (1991, 1992, 1995, and 1996) and Killarney (1995 and 1996). Species composition among years, and at all the sites, was similar, with a mean (±S.D.) proportion of 0.86 (± 0.08) species shared between assemblages. Pairwise correlations of rank abundance (of annual totals of species) among the years at Fota were typically significant (five of six comparisons), and a correlation of rank abundance was also significant between the two years at Killarney. However, at Moorepark, similar rank abundance correlations between the two years were not significant. A more detailed consideration of differences in the relative abundance of species is presented below.

(a) Spring



(b) Early summer



(c) Late summer

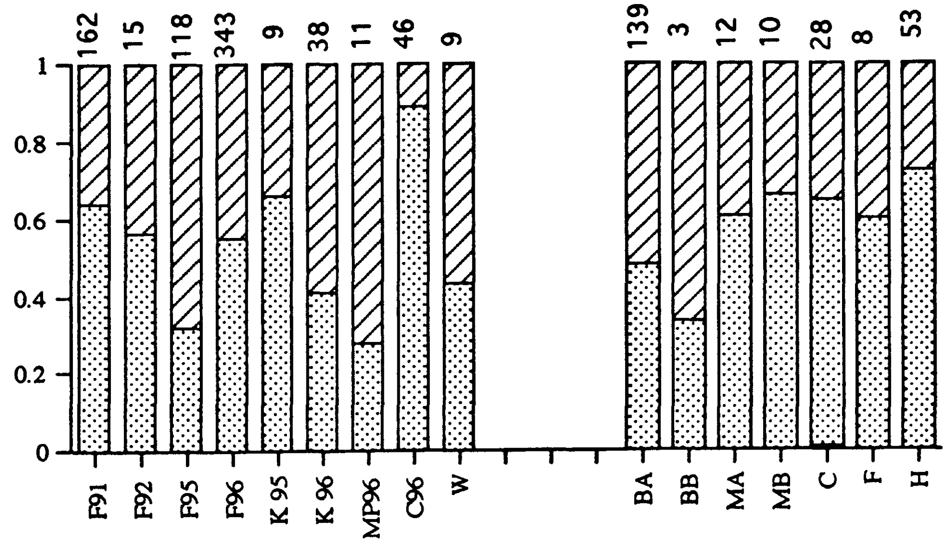


Fig. 5. Proportional contribution of *Sphaeridium* species in the spring, early summer and late summer time periods. Indicated above each column is the sum of the mean numbers of *Sphaeridium* in each trapping interval for the time period. Key to species; ⬚ *S. lunatum*, ▨ *S. scarabaeoides.*

Very low abundances of *A. granarius* occurred at Moorepark in 1991 (one individual at MA), while 5 years later it was the most abundant species in the spring and early summer. This was accompanied by a decrease in the relative abundance of *A. prodromus*. Comparing 1991 and 1996, in 1996 there was a higher combined percentage contribution of *A. rufus* and *A. erraticus* at Moorepark as well as a significant increase in the proportion of *S. scarabaeoides* relative to *S. lunatum* (cf. MP96, MA, MB), particularly in early summer, when highest abundances occurred (e.g. comparing *Sphaeridium* species frequencies for MP96 and MB in early summer, $\chi^2 = 164.7$, d.f. = 1, $p < 0.001$).

In comparison, at Fota, *A. granarius* decreased from modest numbers in 1991 and 1992 to being absent in 1995 and 1996. In the early summer period at Fota, there was a pronounced decrease in the relative abundance of *A. rufipes* and *A. rufus* from 1991 to 1996, accompanied by increases in the relative abundances of *A. ater*, *A. depressus*, and *A. prodromus*. The species frequencies of *S. lunatum* and *S. scarabaeoides* at Fota in 1991 and 1996 were significantly different within all three time periods (spring, $\chi^2 = 12.97$, $p < 0.001$; early summer, $\chi^2 = 5.485$, $p < 0.05$; late summer, $\chi^2 = 18.57$, $p < 0.001$; all d.f. = 1).

There was a change between the two years in the spring period at Killarney, mainly due to the increase in the relative abundance of *A. sphacelatus* and a decrease in the relative abundance of *A. prodromus* and *A. rufipes*. Comparing the early and late summer periods between the two years at Killarney, there was less of a change than that observed in the spring period, but in 1996 there was an increase in the percentage contribution of *A. sphacelatus* and *A. depressus*, apparently at the expense of *A. prodromus*. Significant differences in *Sphaeridium* species frequencies occurred between 1995 and 1996 at Killarney (sufficient data for late summer period only; $\chi^2 = 9.409$, d.f. = 1, $p < 0.01$).

Despite such statistical differences in species frequencies, the biological significance or persistence of any such changes are unknown.

Analyses of assemblage variability

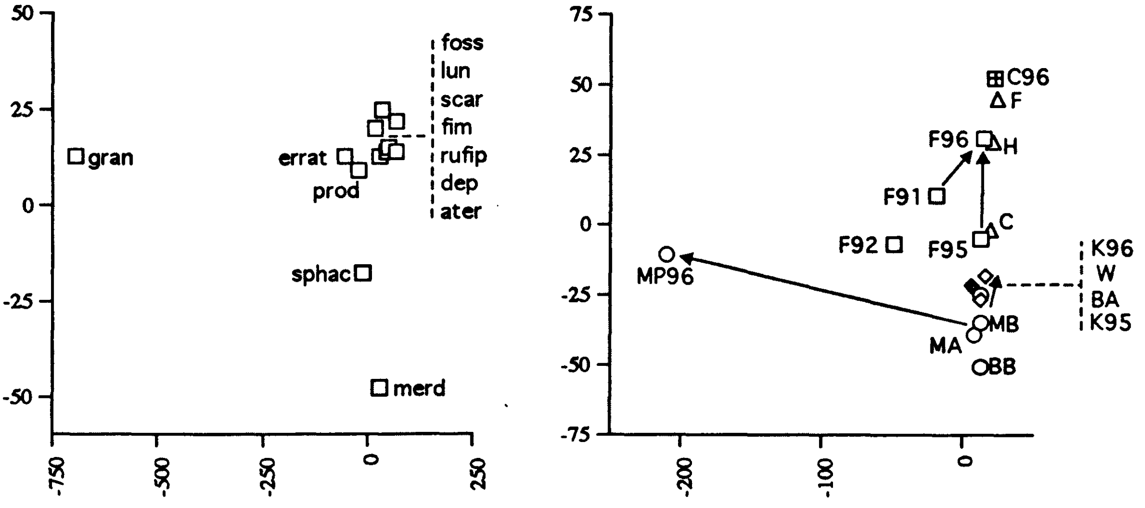
The ordinations of both the species and site sample scores of the three subsets of the annual *Aphodius* assemblage are presented in Fig. 6. In the interpretation of the DCA analyses, the closer the data sets are to each other, the more similar the assemblage structures are. The relative similarity of the assemblages changes across the seasons.

In the spring ordination, some separation occurred on axis 2, but most sites tended to cluster along axis 1, with the Moorepark 1996 and Fota 1991 and 1992 data sets forming outliers, largely due to the occurrence of *A. granarius* in these outlying samples. In the early summer period, most sites formed a well-grouped cluster, with Killarney 1996, Wexford 1996 and Moorepark 1996 data sets as outliers. The species ordinations suggest strongly that this is due to the high abundances in Killarney and Wexford of *A. sphacelatus*, and high abundances of *A. granarius* in Moorepark 1996. In both the early and late summer ordinations, the upland (C, F, and H) and lowland (MA, MB, BA, and BB) Fermoy sites separate consistently. This may be related to environmental differences amongst sites influencing the fauna (e.g. temperature). The Killarney site tended to cluster with the Fermoy upland sites, particularly along axis 1. Depending upon the season, some or all of the Fota data sets show affinity with the Fermoy lowland sites. This is most evident in the early and late summer periods. Axis 2 tends to separate sites within these clusters.

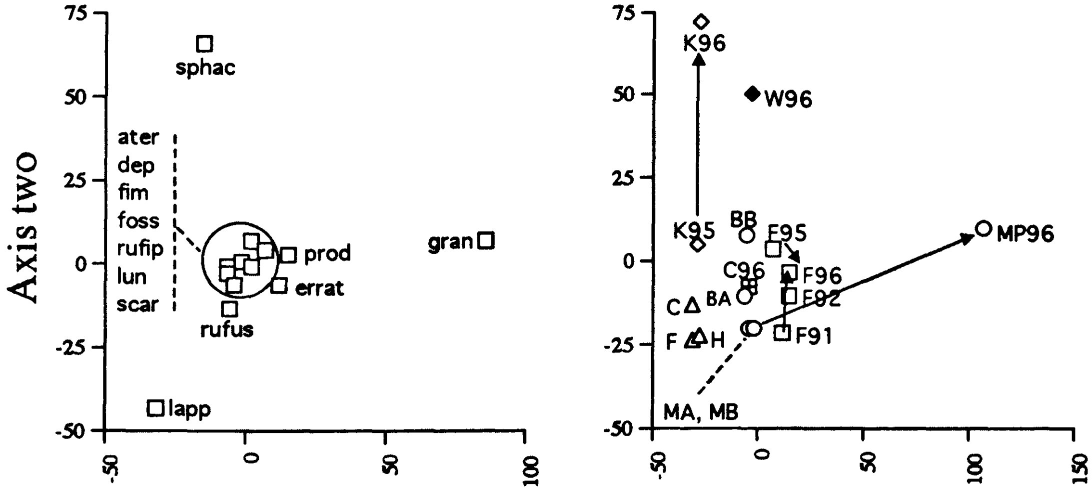
In the species ordinations, the *Sphaeridium* species are generally located amongst the main group of *Aphodius* species, particularly in the spring and early summer ordinations. The ordinations of the combined *Aphodius*, *Sphaeridium*, and *Geotrupes* species were qualitatively very similar to those obtained when analysing *Aphodius* species only, and the latter ordinations are not presented here.

Fig. 6. (Overleaf) Detrended Correspondence Analysis ordinations of dung beetle assemblages in southern Ireland from various sites and years. Analyses are presented for the spring, early summer, and late summer time periods (see text). Arrows indicate the magnitude and direction of comparisons of inter-annual changes (see text). The sums of the eigenvalues for each analysis were 0.402 (spring), 0.333 (early summer) and 0.277 (late summer). For each time period, species ordinations are presented on the left and sample (sites and year) ordinations are presented on the right. □ Fota, ◇ Killarney, ○ Fermoy lowlands, △ Fermoy uplands, ⊞ Carrigaline, ◆ Wexford. Key to species codes: ater = *Aphodius ater*, bip = *Sphaeridium bipustulatum*, dep = *A. depressus*, errat = *A. erraticus*, fim = *A. fimetarius*, foss = *A. fossor*, gran = *A. granarius*, lapp = *A. lapponum*, lun = *S. lunatum*, merd = *A. merdarius*, prod = *A. prodromus*, rufip = *A. rufipes*, rufus = *A. rufus*, scar = *S. scarabaeoides*, sphac = *A. sphacelatus*, spin = *Geotrupes spiniger*.

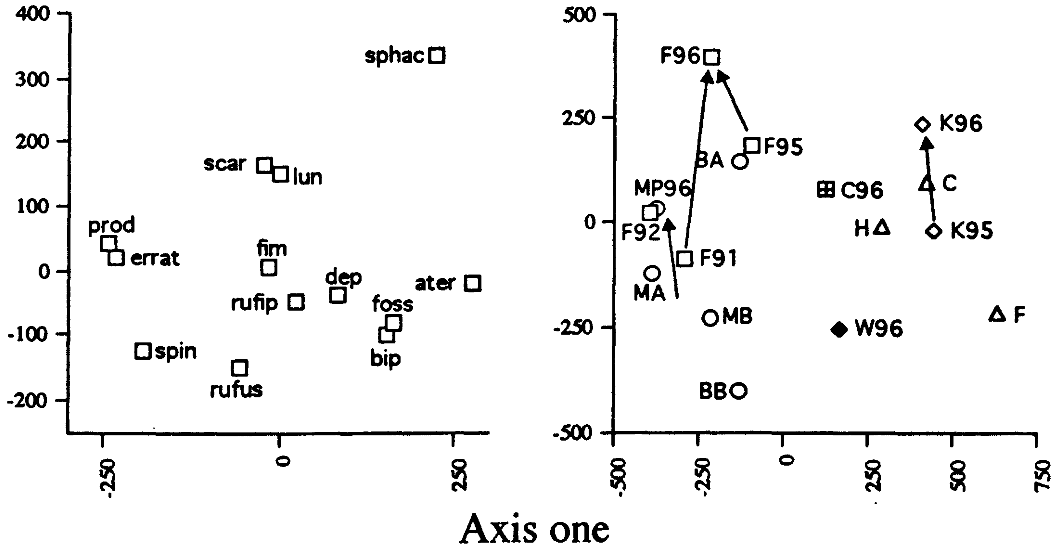
(a) Spring



(b) Early summer



(c) Late summer



Overall, the ordinations of the sites indicate that the variability in assemblage structure at the regional scale between Killarney 1995 (and sometimes Killarney 1996) and the Fermoy upland sites is similar to that at the local scale within the Fermoy upland sites. Moreover, in each ordination, the variability between at least one of the Fota and Fermoy lowland data sets is similar to the between-field variability in the Fermoy lowland sites. The between-year temporal variability at Fota, Fermoy, and Killarney is of the same order as the spatial variability between Fota, Carrigaline, Fermoy, Killarney, and Wexford. To summarise, these ordinations indicate that variability in dung beetle assemblage structure among these study sites in southern Ireland is generally of a similar order of magnitude between sites and between years (as measured by their separation in the ordination biplots), although there is some indication that the greatest variability may occur among the more distant sites.

Discussion

This study was entirely based on data collected by pitfall trapping. There are some problems involved in the interpretation of data collected by pitfall trapping (see Gittings, 1994). In particular, weather conditions and cattle movements in rotationally grazed pastures may change the relationship between pitfall captures and absolute population size, while *Sphaeridium* species are less efficiently sampled by pitfall trapping, in comparison with cohort pat samples. Despite these problems, pitfall trapping is a relatively efficient method of sampling, in logistical terms. More importantly, while there may be significant differences in comparisons of absolute abundances and species frequencies from pitfall traps and cohort pat samples, the rank orders of abundance are usually highly correlated (Doube & Giller, 1990; Gittings, 1994). In this study, the use of subannual assemblages for analyses of assemblage variation was deliberately chosen to overcome some of the biases arising from pitfall trapping (see Finn *et al.*, 1998).

The effect of habitat heterogeneity was largely obviated by locating all pitfall traps in open pastures. However, the location of pitfall traps in near proximity to a dirt road (~ 1.5 m distant) at Moorepark in 1996 was strongly suspected to have led to a reduced catch of dung beetles. In another study, significantly lower abundances of Staphylinidae were captured nearer a road than in the middle of a pasture (Barth *et al.*, 1994). However, low numbers of Hydrophilidea and Scarabaeidea probably did not facilitate comparisons in that study.

Temporal and spatial variability in dung beetle assemblages

There was little difference either in species richness or species composition among the sites and years, and rank orders of abundance of species annual totals were usually highly correlated; out of 120 pairwise comparisons, correlations of rank abundance ranged from 0.368 to 0.978 (mean $r_s = 0.771$; s.e. = 0.0098; mean d.f. = 16), with only three correlations with $r_s < 0.5$. Despite the variability in absolute measures of biomass among data sets, overall there was remarkable predictability in seasonal patterns of biomass of the various taxonomic groups. This is a direct consequence of the fidelity of the phenology of the constituent species in the assemblages, both between years and sites. For example, if the flight activity period of a species is defined as that period within which 90% of the total annual catch of a species was captured, there was only infrequently a difference of more than approximately 10 days between the beginning or the end of the flight activity periods of a species among the data sets (where sufficient numbers were captured to allow comparisons) (Gittings & Giller, 1997; Finn, unpublished data). It is this phenological consistency that gives rise to species turnover within a year, which in turn accounts for a lot of the variation in species richness among the different time periods at any site. The present study and data from other recent studies (Sowig & Wassmer, 1994; Palmer, 1995) support the contention of Finn *et al.* (1998) that *Aphodius* assemblages are more appropriately studied in terms of their seasonal sub-assemblages (the time periods considered here) rather than as annual assemblages.

Whilst there is clear similarity in species composition, the relative contributions of the genera and the relative abundances of component species of these genera varied considerably. It appears that the latter provided greatest differences among assemblages. In addition, ordinations indicated an overall equivalent contribution of both space and time (at the studied scales) in promoting assemblage variability.

Temporal scale

There are few examples indicating the time scales at which populations of north temperate dung beetles may change. In this present study, abundances of *A. granarius* were far smaller at the Moorepark site in 1991 than in 1996, and numbers of *A. rufipes* and *A. rufus* declined at Fota from 1991 to 1996. Other temporal comparisons of assemblages from consecutive years are present in the literature (White, 1960; Rainio, 1966; Kessler and Balsbaugh, 1972; Breymeyer, 1974; Finn *et al.*, 1998). On the basis of the overall evidence, however, assemblages usually appear quite similar at the scale of 1 to 5 years, and indicate relatively little difference due to turnover in species, and greater differences in relative abundance of the species present.

There are also few examples of comparisons of assemblages from the same site at the scale of about 10 years. A re-analysis of Belgian data in De Graef and Desière (1984) indicates a low correlation of the rank order of abundances of the eight commonest species between 1972 and 1982-83 (r_s = -0.5), in contrast to the usual strong positive correlations of data sets from consecutive years (see above; Finn *et al.*, 1998). Comparison of data sets from two periods of sampling from 1972-1977 and 1978-1980 in Denmark (Holter, 1982) showed a relatively low correlation of rank order of abundance of *Aphodius* species (r_s = 0.28, n = 13). Comparisons of regional data sets at temporal scales of ~60 years reveal apparent changes in abundance and some turnover of species (usually a loss of species, in the data sets available; Johnson, 1962; Biström *et al.*, 1991).

Spatial scale

Data on *Aphodius* assemblages from different geographical regions in northern Europe indicate that major changes in *Aphodius* assemblage structure occur at large spatial scales of > 300 km (Finn *et al.*, 1998). Such changes in species composition and relative abundance will be expected on the basis of biogeographical processes that generally operate on such large spatial and temporal scales, e.g. geographical barriers, climatic differences, and historical factors. While a more in-depth consideration is beyond the scope of this paper, the importance of such processes in determining assemblage composition within the meso-scales considered here is greatly diminished. Indeed, compared to changes in assemblage composition at the geographical scale, the variability in assemblage composition documented here is almost negligible.

The present data indicated that the greatest variability in assemblage structure occurred in the late summer, with equivalent variability among sites. In spring and early summer, while overall variability was less, the degree of variability among sites was more dissimilar. This was particularly so in early summer among three regionally separated sites (~100 - 180 km). At this scale, there was some relatively low turnover of species richness. Typically, differences between assemblages were due to differences in the relative abundances of several species that were common to most sites, whereas in a few examples the greatest assemblage variability was derived from an extreme change in the relative abundance of a single species (Fig. 6). Indeed, assemblage variability was not necessarily related to the actual distance seperating sites. At the local spatial scale (1 to 15 km), assemblages examined around Fermoy in 1991 revealed differences between the upland and lowland sites in the relative abundance of a few shared species, most likely due to differences in altitude, weather, and soil type, or a combination of these.

Processes potentially involved in assemblage structure at meso-scales

So, what processes may be important in regulating community structure at the regional scale? Habitat preferences may be important at the macrohabitat scale (e.g. forests vs. pastures). However, in the present study sampling was essentially restricted to one macrohabitat (open pastures). Factors which may be important in affecting assemblage variation within one macrohabitat type include altitude (Key, 1982; Finn *et al.*, 1998), soil type (Sowig, 1995), and pasture quality (through its effect on dung quality, which is known to influence colonisation and reproductive performance in *Aphodius* beetles; Gittings, 1994; Gittings and Giller, 1998). Species with saprophagous larvae (e.g. *A. prodromus* and *A. sphacelatus*) may be particularly affected by pasture quality and soil type. Landscape-scale features, such as the amounts and distribution of pastures and woodlands, may also be important if metapopulation theories are applicable to these assemblages.

However, while it is tempting to try and explain assemblage variation in the context of environmental variation, the similarity in the extent of assemblage variation at the inter-annual and loca-regional scales suggests an alternative approach. This similarity indicates that any factors which may affect assemblage variation among sites have no greater influence on assemblages than those factors which affect assemblage variation among years at any one site. Assemblage variation among years is the product of annual variation in individual species populations, which in turn may be affected by site-specific and/or chance events. Therefore, it may be reasonable to suppose that inter-annual patterns of assemblage variation may not be synchronous between sites. This supposition is supported by comparisons of the magnitude and direction of change in assemblage variation (Fig. 6) between MA/MB - MP96 compared to F91 - F96, and between K95 - K96 compared to F95 - F96. In this context, asynchronous patterns of inter-annual variation among sites could explain a lot of the apparent spatial variation at the local - regional scale.

Suggestions for future research

There is a rich literature that attempts to explain the distribution and abundance of species in comparable communities at the regional scale (e.g. Hanski, 1982; Brown, 1984, 1995). Most of this is theoretical and there have been difficulties in translating theory-derived hypotheses to experimentation in the field. There is no single correct scale at which to study the factors affecting populations or communities (Wiens, 1989; Levin, 1992) and it is important to match the scale of predictive models to that of processes occurring in natural ecosystems (Nisbet *et al.*, 1997). One of the problems has therefore been to determine the appropriate scale for studies, e.g. metapopulation studies rely on delimiting distinct populations in space, and there are few data on turnover rates of, or changes in, species populations either at the landscape level or in time. The data from this study may thus provide some indications of the spatio-temporal scales at which species composition and relative abundance vary, and at which studies of *Aphodius* assemblage stability may be more profitably conducted.

On the basis of the results presented here, the following suggestions are offered for the design of future investigations into the organisation of dung beetle species assemblages. Any suggestions, however, are based on data from southern Ireland, and may not be applicable without modification to dung beetle assemblages at other Northern European sites. Following Finn *et al.* (1998), while dependence on a single sampling site at a local scale may not provide an adequate description of the community, once the local assemblage has been defined (from a number of sites), this may be representative up to the regional scale. This is useful, considering that most studies, and experimental studies in particular, are conducted at small spatial scales. Small-scale temporal replication within the sub-annual assemblages is required for the purposes of generality and to overcome the biases of changes in weather conditions (Finn *et al.*, 1998). Sites located ≥ 50 km apart are more likely to incorporate species turnover at the regional level. There is a need for consistency in the sampling methodology among studies to allow better collation of data. Most importantly, long-term continuous monitoring and experimental studies of dung beetle assemblages will greatly enhance knowledge of the extent, and significance, of changes in the relative composition of taxonomic groups as well as species composition and relative abundance within these groups. Given the recent apparent declines and extinctions in dung beetle species (Väisänen & Rassi, 1990; Biström *et al.*, 1991) in tandem with changes in farming practices, studies documenting and analysing patterns of assemblage variation are urgently required.

Acknowledgements

We thank the following for permission to conduct pitfall trapping and assistance at the various sites; the Finn family at Killarney; Noel Culleton and John Murphy at Teagasc, Johnstown Castle; Jervis Good, Carrigaline; Gearóid Stakelum and staff at Teagasc, Moorepark and staff of Fota Wildlife Park. We also thank Frances Gallager for drawing Fig. 1, and two anonymous referees for their comments.

References

Barth, D., Karrer, M., Heinz-mutz, E.M. & Elster, N. (1994) Colonisation and degradation of cattle dung: aspects of sampling, fecal decomposition and artificially formed pats. *Environmental Entomology*, **3**, 571-578.

Biström, O., Silfverberg, H. & Rutanen, I. (1991) Abundance and distribution of coprophilous Histrini (Histeridae), *Onthophagus* and *Aphodius* (Scarabaeidae) in Finland (Coleoptera). *Entomologica Fennica*, **2**, 53-66.

Breymeyer, A. (1974) Analysis of a sheep pasture ecosystem in the Pieniny mountains (The Carpathians). XI. The role of coprophagous beetles (Coleoptera: Scarabaeidae) in the utilisation of sheep dung. *Ekologia Polska*, **22**, 617-634.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255-279.

Brown, J.H. (1995) *Macroecology*. The University of Chicago Press, Chicago.

De Graef, F. & Desière, M. (1984) Écologie des coléoptères coprophiles en prairie permanente pâturée. III. Dynamique et phénologie des guildes d'Hydrophilidae de Scarabaeidae et de Geotrupidae. *Bulletin de la Société Royale des Sciences de Liège*, **53**, 158-172.

Doube, B. (1987) Spatial and temporal organization in communities associated with dung pads and carcasses. *Organisation of Communities: Past and Present.* (ed. by J. H. R. Gee and P. S. Giller), pp 255-280. Blackwell Scientific Publications, Oxford.

Doube, B.M. & Giller, P.S. (1990) A comparison of two types of trap for sampling dung beetle populations (Coleoptera: Scarabaeidae). *Bulletin of Entomological Research*, **80**, 250-263.

Finn, J., Gittings, T. & Giller, P.S. (1998) *Aphodius* dung beetle assemblage stability at different spatial and temporal scales. *Applied Soil Ecology*, **241**, in press.

Gittings, T. (1994) *The community ecology of* Aphodius *dung beetles.* Unpublished PhD thesis, National University of Ireland.

Gittings, T. & Giller, P.S. (1997) Life history traits and resource utilisation in an assemblage of north temperate *Aphodius* dung beetles (Coleoptera, Scarabaeidea). *Ecography*, **20**, 55-66.

Gittings, T. & Giller, P.S. (1998) Resource quality and the colonisation and succession of coprophagous dung beetles. *Ecography*, in press.

Hanski, I. (1982) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, **38**, 210-221.

Hanski, I. (1986) Individual behaviour, population dynamics and community structure of *Aphodius* (Scarabaeidae) in Europe. *Acta Oecologia, Oecologia Generalis,* **7**, 171-187.

Hanski, I. (1991) North temperate dung beetles. *Dung Beetle Ecology* (ed. by I. Hanski and Y. Cambefort), pp. 75-96. Princeton University Press, Princeton, New Jersey.

Holter, P. (1982) Resource utilisation and local coexistence in a guild of scarabaeid dung beetles (*Aphodius* spp.). *Oikos*, **39**, 213-227.

Johnson, C. (1962) The Scarabaeoid (Coleoptera) fauna of Lancashire and Cheshire and its apparent changes over the last 100 years. *The Entomologist*, **95**, 153-165.

Kessler, H. & Balsbaugh, E.U. (1972) Succession of adult coleoptera in bovine manure in east central South Dakota. *Annals of the Entomological Society of America*, **65**, 1333- 1336.

Key, R.S. (1982) Cluster analysis of dung inhabiting beetle communities from different altitudes in Jostedalen, South-West Norway. *Fauna Norvegica Series B*, **29**, 24-33.

Kiely, J., Diamond, S. & Feeney, P. (1984) *Soils of Fota Island.* Soil Survey Bulletin No. 38, An Foras Talúntais, Dublin.

Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943-1967.

Nisbet, R.M., Diehl, S., Wilson, W.G., Cooper, S.D., Donalson, D.D. & Kratz, K. (1997) Primary productivity gradients and short-term population dynamics in open systems. *Ecological Monographs,* **67**, 535-553.

Palmer, M. (1995) Testing for seasonal diplacement in a dung beetle guild. *Ecography*, **18**, 173-177.

Rainio, M. (1966) Abundance and phenology of some coprophagous beetles in different kinds of dung. *Annales Zoologici Fennici*, **3**, 88-98.

Sowig, P. (1995) Habitat selection and offspring survival in three paracoprid dung beetles: the influence of soil type and soil moisture. *Ecography* **18**, 147-154.

Sowig, P. & Wassmer, T. (1994) Resource partitioning in coprophagous beetles from sheep dung: phenology and microhabitat preferences. *Zoologische Jahrbuecher, Abteilung Systematik*, **121**, 171-192.

Tyndale-Biscoe, M., Wallace, M.M.H. & Walker, J.M. (1981) An ecological study of an Australian dung beetle, *Onthophagus granulatus* Boheman (Coleoptera: Scarabaeidae), using physiological age-grading techniques. *Bulletin of Entomological Research*, **71**, 137-152.

Väisänen, R. & Rassi, P. (1990) Abundance and distribution of *Geotrupes stercorarius* in Finland (Coleoptera, Scarabaeidae). *Entomologica Fennica*, **1**, 107-111.

Van Berge Henegouwen, A. (1989) *Sphaeridium marginatum* reinstated as a species distinct from *S. bipustulatum*. *Entomologische Berichten, Amsterdam*, **49**, 168-173.

White, E. (1960) The natural history of some species of *Aphodius* (Col., Scarabaeidae) in the northern Pennines. *Entomologist's Monthly Magazine*, **96**, 25-30.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385-397.

Appendix 1 : Supplementary data on species abundances, tibial wear and weather patterns.

The data and analyses presented in Chapter 2 are derived from an extensive data set of dung beetle captures from dung baited pitfall trapping that was conducted at several sites and over several years in southern Ireland (see Chapter 2). The value of these data is in the extent of the spatial and temporal ranges considered (up to 6 years to and ~180 km), the temporal resolution of the data (sampled at 10-day intervals) and the lack of data on dung beetle assemblage structure at these spatio-temporal scales. Chapter 2 provides comparisons between sites and years, after pooling data within each of the identified annual subsets of the dung beetle assemblage, i.e. spring, early summer, late summer and autumn (Chapter 2).

Here, I provide more detailed data of pitfall captures from the 10-day trapping intervals, upon which Chapter 2 is based. More detailed information on the Fermoy and Fota sites sampled prior to 1993 are presented in Chapter 2 of Gittings (1994). However, the seasonal patterns of dung beetle biomass at each of the Fermoy sites sampled in 1991 are presented (Fig. 2). For each of the sites at Fota (1995 and 1996), Killarney (1995 and 1996), Carrigaline, Wexford and Moorepark, data is provided on the seasonal changes in various assemblage characteristics e.g. seasonal changes in biomass (Fig. 2), *Aphodius* species richness (Fig. 3), dung beetle flight activity periods (Table 2), seasonal patterns of pitfall captures of dung beetles (Figs. 4 - 10) and seasonal changes in the age composition of *Aphodius* dung beetles (Figs. 11 - 19), the latter based on patterns of tibial wear. In addition, weather conditions during the trapping period at each of the sites during the period are presented (Fig. 20).

Tibial wear age-grading was conducted according to the criteria of Gittings (1994), which was based upon the method of Tyndale-Biscoe (1978). All *Aphodius* and *Geotrupes* beetles in the Fota (1995 and 1996), Killarney (1995 and 1996), Carrigaline, Moorepark and Wexford data sets. Age-grading was conducted by assigning beetles to various classes (N, S_1, S_2, M and H) based on the degree of wear on the foretibia. Thus, class N represented unworn tibia; class S_1 indicated beetles with slightly worn tibia, but with no reduction in tibial length; class S_2 referred to slightly worn tibia with 2/3- 1/2 reduction in tibial length; class M referred to moderately worn tibia and class H indicated heavily worn tibia (see Gittings [1994] for details and diagrams). For *Aphodius* species in which f_1 and f_2 generations overlapped, individuals were assigned to generations as in Gittings (1994).

Weather data were obtained from weather stations located on both the Teagasc farms at Moore Park and Wexford, and from a weather station located within several miles of the Killarney trapping site. Weather data for both the Carrigaline and Fota trapping sites were obtained from the weather station located at Cork Airport.

For detailed comparisons of assemblage structure among a number of sites and years in southern Ireland, see Chapter 2. *Aphodius* species richness typically peaked around mid May, and declined over the following two or three months. Distinct troughs in both species richness and abundances of beetles coincided with relatively heavy rainfall e.g. Moorepark, late July, 1996 and Killarney, mid August, 1996. The flight activity period of various dung beetle species was generally quite consistent among the various sites and years, and were similar to those in Gittings (1994).

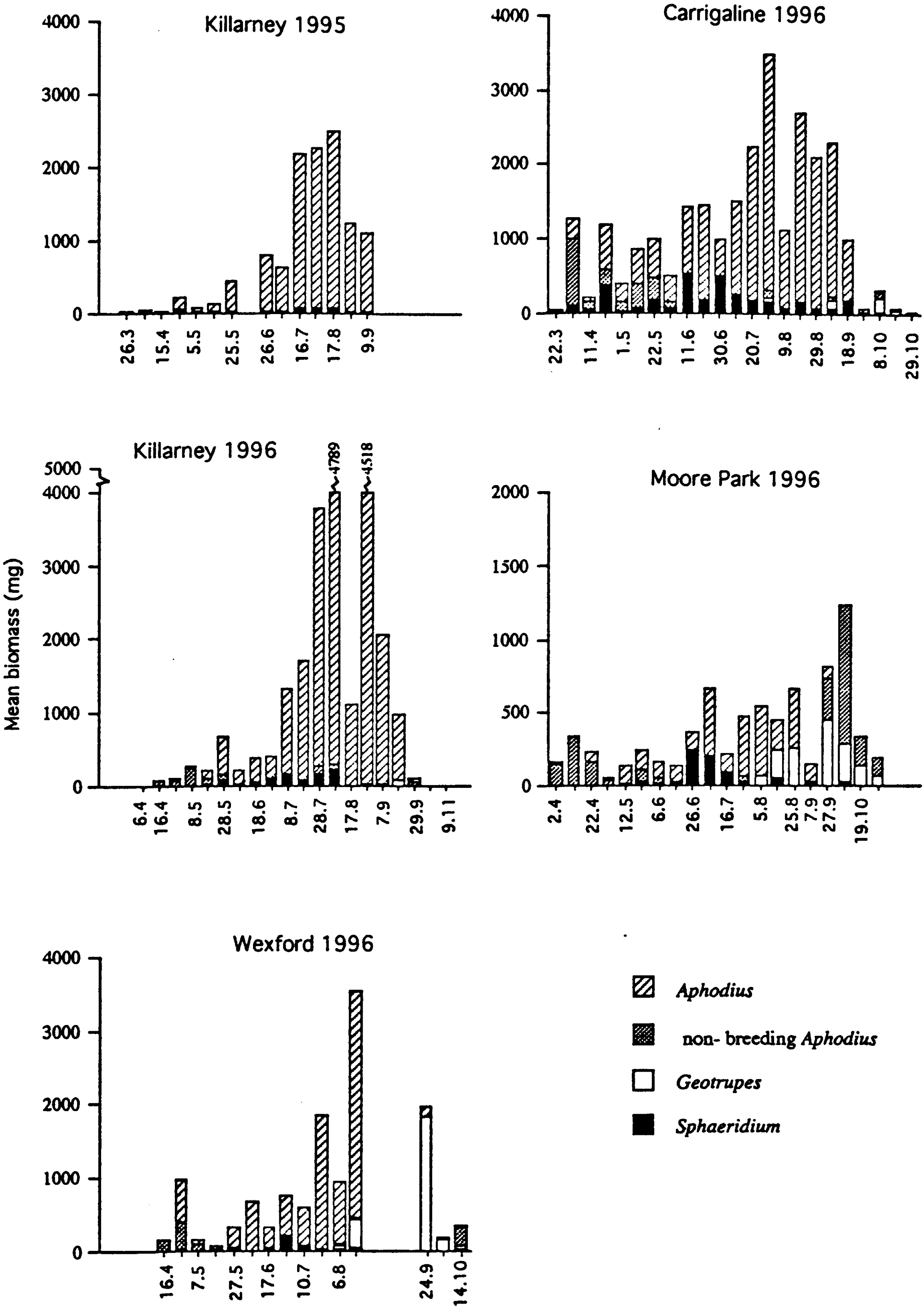


Fig. 1. Seasonal changes in dung beetle biomass captured in baited pitfall traps at Killarney 1995 - 1996 and at other sites in southern Ireland during 1996. Note the change in scale of Moore Park y-axis. See legend for key to taxocenes.

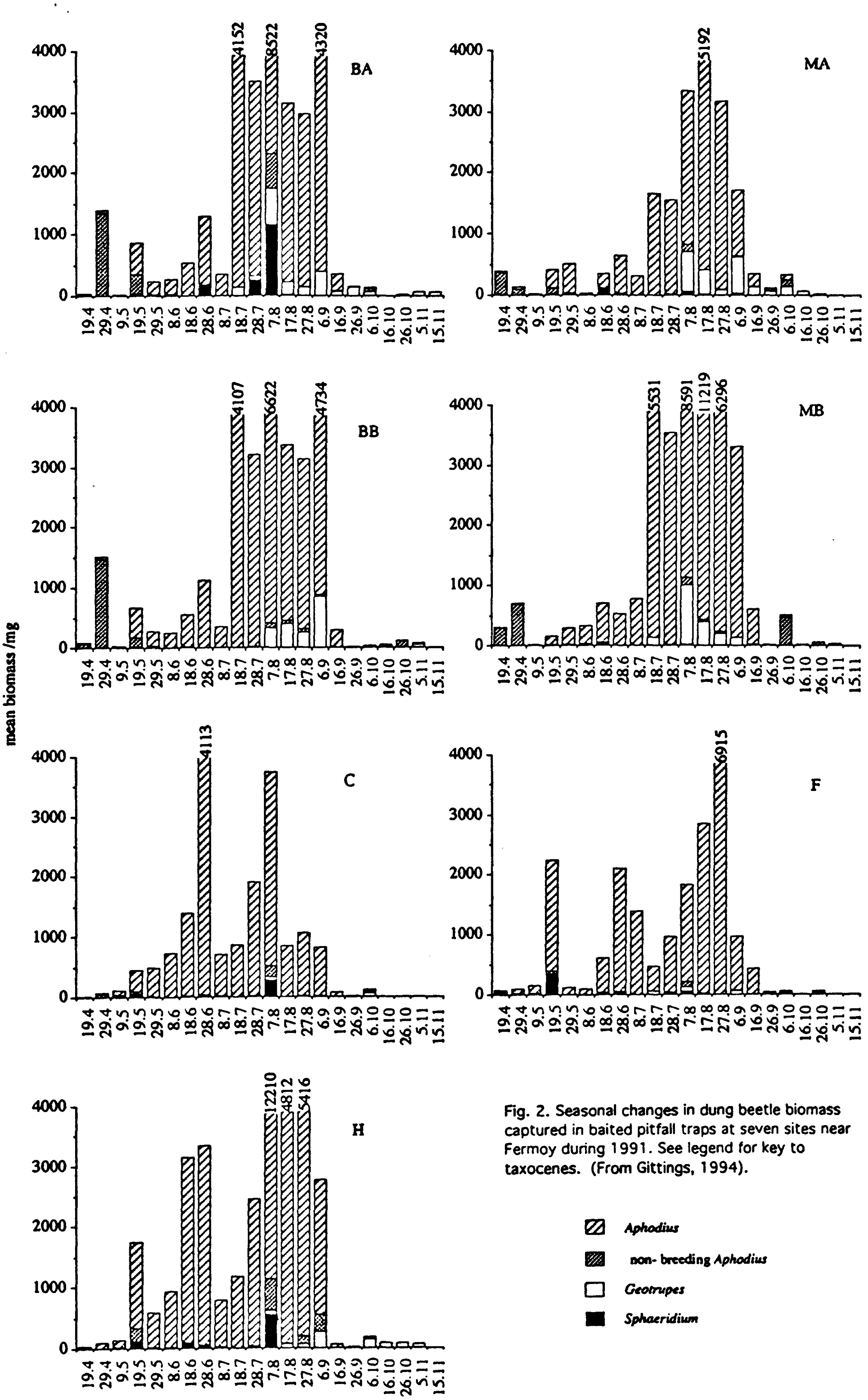


Fig. 2. Seasonal changes in dung beetle biomass captured in baited pitfall traps at seven sites near Fermoy during 1991. See legend for key to taxocenes. (From Gittings, 1994).

Table 1. Total annual pitfall captures over various sites and years in southern Ireland. Indicated are the first and last dates when pitfall trapping was conducted, as well as the number of trapping intervals. Where appropriate, totals for the f_1 and f_2 generations are given seperately. The data from Fota 1991 and 1992 are from Gittings (1994).

		Fota 1991	Fota 1992	Fota 1995	Fota 1996	Killarney 1995	Killarney 1996	Moorepark 1996	Wexford 1996	Carrigaline 1996
Duration		20/3-11/12	20/3-20/10	10/3- 8/11	25/3 - 6/11	26/3- 9/9	16/4 -24/10	12/4 - 8/11	26/4 -24/10	1/4 - 8/11
No. of intervals		27	22	25	23	14	19	20	15	23
A. ater (De Geer)		224	650	230	548	52	237	185	1145	888
A. depressus (Kugel.)	f1	120	357	137	354	134	564	45	52	870
	f2	30	169	22	31	67	54	4	6	61
A. erraticus (L.)	f1	16	125	19	30	2	-	13	5	1
	f2	6	35	7	11	-	-	25	1	3
A. fimetarius (L.)	f1	29	47	1152	45	16	41	33	201	226
	f2	34	13	39	68	-	68	61	34	58
A. fossor (L.)		36	62	39	74	37	50	20	203	151
A. granarius (L.)		27	34	-	-	-	-	427	6	-
A. merdarius (Fabr.)		2	-	-	-	-	-	-	-	-
A. prodromus (Brahm)	f1	1433	696	3250	1821	53	65	596	215	1633
	f2	2615	853	487	804	0	31	1043	55	115
A. rufipes (L.)		10754	2242	4676	979	1527	3171	375	998	2620
A. rufus (Moll)		1845	42	65	27	-	-	19	129	59
A. sphacelatus(Panz.)	f1	138	18	126	420	24	585	127	565	26
	f2	102	87	162	102	0	26	89	243	7
G. spiniger (Marsh.)		149	32	29	42	-	1	22	38	7
S. bipustulatum Fabr.		1	-	2	-	-	-	-	-	-
S. lunatum Fabr.		1045	287	888	2132	30	240	66	46	1347
S. scarabaeoides (L.)		575	131	965	2486	33	216	315	214	145
unidentified Sph.		91	34	-	-	-	-	-	-	-
M. carbonarius (Illiger)		780	1307	-	389	-	110	13	114	280

Table 2. Flight activity periods of dung beetles from various sites and years in southern Ireland.
Flight activity periods indicate the beginning of those trapping intervals in which 90% of the annual catch of each species was captured in cow dung-baited pitfall trapping. Seperate ranges are given for those species with f_1 and f_2 generations. Flight activity periods were not calculated for species or generations with less than 10 individuals captured. Note that the interruption of trapping in Wexford around September will affect calculations of the activity period of the late summer summer species at this site.

		Fota	Fota	Killarney	Killarney	Carrigaline	Moore Park	Wexford
		1995	1996	1995	1996	1996	1996	1996
A. ater		10/4 - 12/7	9/4 - 18/7	15/4 - 16/7	28/4 - 28/7	21/4 - 10/7	22/4 - 6/7	26/4 - 19/7
A. depressus	f1	30/4 - 12/7	29/4 - 18/7	15/5 - 5/8	18/5 - 18/7	12/5 - 10/7	22/4 - 26/7	27/5 - 19/7
	f2	12/7 - 20/10	18/7 - 29/7	5/8 - 19/9	28/7 - 6/9	30/7 - 18/9	-	19/7 - 16/8
A. erraticus	f1	30/5 - 2/7	29/4 - 29/7	-	-	-	22/5 - 16/7	-
	f2	11/8 - 21/8	29/7 - 7/9	-	-	-	26/7 - 5/8	-
A. fimetarius	f1	10/4 - 12/7	30/3 - 8/7	5/4 - 6/7	18/4 - 18/7	1/4 - 21/6	2/4 - 26/7	26/4 - 27/6
	f2	21/7 - 29/9	29/7 - 27/9	-	28/7 - 27/8	10/7 - 8/10	4/9 - 7/10	10/7 - 14/10
A. fossor		30/5 - 11/8	19/5 - 18/7	5/5 - 5/8	28/5 - 27/8	12/5 - 29/8	6/6 - 16/7	27/5 - 19/7
A. granarius		-	-	-	-	-	2/5 - 26/6	-
A. prodromus	f1	31/3 - 20/5	30/3 - 29/5	15/4 - 25/5	18/4 - 28/5	1/4 - 22/5	2/4 - 22/5	16/4 - 27/5
	f2	29/9 - 29/10	17/9 - 27/10	-	6/9 - 24/10	8/9 - 29/10	17/9 - 29/10	3/10 - 14/10
A. rufipes		29/6 - 20/10	9/6 - 17/9	6/7 - 19/9	8/7 - 6/9	21/6 - 18/9	26/6 - 4/9	10/7 - 16/8
A. rufus		1/8 - 20/10	8/7 - 27/9	-	-	20/7 - 8/9	5/8 - 29/10	10/7 - 16/8
A. sphacelatus	f1	10/3 - 19/4	15/3 - 29/4	5/4 - 15/5	10/4 - 28/5	1/4 - 21/4	2/4 - 22/4	16/4 - 27/5
	f2	29/9 - 29/10	18/10 - 27/10	-	27/8 - 24/10	19/8 - 29/8	7/10 - 29/10	3/10 - 24/10
G. spiniger		11/8 - 19/10	18/8 - 18/10	-	-	-	15/8 - 17/10	6/8 - 27/8
S. lunatum		20/5 - 19/10	19/5 - 17/9	26/5 - 17/8	28/5 - 7/8	21/4 - 8/9	6/6 - 7/10	26/4 - 14/10
S. scarabaeoides		30/5 - 9/10	9/6 - 28/8	26/5 - 29/7	18/5 - 7/8	1/4 - 18/9	6/6 - 15/8	17/5 - 16/8

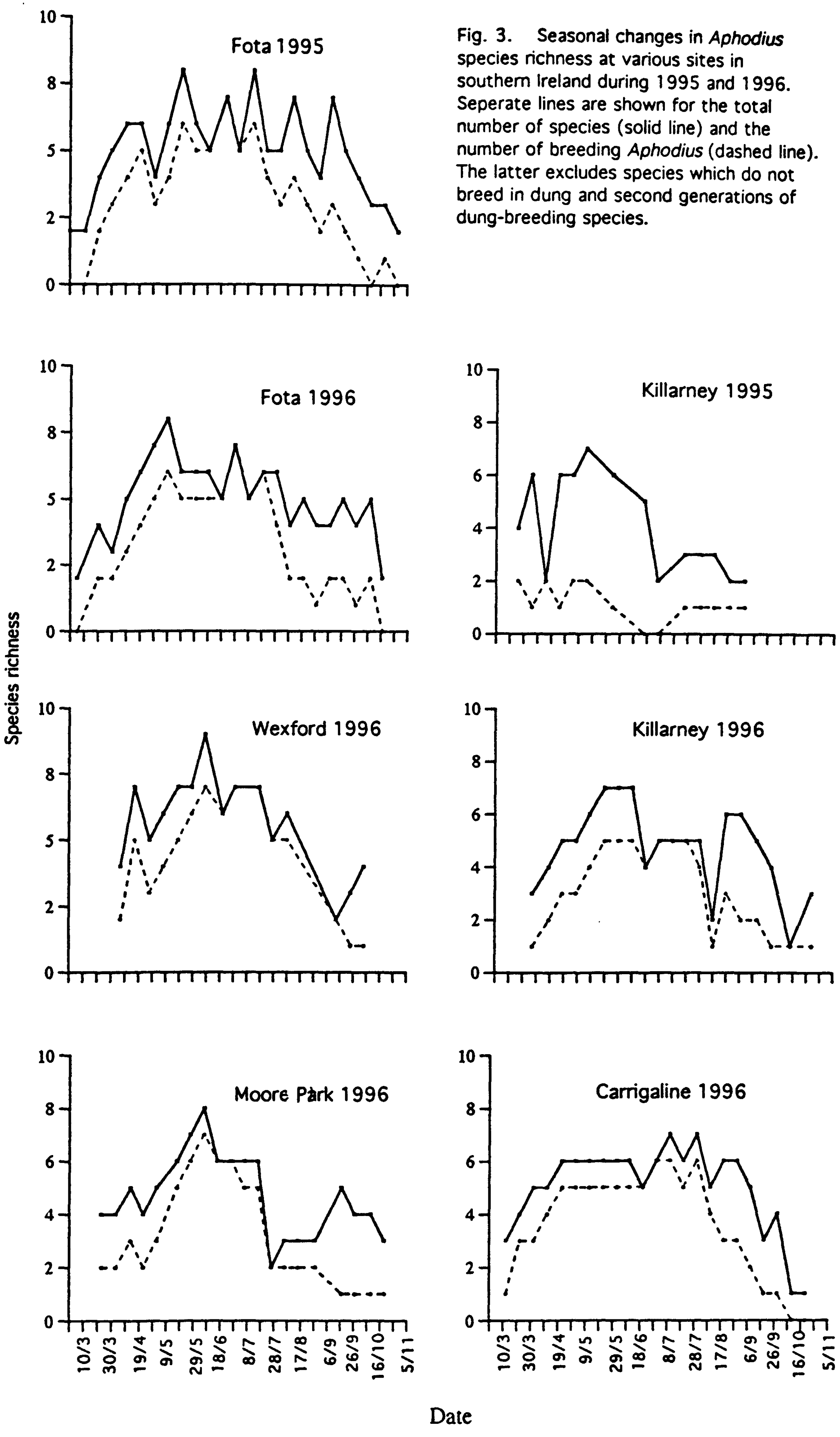


Fig. 3. Seasonal changes in *Aphodius* species richness at various sites in southern Ireland during 1995 and 1996. Seperate lines are shown for the total number of species (solid line) and the number of breeding *Aphodius* (dashed line). The latter excludes species which do not breed in dung and second generations of dung-breeding species.

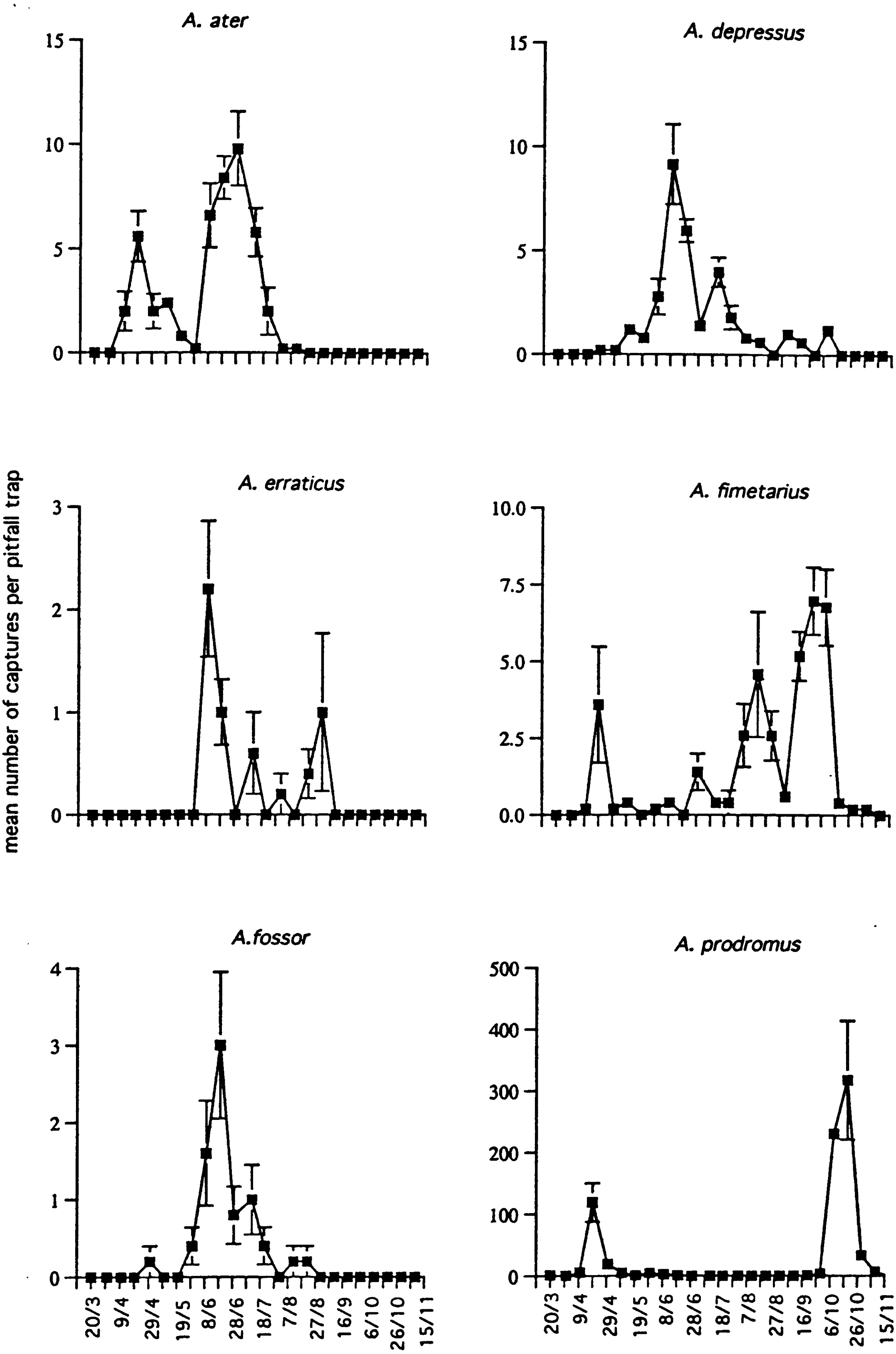


Fig. 4. Seasonal patterns of pitfall captures of dung beetle species at Fota during 1995 (mean ± s.e.).

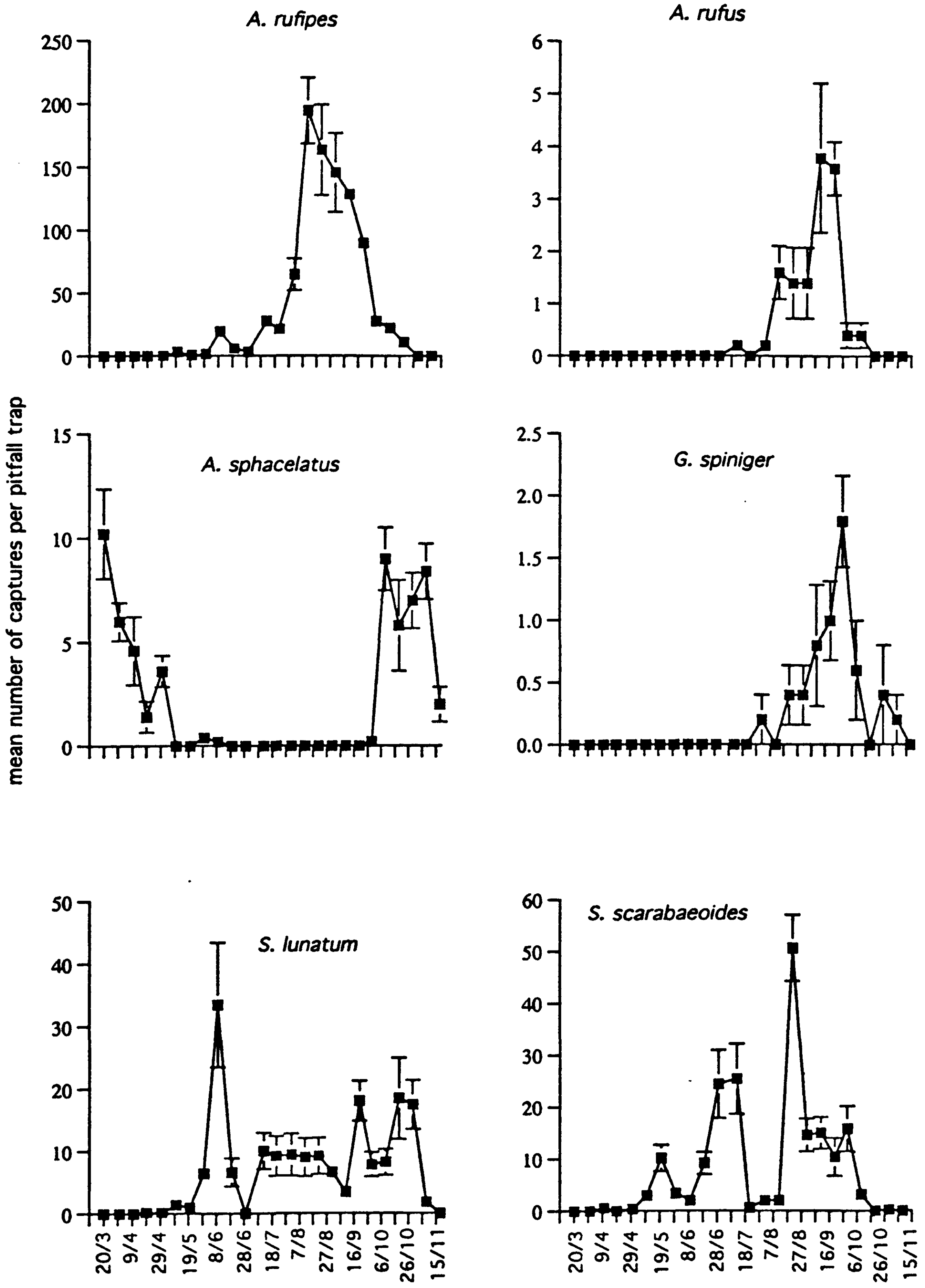


Fig. 4 -contd. Pitfall captures at Fota during 1995.

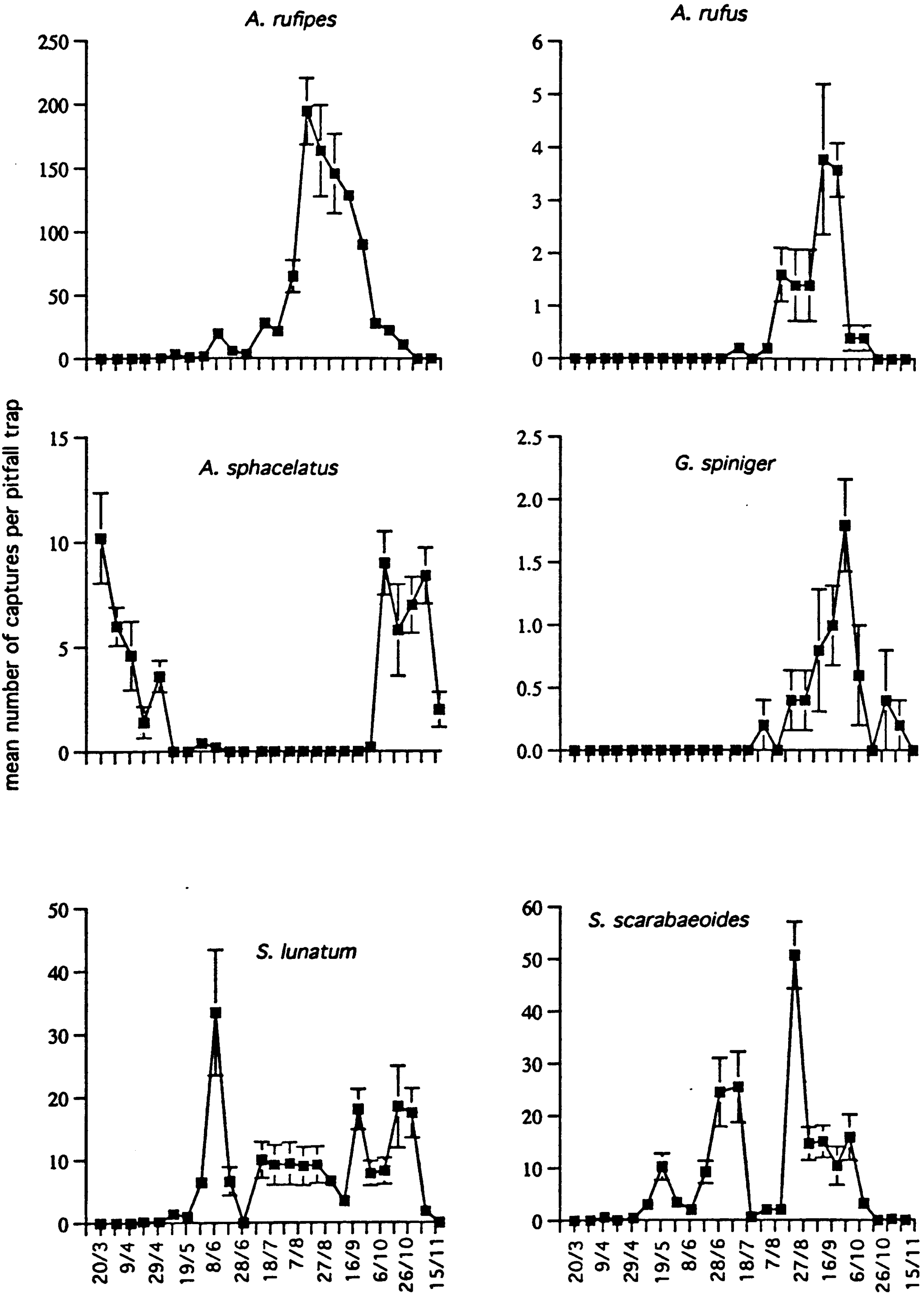


Fig. 4 -contd. Pitfall captures at Fota during 1995.

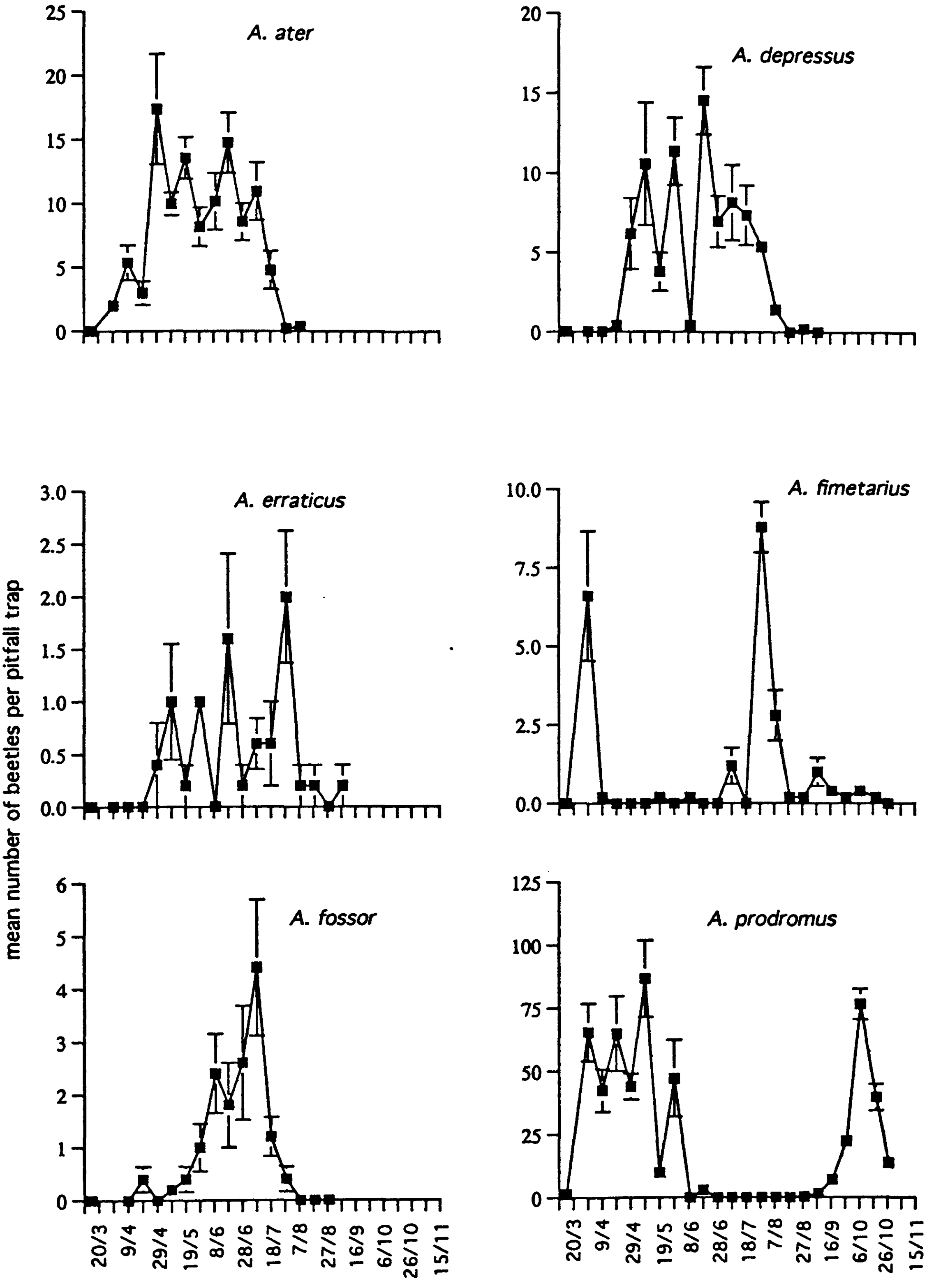


Fig. 5. Seasonal patterns of pitfall captures of dung beetle species at Fota in 1996 (mean ± s.e.). Five replicate pitfall traps were baited with cow dung.

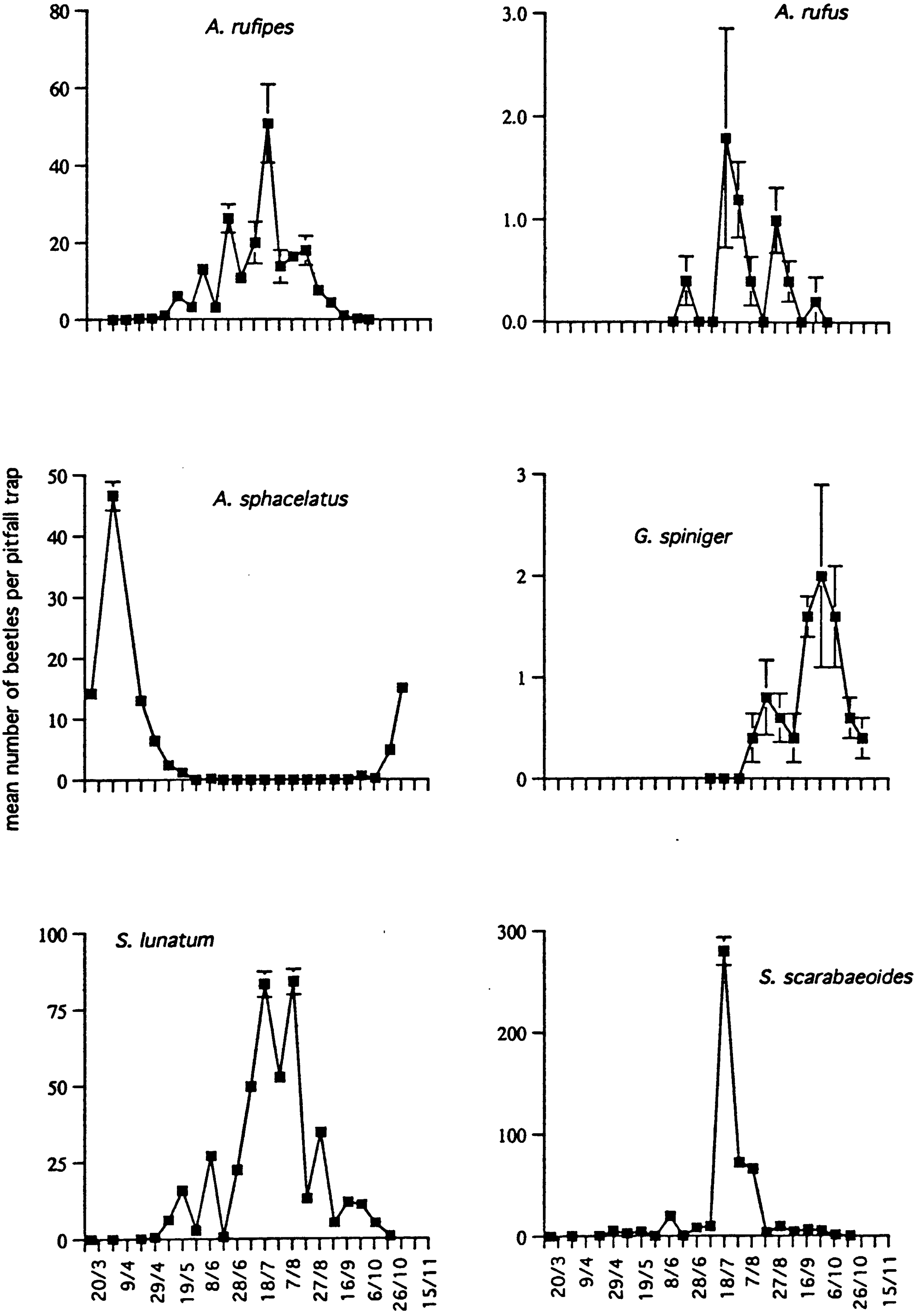


Fig. 5 - contd. Pitfall captures of dung beetles in Fota in 1996.

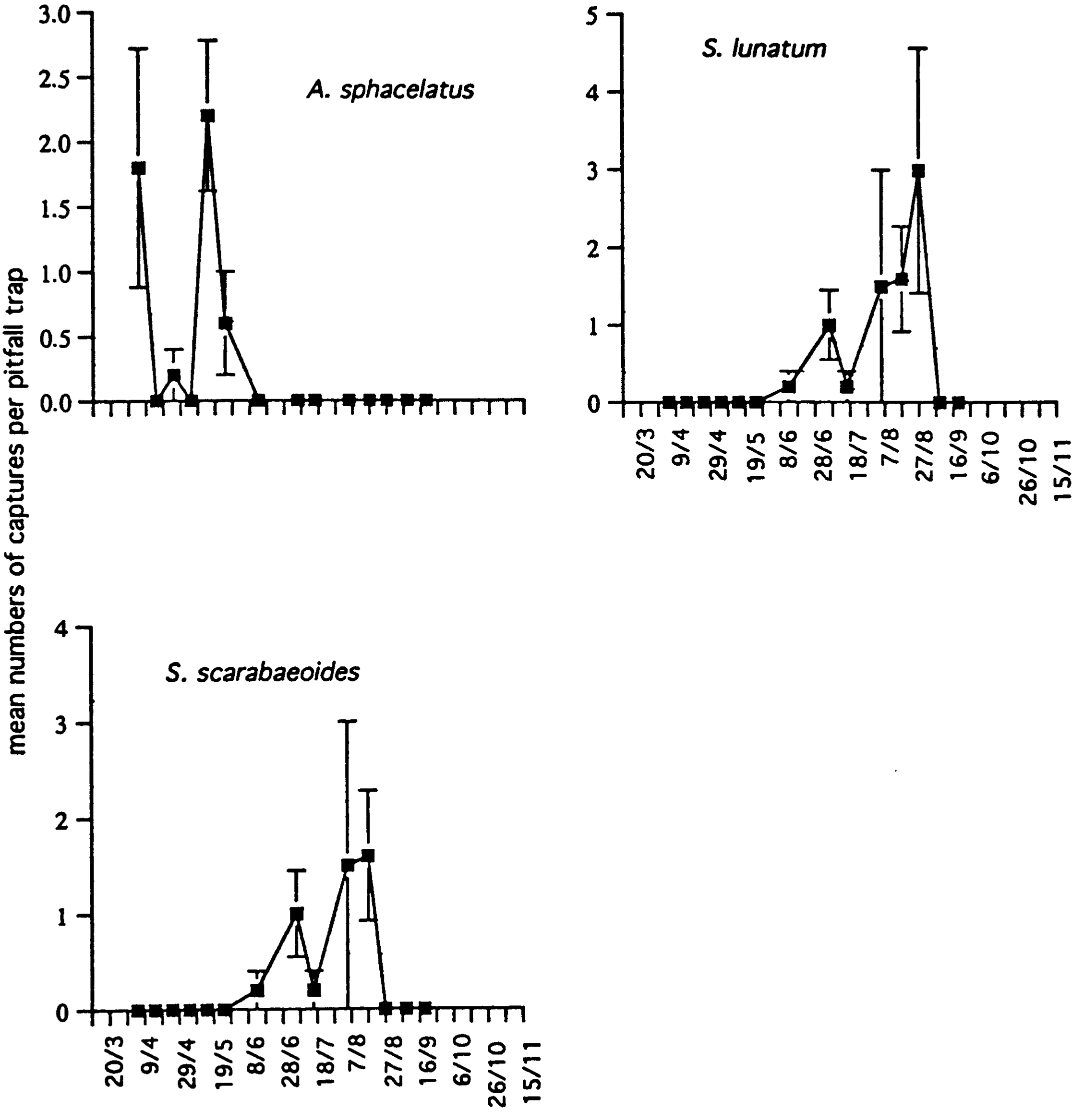


Fig. 6 -contd. Pitfall captures at Killarney during 1995.

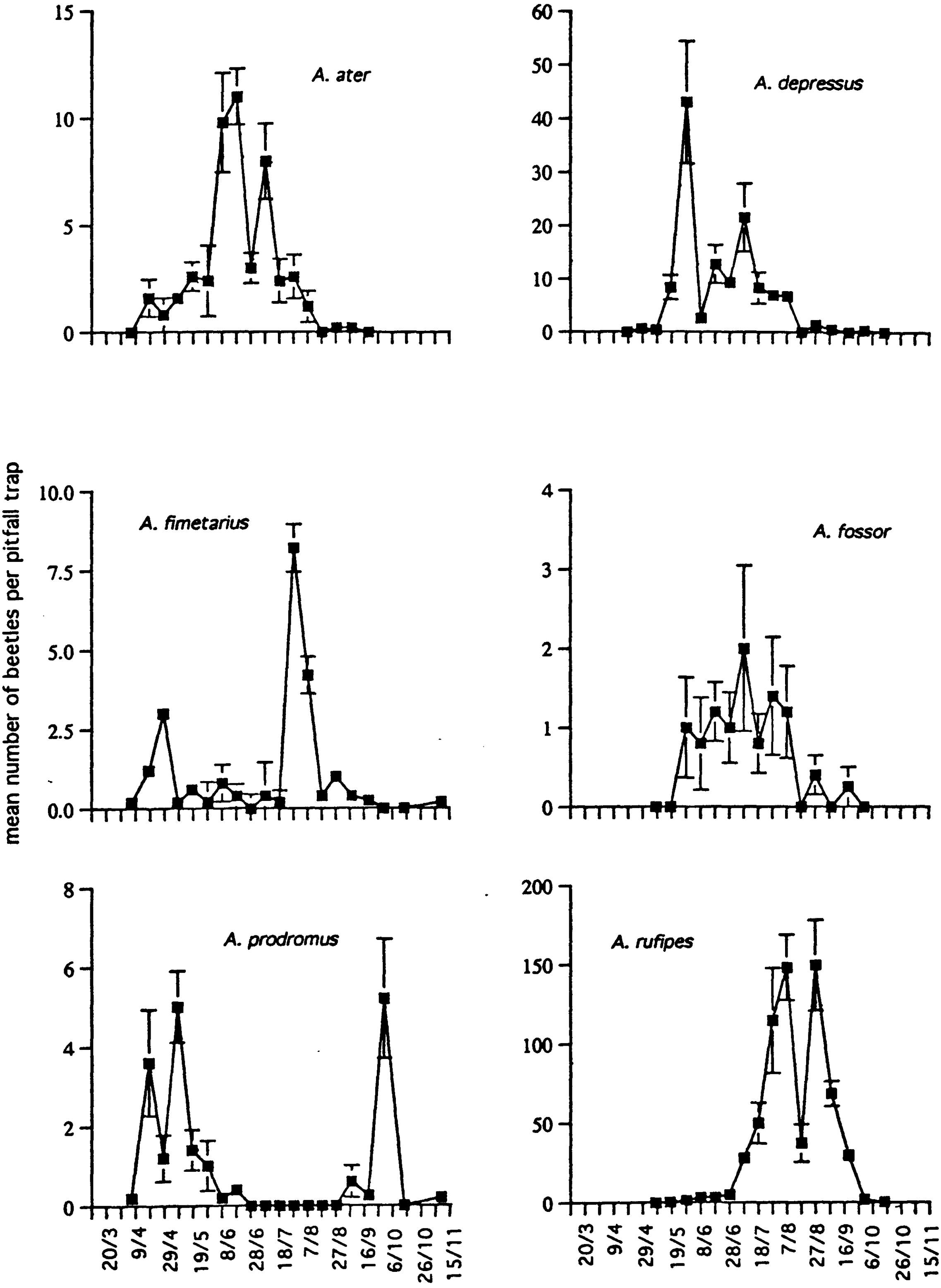


Fig. 7. Seasonal changes in pitfall captures of dung beetle species at Killarney during 1996 (mean ± s.e.).

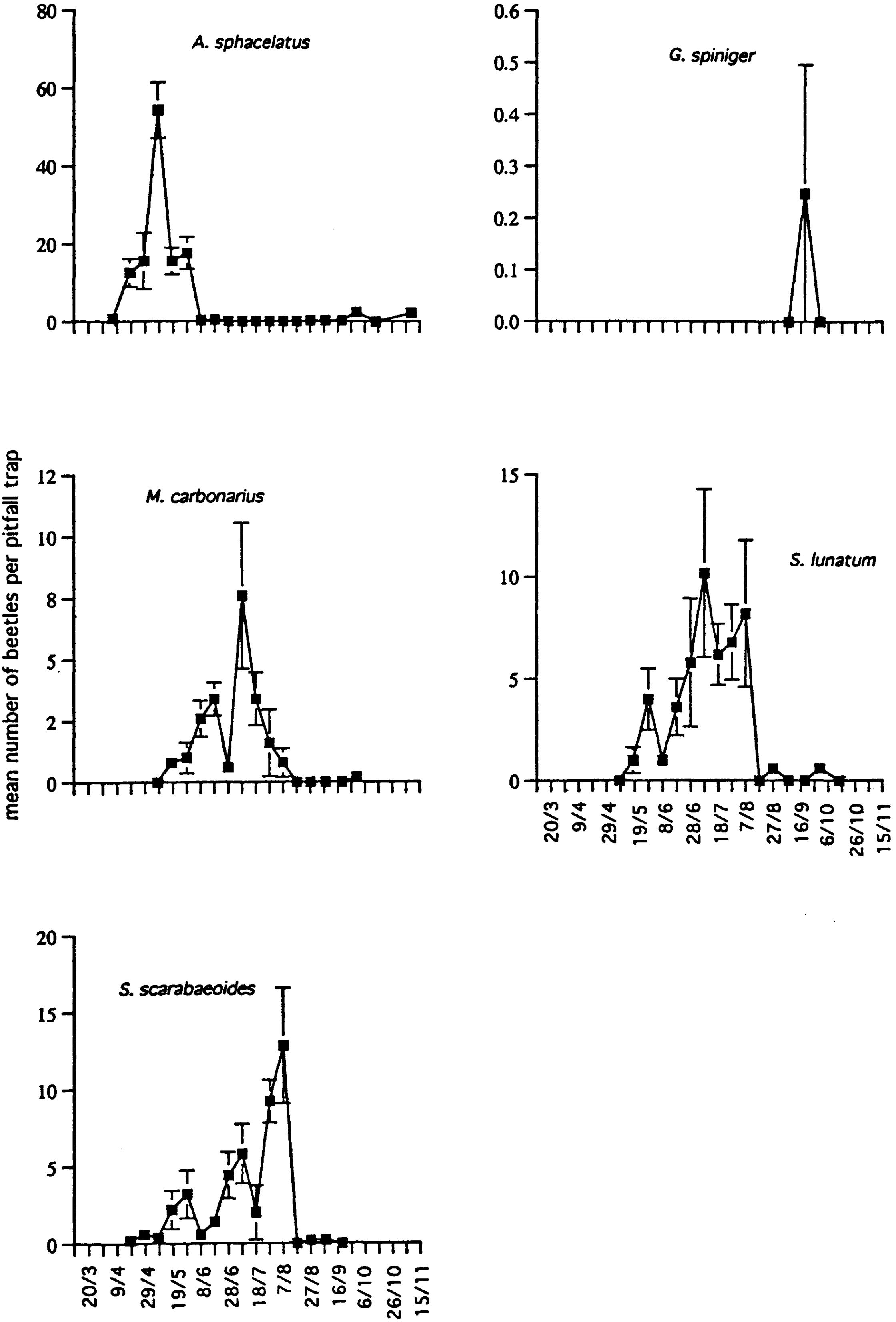


Fig. 7 -contd. Pitfall captures at Killarney during 1996.

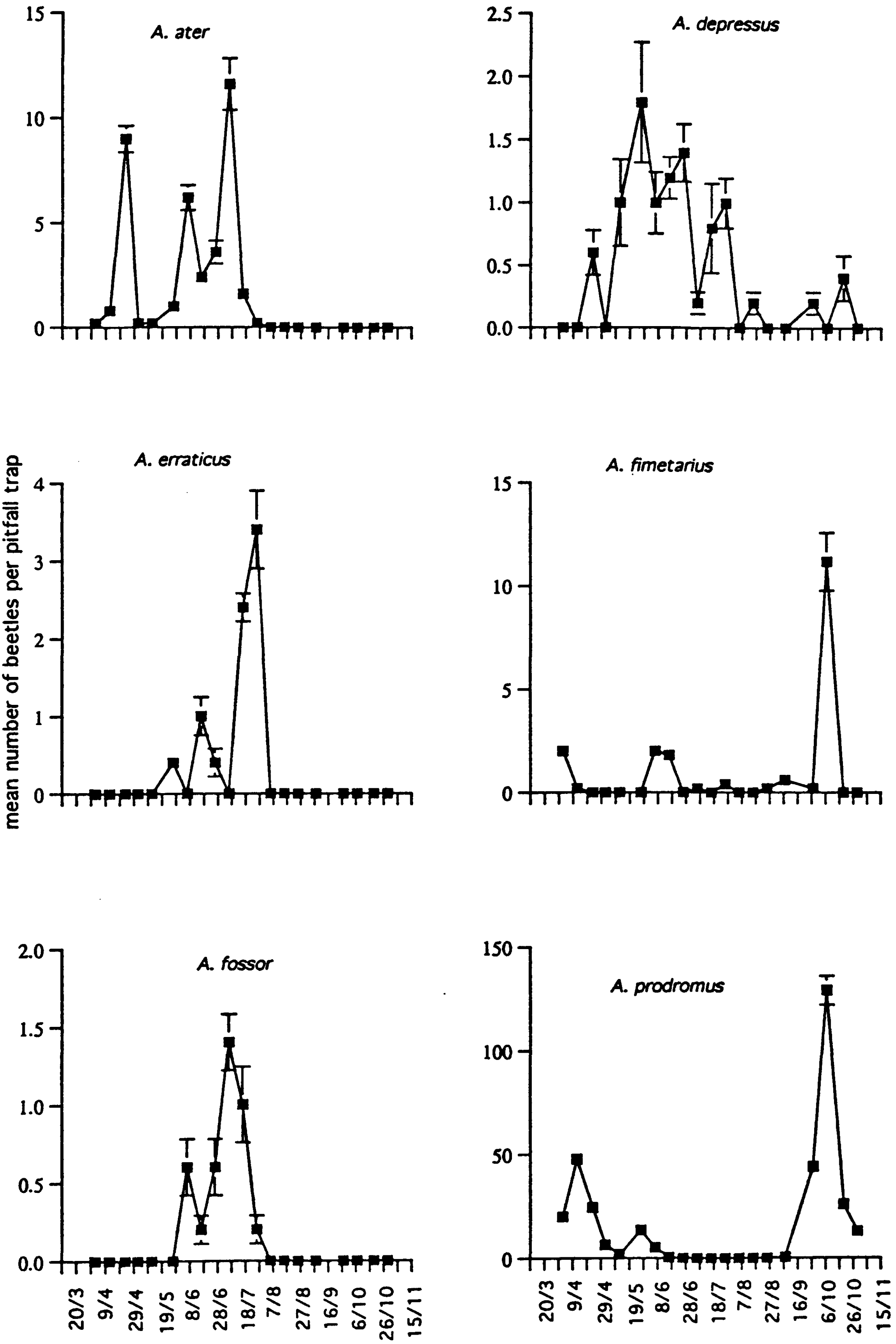


Fig. 8. Seasonal changes in pitfall captures of dung beetle species at Moorepark during 1996 (mean ± s.e.).

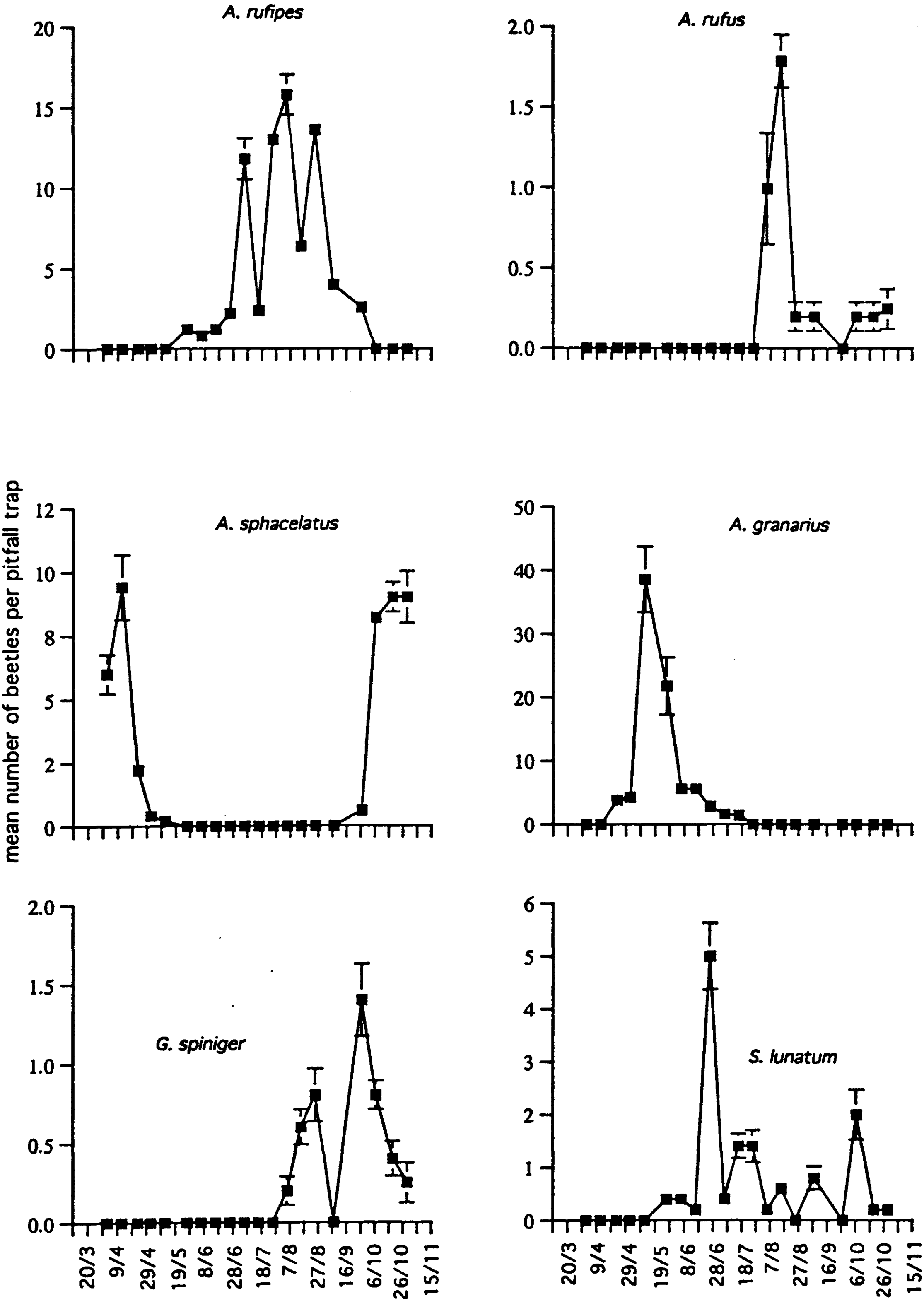


Fig. 8 -contd. Pitfall captures at Moorepark in 1996.

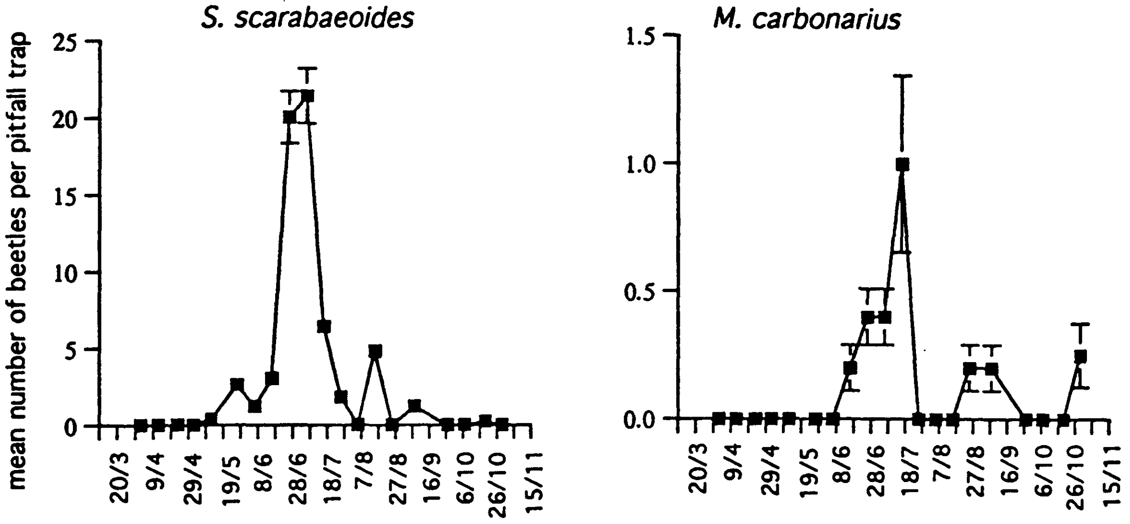


Fig. 8 - contd. Pitfall captures at Moorepark during 1996.

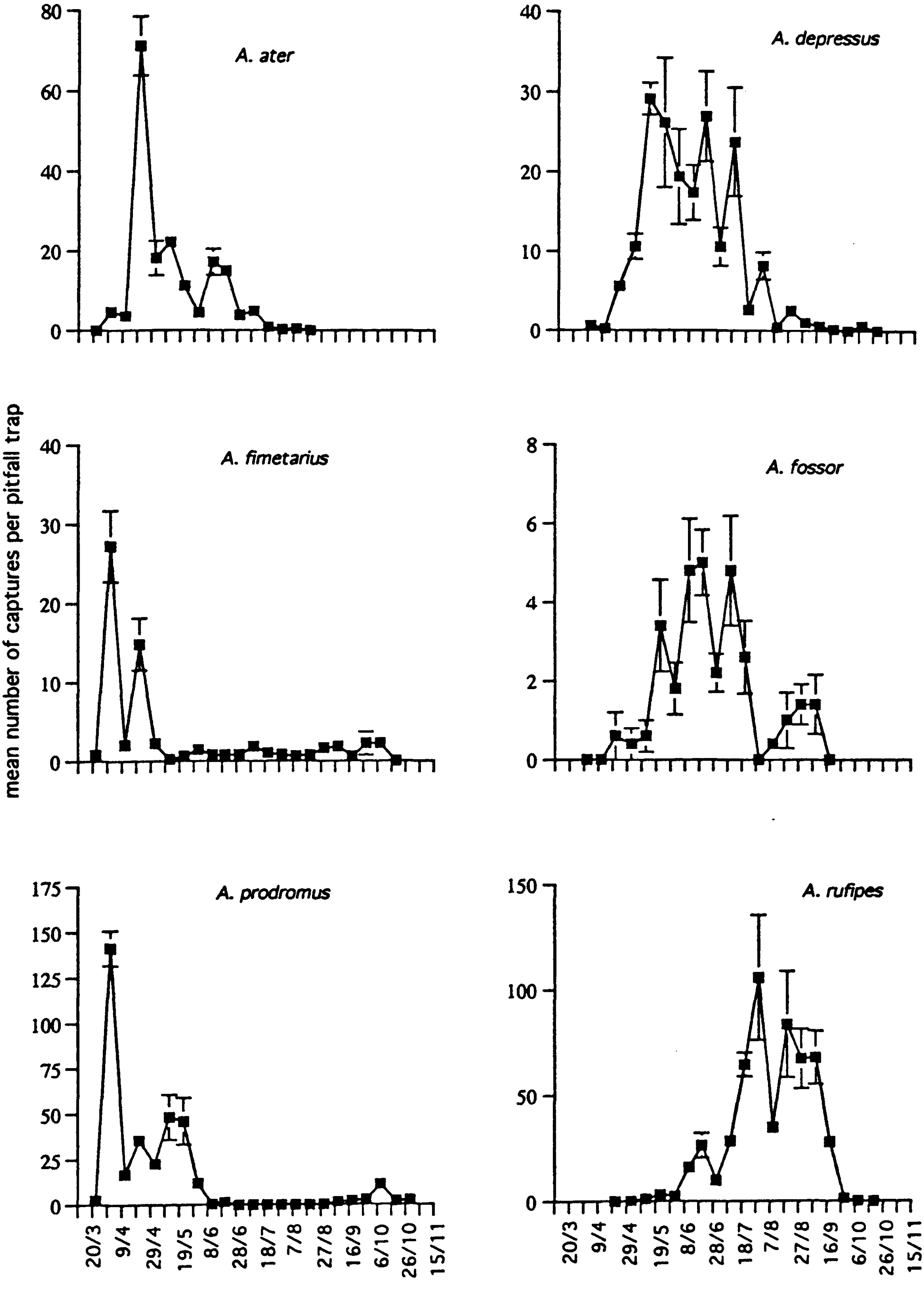


Fig. 9. Seasonal patterns of pitfall captures of dung beetle species at Carrigaline during 1996 (mean ±s.e.).

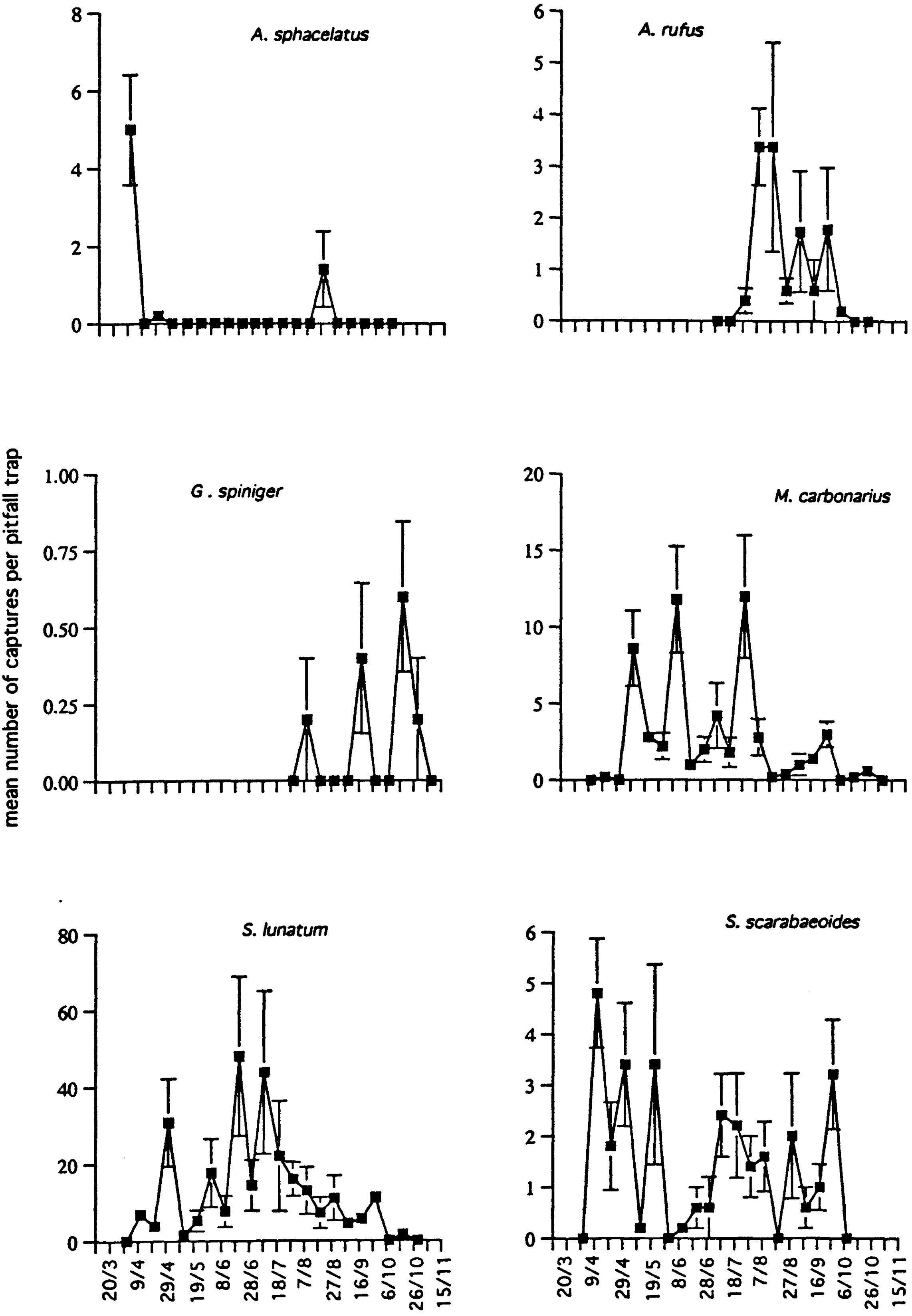


Fig. 9 - contd. Pitfall captures of dung beetle species at Carrigaline during 1996.

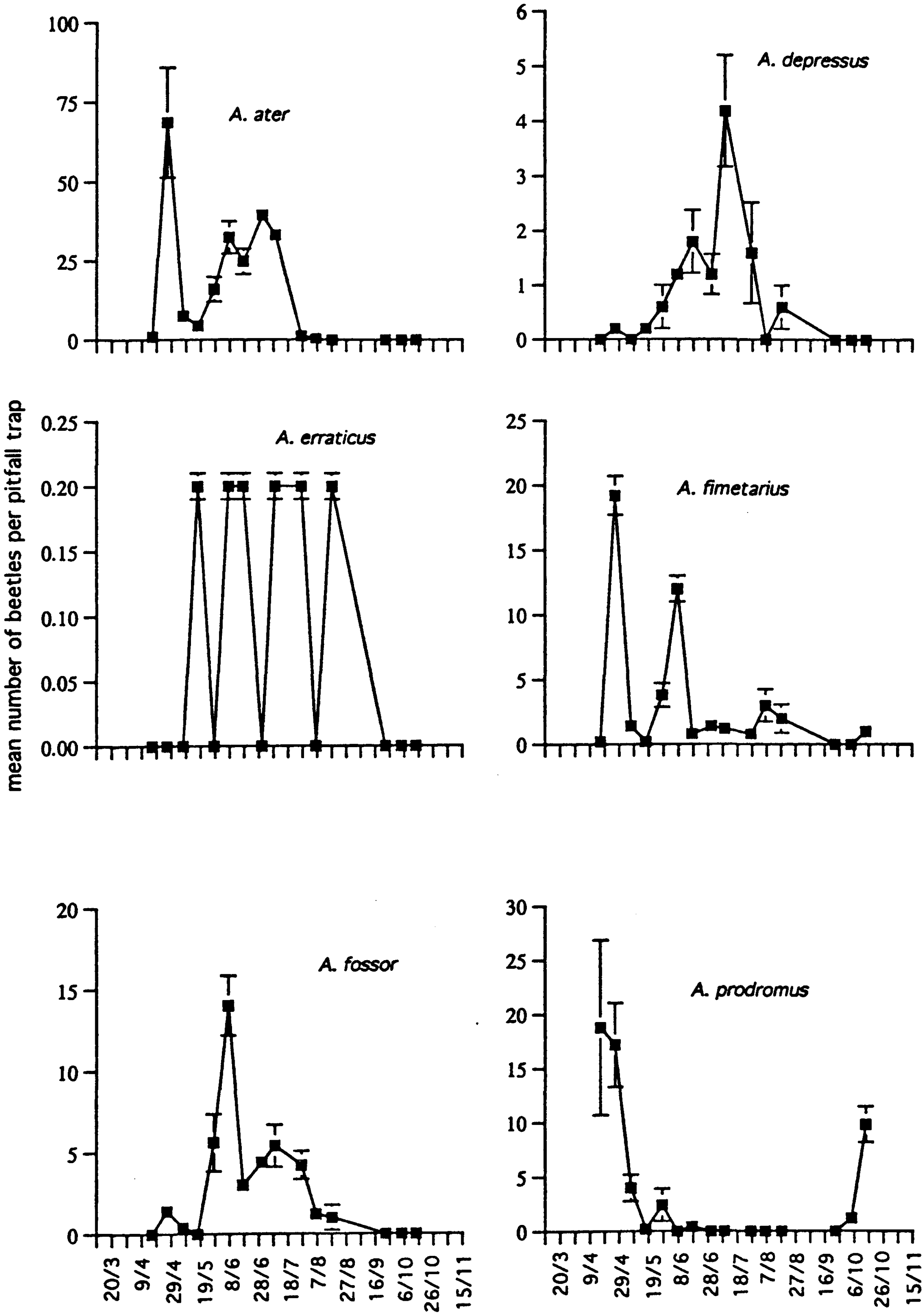


Fig. 10. Seasonal patterns of pitfall captures of dung beetles at Johnstown Castle, Co. Wexford during 1996 (mean ±s.e.).

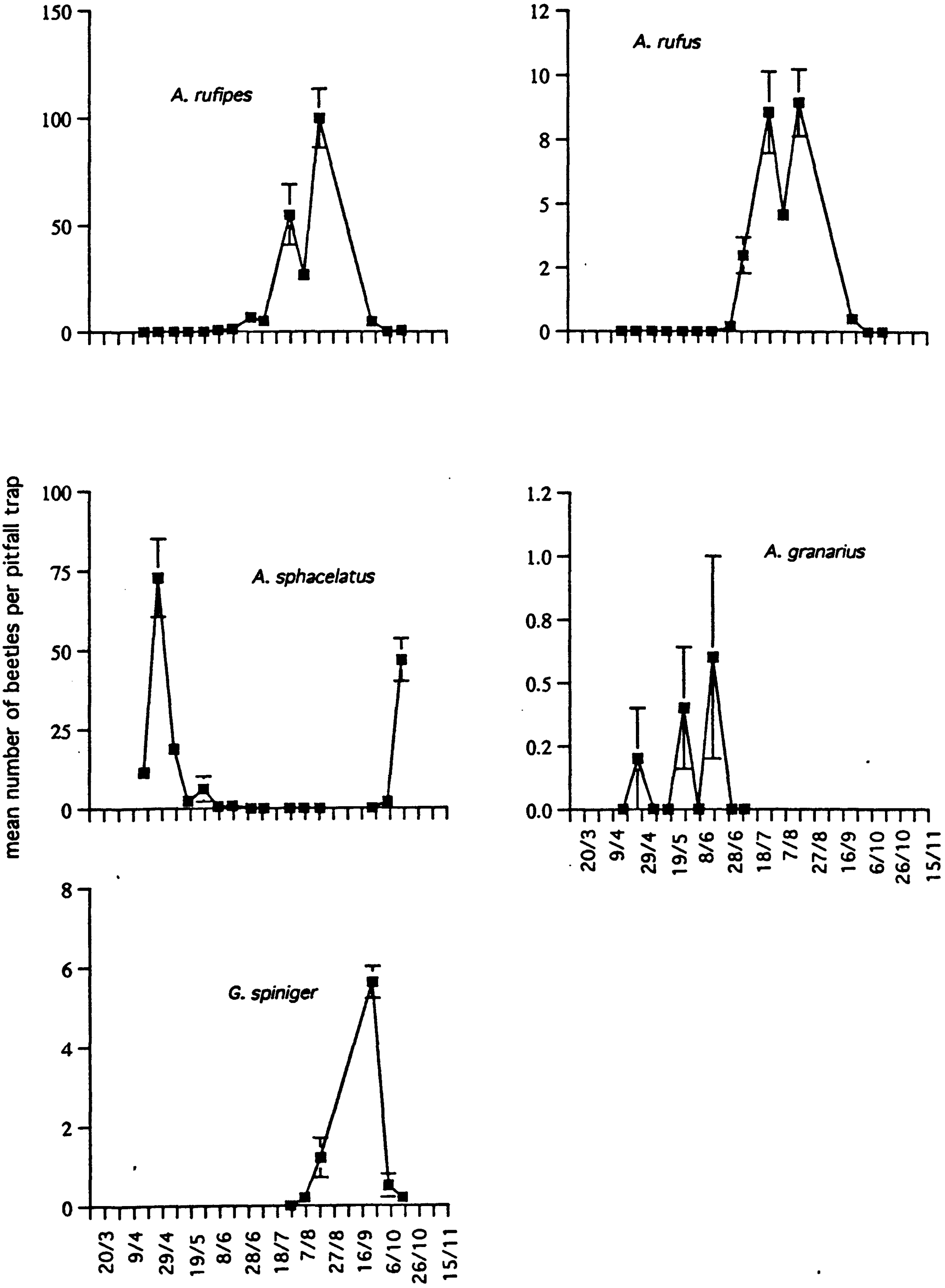


Fig. 10 -contd. Pitfall captures at Wexford during 1996.

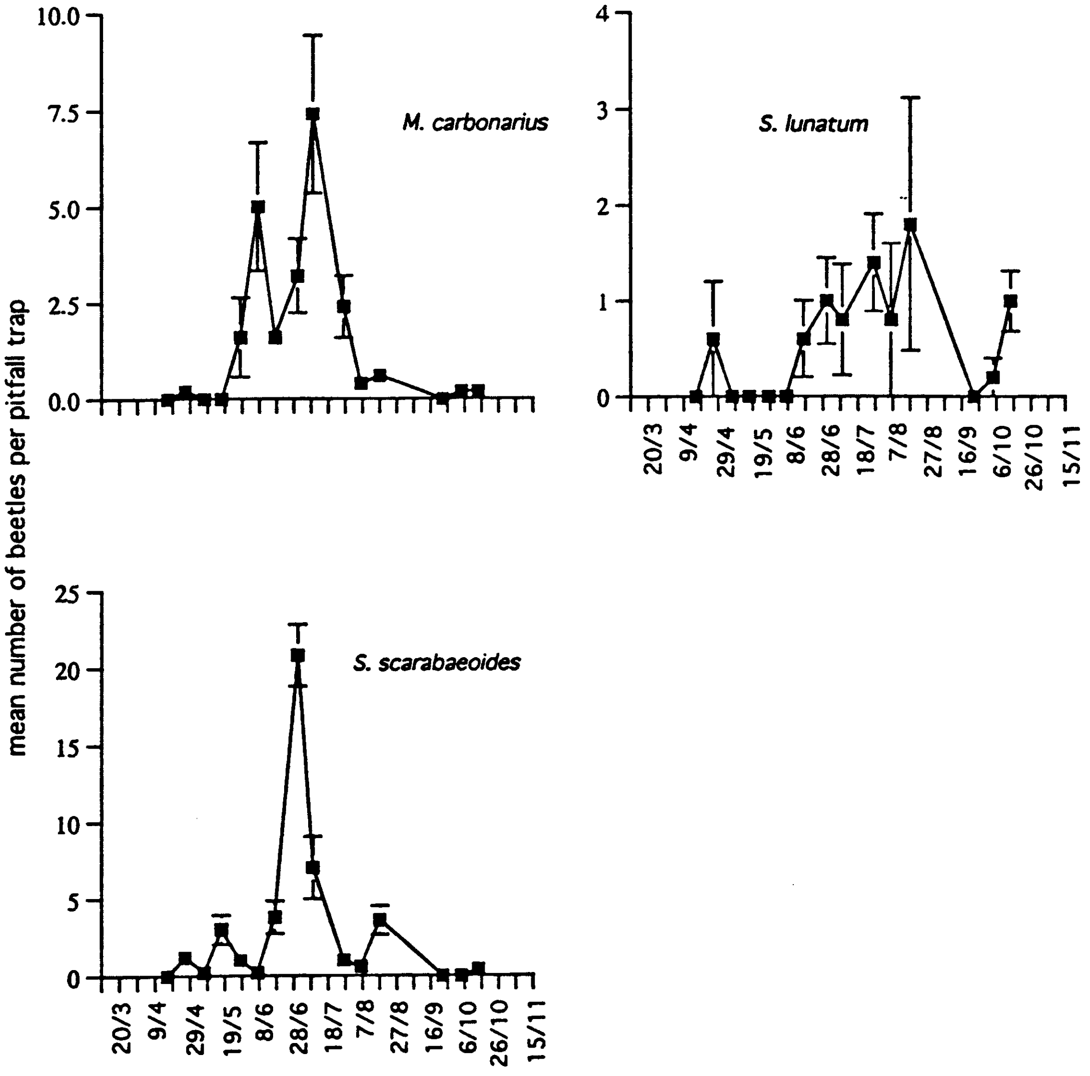


Fig. 10 -contd. Pitfall captures at Wexford during 1996.

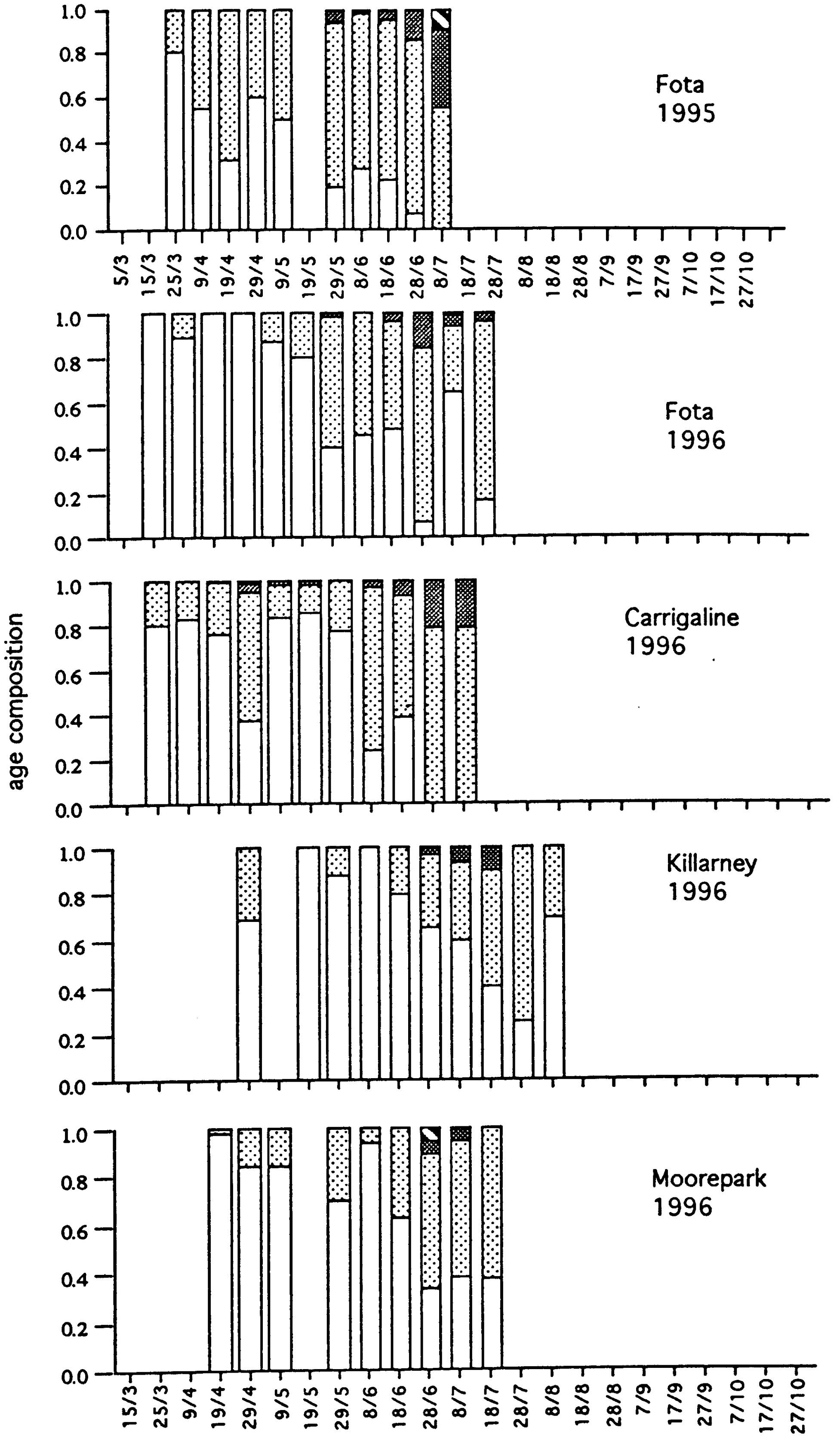


Fig. 11. Seasonal changes in the age composition of *A. ater* at several sites in southern Ireland. Insufficient data was available from the Killarney 1995 data set. Beetles were aged by the degree of tibial wear on their foretibia, which varied from no tibial wear (class N) to heavily worn (class H). Histograms represent age composition when ≥10 individuals were available. See text for details.

■ H
▧ M
▩ S2
⬚ S1
□ N

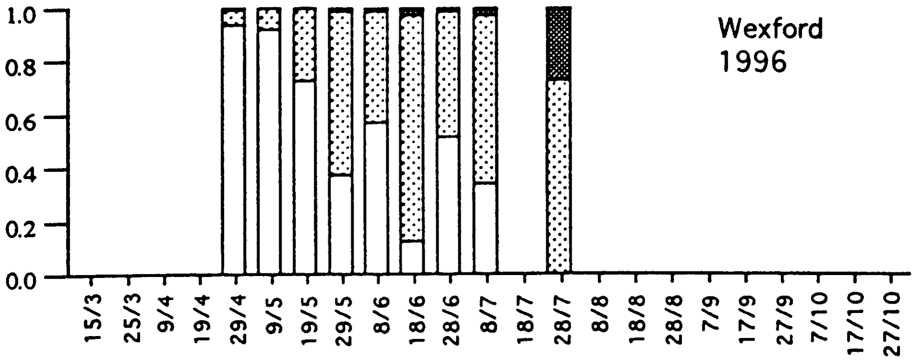


Fig. 11 -contd. Tibial wear composition of *A. ater.*

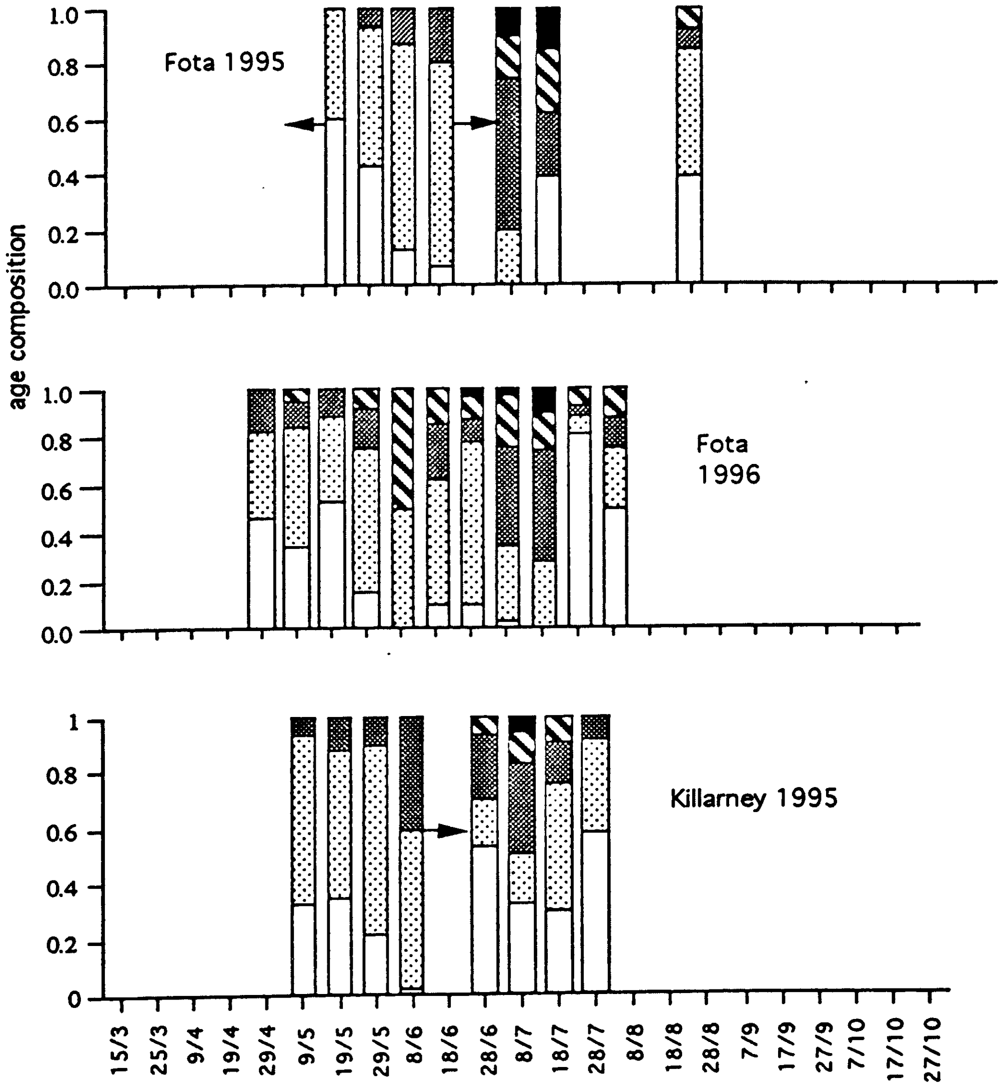


Fig. 12. Seasonal changes in the age composition of *A. depressus* at several sites in southern Ireland. Data from both 1995 and 1996 are presented for Fota and Killarney. Beetles were aged by the degree of wear on the foretibia, which varied from no tibial wear (class N) to heavily worn (class H). See text for details. Histograms represent age composition when ≥ 10 individuals were available. Arrows indicate where data for one (one arrow) or two (two arrows) trapping intervals were combined.

■ H
▧ M
▩ S2
⬚ S1
☐ N

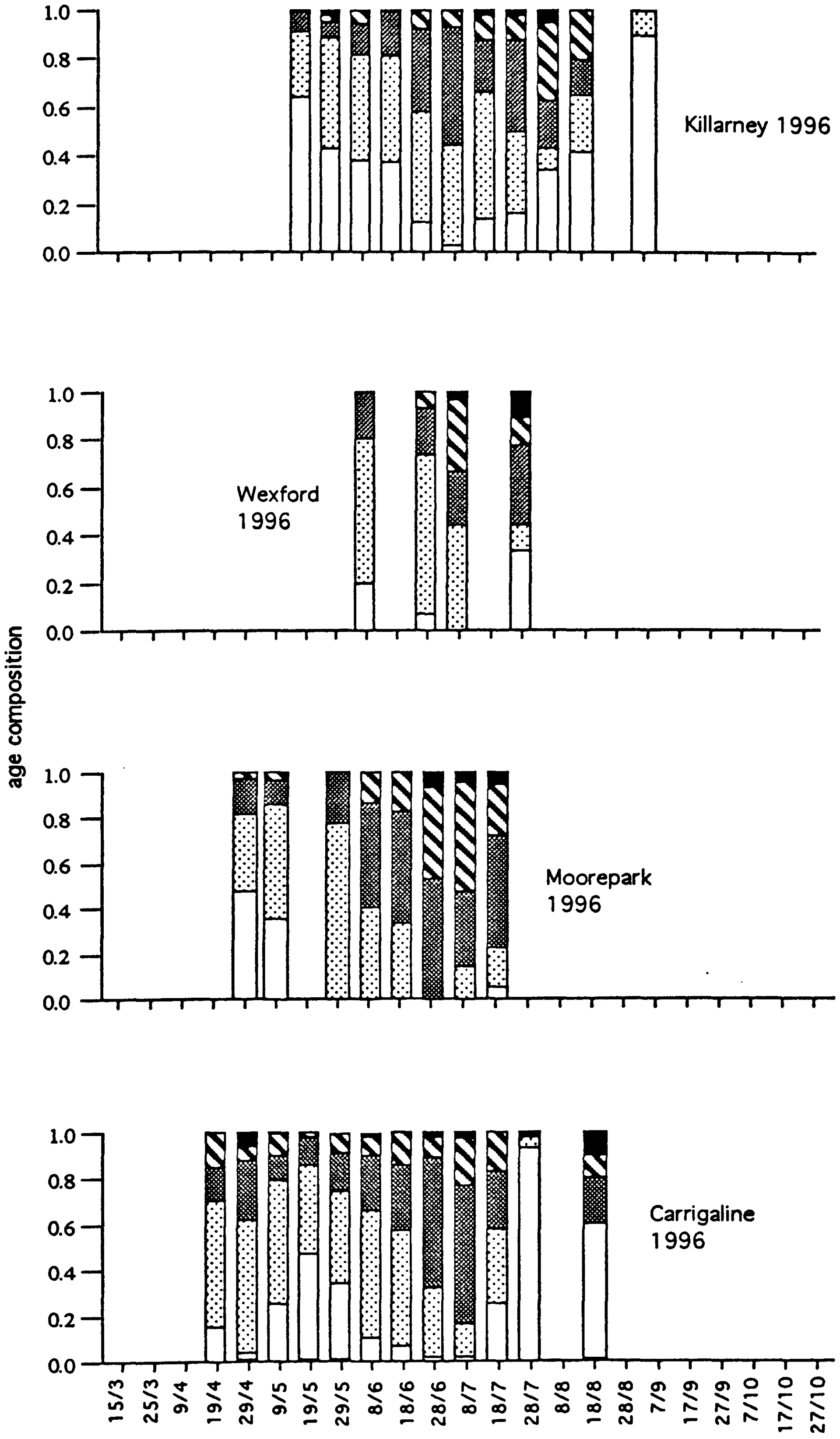


Fig. 12 -contd. Age composition of *A. depressus*.

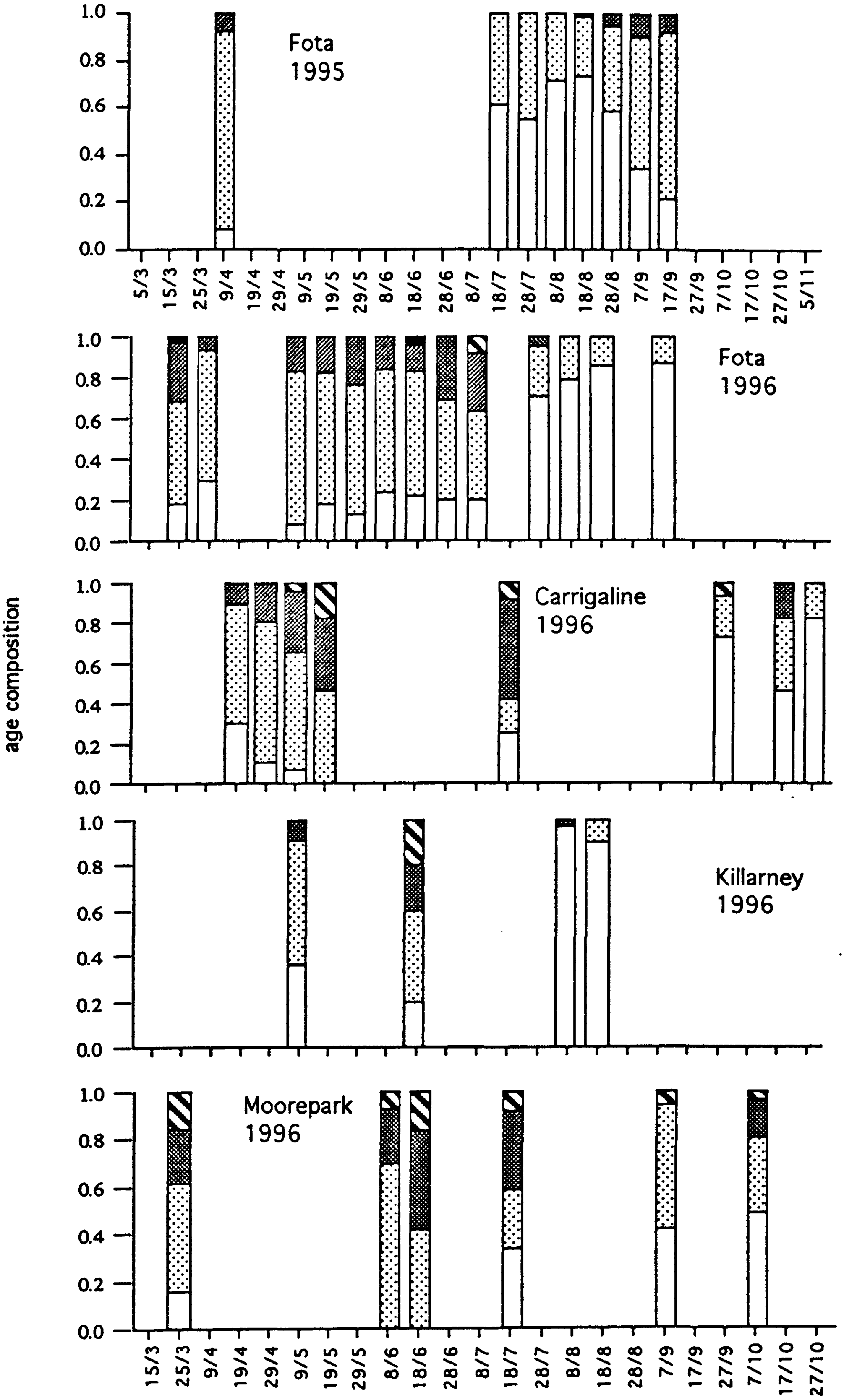


Fig. 13. Seasonal changes in the age composition of *A. fimetarius* at several sites in southern Ireland. Insufficient data was available from the Killarney 1995 data set. Beetles were aged by the degree of tibial wear on their foretibia, which varied from no tibial wear (class N) to heavily worn (class H). Histograms represent age composition when ≥10 individuals were available. See text for details.

■ H
▧ M
▩ S2
▒ S1
□ N

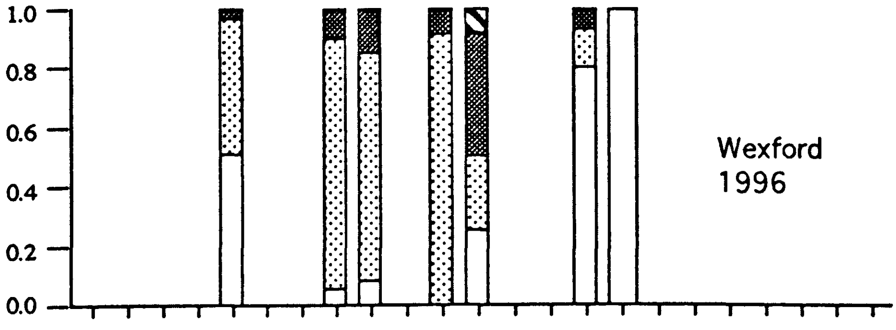


Fig. 13 - contd. Seasonal changes in the age composition of *A. fimetarius* at several sites in southern Ireland.

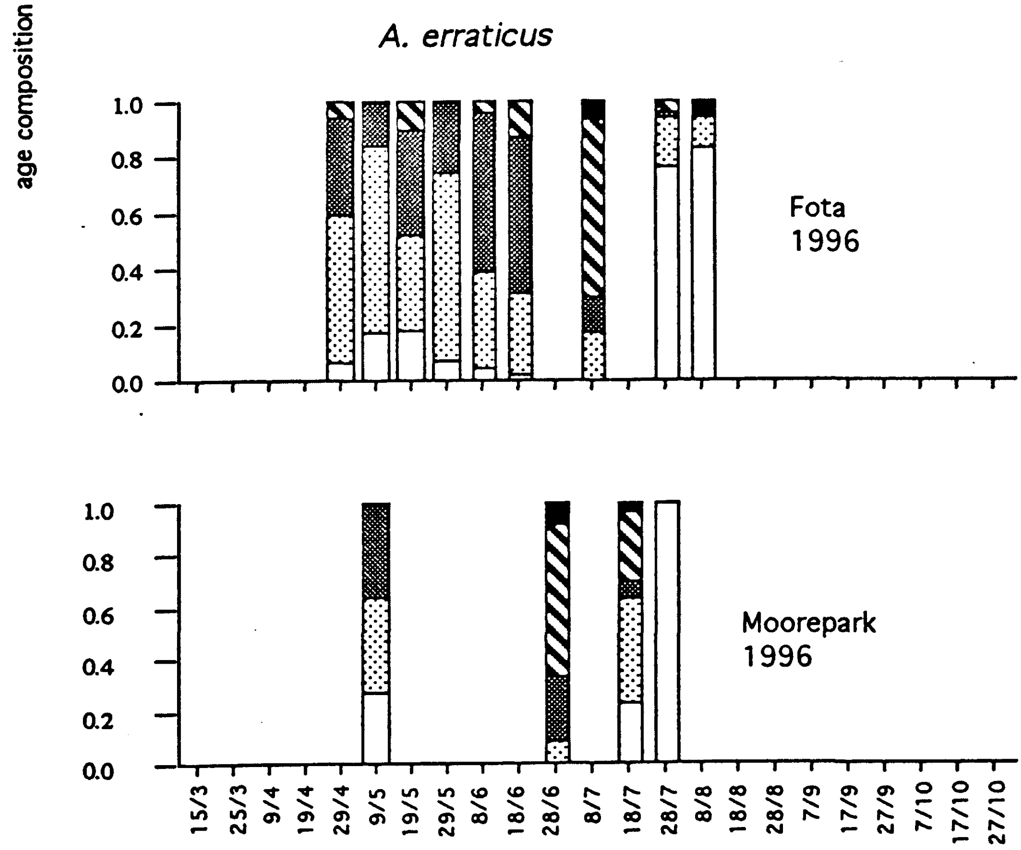


Fig. 14. Seasonal changes in the age composition of *A. erraticus* at several sites in southern Ireland. Sufficient data were available for Fota 1996 and Moore Park 1996 only. Histograms represent age composition when ≥ 10 individuals were available. See text for details.

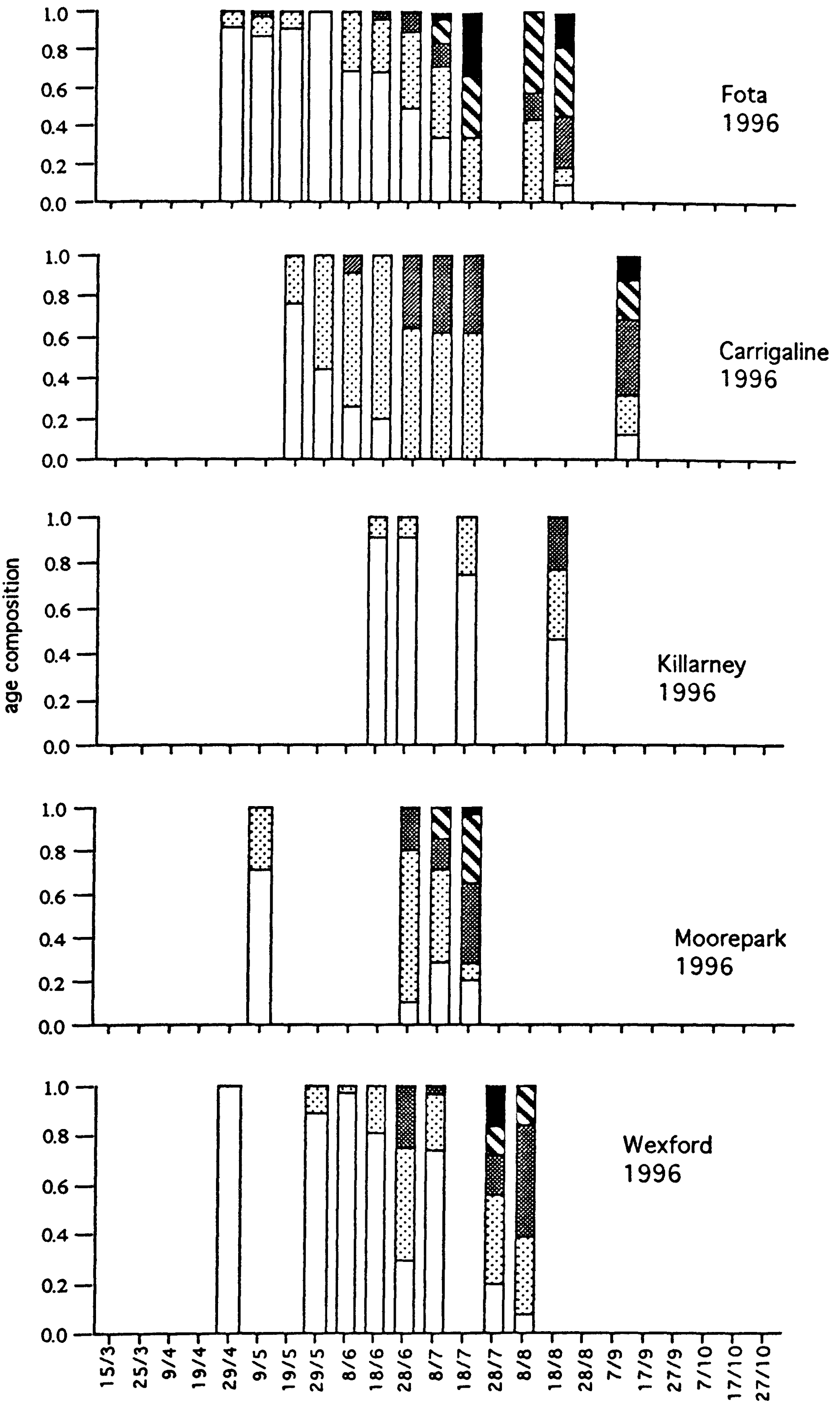


Fig. 15. Seasonal changes in the age composition of *A. fossor* at several sites in southern Ireland. Insufficient data was available from 1995 data sets. Beetles were aged by the degree of tibial wear on their foretibia, which varied from no tibial wear (class N) to heavily worn (class H). Histograms represent age composition when ≥10 individuals were available. See text for details.

■ H
▧ M
▩ S2
⬚ S1
☐ N

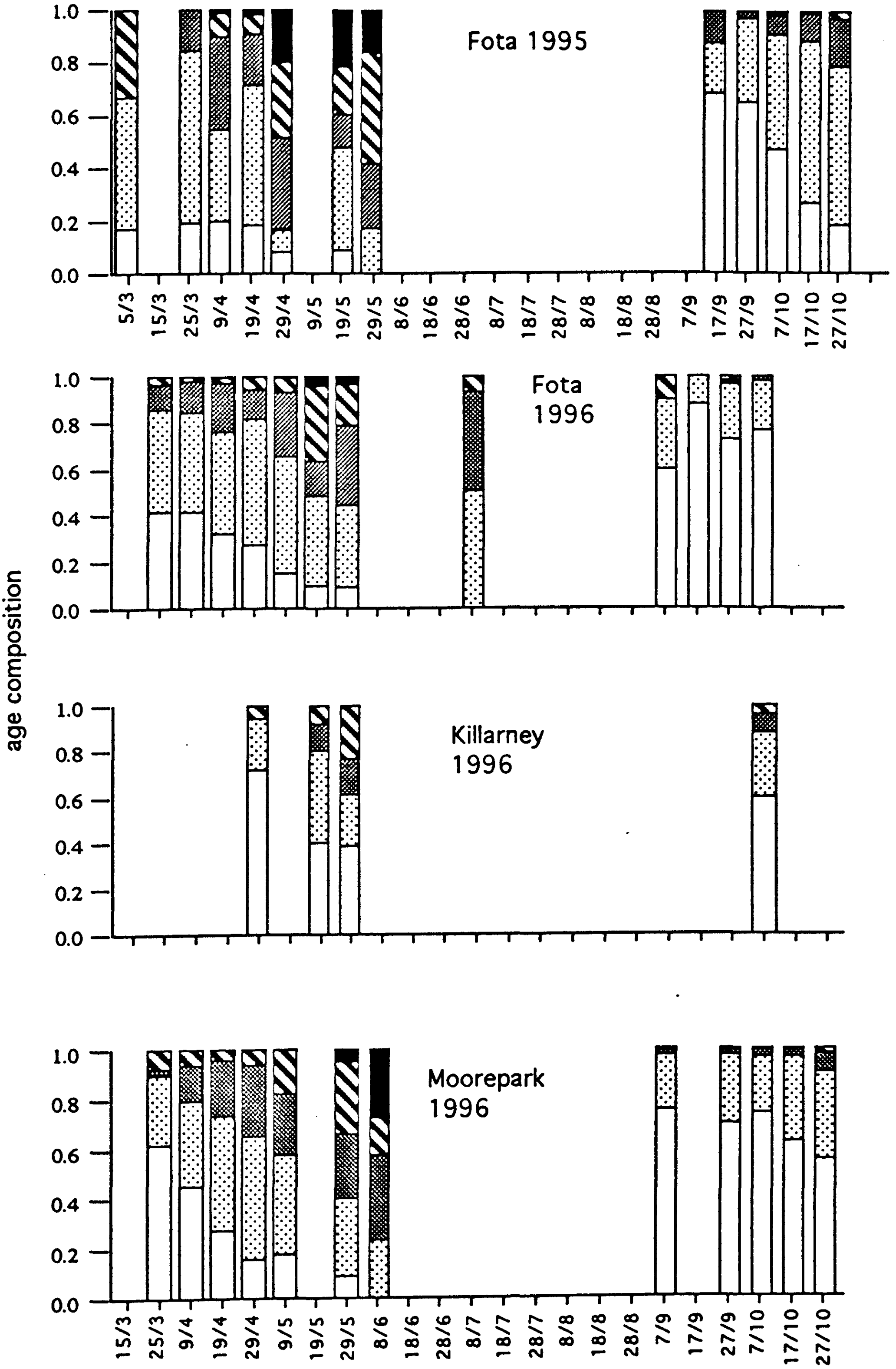


Fig. 16. Seasonal changes in the age composition of *A. prodromus* at several sites in southern Ireland. Data from both 1995 and 1996 are presented for Fota. Beetles were aged by the degree of wear on the foretibia, which varied from no tibial wear (class N) to heavily worn (class H). See text for details. Histograms represent age composition when ≥ 10 individuals were available. Arrows indicate where data for one (one arrow) or two (two arrows) trapping intervals were combined.

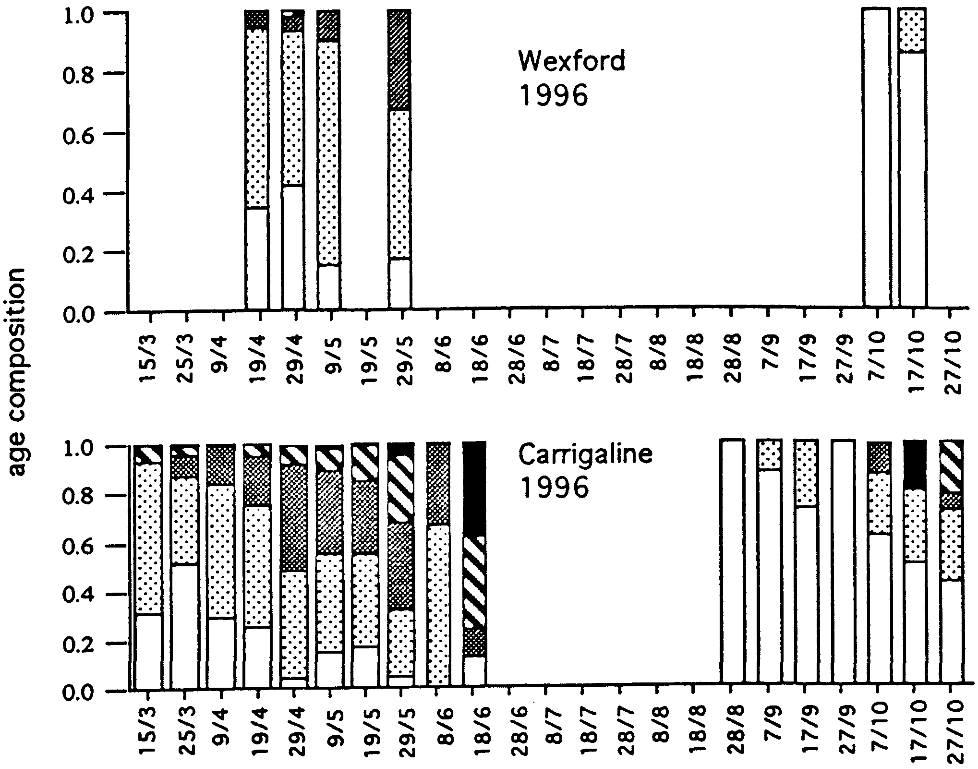


Fig. 16 -contd. Age composition of *A. prodromus.*

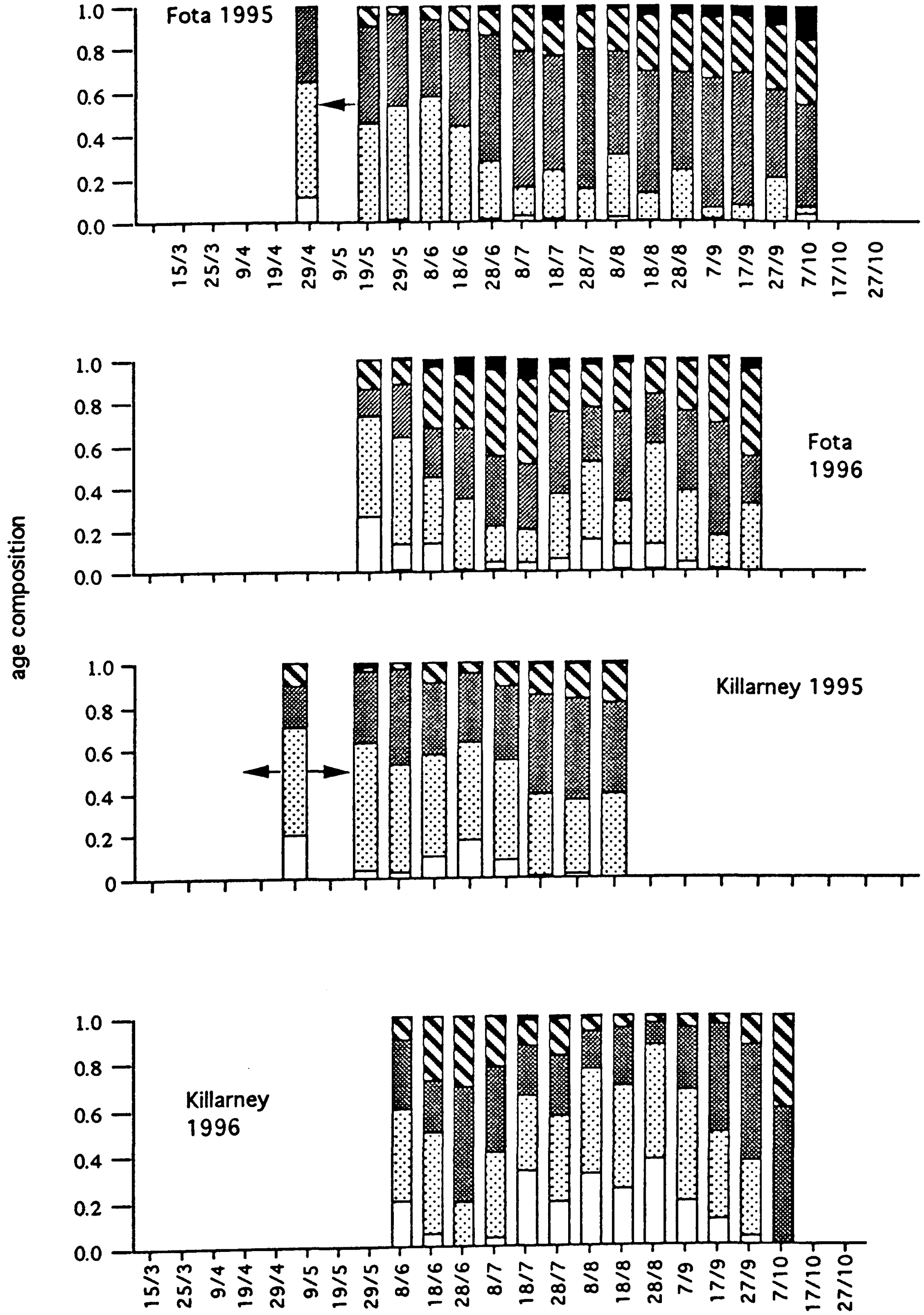


Fig. 17. Seasonal changes in the age composition of *A. rufipes* at several sites in southern Ireland. Data from both 1995 and 1996 are presented for Fota and Killarney. Beetles were aged by the degree of wear on the foretibia, which varied from no tibial wear (class N) to heavily worn (class H). See text for details. Histograms represent age composition when ≥ 10 individuals were available. Arrows indicate where data for one (one arrow) or two (two arrows) trapping intervals were combined.

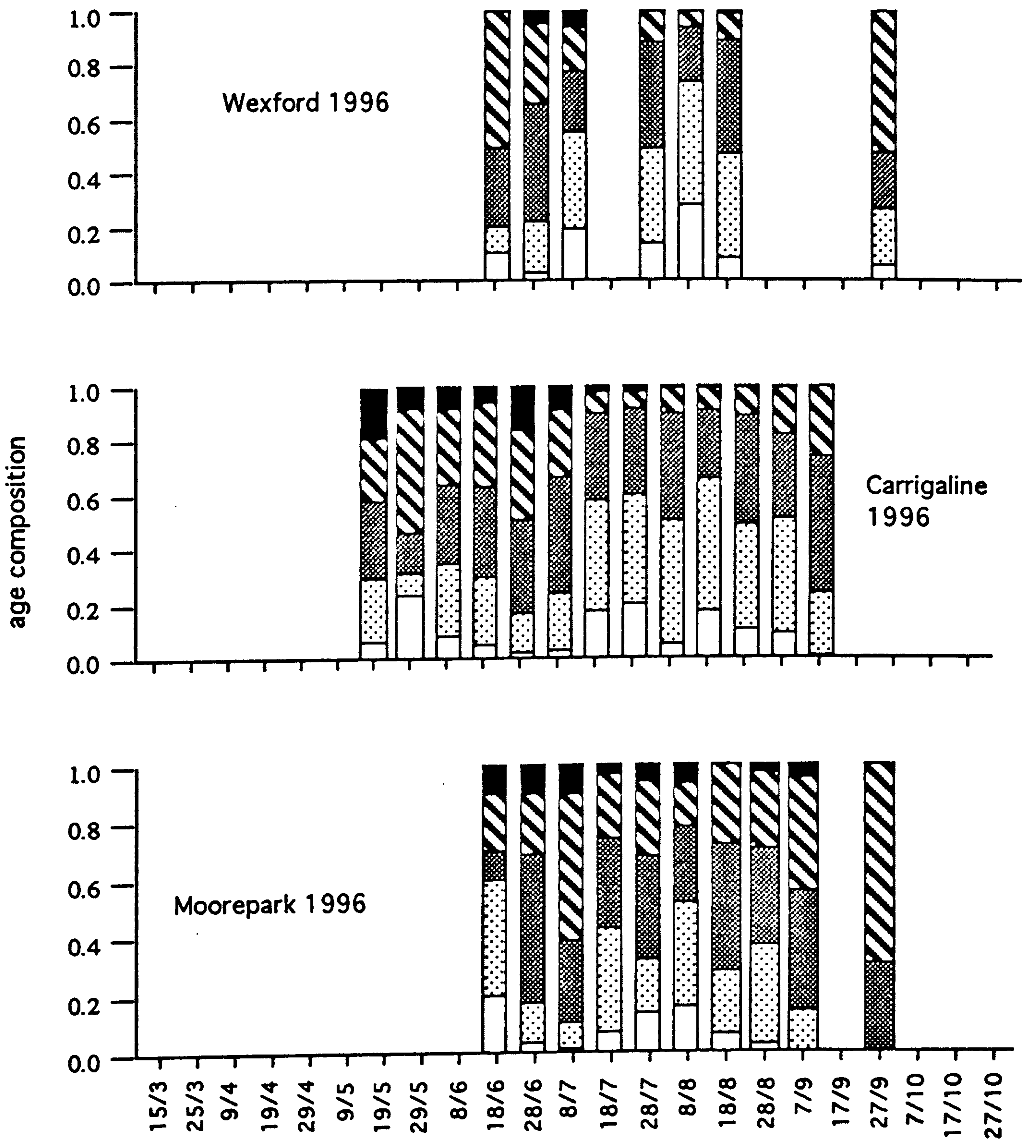


Fig. 17 - contd. Tibial wear age-composition of *A. rufipes*.

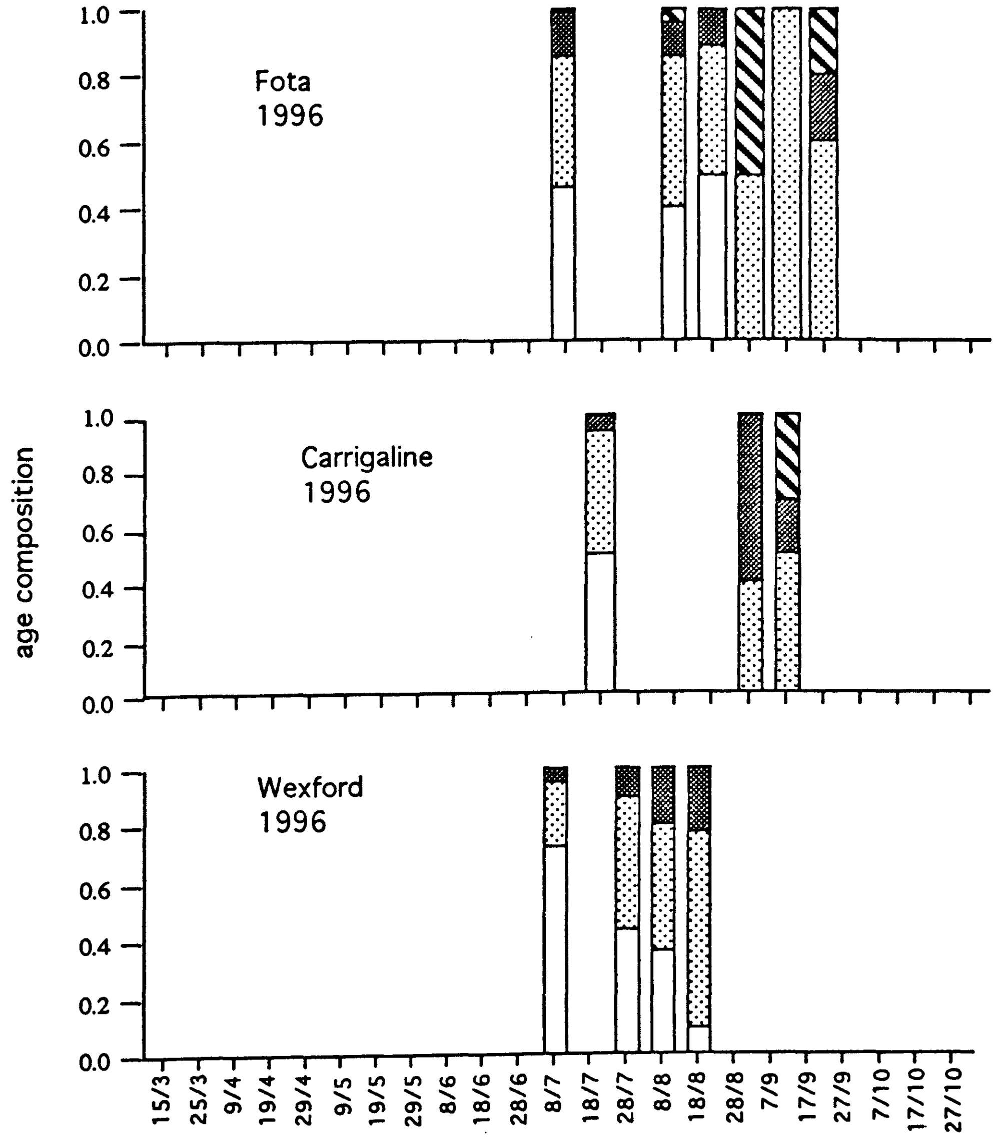


Fig. 18. Seasonal changes in the age composition of *A. rufus* at several sites in southern Ireland, where sufficient data was available. Beetles were aged by the degree of tibial wear on their foretibia, which varied from no tibial wear (class N) to heavily worn (class H). Histograms represent age composition when ≥10 individuals were available. See text for details.

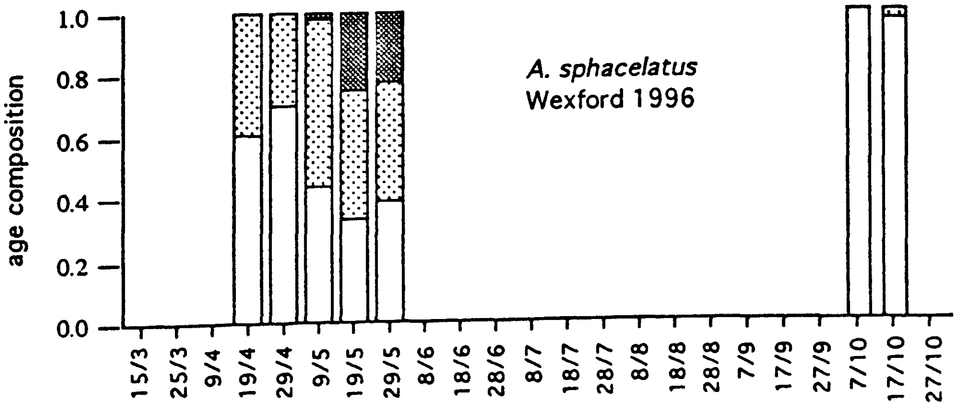


Fig. 19. Tibial wear age-composition of *A. sphacelatus*. See overleaf.

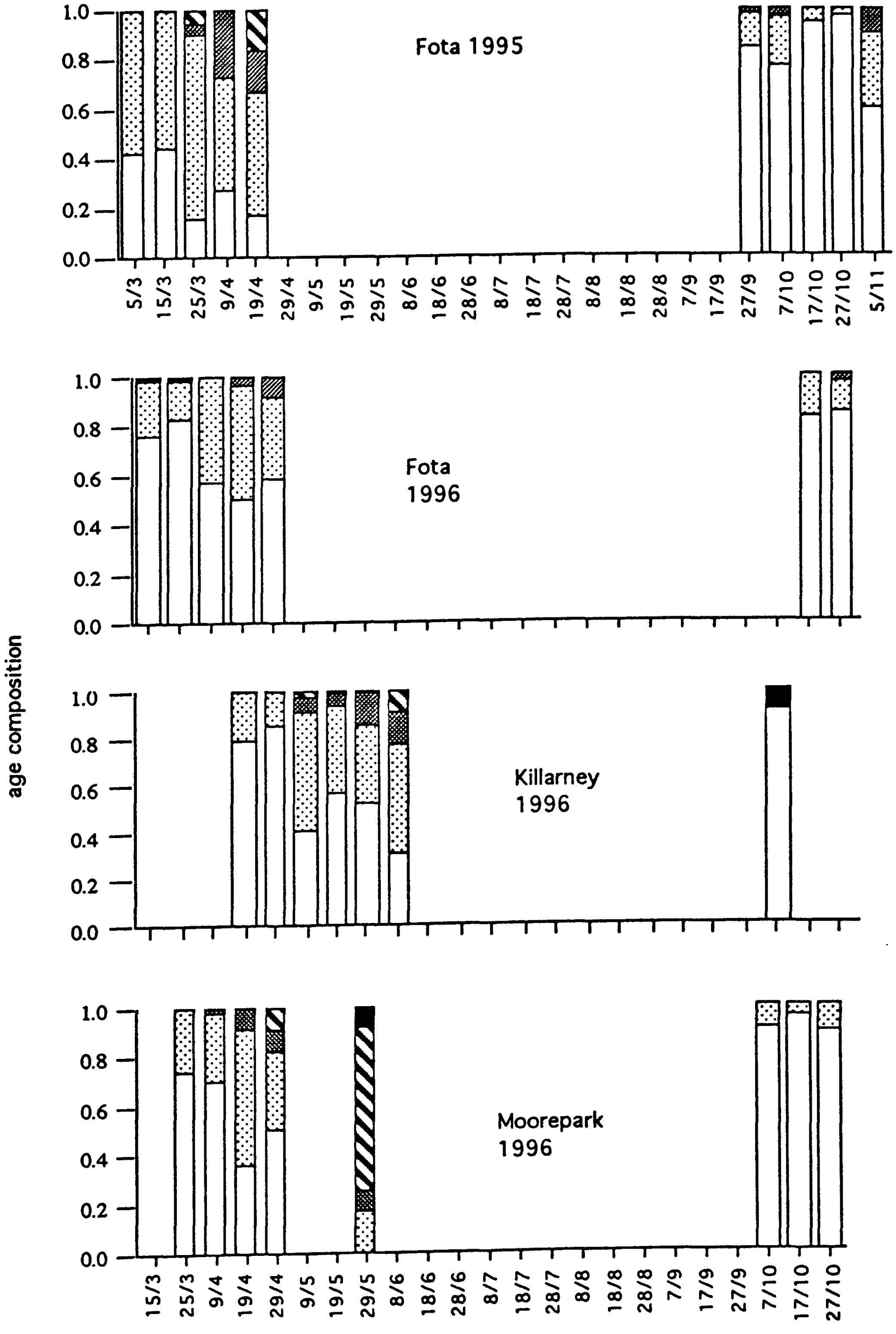


Fig. 19. Seasonal changes in the age composition of *A. sphacelatus* at several sites in southern Ireland. Data from both 1995 and 1996 are presented for Fota. Beetles were aged by the degree of wear on the foretibia, which varied from no tibial wear (class N) to heavily worn (class H). See text for details. Histograms represent age composition when ≥ 10 individuals were available. Arrows indicate where data for one (one arrow) or two (two arrows) trapping intervals were combined.

■ H
▧ M
▩ S2
⬚ S1
☐ N

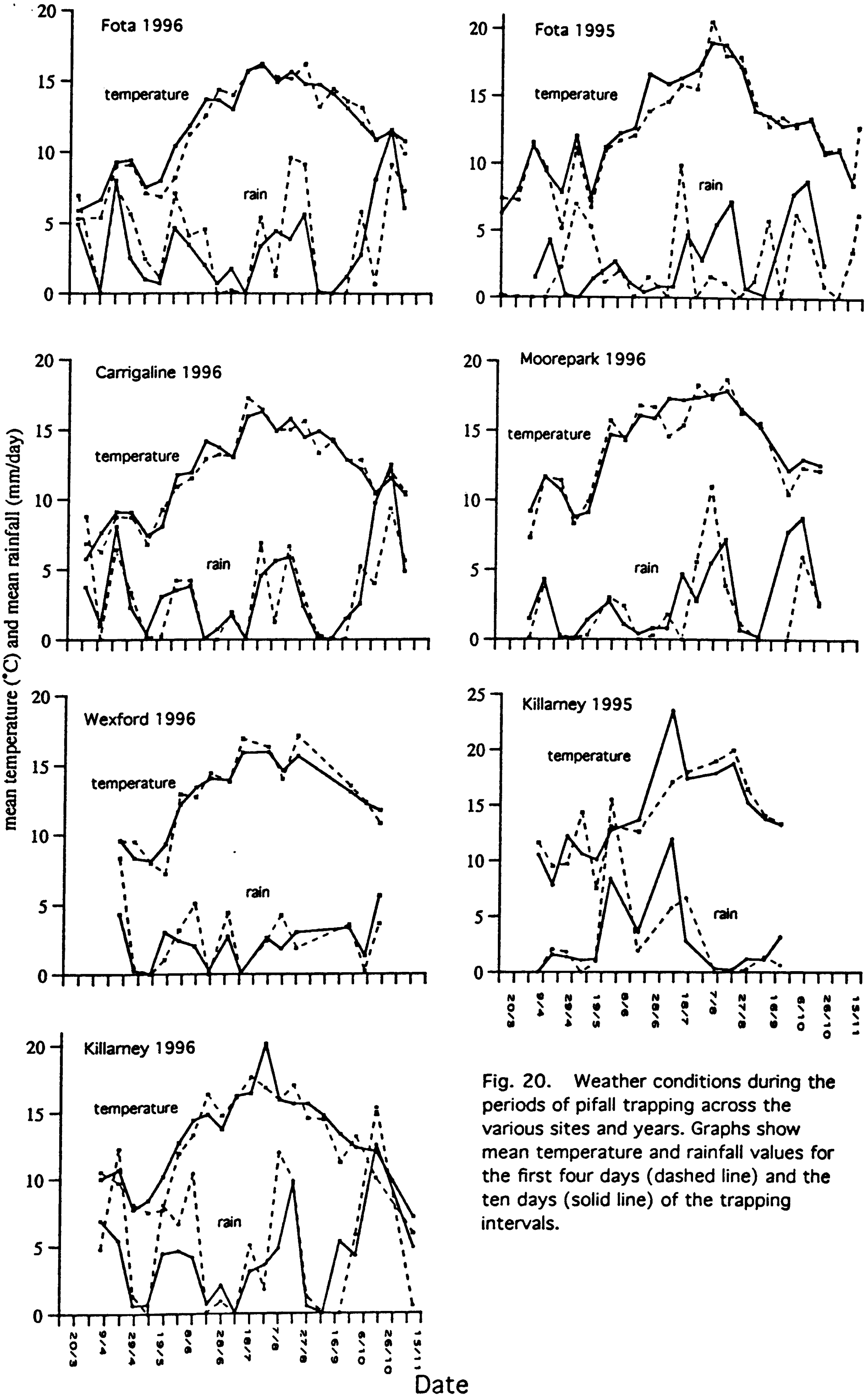


Fig. 20. Weather conditions during the periods of pifall trapping across the various sites and years. Graphs show mean temperature and rainfall values for the first four days (dashed line) and the ten days (solid line) of the trapping intervals.

Chapter 3

Effect of patch size on colonisation and utilisation of ephemeral resources: an experimental analysis using north temperate coprophagous dung beetles

John A. Finn and Paul S. Giller
Dept of Zoology and Animal Ecology, University College Cork, Ireland

Submitted to Oikos, May 1998

Chapter 3

Effect of patch size on colonisation and utilisation of ephemeral resources: an experimental analysis using north temperate coprophagous dung beetles

Abstract

The relationship between dung pad size and both adult colonisation and larval development was investigated in an assemblage of north temperate dung beetles (*Geotrupes*, *Aphodius* and *Sphaeridium*) using both dung pads and baited pitfall traps. Pad size of natural dung pads was found to vary widely in the field (< 100 g to > 1000 g). Across all sampling dates in field experiments, dung pad size had a significant influence on dung beetle biomass sampled from pads. Closer examination of experimental dung pads on the second day after deposition, when beetle biomass was at a maximum, revealed not only a general positive relationship between pad size and dung beetle biomass but, more importantly, a positive effect of dung pad size on a measure of dung beetle density (dung beetle biomass per unit dung volume). There was a strong trend for *Aphodius* species richness to increase, and maintain higher values for longer periods of time, in larger pads. Although dung pad and pitfall trap samples could differ in the actual numbers of beetles captured, the relationship between different dung sizes and dung beetle biomass was similar. Pat residence times of *A. rufipes* in the laboratory were significantly negatively correlated with dung pad size. In two field experiments, positive correlations were found between dung pad size and numbers of larvae in pads of different sizes and in one of these experiments larval densities were significantly and positively correlated with dung pad size. We discuss how variation in pad size may play a greater role in the distribution of dung beetles than intrinsic patterns of aggregation, as well as the implications of our findings in the context of resource utilisation and the aggregation model of coexistence.

Introduction

Fruits, mushrooms, carcasses and dung pads are ephemeral resources which are patchily distributed in space and time, and their discreteness facilitates their manipulation and replication as well as a complete censusing of associated fauna. Over the past two decades, a large body of theory has been developed in relation to insect community ecology in ephemeral patches, particularly towards the investigation of the role of resource patchiness in promoting species coexistence (e.g. Shorrocks et al. 1979, Atkinson and Shorrocks 1981, Hanski 1981, Ives 1988). Simply put, theoretical models of competition predict that species coexistence in patchy resources may be promoted where species have strong and independent aggregations across patches (e.g. Atkinson and Shorrocks 1981, Shorrocks and Rosewell 1987).

The majority of empirical studies have been experimental, controlling for patch size and ignoring the variability in patch size frequently observed in nature (but see Jaenike and James 1991, Sevenster and van Alphen 1996, Worthen et al. 1996, 1998), and some resource types have been better studied than others, e.g. carrion and fruits. In a critical appraisal of the aggregation model of coexistence, Sevenster (1996) and Sevenster and van Alphen (1996) emphasised that when patches differ in size it is the density of competitors, as opposed to their number, that determines the crowding experienced by individuals in patches. Using data from a frugivorous *Drosophila* community, log- log regressions revealed that larger fruits supported higher numbers, but lower densities of insects. In the words of the authors, 'while larger fruits seem to be aggregations when numbers are considered, they in fact tend to be low density refuges. This convincingly emphasises the general need to take patch size into account when quantifying aggregation,' (Sevenster and van Alphen 1996). Most experimental studies of dung beetle ecology to date are no different and have been performed on replicate standardised dung pads, leading Sowig and Wassmer (1994) to comment that, "A common method in experimental dung beetle ecology is to exclude the influence of patch size..." However, under natural conditions, pad quality, size and morphology can be observed to vary considerably. Dung pad size may differ due to the size of the defecating animal, the consistency of the faecal material and/or the conditions under which defecation occur (e.g. whether an animal is walking during defecation). A dearth of knowledge on the effects of variability in dung pad size is evident, despite some known effects of dung size on reproductive performance (Landin 1961, Lumaret and Kirk 1987, Gittings 1994) and the known influence of patch size on ecological sampling in general. Little standardisation is evident among dung beetle ecologists in relation to methods of sampling, and this extends to the size of the dung pad employed. This varies from the use of discrete volumes (0.25, 0.5

and 1.0 litre, Gittings 1994; 2 and 200 ml, Peck and Howden 1984; 1.0 litre, Kohlman and Sanchez Colon 1984; Peck and Forsyth 1982), to dung weights (50 g, Hirschberger 1996; 2 kg, Holter 1982), or in some cases no description is provided at all!

Aphodius species (ca. 10 - 20 mg dry weight) are known as dwellers (the larvae living and feeding within the pad) and the adults typically feed on the liquid content of dung. Depending on the species, adults lay either single eggs or clutches of eggs in the pad or at the pad/soil interface. Upon hatching, the larvae undergo three larval stages and a pupal stage before an adult emerges. *Geotrupes* beetles (ca. 300 mg dry weight) are known as tunnellers (the larvae develop in brood masses of dung buried underneath the dung pad) and can bury substantial proportions of single pads. They are usually of relatively low abundance. *Sphaeridium* species (ca. 12 mg dry weight) can occur in considerable abundances in pads; the adults are coprophagous, whereas the larvae are carnivorous within the pad.

In this study, we investigate the influence of patch size on the ecology of dung beetles and, in particular, the nature of the relationship between pad size and colonisation and larval production in dung beetles. When pad sizes were estimated in the field, dung pad weights could differ by more than a factor of ten. From field experiments, we describe significant relationships between dung beetle biomass and density, and pad size, as well as significant relationships between larval numbers and density, and pad size. We also discuss our findings in terms of other experimental studies and assess some of the implications of variability in dung pad size, and patch size in general, in aggregation theory.

Materials and Methods

Field experiments were carried out at Fota, County Cork, in southern Ireland. Fota is located approximately 20 km from Cork city and the area consists of a wildlife park and pasture, the latter being grazed by one or two herds of cattle. The soils are glacial tills and gravels.

Experimental design

Colonisation experiments

A set of five field experiments (S1-S3 and C2-C3) were conducted to investigate the influence of dung patch size on adult beetle colonisation. In addition, data from a comparable field experiment (C1) conducted by Gittings (1994) are included in this analysis. Dung pads of different sizes in experiments C1, C2 and C3 formed part of larger experiments investigating dung beetle colonisation. Experiments varied in the

Table 1. Description of colonisation field experiments employing different dung sizes. Columns indicate experiment type, dung types and sizes used in the experiments and the days after deposition on which pads were sampled. Data in experiment C1 is from Gittings (1994).

Expt.	**Dung types and sizes**	**Sampling days**
S1: 29 August, 1995	cow; 0.25, 0.5, 1.0 and 1.5 L	2 and 4
S2: 7 May, 1996	cow; 0.25, 0.5, 1.0 and 1.5 L	2, 6 and 10
S3: 10 July, 1996	cow; 0.25, 0.5, 1.0 and 1.5 L	2 and 6
C1: 8 July, 1990	cow & red lechwe; 0.25, 0.5, and 1.0 L	2 and 6
C2: 19 June, 1996	sheep; 0.25 and 1.0 L	2, 4 and 6
C3: 11 August, 1996	sheep; 0.25 and 1.0 L	2, 4 and 6

number of dung sizes, the dung type employed, days after deposition on which samples were collected and the number of sampling days (Table 1). Experiment C1 included data from different sizes of cow and red lechwe (*Kobus leche leche*) dung, these two types being presented and analysed separately. At the start of some experiments, pitfall traps were baited with the same dung types and sizes used to form pads. When the contents of these traps were collected, the baits were not changed; thus, these pitfall traps provide a measure of dung beetle immigration to aging dung of different sizes ("findability", Gittings and Giller 1998).

The basic experimental design consisted of replicate standardised pads, and (in some experiments only) pitfall traps, of the various dung volumes, placed in a grid of replicate randomised blocks with each row and each dung pad/pitfall trap a similar interval (5 m) apart. There were five blocks, with single pitfall traps baited with each dung volume and a fixed number of dung pads of each volume in each block. Pad sizes were composed of 0.25, 0.5, 1.0 or 1.5 litre (L) of fresh homogenised dung, deposited in plastic formers of 8, 12, 16 and 22 cm diameter, respectively. On each sampling day (see Table 1), contents of the pitfall traps were collected and one dung pad of each volume and the underlying soil to a depth of approximately 5 cm were sampled from each block. Dung pad samples were immediately transported to the laboratory and stored briefly at 4 °C before using Tullgren funnels to extract beetles from both the dung pad sample and underlying soil. Deposition and collection of the pads was conducted between 09.00 and 13.30.

Larval abundance

The relationship between larval abundance and dung pad size was investigated in the field in the summer of 1995. In the first study (L1), five artificial replicate cow pads of each of sizes 0.5, 1.0 and 1.5 L (deposited in plastic formers of diameter 12, 16 and 22 cm, respectively) were deposited in a grid in which pads were placed 5 m apart. At the time of deposition, the lower third of the volume of the 0.5 and 1.5 litre pads were seperated by plastic mesh (mesh size ca. 0.75 cm), whereas the lower and upper half of the 1.0 L pads were separated by the mesh (after Holter, 1982). Pads were deposited on 2nd August, and collected on 15th August. Upon collection, the upper and lower sections of the pads were carefully seperated and the top section and both the lower section and underlying soil (to 5 cm) were hand sorted for larvae.

In a second study (L2), naturally dropped dung pads (n = 24) incorporating a range of dung sizes were collected at Fota on 25 August, 1995. We collected each pad encountered in a field in which cattle had been present about 22 days earlier. The pads were transported to the lab, weighed and each pad and the underlying soil were hand sorted for live larvae.

Pat residence times

A laboratory experiment was also conducted to investigate the effect of dung pad size on pad residence times of the abundant *A. rufipes* L. beetles. The experimental arenas consisted of a plastic container of approximately 20 cm diameter and 15 cm height, filled to about 7 cm with damp, loose soil which had been passed through a coarse sieve. There were five replicate arenas for each of three dung sizes employed in the experiment (0.25, 0.5 and 1.0 L of cow dung). Dung volumes were measured and each placed on the soil. The arenas were placed in a bucket with a few cm of water in the bottom. Twenty beetles were added to each pad before the bucket was covered with nylon net (mesh size 1.5 mm diameter). Replicates were checked every day for emigrating beetles which would be trapped in the water. Replicates were kept in the laboratory where temperatures for the first three days were about 23 °C and ranged between 19 °C and 23 °C for the 12 days duration of the experiment.

Data analysis

Data consisted of numbers of adults of each beetle species identified in each replicate pad or pitfall trap. Calculations of beetle biomass are based on dry weights of species (Gittings 1994) grouped into breeding and non-breeding *Aphodius*, *Sphaeridium* and *Geotrupes*. The non-breeding *Aphodius* included species with saprophagous larvae (*A. prodromus* (Brahm) and *A. sphacelatus* (Panz.)) and the immature f_2 generations of dung-breeding species. For *Aphodius* species in which f_1 and f_2 generations overlapped, individuals caught during the overlap period were assigned to one of the two generations on the basis of their tibial wear (Gittings and Giller, 1997). In this study, our analyses of data from the field experiments are primarily based on comparisons of dung beetle biomass. We consider that this is most appropriate given the range in size between the dung beetle species and evidence that there is greater resource utilisation by larger species of dung beetles (e.g. Halffter and Matthews 1966, Nealis 1977, Doube, Giller and Moola 1988). Nevertheless, we do provide a comparison of analyses based on data from both beetle numbers and biomass (cf. Table 3 and Table 4).

The effect of dung pad size and day of sampling on dung beetle biomass was examined by ANOVA using factors 'block', 'size', 'day', and 'size x day'. The F-value of the 'size x day' interaction term indicates the significance of differences in the successional pattern between different dung sizes. The role of succession is considerable in dung beetle communities (e.g. see Fig. 1) and, employing the above analysis, the effect of dung size may be confounded by the duration of an experiment i.e. relative to the effects of size, successional effects will be greater in experiments of longer duration. Therefore, as highest numbers of beetles in dung pads were almost always found on day 2, the relationship between dung size and beetle colonisation was investigated in more detail by linear regression of dung beetle biomass on both pad and pitfall trap samples from day 2 in those experiments with three or more dung sizes (S1-S3 and C1). Regression slopes were used to compare beetle colonisation between pitfall trap and dung pad samples. Regressions employed log transformed data. For comparison of data based on beetle numbers rather than biomass, we also used pad samples from day 2 to perform regression analyses of dung beetle numbers and numerical density (numbers of beetles/unit dung size) on dung size. In experiments C2 and C3, which employed two sizes of dung, ANOVA was used to analyse differences between the sizes, and data was transformed where necessary. As biomass was used as a measure of beetle colonisation references to 'biomass' and 'biomass density' indicate dry weight of beetle abundances and beetle biomass per unit dung volume, respectively.

The relationship between pad size and both larval numbers and density were investigated using Spearman rank correlation. In L1, larval density was expressed as number of larvae per unit dung volume, while in L2, larval density was calculated as larval number per unit dung weight. All analyses were performed on the Minitab application program.

Results

Dung Size and Colonisation

Dung pads

The composition of the dung beetle assemblage varied between experiments, due to the different phenologies of species. Experiments S1, C1, C2 and C3 (conducted in early - late summer) were dominated by breeding *Aphodius* and *Sphaeridium.* Experiment S2 (conducted in spring)was dominated by such large numbers of non-breeding *Aphodius* (*A. prodromus*) that pads were observed to be considerably 'shredded' over the course of the experiment. Experiment S3 (mid-summer) was dominated by *Sphaeridium.* Mean biomass of dung beetles colonising dung pads varied significantly between pad sizes and days (Fig. 1, Table 2). 'Size' explained more of the variance in dung beetle biomass than 'day' in five of the seven analyses. Note, however, that this is probably dependent on the temporal scale of sampling; sampling over a longer successional duration may well increase the relative amount of variance attributable to succession ('day') in relation to size. Patterns of succession between dung sizes were significantly different in four of the seven analyses (Table 2). Note that the F-value for the 'dung type x size x day' interaction term in experiment C1 was significant (total biomass, square root transformed: $F_{2, 59} = 4.96$, $p < 0.011$), indicating a different pattern of succession between the cow and red lechwe dung types employed in that experiment. Greater biomass was found in larger sizes of pads, and on day 2 of the experimental periods. Biomass density of beetles showed a clear, but less strong, relationship with dung size, and no relationship was observed in experiment S2 (Fig. 1).

In experiments S1 - S3 and C1, log-log regressions of beetle biomass from day 2 samples on pad size revealed significant and positive relationships between biomass and pad size and quite a large amount of the variance was explained (Fig. 3, Table 3). With the exception of experiment S2, there was a significant positive relationship between biomass density and pad size, although the slopes were lower than those obtained using biomass. In experiments C2 and C3, ANOVAs of beetle biomass from day 2 samples indicated that biomass in 1.0 L pads was significantly greater than that of 0.25 L pads (Expt. C2: $F = 6.52$, $p < 0.04$, untransformed; Expt. C3, $F = 163.5$, $p < 0.001$, square root transformed). Biomass densities in 1.0 L pads were significantly greater than those of 0.25 L pads in C3 only ($F = 29.1$, $p < 0.001$, untransformed). Regressions of beetle number and numerical density (numbers/ unit dung size) were comparable to regressions based on beetle biomass (cf. Table 3 and 4), the only effective difference being the non-significant regression of numerical density on pad size in C1 (red lechwe dung). In experiments C2 and C3, beetle

Fig. 1. Biomass of dung beetles in dung pads of different sizes. For experiments S1-S3 and C1, two graphs are presented. Left-hand graphs indicate biomass sampled in dung pads, whereas right-hand graphs present the biomass density (biomass/ unit dung volume). For experiments C2 and C3, the graph of biomass density in 0.25 L pads is presented beside the 0.25 L biomass graph. Note the different scales between graphs. (░) *Sphaeridium* spp., (▥) non dung-breeding *Aphodius* spp. (including non-breeding f2 generations), (▓) breeding *Aphodius* spp. and (▨) *Geotrupes.*

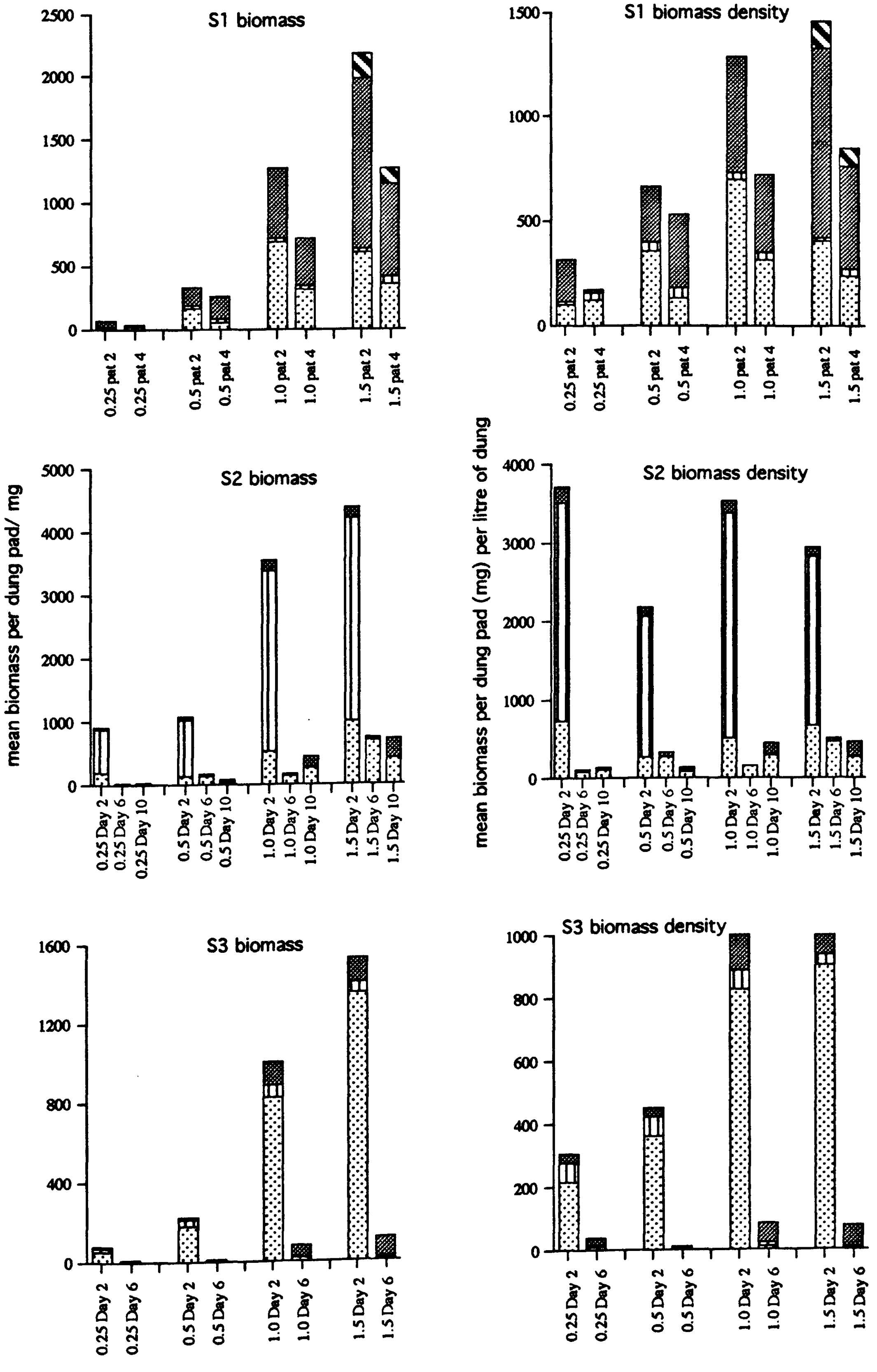


Fig. 1 (b)

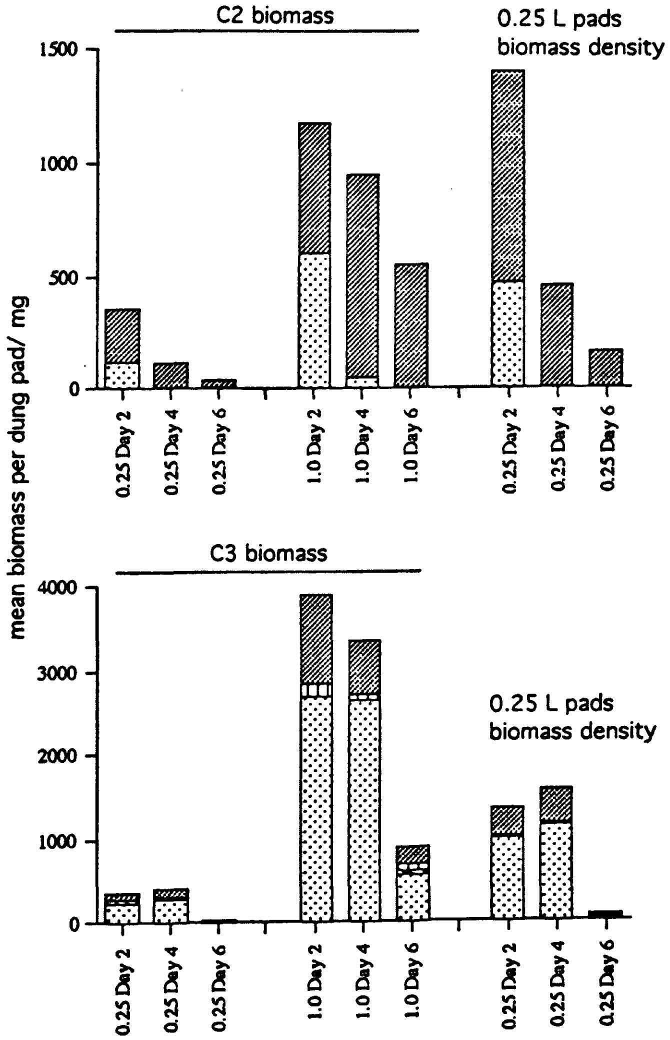
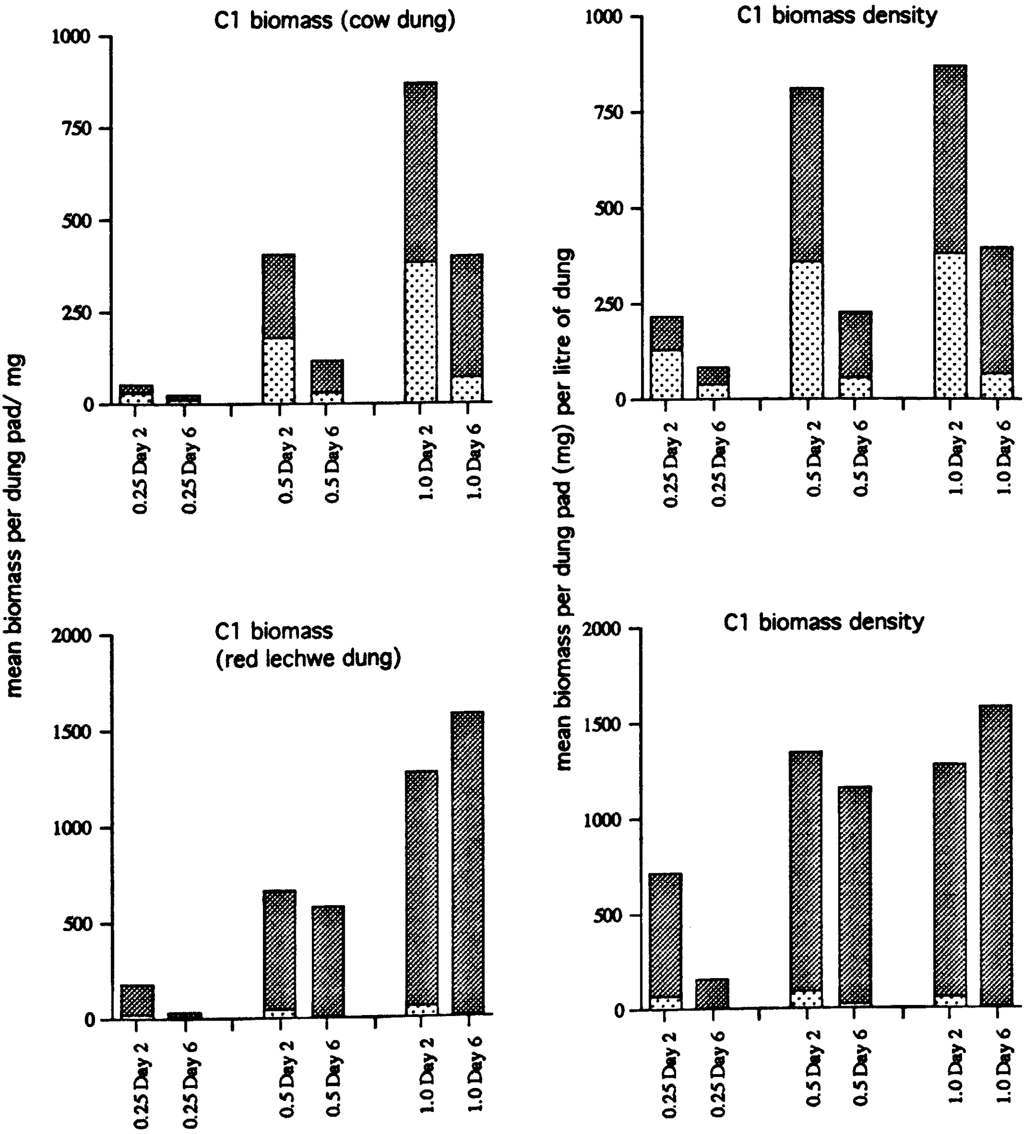

mean biomass per dung pad/ mg
C2 biomass
0.25 L pads
biomass density
1500
1000
500
0
0.25 Day 2
0.25 Day 4
0.25 Day 6
1.0 Day 2
1.0 Day 4
1.0 Day 6
0.25 Day 2
0.25 Day 4
0.25 Day 6
C3 biomass
4000
3000
2000
1000
0
0.25 L pads
biomass density
0.25 Day 2
0.25 Day 4
0.25 Day 6
1.0 Day 2
1.0 Day 4
1.0 Day 6
0.25 Day 2
0.25 Day 4
0.25 Day 6

Fig. 1 (c)


C1 biomass (cow dung)
C1 biomass density
C1 biomass
(red lechwe dung)
C1 biomass density
mean biomass per dung pad/ mg
mean biomass per dung pad (mg) per litre of dung
0
250
500
750
1000
1500
2000
0.25 Day 2
0.25 Day 6
0.5 Day 2
0.5 Day 6
1.0 Day 2
1.0 Day 6

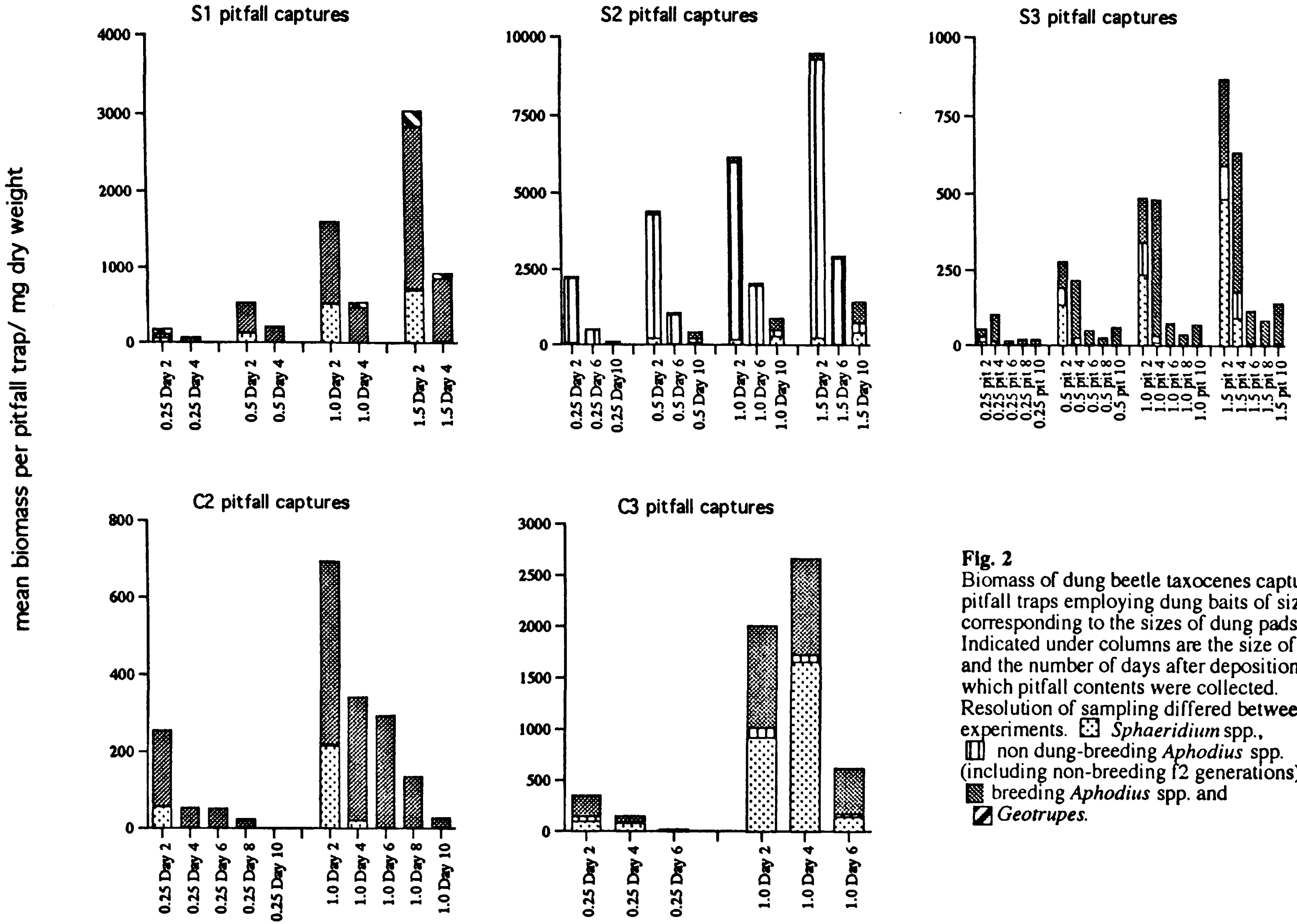


Fig. 2
Biomass of dung beetle taxocenes captured in pitfall traps employing dung baits of size corresponding to the sizes of dung pads. Indicated under columns are the size of baits, and the number of days after deposition on which pitfall contents were collected. Resolution of sampling differed between experiments. ⛆ *Sphaeridium* spp., ▥ non dung-breeding *Aphodius* spp. (including non-breeding f2 generations), ▩ breeding *Aphodius* spp. and ◩ *Geotrupes*.

Table 2. Effect of dung size and day of sampling on dung beetle biomass in field experiments. The data was analysed by randomised block analysis of variance. Indicated are F-values for 'size', 'day' and 'size x day' terms. The 'size x day' interaction term compares the pattern of succession between dung sizes. Significance of the F-values indicated as follows: * $p < 0.05$, ** $p < 0.01$ ***$p < 0.001$. Data was transformed by square-root (sq) or $\log_{10}$ (log) transformation.

		Size	Day	Size x day
S1	sq	$178.9_{3,27}$ ***	$26.7_{1,27}$ ***	$4.68_{3,27}$ **
S2	log	$14.8_{3,44}$ ***	$36.8_{2,44}$ ***	$1.5_{6,24}$ n.s.
S3	sq	$56.1_{3,28}$ ***	$194.4_{1,28}$ ***	$16.9_{3,28}$ ***
†C1- cow	sq	$48.1_{2,20}$ ***	$20.8_{1,20}$ ***	$1.6_{3,20}$ n.s.
†C1- red lechwe	sq	$101.5_{2,20}$ ***	$1.2_{1,20}$ n.s.	$3.8_{2,20}$ *
C2	sq	$118.7_{1,20}$ ***	$15.5_{2,20}$ ***	$0.8_{2,20}$ n.s.
C3	sq	$348.9_{1,20}$ ***	$59.4_{2,20}$ ***	$10.29_{2,20}$ **

numbers in 1.0 L pads were significantly greater than those in 0.25 L pads (Expt. C2: $F = 9.86$, $p < 0.02$, untransformed; Expt. C3, $F = 112.4$, $p < 0.001$, square root transformed). There was no significant difference in numerical density of beetles between 1.0 and 0.25 L pads in C2, but there were significant differences between these two sizes in C3 ($F = 24.4$, $p < 0.001$, untransformed).

Pitfall traps

Mean biomass of dung beetles colonising pitfall traps varied considerably between pad sizes and days (Fig. 3). Typically, pitfall captures were highest on the first sampling day (day 2) and, on any day, larger dung sizes captured a greater biomass of beetles than smaller dung sizes. Log-log regressions of day 2 pitfall captures from experiments S1 - S3 on dung size all yielded significant positive relationships (Table 3). The interaction term of the pit/pat regression lines for each of S1 - S3 were not significant; S1, $p = 0.272$; S2, $p = 0.167$; S3, $p = 0.253$ (Table 3). Therefore, while the two sampling methods (dung pad sampling and pitfall trapping) can differ in the actual numbers of beetles captured, the relationship between different dung sizes (the regression slope) and dung beetle biomass was similar between the two methods in these experiments.

Fig. 3. Log- log regressions of dung beetle biomass and biomass density (biomass/ unit dung size) against size of dung pads collected on day 2. Closed circles indicate pitfall trap samples; open squares indicate pad samples. Regression lines for pitfall trap and pad samples are indicated by dashed and solid lines, respectively. See Table 3 for details.

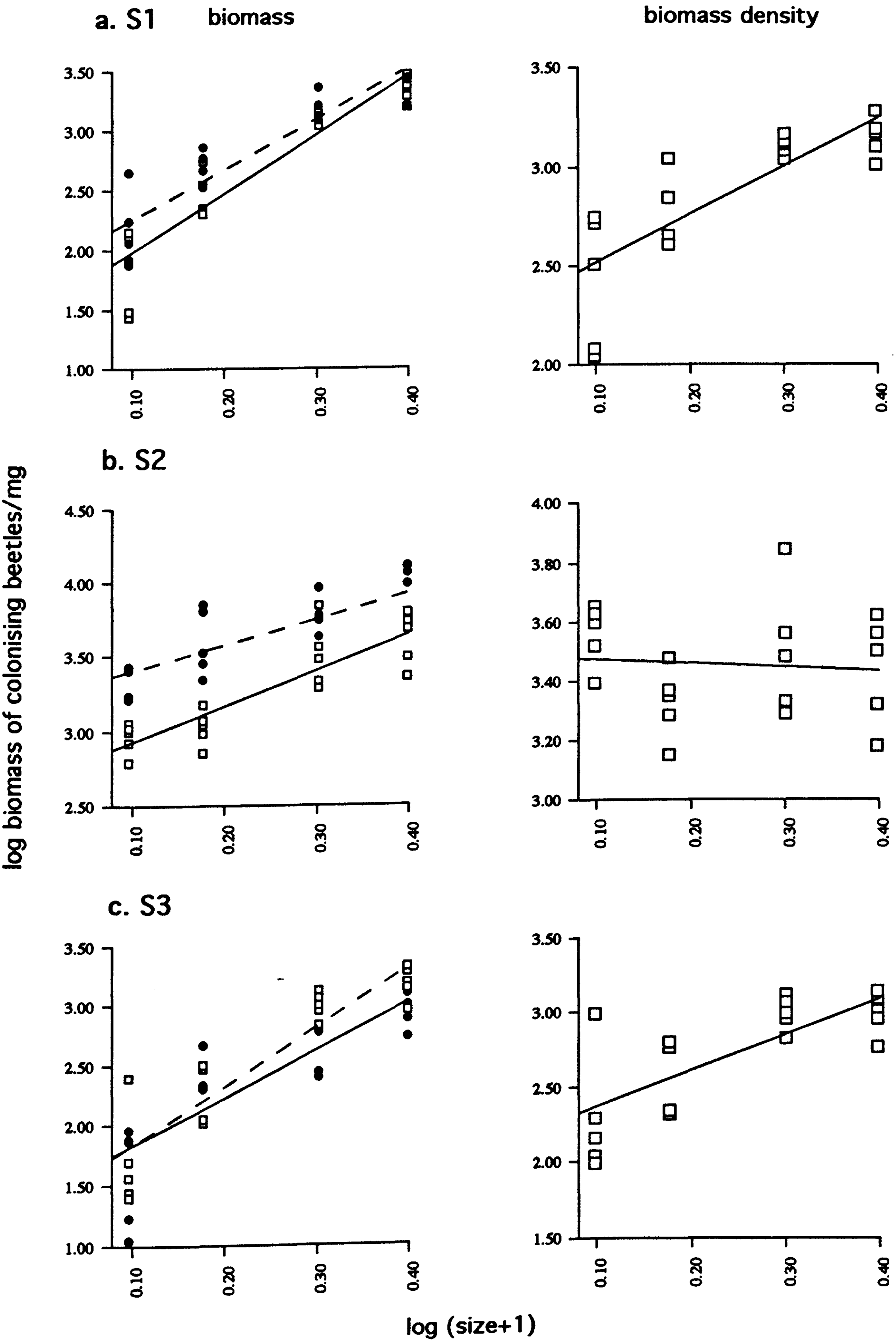


Fig. 3 (b)

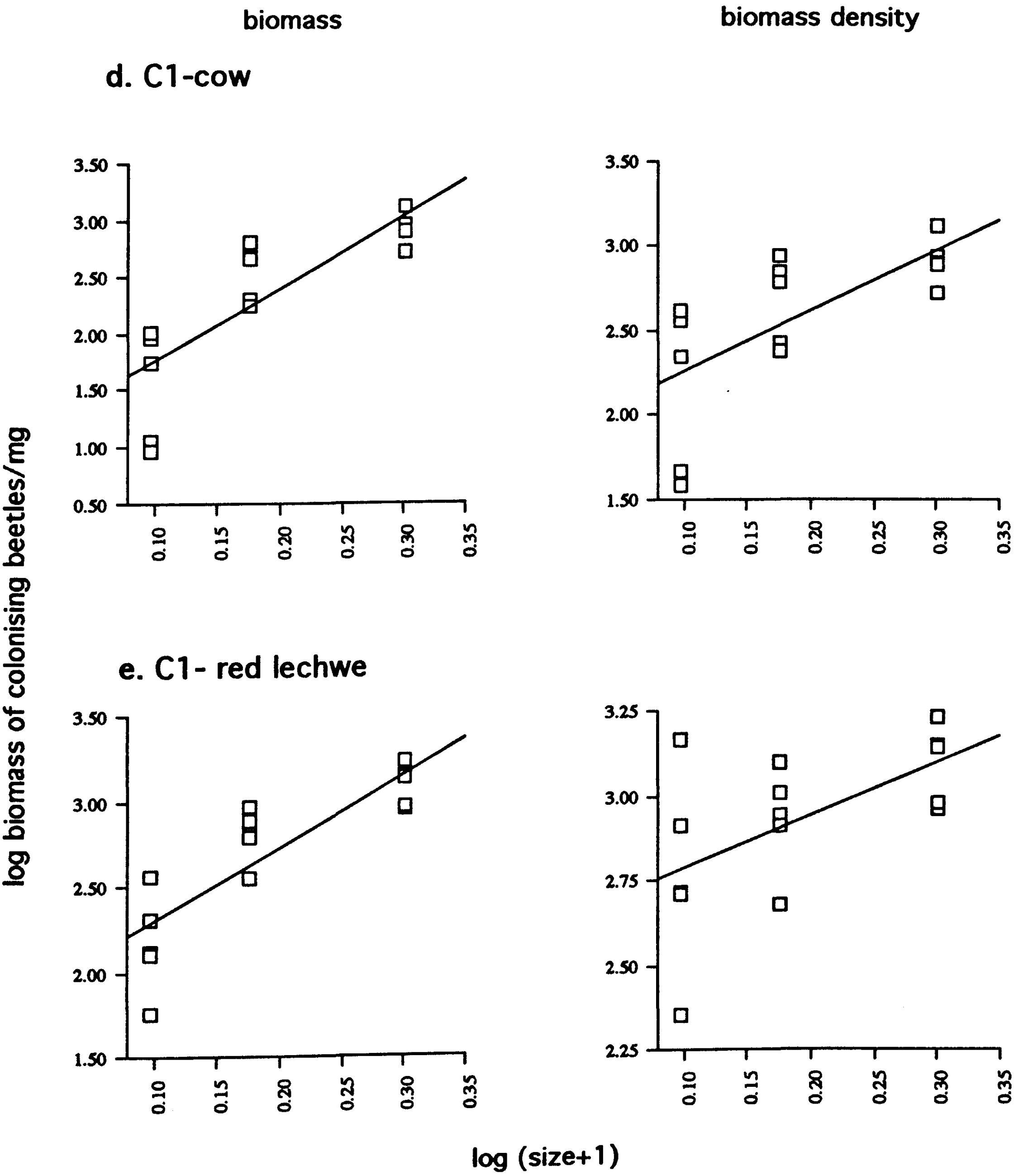

biomass
biomass density
d. C1-cow
e. C1- red lechwe
log biomass of colonising beetles/mg
log (size+1)
3.50
3.00
2.50
2.00
1.50
1.00
0.50
3.25
2.75
2.25
0.10
0.15
0.20
0.25
0.30
0.35

Table 3. Regression of dung beetle abundance (log [insect weight]) and density (log [insect weight/dung size]) on log (size + 1). Sizes are expressed in litres and data use day 2 samples only. Indicated are regression type, sample size (n), the slope of the regression, the coefficient of determination (r^2) and the significance level (p).

Regression	n	slope	r^2 (%)	p
S1 biomass- pads	20	5.00	87	<0.001
S1 biomass- pits	18	4.29	86	<0.001
S1 biom. density- pads	20	2.43	65	<0.001
S2 biomass- pads	20	2.44	75	<0.001
S2 biomass- pits	20	1.75	57	<0.001
S2 biom. density	20	-0.13	0.8	0.709
S3 biomass- pads	20	4.97	82	<0.001
S3 biomass- pits	20	4.02	71	<0.001
S3 biom. density- pads	20	2.41	56	<0.001
C1 biomass- cow pads	15	6.58	68	<0.001
C1 biom. density- cow pads	15	3.73	48	0.004
C1 biomass- red lechwe pads	15	4.44	73	<0.001
C1 biom. density- red lechwe pads	15	1.58	33	0.025

Table 4. Regression of dung beetle abundance (log [insect number + 1]) and density (log [{insect number + 1}/pad size]) on log (pad size + 1). Pad sizes are expressed in litres and data use day 2 samples only. Indicated are regression type, sample size (n), the slope of the regression, the coefficient of determination (r^2) and the significance level (p).

Regression	n	slope	r^2 (%)	p
S1 abundance	20	4.35	84	<0.001
S1 density	20	2.01	55	<0.001
S2 abundance	20	2.39	76	<0.001
S2 density	20	-0.15	1	0.664
S3 abundance	20	4.65	81	<0.001
S3 density	20	2.36	50	<0.001
C1 abundance- cow	15	5.13	75	<0.001
C1 density- cow	15	2.65	40	0.011
C1 abundance- red lechwe	15	3.01	75	<0.001
C1 density- red lechwe	15	0.22	2	0.642

Table 5. Mean (± S.D.) values of *Aphodius* species richness of replicate dung pads (n=5) in artificial dung pads of standard sizes (0.25, 0.5, 1.0 and 1.5 litre) deposited in field experiments. Not all experiments employed all sizes. Columns indicate experiment, day of sampling and dung pad size, and the final column indicates the relationship between dung pad size and *Aphodius* species richness in day 2 samples (Spearman correlation coefficient).

	Day	**0.25 litre**	**0.5 litre**	**1.0 litre**	**1.5 litre**	r_s
Expt. S1	Day 2	1.00± 0.71	2.40± 0.89	3.20± 0.45	3.20± 0.45	0.781, n=20
	Day 4	0.80± 0.45	2.00± 1.23	2.80± 1.48	3.00± 0.00	p < 0.01
Expt. S2	Day 2	3.80± 0.45	4.00± 1.00	5.20± 0.84	5.00± 0.71	0.602, n=20
	Day 6	1.00± 0.71	1.40± 1.34	0.60± 0.90	3.40± 1.34	p < 0.01
	Day 10	0.20± 0.45	0.80± 1.30	1.40± 0.89	2.40± 0.55	
Expt. S3	Day 2	1.60± 0.55	2.20± 0.84	4.20± 0.45	4.40± 0.55	0.866, n=20
	Day 6	0.40± 0.80	0.40± 0.55	1.60± 0.89	2.80± 1.10	p < 0.01
Expt. C1	Day 2	1.40± 0.89	3.20± 0.84	4.40± 1.52		0.774, n=15
(cow)	Day 6	0.60± 0.89	1.80± 1.01	2.80± 0.45		p < 0.01
Expt. C1	Day 2	2.80± 0.84	4.60± 0.55	5.60± 1.34		0.799, n=15
(red lechwe)	Day 6	1.60± 0.55	3.8± 0.84	4.40± 0.55		p < 0.01
Expt. C2	Day 2	4.00± 1.23	-	6.00± 0.71		
	Day 6	2.80± 1.48	-	5.2± 0.45		
	Day 10	2.00± 0.71	-	4.00± 1.00		
Expt. C3	Day 2	3.40± 1.14	-	4.60±0.55		
	Day 4	3.20± 0.45	-	4.60± 1.14		
	Day 6	1.20± 0.45	-	3.00± 1.23		

Dung Pad Size and Species Richness

A clear pattern emerged in which mean values of *Aphodius* species richness on any day were greater both in larger pads and in the earlier days of the succession (Table 5). (The 1.0 L pads on day 6 in experiment S2 were anamolous.) Note that in experiment C1, mean species richness was always greater in red lechwe dung pads when compared with cow dung pads of the same size and age. Correlations indicated positive and significant relationships ($p < 0.01$) between pad size and *Aphodius* species richness from day 2 pads in each of experiments S1, S2, S3 and C1 (Table 5).

Dung Pad Size and Larval Numbers

Both studies were numerically dominated by larvae of *A. rufipes*. Larvae in L1 were mostly first and second instars, whereas pads in experiment L2 contained second and (mostly) third instar larvae.

In each of the three pad sizes examined, larvae were found to occur in the basal section of the pad, near the pad-soil interface. In addition, there was generally no evidence of much larval activity having occurred in the top sections of pads. There was a significant positive correlation between initial dung pad size and total larval number after 13 days in these artificially deposited dung pads (Spearman rank correlation; $r_s = 0.705$, $n = 15$, $p < 0.01$), but there was no significant correlation ($r_s = -0.043$, $n = 15$, n.s.) between pad size and larval density (expressed as larval number per unit dung volume at deposition).

The 22 day old naturally dropped dung pads in L2 displayed a significant positive correlation between dung pad size and the number of larvae (Spearman rank correlation; $r_s = 0.845$, $n = 24$, $p < 0.01$) and, more importantly, between pad size and larval density (expressed as larval number per unit dung weight) ($r_s = 0.495$, $n = 24$, $p < 0.02$) (Fig. 4). Note the considerable range in size of the naturally dropped pads that were sampled.

Dung pad size and emigration rates.

Mean (± sd) pad residence times of beetles in pad sizes of 0.25, 0.5 and 1.0 L were 2.71 (± 0.52) days, 3.08 (± 0.40) days and 3.67 (± 0.59) days, respectively. There was a significant positive correlation between average pad residence times per replicate and dung pad size ($r_s = 0.567$, $p < 0.05$, $n = 15$).

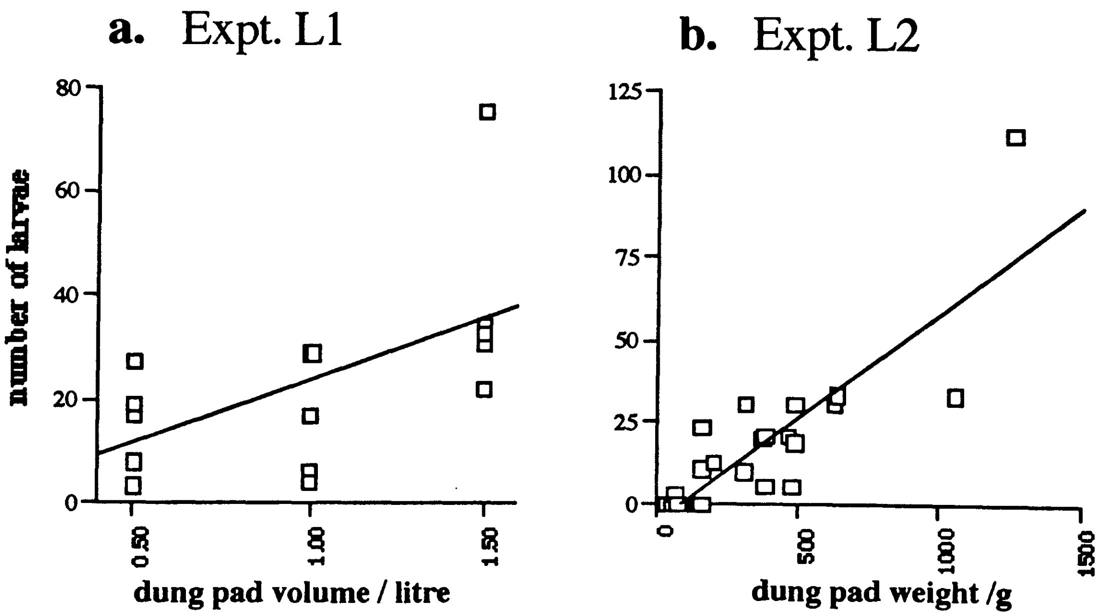


Fig. 4. Number of larvae collected in August, 1995 in different sizes of a) artificial dung pads of known size, collected 13 days after deposition and b) naturally dropped dung pads collected about 22 days after deposition. Most of the larvae were individuals of *A. rufipes*.

Table 6. Within-pad spatial distribution of *Aphodius* larvae in 13 day old dung pads (Expt. L1). The top and bottom sections of pads were separated by plastic mesh (see text for details) in three different sizes of dung pads (n=5).

replicate	**0.5 Litre**		**1.0 Litre**		**1.5 Litre**	
	Top	Bottom	Top	Bottom	Top	Bottom
1	0	17	0	6	20	17
2	0	8	2	27	2	74
3	0	27	0	17	1	30
4	5	14	6	23	0	22
5	0	3	0	4	0	33

Discussion

Abundance and density in different patch sizes

Although a large number of papers have discussed colonisation and coexistence in ephemeral patches, relatively few theoretical or empirical studies are concerned with size differences in ephemeral patches, despite the variability in patch size that is evident in nature. It should be stressed that there is no a priori reason to expect that the actual density of insects in ephemeral patches would increase or decrease in relation to patch size. This is evident from some other data in the literature which allow comparisons of colonisation on patches of different sizes (summarised in Table 7). These kinds of relations appear even less consistent when one considers stand size of host plants and density of herbivores (cf. Cromartie 1975, Kareiva 1983, Stanton 1983, Bach 1988). In a critical appraisal of the aggregation model of coexistence, Sevenster (1996) and Sevenster and van Alphen (1996) emphasised that when patches differ in size it is the density of competitors, as opposed to their number, that determines the crowding experienced by individuals in patches. In contrast to the patterns observed in frugivorous *Drosophila* (Sevenster 1996, Sevenster and van Alphen 1996), which revealed a reduction in density with increasing patch size, our data showed that larger patches hold higher densities of beetles, which thereby experience greater crowding (Fig. 3). Thus, it would seem that any treatment of density-dependent patterns or processes in dung beetle ecology should take into consideration the possible effects of different dung sizes.

Here, we first discuss the relationship between dung pad size and the ecology of dung beetles, then using examples from dung beetle ecology, we present some more general discussion on the role of patch size in aggregation theory.

Dung pad size and adult dung beetles

Overall, dung pad size generally had a significant effect on both biomass and biomass density of dung beetles. Note that an obvious exception to this pattern in our data was found in experiment S2. This was the only experiment dominated by non-breeding *Aphodius*; all other experiments were dominated by dung-breeding beetles (*Aphodius* or *Sphaeridium*). There were significant relationships between dung pad size and *Aphodius* species richness. Larger pads were typically colonised by more species, and more species tended to remain in larger pads for longer than in smaller pads.

Table 7. Comparison of patterns of colonisation of insects on patches of different size. Where possible, we indicate increases (↑), decreases (↓), or no apparent change (↔) in measures of abundance, density, species richness and diversity. Symbols in brackets are estimated. Sources: [1] this study; [2] beetles colonising dung (Gittings 1994); [3] flies emerging from fruit (Sevenster and van Alphen 1996); [4] mayfly nymphs colonising substrate trays (Giller and Cambell 1989); [5] flies colonising carrion (Hanski 1982); [6] flies emerging from carrion (Hanski 1982); [7] flies emerging from mushrooms (Worthen *et al.* 1996).

Insect type	**Abundance**	**Density**	**Species no.**	**Diversity**
[1]*Aphodius* dung beetles	↑	↑	↑	-
[2]*Aphodius* dung beetles	↑	↑	↑	↑
[3]*Drosophila* flies	↑	↓	-	-
[4]Mayfly nymphs	↑	↓	↑	↑
[5]Carrion flies	↔	(↓)	-	-
[6]Carrion flies	↑	-	-	-
[7]*Drosophila* flies	↑	↔	↑	↑

The observed patterns of colonisation of dung pads are due to a combination of immigration/ emigration rates, which may vary in relation to pad size. Pitfall trapping data also demonstrated that there are differential patterns of colonisation, with larger dung baits attracting significantly more beetles than smaller baits, validating the notion of superior 'findability' of larger dung pads. In addition, pitfall trap data (especially from those experiments with greater temporal sampling resolution i.e. S3, C2 and C3), indicated that over several days, larger dung sizes remained more 'findable' than smaller sizes. Presumably, the findability of a dung pad is related to the odour dispersion from the pad, which in turn may be related to the surface area of the pad. Crust formation on pads appears to affect dung beetle colonisation (Desière and Thome 1977), possibly due to its effect on odour dispersal: smaller pads may undergo more rapid and extensive crust formation than larger pads. Note that pitfall traps of any size regularly collected far larger total biomass of dung beetles than were found in pads, presumably as both the interactions within the pad and emigration were not possible for beetles in pitfall traps.

We are aware of only a few other examples in the literature which consider interactions between dung pad size and beetle ecology. Landin (1961) demonstrated that emigration from dung can be dependent on dung pad size, using experiments in which twenty individuals were placed in containers with 35, 15 or 5 cm^3 of sheep dung (*A. zenkeri* (Germar) and *A. ictericus* (Laich.)). Calculations showed that emigration rates increase when beetles have less than 25-70 times their body volume of dung available. These calculations would correspond to densities of greater than 100 individuals of *A. rufipes* per litre of dung, which is very uncommon in the field. In the present study, evidence indicated that emigration rates of adult *A. rufipes* may be density-dependent at densities that are common in the field.

Olechowicz (1974) found that numbers of scarabaeid beetles in sheep dung increased exponentially in relation to pad size (10-100 g fresh weight). Calculations using data in Sowig and Wassmer (1994) indicated an increase in the mean number of coprophagous beetles per sample in size classes of smaller to larger sheep pads. Data from Gittings (1994), showed significant differences in diversity (Simpson's Index) of *Aphodius* species in cow dung pads of different sizes (0.25, 0.5 and 1.0 litres), with larger dung pads having higher species numbers and species diversities. In a comparison of tropical dung beetles from pitfall traps with 200 ml and 2 ml dung baits, Peck and Howden (1984) found that beetles larger than 10 mm were almost exclusively found in the traps with the 200 ml dung baits. In addition, beetles less than 10 mm in length preferred small amounts of dung even when the large species were excluded from the baits with a screen. Data from Gittings (1994) showed that in north temperate European dung beetles, larger species showed a preference for larger pads in only one of three field experiments. Note, however that the one experiment which revealed a preference had a range of three dung sizes (0.25, 0.5 and 1.0 L) whereas the other two experiments compared two dung sizes only (0.5 and 1.0 L). We performed a similar analysis with data from the present experiments; only experiments S2 and C2 (and C3, omitting one outlying point) displayed a significant positive relationship between dung beetle size and pad size.

Pad size and *Aphodius* larvae

Aphodius dung beetle larvae have been less studied than the adults, but some references are pertinent in relation to pad size. Lumaret and Kirk (1987), for example, describe how the adults of *Aphodius constans* rely on the extended aging of the pad under Meditteranean conditions from February to April to oviposit in a zone of dung ranging from 55 - 75% humidity, while the larvae move inwards from the drier peripheral regions of the pad to avoid dessication. In relation to the suitability of pads over the duration of larval development, Lumaret and Kirk (1987) state that "the initial size of the dung when dropped is the most determinant factor." This is presumably because larger pads dessicate at a slower rate and provide a larger zone that is suitable for larval development than do smaller pads. In another study, significant differences in survival of *A. rufipes* larvae in 0.25 and 0.5 litres of the same dung type have been demonstrated under laboratory conditions (Gittings 1994).

Our present data show differences in the relationship between larval density and pad size when we compared 13 day old pads and 22 day old pads, which were deposited at about the same time. The 13 day old pads were largely composed of small larvae of *A. rufipes* and although larval numbers were correlated with pad size, their densities were not. In contrast, the 22 day old pads typically contained older, larger larvae of *A. rufipes* and larval densities were significantly correlated with pad size. This may be due to one or more mortality factors which are dependent on pad size, the most likely of which would be dessication, as smaller pads dry out faster than larger pads (Gittings 1994, see above). It is also possible that larval competition would intensify as the larvae age and the availability of dung in a pad decreases due to dessication and/or decomposition (Lumaret and Kirk 1987, Gittings 1994, Hirschberger 1996, Worthen et al. 1998). Observations of dead larvae in some of the smaller pads would further support this. Other factors may influence the relationship between pad size and larval abundance in the naturally dropped pads, particularly in relation to adult colonisation, such as the time of pad deposition (Holter 1979) and patterns of aggregation (Hanski 1980, Holter 1982). It should also be noted that wet weights of 22 day old pads in Fig. 4b were most likely quite different to the wet weights of those pads at deposition, largely due to dessication.

The results of this present study indicate that because of increases in adult beetle and larval density in relation to pad size, proportionally more intense biological activity may be expected in larger dung pads than in smaller dung pads. This may have important consequences for the decomposition of dung, considering that the biological activity of dung beetles and larvae is an important direct factor in decomposition and is considered to influence the aggregation of earthworms in dung pads (Holter 1983). We are not aware of any data which investigate the significance of dung pad size on the biology of the adults and larvae of dung beetles and earthworms in relation to decomposition rates.

Applicability of the aggregation model to dung beetles

North temperate dung beetles typically display aggregated distributions, even when artificial homogenised pads are employed (Hanski 1979, Holter 1982), but whether species are independently aggregated or not is unclear (cf. Holter 1982, Hanski 1991). Nevertheless, the aggregation model of coexistence has been often quoted in, and inspired in part by, examples from dung beetle ecology. Our present data indicate that patch size should be incorporated in applications of the aggregation model, to dung beetle ecology at least (see Sevenster and van Alphen 1996). Reasons include the large variability in pad sizes observed in the field and the frequent increases in density of both adult beetles and, sometimes at least, larvae in relation to pad size. Indeed, it seems that the response of dung beetles to variation in dung pad size may well account for more between-pad variability in abundance, biomass or density of beetles in the field than would inherent patterns of aggregation. However, these experiments were not specifically designed to test such a hypothesis.

Assumptions of the aggregation model of coexistence include that species are independently aggregated to a degree, that competition occurs and that the distribution of individuals is known before competition occurs. Competition in the adult stages of north temperate dung beetles is not well documented and is cited as occurring only infrequently. Some experimental evidence indicates density-dependent emigration from cow pads by *Aphodius* (Landin 1961, this study). Holter (1979) found that eggs of *A. rufipes* in cow pads in the field were distributed less contagiously than were adults, and his laboratory experiments demonstrated an inverse relationship between oviposition rates of *A. rufipes* and beetle density. Given the high energy content of dung and the frequently low numbers of individuals in pads, competition in north temperate dung beetles, when it occurs, is probably not exploitative for dung directly. Interference competition for space by larvae is considered most likely and evidence of larval competition and dynamics is slowly emerging (Holter 1975, 1979, Lumaret and Kirk 1987, Gittings 1994, Hirschberger 1996, Sowig 1997, Sowig et al. 1997). Thus, it may be that testing the aggregation theory using data on adult distribution is one step removed and, although it is logistically more difficult, such testing should concern itself more with larval distribution and competition. The question remains also whether adult density will be indicative of future larval production.

Resource availability versus resource utilisation

Other data further indicate that the aggregation model may not be entirely applicable to dung beetles, at least not without some further modification. Although larger pads may provide an apparent increase in resource, this may not actually be the case if not all of the pad is equally utilised. We suggest that the latter may be the case given the nature of within-pad spatial distribution of north temperate dung beetles, and the relative habitat suitability of pads across dung sizes.

Many beetles colonising dung pads are usually found not within the pad, but at the pad-soil interface or in the underlying soil {Desière 1983 (but see associated methodological problems on p.4 of Introduction), Gittings and Giller unpublished}.

Of those individuals found within the pad, larvae (at least in relatively fresh dung pads) and adults preferentially occupy the basal and peripheral parts of the pad (Holter 1982, Gittings 1994, this study Table 6). In terms of the aggregation model, this within-patch microhabitat partitioning inspires an interesting conundrum; crowding in preferred segments of patches may actually be much higher than estimates of crowding calculated from numbers per total patch size. It remains to be determined in detail what proportion of dung pads is utilisable by dung beetles and how the utilisable proportion may change in relation to dung pad size, successional age and the influence of environmental factors.

Adult and larval stages of north temperate dung beetles differ in their patterns of dung pad utilisation. Adults typically colonise fresh dung, occupying the pad for a relatively short time of several days, e.g. Fig. 1. In contrast, larvae typically inhabit and feed in older dung for a considerably longer period of a few weeks. Therefore, dung pad size may affect adults and larvae in different ways that are outlined in more detail below.

Dung beetles are exposed to anoxic conditions in the centre of fresh dung pads that may give rise to physiological stress (Holter 1991, 1994). However, Holter (1997) indicated that methane production from pads of sizes 0.25 L, 0.75 L, 1.0 L, 1.25 L and 1.5 L was proportional to the weight of the pad, which would indicate that there is a similar ratio of aerobic : anaerobic volume of dung across the dung sizes. In field and laboratory experiments, moisture contents of pads (between dung types) of the same size appeared to be an important factor in *Aphodius* dung beetle colonisation (Gittings and Giller 1998) and reproductive parameters (Gittings 1994), with wetter dung types regularly being the least favoured. The relative severity of these anoxic and fluidic conditions in pads of different sizes is unknown, but it might be expected to be more intense in the centre of larger fresh pads, considering the surface area: volume ratio in pads of different sizes. Note also that although beetles may be adapted to cope with the conditions of physiological stress that can occur in dung pads (Holter 1991, 1994), they may still prefer to avoid the centre of pads where the stress may be greatest. Despite the potential for larger pads to be more unfavourable habitats for adult dung beetles, the present data suggest that greater numbers and densities of beetles colonise larger pads. Thus, it may be that the beetles are forced to utilise more of the unfavoured proportion of the pad, or that they experience greater crowding in the preferred locations of the pad.

Even less work has been done on within-pad spatial distribution of dung beetle larvae. While larvae of soil-ovipositing species (see Gittings and Giller 1997) appear to remain at the soil-pad interface, at least in the earlier stages of development (Table 6), later instars can be found throughout the pad (personal observations). During dry summer periods, larger pads have lower dessication rates than smaller pads (Lumaret and Kirk 1987). Therefore, larger pads will have higher moisture contents for longer, which appears to be important for the suitability of the larger pads for larvae, in terms of providing dessication-resistant habitat and/or dung of acceptable nutritional quality.

In conclusion, the ecology of north temperate dung beetles is significantly affected by dung pad size. This appears primarily due to an interaction between the greater findability of larger pads and their greater suitability as habitats for larvae. The lower surface area : volume ratio of larger pads probably has different consequences for the adult and larval life stages. Thus, it may be that the tolerance by adults of relatively unfavourable conditions in larger pads is a trade-off for the greater suitability of larger pads for larvae. This may be a reflection of important processes occurring during the larval stage. More generally, we found that the density of both dung beetle adults and older larvae increased with patch size, which provides additional empirical data that advocate the incorporation of patch size as a variable in aggregation theory (Sevenster and van Alphen 1996). Finally, measures of crowding would appear to assume that all of the patch is equally utilisable and, more importantly, that different-sized patches are utilised in a similar manner. A measure of the utilisable proportion of different-sized patches, and the level of crowding experienced by organisms, can be confounded by several factors. These can include within-patch spatial distribution of organisms, which in the present study was possibly mediated through within-patch differences in resource quality, and disproportionate effects of environmental conditions (such as dessication) on patches of different size.

Acknowledgements

We are very grateful to Tom Gittings for providing data for experiment C1, helpful discussion and comments on earlier drafts. We thank Peter Holter for providing information and comments, Derek Casey and Linda Moloney for assistance with fieldwork, and John Murphy for comments on an earlier draft.

References

Atkinson, W. D. and Shorrocks, B. 1981. Competition on a divided and ephemeral resource: a simulation model. - J. Anim. Ecol. 50: 461-471.

Bach, C. E. 1988. Effects of host plant size on herbivore density: patterns. - Ecology 69: 1090-1102.

Cromartie, W. J. 1975. The effect of stand size and vegetational background on the colonisation of cruciferous plants by herbivorous insects. - J. Appl. Ecol. 12: 517-533.

Desière, M. and Thome, J. P. 1977. Variations qualitatives et quantitatives de quelques populations de coléoptères coprophiles associès aux excréments de 3 types d'herbivores. Rev. Ècol. Biol. Sol - 14: 583-591.

Desière, M. 1983. Écologie des coléoptères coprophiles en prairie permanente pâturée. 1.-Caractéristiques des populations de Coléoptères adultes coprophiles. Phénologie et dynamique saisonnière. - Bull. d'Écol. 14: 99-117.

Doube, B. M., Giller P. S. and Moola, F. 1988. Dung burial strategies in some South African coprine and onitine dung beetles (Scarabaeidae, Scarabaienae). - Ecol. Entomol. 13, 251-261.

Finn, J. A. , Gittings, T. and Giller, P. S. (1998) *Aphodius* dung beetle assemblage stability at different temporal and spatial scales. - Appl. Soil Ecol. 241:In press.

Giller, P. S. and Cambell, R. N. B. 1989. Colonisation patterns of mayfly nymphs (Ephemeroptera) on implanted substrate trays of different size. - Hydrobiol. 178: 59-71.

Gittings, T. (1994) The community ecology of *Aphodius* dung beetles. Unpublished PhD thesis, National University of Ireland.

Gittings, T. and Giller, P. S. 1997. Life history traits and resource utilisation in an assemblage of north temperate *Aphodius* dung beetles (Coleoptera, Scarabaeidea). - Ecography 20: 55-66

Gittings, T. and Giller, P. S. 1998. Resource quality and the colonisation and succession of coprophagous dung beetles. Ecography (in press).

Halffter, G. and Matthews, E. G. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidea). - Fol. Entomol. Mex. 12-14, 1-312.

Hanski, I. 1980. Spatial patterns and movements 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. 1986. Individual behaviour, population dynamics and community structure of *Aphodius* (Scarabaeidae) in Europe. - Acta Oecol., Oecol. Gen. 7: 171-187.

Hanski, I. 1987. Carrion fly community dynamics: patchiness, seasonality and coexistence. - Ecol. Entomol. 12: 257 - 266.

Hanski, I. 1991. North temperate dung beetles. - In: Hanski, I. and Cambefort, Y. (eds.), Dung beetle ecology. Princeton University Press, Princeton, New Jersey, pp. 305-329.

Hirschberger, P. and Drego, H. N. 1996. Oviposition of the dung beetle *Aphodius ater* in relation to the abundance of yellow dungfly larvae (*Scatophaga stercoraria*). - Ecol. Entomol. 21: 352-357.

Holter, P. 1975. Energy budget of a natural population of *Aphodius rufipes* larvae (Scarabaeidae). - Oikos 26: 177-186.

Holter, P. 1979. Abundance and reproductive strategy of the dung beetle *Aphodius rufipes* (L.) (Scarabaeidae). - Ecol. Entomol. 4: 317-326.

Holter, P. 1982. Resource utilisation and local coexistence in a guild of scarabaeid dung beetles (*Aphodius* spp.). - Oikos 39: 213-227.

Holter, P. 1983. Effect of earthworms on the disappearance rate of cattle droppings. - In: Satchell, J.E. (ed.), Earthworm Ecology. Chapman and Hall, London, pp. 49-57.

Holter, P. 1991. Concentration of oxygen, carbon dioxide and methane in the air within dung pats. - Pedobiologia 35: 381-386.

Holter, P. 1994. Tolerance of dung insects to low oxygen and high carbon dioxide concentrations. - Eur. J. Soil Biol. 30: 187-193.

Holter, P. 1997. Methane emissions from Danish cattle dung pats in the field. - Soil Biol. Biochem. 29: 31-37.

Ives, A. R. 1988. Covariance, coexistence and the population dynamics of two competitors using a patchy resource. - J. Theor. Biol. 115: 65- 92.

Jaenike, J. and James, A. C. 1991. Aggregation and the coexistence of mycophagous *Drosophila*. - J. Anim. Ecol. 60: 913-928.

Kareiva, P. 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. - In: Denno, R. F. and McClure, M. S. (eds.), Variable plants and herbivores in natural and managed systems. Academic Press, New York, New York, USA., pp. 259-298.

Kohlman, B.and Sanchez-Colon, S. 1984. Structure of a scarabaeinae community: a numerical behavioural study (Coloeptera: Scarabaeinae). - Acta Zool. Mex. 2: 1-27.

Kuusela, S. and Hanski, I. 1982. The structure of carrion fly communities; the size and type of carrion. - Hol. Ecol. 5: 337-348.

Landin, B. -O. 1961. Ecological studies on dung beetles (Col. Scarabaeidae). - Opusc. Entomol. (Suppl.) 19: 1-277.

Lumaret, J. P. and Kirk, A. A. 1987. Ecology of dung beetles in French mediterranean region (Coleoptera: Scarabaeinae). - Acta Zool. Mex. (ns) 24: 1-55.

Nealis, V. G. 1977. Habitat associations and community analysis of South Texas dung beetles (Coleoptera: Scarabaeinae). - Can. J. Zool. 55, 138-147.

Olechowicz, E. 1974. Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). X. Sheep dung and the fauna colonizing it. - Ekol. pol. 22: 589 - 616.

Peck, S. B. and Howden, H. F. 1984. Response of a dung beetle guild to different sizes of dung bait in a Panamanian rainforest. Biotropica 16: 235 - 238.

Sevenster, J. G. and van Alphen, J. J. M. 1996. Aggregation and Coexistence. II. A neotropical *Drosophila* community. - J. Anim. Ecol. 65: 308 - 324.

Sevenster, J. G. 1996. Aggregation and coexistence. I. Theory and analysis. - J. Anim. Ecol. 65: 297-307.

Shorrocks, B. Atkinson, W. and Charlesworth, P. 1979. Competition on a divided and ephemeral resource. - J. Anim. Ecol. 48: 899-908

Shorrocks, B. and Rosewell, J. 1987. Spatial patchiness and community structure: coexistence and guild size of drosophilids in ephemeral resources. - In: Gee, J. H. R. and Giller, P. S. (eds.), Organisation of communities: past and present. Blackwell Scientific Publications, Oxford, pp 29-51.

Sowig, P. 1997. Predation among *Sphaeridium* larvae: the role of starvation and size differences (Coleoptera: Hydrophilidae). - Ethology Ecology and Evolution 9: 241-251.

Sowig, P. and Wassmer, T. 1994. Resource partitioning in coprophagous beetles from sheep dung: Phenology and microhabitat preferences. - Zool. Jb. Syst. 121: 171-192.

Sowig, P., Himmelsbach, R. and Himmelsbach, W. 1997. Predator-prey relationships between insect larvae: growth of *Sphaeridium* larvae (Coleoptera: Hydrophilidae) under time constraints through predation on *Musca autumnalis* maggots (Diptera: Muscidae). - Can. J. Zool. 75: 2069-2076.

Stanton, M. L. 1983. Spatial patterns in the plant community and their effect upon insect search. - In: Ahmad, S. (ed.), Herbivorous insects: host-seeking behaviour and mechanisms. Academic Press, New York, New York, USA., pp.125-155.

Worthen, W. B., Carswell, M. L. and Kelly, K. A. 1996. Nested subset structure of larval mycophagous fly assemblages: nestedness in a non-island system. - Oecologia 107: 257-264.

Worthen, W. B., Jones, M. T. and Jetton, R. M. 1998. Community structure and environmental stress: dessication promotes nestedness in mycophagous fly communities. - Oikos 81: 45-54.

Appendix 1

Decomposition of different dung pad sizes

In the summer of 1995, dung pad decomposition in relation to dung pad size was investigated in a field experiment. The experiment was conducted at Moore Park. The dung pad sizes employed were 0.25 L, 0.5 L, 1.0 L and 1.5 L. Fresh dung was collected on the evening prior to deposition from the surrounding fields and from a cowshed. Experimental pads were artificially deposited on 16 August, 1995. Control pads were also deposited, and these were used to investigate the effect on decomposition rates of excluding dung beetle colonisation over the first 10 days as well as the exclusion of earthworms. About four days before the experiment began, the soil about each control pad was removed as a single sod to a depth of ca. 10 cm, and extending to ca. 10 cm from where the perimeter of the pad would eventually lie. The exposed hollow was lined with nylon mesh, the sod replaced and, with the aid of pegs, the nylon was raised to a height of not less than 5 cm from the ground. This was intended to prevent earthworm activity at the pad from below- and above-ground colonisation. Dung beetle colonisation of the control pads was prevented by the use of a metal frame similar in design to that in Holter (1977). Pads were collected on 20, 40, 60 and 80 days after deposition, and the proportion of initial dry weight remaining was calculated for pads on each date of collection.

Inspection of the pads and results from a concurrent colonisation study immediately adjacent to the decomposition experiment indicated that there was negligible colonisation of pads by dung beetles at this time. I cannot readily explain why this was so, as weather conditions appeared to be optimal for beetle colonisation. Earthworm activity appeared to be negligible for the first 40 days, most probably due to the drought-like conditions that prevailed during this time. However, the increased rainfall from day 40 onwards coincided with an observable increase in earthworm activity in the field, with the pads showing visible signs of 'grazing', particularly at the edges, which appeared to be due to earthworms. The control pads were relatively unaffected in this way for the duration of the experiment.

Decomposition rates of the experimental pads were similar across the different pad sizes and the considerable increase from day 40 onwards coincided with the increase in rainfall (Fig. 1) and an observed increase in earthworm activity. While there may have been statistical differences in decomposition between the sizes on some dates (Table 1), it is unclear whether such differences have any biological significance. The control pads showed similar decomposition rates to the experimental pads until

Table 1. ANOVA of the effect of treatment (experimental or control pads) and size (0.25 L, 0.5 L, 1.0 L and 1.5 L) on dung pad decomposition rates. The 'date*treatment*size' interaction term was significant ($F_{9,159} = 2.09^{*}$), so analyses were conducted for each separate date of sampling. Significance levels are indicated as follows: ^{ns} $p > 0.1$, † $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.005$, **** $p < 0.001$.

	Treatment	Size	Treatment*Size
Day 20	$F_{1,39} = 2.67^{ns}$	$F_{3,39} = 4.66^{**}$	$F_{3,39} = 0.11^{ns}$
Day 40	$F_{1,39} = 7.23^{*}$	$F_{3,39} = 2.13^{ns}$	$F_{3,39} = 0.27^{ns}$
Day 60	$F_{1,39} = 5.66^{*}$	$F_{3,39} = 9.72^{****}$	$F_{3,39} = 0.88^{ns}$
Day 80	$F_{1,39} = 132.8^{****}$	$F_{3,39} = 5.68^{***}$	$F_{3,39} = 3.68^{*}$

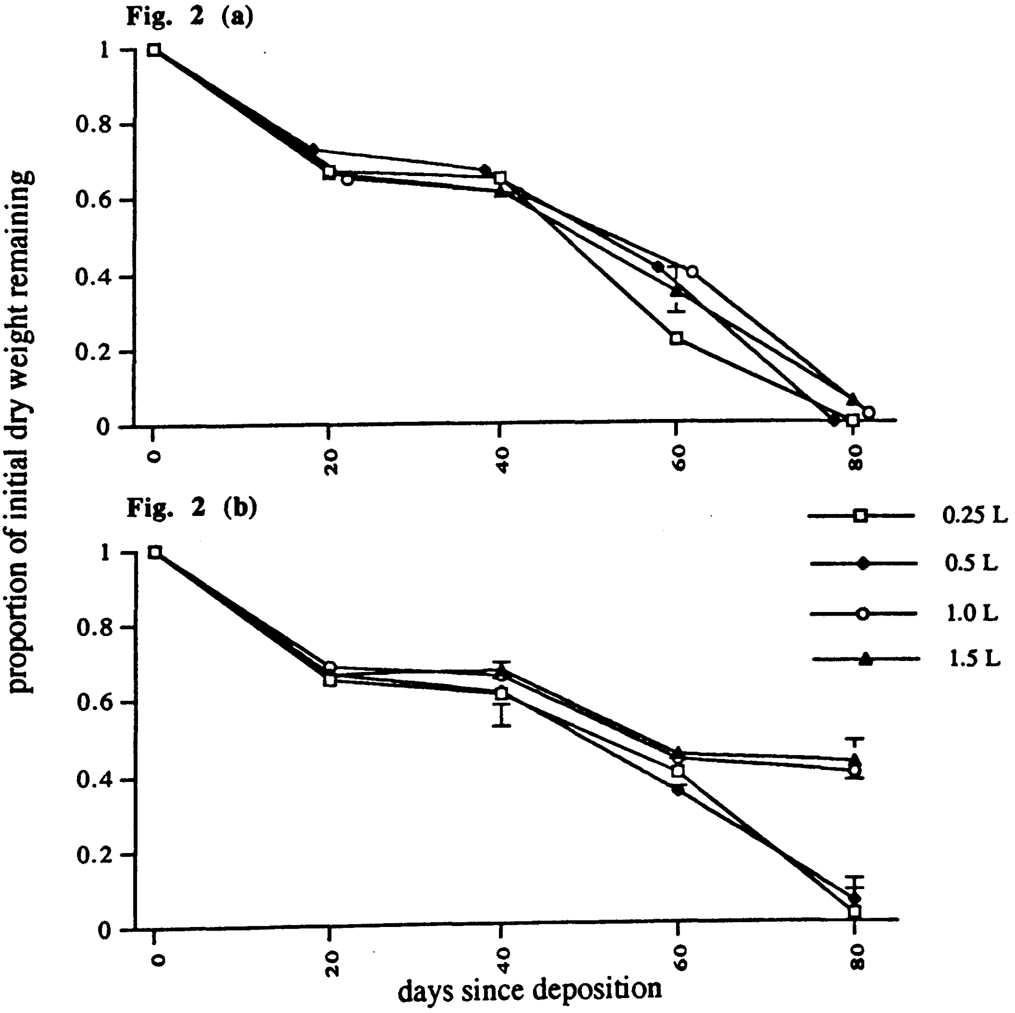


Fig. 2. Decomposition of (a) experimental and (b) control pads of different sizes over time since deposition. Data points represent mean proportion of initial dry weight remaining on days 20, 40, 60 and 80. Data points in (a) are horizontally displaced for clarity. See legend for key to different-sized pads.

day 40. From day 40, decomposition of the control pads was significantly lower than decomposition of the experimental pads. Decomposition rates between the different sizes of the control pads were similar until day 60. Over the last 20 days of the experiment, the 0.25 L and 0.5 L lost significantly greater proportion of mass than the 1.0 L and 1.5 L pads.

Unfortunately, the negligible dung beetle and/or earthworm activity which occurred at the beginning of this experiment had the effect of decreasing the degree of differences which were originally intended between the treatments. Nevertheless, the differences between the control pad sizes at the end of the experiment are notable (Fig. 2, Table 1). I suspect that the smaller pads are either more susceptible to the effects of weathering and/or the effect of any few earthworms that did cross the experimental earthworm barriers. The differences between the larger of the control and experimental pads also seem to underline the importance of earthworm activity in decompostion in north temperate pastures. Nevertheless, it would be very interesting to further examine the relative decomposition rates with typical levels of dung beetle colonisation, and to investigate whether earthworms tend to aggregate at the larger pads.

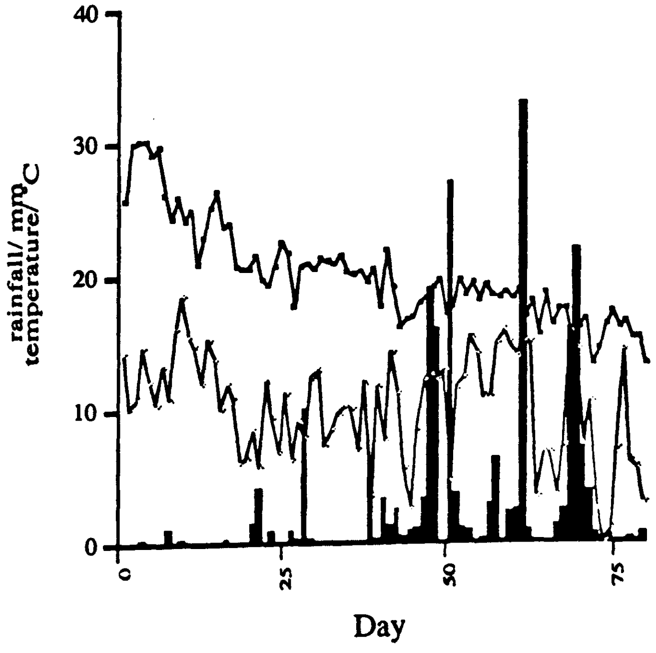


Fig. 1. Weather patterns over the duration of the decomposition experiment. The upper and lower lines indicate daily maximum and minimum air temperatures, histograms represent daily rainfall.

Chapter 4

The colonisation of native herbivore dung types by north temperate coprophagous dung beetles

Chapter 4

The colonisation of native herbivore dung types by Northern European coprophagous dung beetles.

Abstract

1. In order to investigate the role of dung quality in colonisation preferences of dung beetles, field experiments were used to compare the colonisation by dung beetles of standardised dung pads from a number of native large herbivore species (cow, horse and sheep). An additional experiment compared the colonisation by dung beetles of five different types of cow dung.

2. There were significant differences between dung types in moisture content and organic matter. There were also significant differences in the biomass, species richness and diversity of dung beetles colonising pads.

3. Laboratory experiments provided evidence that adult emigration and larval production were highest on sheep dung, which was typically colonised by the highest abundances of beetles.

4. Data from this study, and re-analysis of previously published data facilitated comparisons of dung beetle colonisation on different dung types. Generally, these data indicated that dung beetle species composition and species richness were quite similar among dung types of native large herbivores. However, significant differences in dung beetle assemblage structure among dung types occurred in terms of absolute abundances and the rank order of species.

5. The lack of a consensus on what constitutes a dung type preference is discussed. These data indicate that while dung beetles can display preferences for dung of different quality, biases in experimental design can confound interpretation. These biases include differences in sampling effort and pad size. Furthermore, the role of natural variability in dung pads (e.g. quality, size etc.) needs to be investigated to clarify the actual role of dung type in structuring dung beetle assemblages in nature.

Introduction

There have been a number of descriptive studies examining the colonisation by dung beetles of different dung types or the breeding performance of dung beetles in response to intraspecific variation in dung quality of herbivores (see below). Few of these studies have been undertaken in northern temperate regions where *Aphodius* species are the dominant coprophages.

In a review, Hanski (1991) stated that *Aphodius* species utilise 'the dung of domestic mammals- cattle, horses, and sheep without much discrimination'. Evidence for the indiscriminate use of dung by north temperate dung beetles may be provided by Landin (1961) and Heijerman (1990). Even then, Heijerman's (1990) analyses are confounded by the pooling of samples from different times of the year; in north temperate dung beetles, seasonal variation in species composition is considerable and may mask differences among dung types if data is pooled across seasons (Finn *et al.*, 1998ab; Chapters 2 and 5) . In comparisons of colonisation of sheep, horse, cow, pig and human dung, Rainio (1966) concluded that dung beetles were not 'wholly specialised to any particular kind of dung'; however, several dung beetle species in that study did display preferences for various dung types (see below).

In contrast, there are several examples in the literature in which north temperate dung beetles displayed preferences for some dung types over others e.g. Rainio (1966), Fincher, Stewart and Davis (1977), Kessler *et al.* (1974), Breymeyer and Zacharieva-Stoilova (1975), Desière and Thome (1977), Krikken (1978), Horgan (1989) and Gittings and Giller (1998). In addition, Hanski and Kuusela (1983) speculated that species abundances in sheep dung are less evenly distributed across pads than in cattle dung. Lumaret *et al.* (1992) found that when dung resources at a site changed from sheep to cow dung, dramatic changes in dung beetle community structure followed. However, in the latter study, it is unclear to what extent differences in dung type were responsible for changes in dung beetle community structure, as opposed to changes in dung pad size.

Attempts to investigate differences of dung beetle colonisation among dung types have sometimes been confounded by a lack of an experimental approach, inappropriate analyses, and the pooling of dung samples of different ages and different dung sizes. Other possible confounding effects include artefacts of macrohabitat preferences, the preference by larger species for larger dung pad sizes (Peck and Howden, 1984), as well as different patterns of succession among dung types (Gittings, 1994).

One might expect that the underlying cause of any differences among dung types, and preferences by dung beetles for different types of dung, are the interspecific differences in physical and chemical parameters of the dung. These parameters are produced by a combination of the digestion processes of herbivores and the material ingested, can be used to define dung quality and may include moisture content, nitrogen content, organic matter content etc. For example, sheep and cow dung are quite distinct in their appearance, but there can also be considerable intraspecific differences in herbivore dung quality (pers. obs). Intraspecific variation in dung quality may be due to seasonal (Greenham, 1972; Kunz, 1980; Matthieson and Hayles, 1983; MacQueen *et al.*, 1986; Edwards, 1991) or spatial (Greenham, 1972; Matthieson and Hayles, 1983) differences in pasture quality, or due to different diets (Palmer and Bay, 1983). Such intraspecific variation in chemical dung quality parameters has been related to reproductive success in dung beetles (MacQueen *et al.*, 1986; Ridsdill-Smith, 1986; Aschenborn *et al.*, 1989; Davis, 1989; Edwards, 1991) and in dung-breeding flies (Greenham, 1972; Kunz, 1980; Matthieson and Hayles, 1983; Palmer and Bay, 1983; MacQueen *et al.*, 1986; Edwards, 1991). For example, dung from cattle grazing in Australian pasture produced larger flies of both *Haemotobia irritans exigua* and *Musca vetustissima,* and more broods from the beetle *Euoniticellus intermedius*, during the summer wet season than from the same pasture in the winter dry season (MacQueen *et al.*, 1986).

In a study based in southern Ireland, Gittings and Giller (1998) employed field experiments to investigate the role of dung quality in dung beetle colonisation of dung from cows and from range of exotic animals (giraffe, zebra, guanaco, ostrich and red lechwe) from a nearby wildlife park. There were significant differences in dung quality parameters among the dung types, and dung beetle species usually displayed distinct and consistent preferences in their colonisation of particular types of dung, and these preferences appeared to be related to their reproductive biology. The present study employed a similar experimental approach to investigate colonisation by north temperate beetles of dung of large domestic native herbivores (sheep, horse and cow) and their colonisation on cow dung collected from cattle that were fed different diets. This facilitated investigation of whether inter- or intraspecific variation in dung quality affects dung beetle colonisation. In addition, a small number of laboratory experiments were conducted to investigate emigration rates and reproductive performance on different dung types. Previously published data from colonisation experiments of different dung types were analysed to further investigate dung beetle preferences for dung types.

Materials and Methods

Experimental design of colonisation experiments

A set of four field experiments (C1-C4) were conducted to investigate the influence of dung quality on dung beetle colonisation. The experiments differed in the dung type employed, days after deposition on which samples were collected and the number of sampling days (Table 1). Experiments C1-C3 employed sheep, horse and cow dung, whereas experiment C4 employed five different types of cow dung. At the start of experiments C1-C3, pitfall traps were baited with the same dung types that were used to form pads. The pitfall trap design follows that of Tyndale-Biscoe *et al.* (1981). When the contents of these traps were collected, the baits were not changed; thus, these pitfall traps provide a measure of dung beetle immigration to aging dung of different types (findability). In experiments C2 and C3, additional pads and pitfall traps with a dung size of 0.25 L of sheep dung were included in the experiment.

Table 1. Description of field experiments investigating colonisation of different dung types. Columns indicate experiment, dung types employed, days after deposition on which pad samples were collected and whether pitfall trapping was conducted.

Experiment and date		Dung types	Sampling days	Immigration pitfall traps
C1	23/5/96	cow, horse (x 2) and sheep	2, 6, 10	all types
C2	19/6/96	cow, horse, and sheep	2, 6, 10	all types
C3	11/8/96	cow, horse, and sheep	2, 4, 6	all types
C4	5/7/96	5 types of cow dung	2, 6	-

In experiment C1, two types of horse dung were used. One type of horse dung [hor (rgh)] was collected from rough pasture near Fota (dominated by *Juncus* and grasses), whereas the other type [hor (imp)] was derived from more improved pasture (regularly fertilised) near Fermoy. Compared to sheep and cow dung, horse dung was the most fibrous in texture and, particularly when fresh, had a very strong odour. Of the two types of horse dung in experiment C1, the former [hor (rgh)] was not liquid in consistency, was composed of clearly visible and relatively undigested plant fibres, and was inclined to fragment. The other type of horse dung [hor (imp)] appeared to be more digested, and had a more paste-like consistency than hor (imp). As the season progressed, the horse dung from Fermoy changed in appearance and texture, becoming more like that of hor (rgh). Of the horse, sheep and cow dung types, sheep dung had the most paste-like and solid texture.

The five different types of cow dung (Gr, F, Sp, Sil, Sum) in experiment C4 were collected at both Fota and Moorepark. The latter is an agricultural research station at Fermoy, County Cork. Cow dung type F was collected at Fota on the same day as experiment C4 commenced, and was quite fibrous in texture. Dung types Gr, Sp, Sil and Sum were collected at Moorepark. Dung type Sp, which had an extremely liquid texture, was collected during the spring and stored frozen until required. Dung types Gr, Sil and Sum were collected from cattle that were housed indoors for a feeding trial in which cattle were fed different grass types with additives (Gr and Sum) or silage and additives (Sil).

The basic experimental design consisted of replicate standardised pads and pitfall traps of the various dung types placed in a grid of replicate randomised blocks with each row and each dung pad/pitfall trap a similar interval (5m) apart (see Chapter 1). There were five blocks with single pitfall traps baited with each dung volume and a fixed number of dung pads of each volume in each block. Pads were composed of 1.0 litre (L) of fresh homogenised dung deposited in a circular plastic former of 16 cm diameter. On each sampling day, one dung pad of each type and the underlying soil to a depth of approximately 5 cm was sampled from each block. Dung pad samples were immediately transported to the laboratory and stored briefly at 4 °C before using Tullgren funnels to extract beetles from both the dung pad sample and underlying soil. On each sampling date the contents of the pitfall traps were also collected. Deposition and collection of the pads and pitfall traps were conducted between 09.00 and 13.30. Field experiments were carried out at Fota, County Cork, in southern Ireland. Fota is located approximately 20 km from Cork and the area consists of a wildlife park and cattle pasture, the latter being grazed by one or two herds of cattle. The soils at Fota consist of glacial tills and gravels (Gittings, 1994).

Laboratory experiments

Four experiments (A1-A4, see Table 2) were conducted to investigate the migration and reproductive performance of *Aphodius* species on the sheep, horse and cow dung types from field experiments C1 (A4) and C2 (A1-A3). In particular, investigations were directed at the production of eggs and larvae by a number of adults in replicate arenas in which dung was available. In general, the arenas consisted of containers with 5-6 cm of soil on which dung was available to a known number of beetles (Table 2). These arenas were kept within larger buckets containing a few centimetres of water, so that emigrating beetles were trapped in the water for collection. Before experiment A1 began, beetles were kept in each of the three dung types for three days, and placed on the same dung type in the experiment. In experiments A2 and A3, beetles were starved for at least one day before the experiment.

Table 2. Details of laboratory experiments investigating *Aphodius* reproductive success on different dung types from experiment C2.

Experiment	species	number of replicates	number of beetles per arena	days	dung size
A1	*A. ater*	4	10	12	0.5 L
A2	*A. depressus*	4	7	11	0.5 L
A3	*A. rufipes*	5	7	9	0.6 L
A4	*A. prodromus*	3	18	11	0.6 L

In all experiments, replicates were checked each day for emigrating beetles, and at the end of the experiments, the number of broods, eggs and larvae in the pad and underlying soil were recorded at the same time, as appropriate. In experiment A4, 18 individuals of *A. prodromus* were introduced to replicates (n = 3) containing 0.6 L of the four dung types in experiment C1. Replicates were checked daily for emigrating beetles, and analysis was based on emigrating beetles only. Although the number of remaining beetles was not recorded, inspection of some of the pads indicated that the vast majority of beetles had emigrated by the end of the eleven days of the experiment.

Dung quality

Moisture and organic matter contents were measured from subsamples of the fresh dung of each type in each of the experiments. From each of the fresh dung types, five subsamples of 80 - 150 g dry weight were collected and oven-dried to constant weight to determine the moisture content. The dried subsample was then ground in a mechanical mill. Organic matter content was determined by igniting dried subsamples of the milled sample in a 500 °C muffle furnace for 18 hours.

Study species

In this study, only the *Aphodius*, *Geotrupes* and *Sphaeridium* genera are considered, by virtue of their dominance of the composition of the biomass of coprophagous beetles in north temperate areas. The above groups also cover the main adult fluid-feeding and larval dung-feeding taxonomic groups. The *Aphodius* species were divided into breeding *Aphodius* and non-breeding *Aphodius*. The non-breeding *Aphodius* included species with saprophagous larvae (*A. prodromus* and *A. sphacelatus*) and the immature f_2 generations of dung-breeding species. For calculation of total catches of f_1 and f_2 generations in *Aphodius* species in which these generations overlapped, individuals caught during the overlap period were assigned to one of the two generations on the basis of their tibial wear (Gittings and Giller, 1997).

Data analysis

Calculations of biomass are based on dry weights of species (Gittings, 1994). The effect of dung pad type and day of sampling on biomass was examined by three-way ANOVA using factors 'block', 'type', 'day' and 'type * day'. The F-value of the 'type * day' interaction term indicates the significance of differences in the successional pattern among different dung types. The role of succession is considerable in dung beetle communities (e.g. see Fig. 1), and may confound investigations of an effect of dung type when analyses are conducted on data collected from a number of sampling dates. For this reason, ANOVA was used to compare biomass values of dung beetles among the dung types on each day of sampling. *Aphodius* species diversity (reciprocal of Simpson's index) was calculated from abundances of beetles, and *Aphodius* species richness was also calculated.

Canonical Correspondence Analysis (CCA) is a multivariate direct gradient analysis which ordinates species and samples by axes which are linear combinations of known environmental variables (see ter Braak, 1986, 1988, 1990). CCA was used to investigate the relationship between species occurrence and dung type in a single analysis combining experiments C1-C3, and including all species. The categorical variable 'expt. no.' was used as a covariable, and 'day' and the dung types were used as the environmental variables. Another CCA included the continuous variable 'size', to investigate the effect of dung size using data from the additional 0.25 L sheep pads in experiments C2 and C3. The raw data for the CCA consisted of the untransformed means of beetle numbers of each species collected in the replicate dung pads and there was downweighting of rare species. Forward selection was used to remove variables that did not explain a significant ($p < 0.02$) amount of the variance in species data, as tested using a Monte Carlo permutation test. A Monte Carlo test was also conducted to test the significance of the overall ordination. CCA analyses were conducted using the CANOCO 3.11 program. Dung quality parameters (organic matter and moisture content) were included as environmental parameters in experiment C4 only (see results). Note that Gittings (1994) reported that separate CCA ordinations that employed dung type, initial dung quality values and sampling day dung quality values all indicated similar relationships between species occurrence and dung types.

Comparisons of sheep, horse and cow assemblages in the literature

Comparisons of dung beetle numbers in different dung types from field studies are included in Rainio (1966), Kessler *et al.*, (1974) and Breymeyer and Zacharieva-Stoilova (1975), and included sheep, horse and cow dung types. Here, re-analyses of these data were conducted to facilitate comparisons of colonisation of the dung types.

Rainio (1966) examined the colonisation of several nearby sites in southern Finland (Tables 3, 4 and 5 of that study). In Table 3 of Rainio (1966), dung beetle numbers were compared in sheep, horse and cow dung, using pad sizes of 1 kg, 2 kg and 2 kg respectively. From the original data, the *Sphaeridium* and scarabaeid species were calculated as numbers per unit dung weight of the original dung size deposited. Table 5 of Rainio (1966) listed numbers of beetles in pig, cow, horse and sheep dung pads with a weight of 200 g at deposition. Pairwise correlations of the rank abundance of the most abundant species (total number of individuals captured > 10) were conducted among the four types of dung.

Kessler *et al.*, (1974) provided a comparison of the colonisation by dung beetles of cattle and sheep dung in South Dakota, USA. Only the *Sphaeridium* and scarabaeid species data collected in that study were utilised in the present calculations. A consideration of the sampling methods employed by Kessler *et al.* (1974) in collecting the two dung types is necessary prior to analysis. Cow pads were formed as "a 22.5 cm diam x 5.0 cm deep bovine manure pile". To facilitate sampling, cow pads were placed over pans which were placed in the soil. As the authors describe, "One pan was selected at random and removed from the exclosure at intervals of 24, 48, 72 and 96 hr. Throughout the season, 8 pans of dung were collected per week for 13 weeks" (Kessler and Balsbaugh, 1972). Thus, each pad was of volume $\pi r^2 h$ = 3.142 x 11.25^2 x 5 cubic centimetres = 1.988 litres. The collection of 8 pans per week for 13 weeks implies that the total volume of cow dung examined was 1.988 L x 8 x 13 = 207 L. Describing the collection of sheep dung, Kessler *et al.*, (1974) stated that sheep dung (24-96 hr old) was collected every seventh day and "each collection period, 2.85 cc of sheep manure was placed into a Burlese funnel for 24 hr". It seems extraordinary that only 2.85 cc of sheep dung would have been collected each week, and it is assumed that the sheep dung was collected using a similar methodology as the cow dung, but with a sheep pad size of 2.85 cc. Thus, from the methods described in Kessler and Balsbaugh (1972), a total of 296 cc (2.85 cc x 8 x 13) of sheep dung was examined in their study. If these calculations are correct, then the volume of cow dung examined was almost 700 times greater than the volume of sheep dung examined.

Breymeyer and Zacharieva-Stoilova (1975) provided data on the *Scarabaeidae* sampled in a Bulgarian pasture which contained both sheep and cattle. They randomly collected 10 naturally dropped pads of each dung type every month from May to September in 1970, totalling 50 pads of each dung type over the year. In Table II of Breymeyer and Zacharieva-Stoilova (1975), the authors indicated that the average numbers of beetles per pad were 38.3 and 89.2 beetles for sheep and cow dung respectively. Thus, a total of 1915 and 4410 beetles in sheep and cow dung were collected respectively (Table I of their study). In addition, they calculated the mean dry weight of sheep and cow pads as 7.5 and 534 g dry weight respectively, which differ by a factor of about 70. Therefore, the data in Table I of their study was derived from a total dry weight of cow dung which was, according to these calculations, 70 times greater than the total dry weight of sheep dung used.

Because of the considerable differences in sampling effort between the sheep and cow dung (see Discussion), only the first fifteen species in Table I of Breymeyer and Zacharieva-Stoilova (1975), plus *Aphodius distinctus* and *A. varians* + *A. varians* ab. *fabrici* (which occurred in sheep dung only, with percentages > 1%) were selected for re-analysis. These species were generally more abundant and/or occurred in both dung types (see Discussion). A correlation of the rank abundance of these species was used to investigate assemblage structure of the dung beetles captured in the two dung types.

Results

Dung Quality parameters

There were significant differences in both organic matter and moisture content levels between dung types in the colonisation experiments (Table 3). Sheep dung consistently had lowest values of organic matter and moisture content.

Dung beetle biomass

Biomass of the various dung beetle groups (*Geotrupes*, *Sphaeridium*, as well as breeding and non-breeding *Aphodius*) varied considerably among the experiments, among the dung types and among days of sampling (Fig. 1). Experiment C1 was dominated by *Sphaeridium* and non-breeding *Aphodius* species (the latter was comprised mostly of *A. prodromus*). In experiment C2, breeding *Aphodius* species were dominant, whereas captures in experiments C3 and C4 were mostly of *Sphaeridium* and breeding *Aphodius* species.

Table 3. Summary of initial (Day 0) organic matter and moisture content levels in the different dung types employed in experiments C1-C3 (a) and (b) C4. Organic matter values are percentages of dry weight, moisture contents are percentages of wet weight. Values are presented as mean ± s.e. Chemical parameters were analysed by ANOVA; values with the same superscript were not significantly different ($p < 0.05$).

a. Experiments C1-C3

	sheep	horse (imp)	cow	horse (rgh)
C1				
organic matter	$76.8^{a} \pm 0.2$	$77.3^{a} \pm 0.2$	$80.8^{b} \pm 0.2$	$80.3^{b} \pm 0.5$
moisture content	$79.3^{a} \pm 0.2$	$85.0^{b} \pm 0.2$	$87.8^{c} \pm 0.1$	$85.1^{b} \pm 0.4$
C2				
organic matter	$81.5^{a} \pm 0.4$	$81.4^{a} \pm 0.3$	$81.5^{a} \pm 0.1$	
moisture content	$82.1^{a} \pm 0.1$	$87.1^{b} \pm 0.1$	$87.1^{b} \pm 0.1$	
C3				
organic matter	$77.5^{a} \pm 0.2$	$82.4^{a} \pm 0.5$	$84.3^{c} \pm 0.5$	
moisture content	$81.8^{a} \pm 0.1$	$86.5^{c} \pm 0.1$	$84.5^{b} \pm 0.3$	

b. Experiment C4

C4	Gr	F	Sp	Sil	Sum
organic matter	$80.8^{a} \pm 0.1$	$86.3^{c} \pm 0.1$	$79.9^{a} \pm 0.7$	$84.1^{b} \pm 0.4$	$87.4^{c} \pm 0.1$
moisture content	$85.0^{b} \pm 0.2$	$87.1^{c} \pm 0.1$	$88.8^{d} \pm 0.1$	$81.0^{a} \pm 0.1$	$84.1^{b} \pm 0.2$

Statistical analyses of the biomass of dung beetles colonising different dung types in experiments C1-C4 are presented in Table 4. Experiments varied in both the absolute levels of dung beetle biomass and the relative proportions of the dung beetle groups that colonised pads. In experiments C1-C3, sheep dung always had the highest total biomass on each day of sampling. In experiment C1, the horse dung from improved pasture had relatively high levels of beetle biomass, but beetle biomass in the horse dung from the unimproved pasture was very low. Compared to dung beetle biomass in sheep dung, cow dung also had very low biomass in experiments C2 and C3. There were significant differences in total dung beetle biomass among some of the different types of cow dung in experiment C4 (Table 4), but significant differences in species abundances among the dung types only occurred in *Aphodius ater, A. depressus, Sphaeridium lunatum* and *S. lunatum* (Table 5).

Pitfall trapping data allowed comparison of findability among the dung types (cf. Figs. 1 and 2). The horse dung from improved pasture appeared to be more attractive to the non-breeding *A. prodomus* and this was evident in the pitfall trapping data (Fig. 2). Note that the horse dung from the rough pasture attracted very few beetles, and

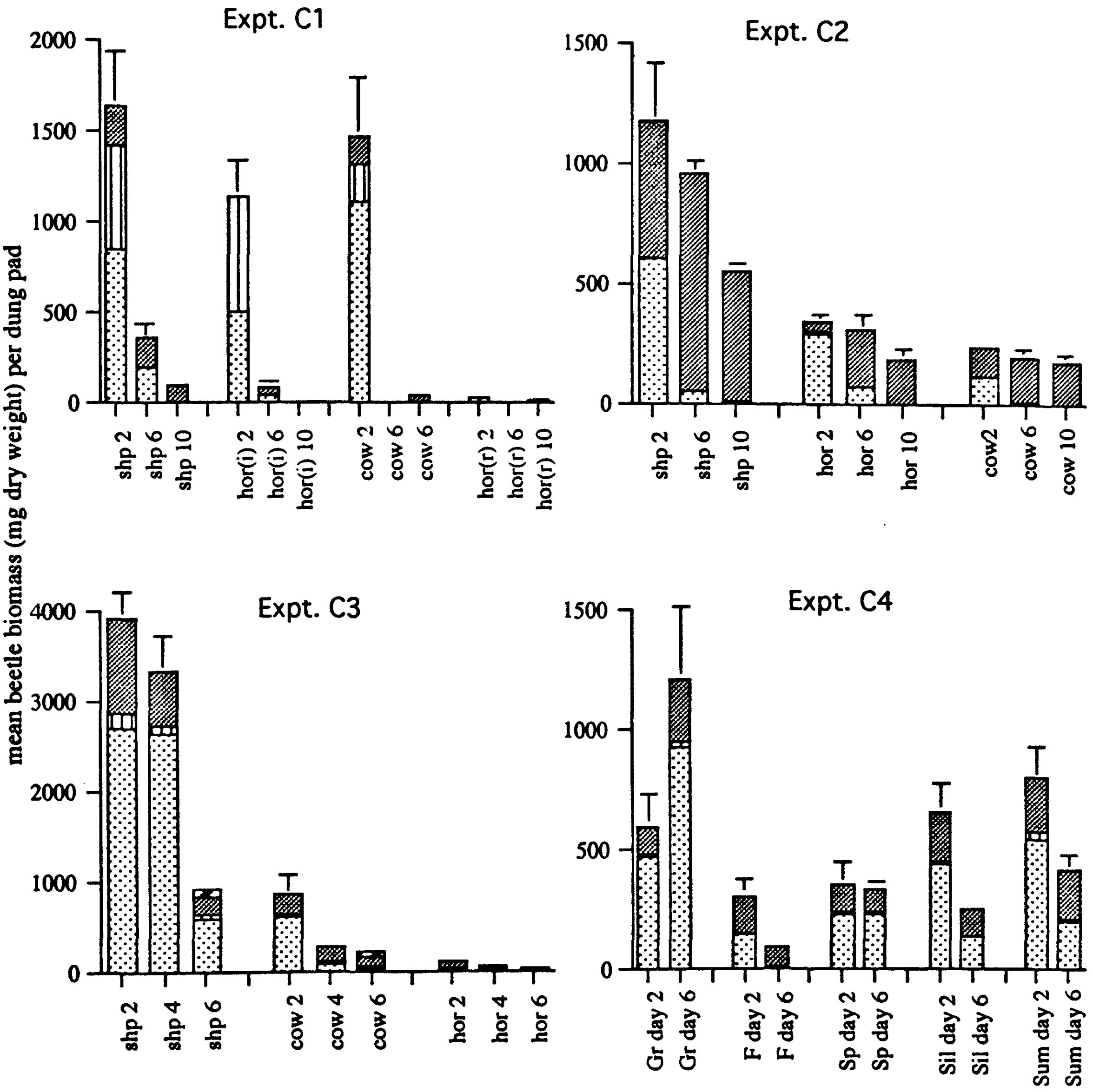


Fig. 1. Biomass (± s.e.) of different dung beetle genera in various types and ages of dung. All experiments used one litre of dung. There were differences between experiments in the number of sampling days and the number of days after deposition on which pads were collected. Two types of horse dung were employed in experiment C1. Numbers after dung types indicate age of dung pads on collection. Experiment C4 employed five different types of cow dung. See text for details. Shp= sheep, hor = horse.

▨ *Geotrupes*
▥ *Aphodius* non-breeding
▩ *Aphodius* breeding
⬚ *Sphaeridium*

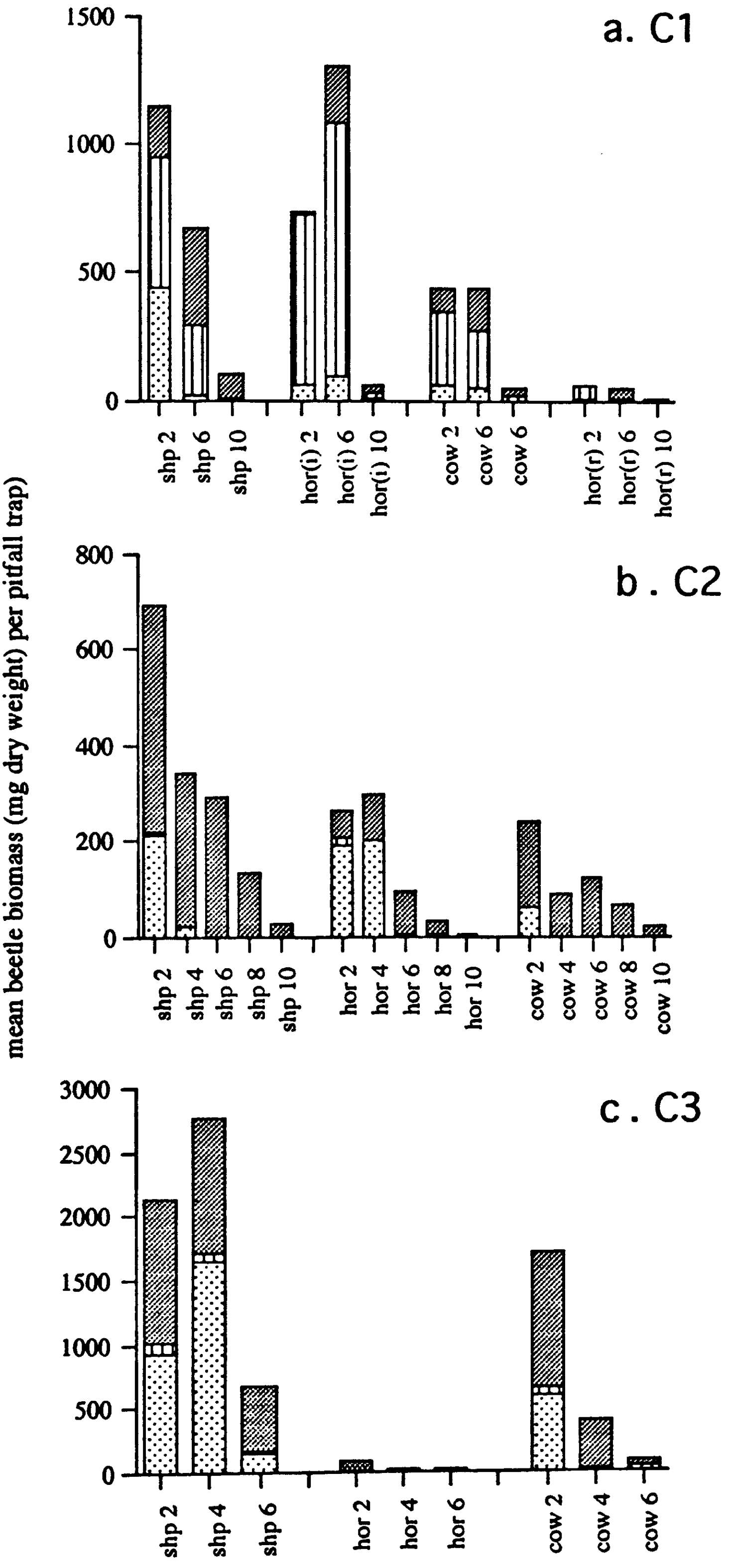


Fig. 2. Biomass of dung beetle genera captured in pitfall traps baited with different types of dung at the beginning of experiments C1- C3. All experiments used one litre of dung. Indicated are the dung type and the number of days after baiting of the pitfall trap on which trap contents were collected. See text for details. Shp= sheep, hor = horse.

Table 4. Effect of dung type on biomass of dung beetles collected from dung pads deposited in filed experiments C1-C4. Significance of F-values are indicated as follows: †p < 0.1, *p < 0.05, **p < 0.01, ***p < 0.005, ****p < 0.001. If necessary, data were transformed by square root (x + 0.5) (sq), log (x+1) (log) or were untransformed (u). Dung types with values of biomass that were not significantly different (p < 0.05) have the same superscript. *Aphodius* species were divided into breeding and non-breeding beetles (see text). The dung types employed were cow, sheep and horse (hor) dung. In experiment C1, two types of horse dung, hor(i) and hor(r), are indicated, and were derived from improved and rough pasture respectively. Because there were frequently significant effects of the 'day' or 'type*day' terms, a seperate analysis was conducted for individual days within each experiment. In some experiments, there were insufficient numbers of captures for analysis of any or all taxonomic groups.

a. Experiment C1

Analysis	Type	Day	Type*Day
Total biomass log	$F_{3,59}$ =38.6****	$F_{2,59}$ = 91.9****	$F_{6,59}$ = 12.7****
Aphodius (b) log	$F_{3,59}$ = 34.8****	$F_{2,59}$ = 4.3*	$F_{6,59}$ = 10.7****
Aphodius (nb)log	$F_{3,59}$ = 38.8****	$F_{2,59}$ = 1606****	$F_{6,59}$ = 33.7****
Sphaeridium log	$F_{3,59}$ = 40.0****	$F_{2,59}$ = 146.9****	$F_{6,59}$ = 22.2****
Day 2			Highest ———>Lowest
Total biomass log	$F_{3,19}$ = 68.7****		sheep^{a} cow^{a} hor(i)^{a} hor(r)^{b}
Aphodius (b) log	$F_{3,19}$ = 21.8****		sheep^{a} cow^{a} hor(i)^{b} hor(r)^{b}
Aphodius (nb)log	$F_{3,19}$ = 52.8****		hor(i)^{a} sheep^{a} cow^{b} hor(r)^{c}
Sphaeridium log	$F_{3,19}$ = 51.2****		cow^{a} sheep^{a} hor(i)^{a} hor(r)^{b}
Day 6			
Total biomass log	$F_{3,19}$ = 24.9****		sheep^{a} hor(i)^{b} hor(r)^{c} cow^{c}
Aphodius (b) log	$F_{3,19}$ = 30.9****		sheep^{a} hor(i)^{a} cow^{b} hor(r)^{b}
Aphodius (nb)log	all values = 0		-
Sphaeridium log	$F_{3,19}$ = 15.5****		sheep^{a} hor(i)^{b} cow^{b} hor(r)^{b}
Day 10			
Total biomass log	$F_{3,19}$ = 24.9****		sheep^{a} cow^{b} hor(r)^{b} hor(i)^{c}

b. Experiment C2

Experiment	Type	Day	Type*Day
Total biomass sq	$F_{2,44}$ = 50.0****	$F_{2,44}$ = 6.8***	$F_{4,44}$ = 1.02ns
Aphodius (b) sq	$F_{2,44}$ = 59.8****	$F_{2,44}$ = 7.8***	$F_{2,44}$ = 1.83ns
Aphodius (nb)sq	$F_{2,44}$ = 3.4*	$F_{2,44}$ = 8.49****	$F_{4,44}$ = 2.2†
Sphaeridium sq	$F_{2,44}$ = 10.6****	$F_{2,44}$ = 72.7****	$F_{4,44}$ = 3.8*
Day 2			Highest—>Lowest
Total biomass sq	$F_{2,14}$ = 16.7****		sheep^{a} hor(i)^{b} cow^{b}
Aphodius (b) sq	$F_{2,14}$ = 25.6****		sheep^{a} cow^{b} hor(i)^{b}
Aphodius (nb)sq	$F_{2,14}$ = 2.7ns		hor(i)^{a} sheep^{a} cow^{a}
Sphaeridium sq	$F_{2,14}$ = 6.2*		sheep^{a} hor(i)^{ab} cow^{b}
Day 6			
Total biomass sq	$F_{2,14}$ = 32.9****		sheep^{a} hor(i)^{b} cow^{b}
Aphodius (b) sq	$F_{2,14}$ = 32.9****		sheep^{a} hor(i)^{b} cow^{b}
Aphodius (nb)sq	$F_{2,14}$ = 1.0ns		hor(i)^{a} sheep^{a} cow^{a}
Sphaeridium sq	$F_{2,14}$ = 6.3*		hor(i)^{a} sheep^{a} cow^{b}
Day 10			
Total biomass sq	$F_{2,14}$ = 11.8****		sheep^{a} hor(i)^{b} cow^{b}
Aphodius (b) sq	$F_{2,14}$ = 11.6***		sheep^{a} hor(i)^{b} cow^{b}

c. Experiment C3

Experiment	Type	Day	Type*Day
Total biomass sq	$F_{2,44} = 235.9^{****}$	$F_{2,44} = 33.9^{****}$	$F_{4,44} = 11.7^{****}$
Aphodius (b) sq	$F_{2,44} = 150.2^{****}$	$F_{2,44} = 48.6^{****}$	$F_{4,44} = 9.0^{****}$
Aphodius (nb)sq	$F_{2,44} = 31.4^{***}$	$F_{2,44} = 2.8^{\dagger}$	$F_{4,44} = 2.2^{\dagger}$
Sphaeridium log	$F_{2,44} = 235.0^{****}$	$F_{2,44} = 57.3^{****}$	$F_{4,44} = 9.5^{\dagger}$
Day 2			Highest—>Lowest
Total biomass sq	$F_{2,14} = 80.4^{****}$		sheep^{a} cow^{b} hor(i)^{c}
Aphodius (b) sq	$F_{2,14} = 43.2^{****}$		sheep^{a} cow^{b} hor(i)^{c}
Aphodius (nb)sq	$F_{2,14} = 17.8^{***}$		sheep^{a} cow^{b} hor(i)^{b}
Sphaeridium log	$F_{2,14} = 45.0^{****}$		sheep^{a} cow^{b} hor(i)^{c}
Day 4			
Total biomass sq	$F_{2,14} = 110.9^{****}$		sheep^{a} cow^{b} hor(i)^{b}
Aphodius (b) sq	$F_{2,14} = 43.3^{****}$		sheep^{a} cow^{b} hor(i)^{c}
Aphodius (nb)sq	$F_{2,14} = 8.3^{**}$		sheep^{a} cow^{ab} hor(i)^{b}
Sphaeridium log	$F_{2,14} = 54.7^{****}$		sheep^{a} cow^{b} hor(i)^{c}
Day 6			
Total biomass sq	$F_{2,14} = 64.7^{****}$		sheep^{a} cow^{b} hor(i)^{c}
Aphodius (b) sq	$F_{2,14} = 25.6^{****}$		sheep^{a} cow^{a} hor(i)^{b}
Aphodius (nb)sq	$F_{2,14} = 7.3^{**}$		sheep^{a} cow^{a} hor(i)^{b}
Sphaeridium log	$F_{2,14} = 154.8^{****}$		sheep^{a} cow^{b} hor(i)^{b}

d. Experiment C4

Experiment	Type	Day	Type*Day
Total biomass sq	$F_{4,49} = 7.3^{****}$	$F_{1,49} = 2.5$ns	$F_{4,44} = 3.52^{*}$
Aphodius (b) sq	$F_{2,44} = 1.7$ns	$F_{2,44} = 0.12$ns	$F_{4,44} = 1.6$ns
Aphodius (nb)sq	$F_{2,44} = 2.93^{*}$	$F_{2,44} = 0.02^{ns}$	$F_{4,44} = 4.12^{**}$
Sphaeridium log	$F_{2,44} = 35.4^{****}$	$F_{2,44} = 21.4^{****}$	$F_{4,44} = 16.0^{****}$
Day 2			Highest—>Lowest
Total biomass sq	$F_{2,14} = 2.69^{\dagger}$		sum^{a} sil^{a} gr^{a} sp^{a} f^{a}
Aphodius (b)	$F_{2,14} = 1.76$ns		sum^{a} sil^{a} gr^{a} sp^{a} f^{a}
Aphodius (nb)	$F_{2,14} = 6.7^{***}$		sum^{a} sil^{ab} gr^{abc} sp^{bc} f^{c}
Sphaeridium log	$F_{2,14} = 2.8^{\dagger}$		sum^{a} sil^{a} f^{a} gr^{a} sp^{a}
Day 6			
Total biomass sq	$F_{2,14} = 8.18^{****}$		gr^{a} sum^{ab} sp^{b} sil^{b} f^{b}
Aphodius (b) sq	$F_{2,14} = 1.8$ns		gr^{a} sum^{a} sil^{a} sp^{a} f^{a}
Aphodius (nb)sq	$F_{2,14} = 2.18$ns		gr^{a} f^{a} sp^{a} sum^{a} sil^{a}
Sphaeridium log	$F_{2,14} = 102.2^{****}$		gr^{a} sp^{b} sum^{b} sil^{b} f^{c}

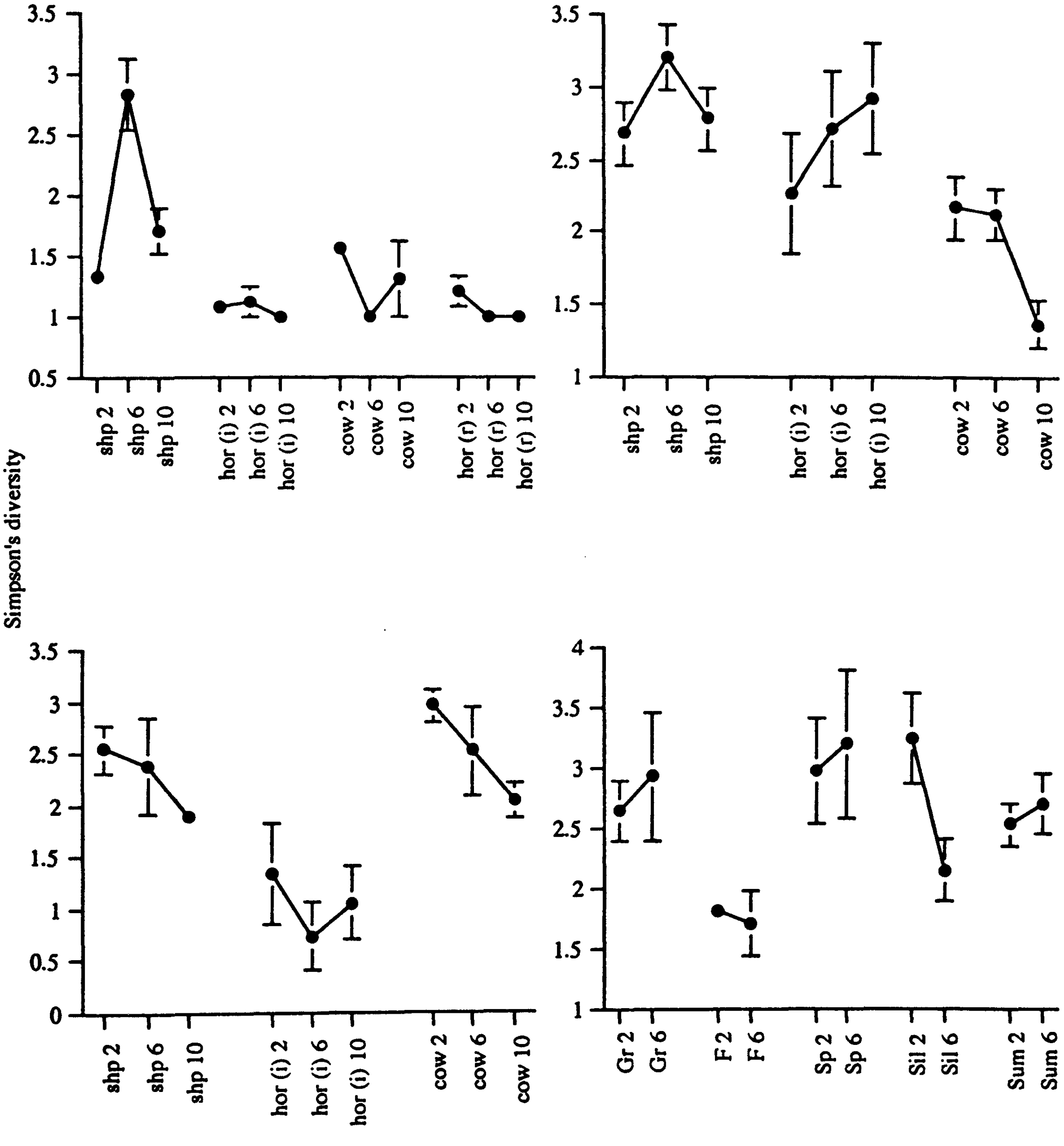


Fig. 3. Simpson's diversity of *Aphodius* species in dung pats of different dung types in field experiments. Day of sampling is indicated after dung type; shp= sheep, hor (i)= horse dung from improved pasture, hor (r)= horse dung from rough pasture.

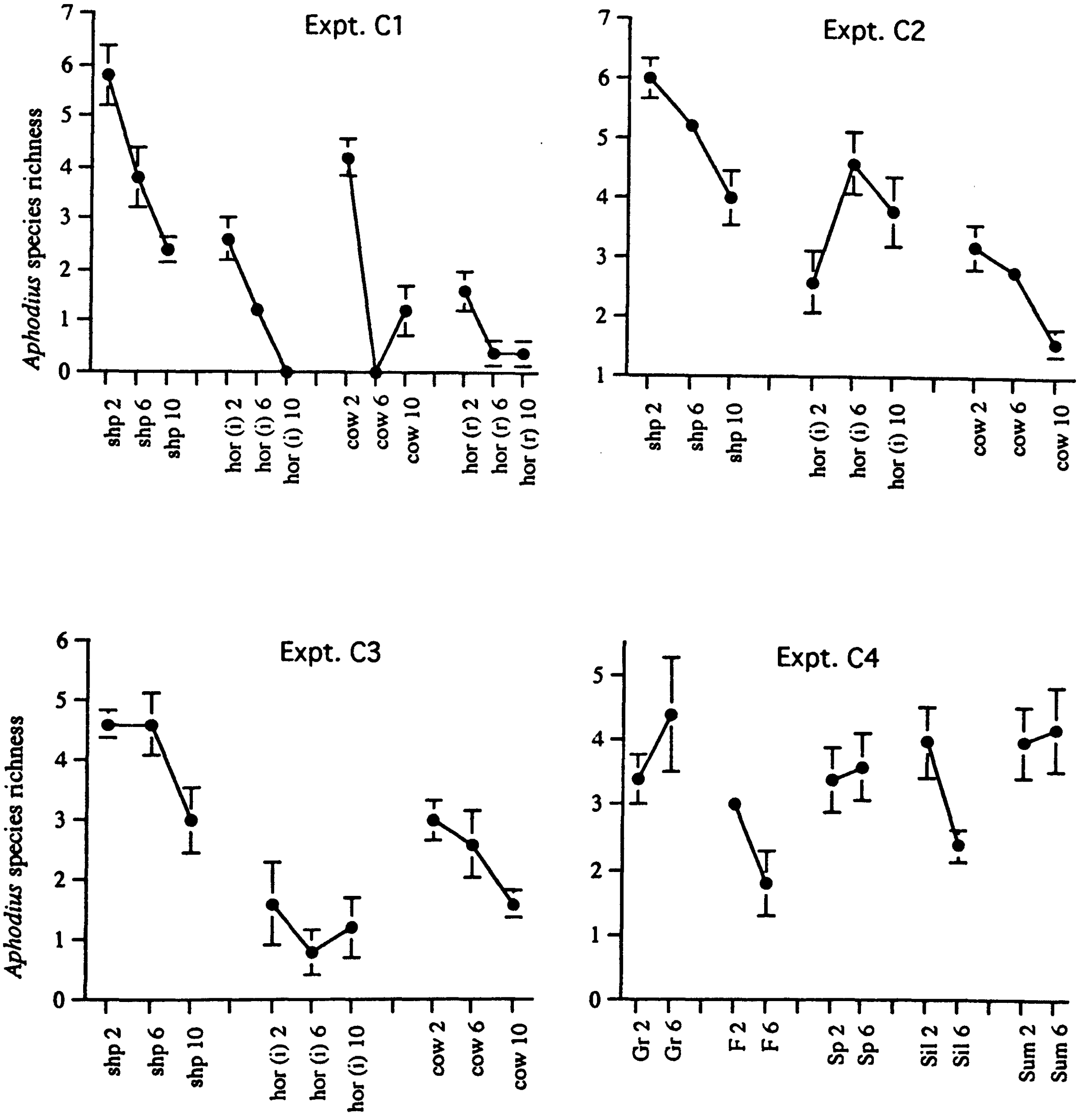


Fig. 4. *Aphodius* species richness (mean ± se) in dung pats of different dung types in field experiments C1-C4. Day of sampling is indicated after dung type; shp= sheep, hor (i)= horse dung from improved pasture, hor (r)= horse dung from rough pasture.

Table 5. Effect of cow dung type in experiment C4 on abundances of species. Analysed by Anova or, in the case of *A. erraticus*, by Friedman's test. Columns indicate the species, the number of individuals captured in the experiment, the test statistic and the dung type preference in ascending order. Significance of analyses indicated as follows: ^{ns} $p > 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.005$, **** $p < 0.001$.

Species	n	F-value	smallest —> largest
A. ater	241	$F_{4,\,24} = 6.48^{***}$	$\mathrm{Sp^{a}\ Sil^{ab}\ Gr^{b}\ F^{b}\ Sum^{b}}$
A. depressus	109	$F_{4,\,24} = 3.56^{*}$	$\mathrm{F^{a}\ Sil^{ab}\ Sp^{ab}\ Gr^{ab}\ Sum^{b}}$
A. erraticus	16	$F_{4,\,24} = 0.154^{ns}$	$\mathrm{F^{a}\ Sp^{a}\ Sil^{a}\ Sum^{a}\ Gr^{a}}$
A. fimetarius	26	$F_{4,\,24} = 0.27^{ns}$	$\mathrm{Sil^{a}\ Gr^{a}\ Sp^{a}\ Sum^{a}\ F^{a}}$
A. fossor	175	$F_{4,\,24} = 1.36^{ns}$	$\mathrm{Gr^{a}\ Sp^{a}\ F^{a}\ Sil^{a}\ Sum^{a}}$
A. rufipes	47	$F_{4,\,24} = 2.09^{ns}$	$\mathrm{F^{a}\ Sp^{a}\ Sil^{a}\ Sum^{a}\ Gr^{a}}$
S. lunatum	680	$F_{4,\,24} = 14.6^{****}$	$\mathrm{F^{a}\ Sp^{b}\ Sil^{bc}\ Sum^{bc}\ Gr^{c}}$
S.scarabaeoides	940	$F_{4,\,24} = 7.17^{***}$	$\mathrm{F^{a}\ Sil^{ab}\ Sp^{ab}\ Sum^{b}\ Gr^{b}}$

Additional rare species: *S. bipustulatum* n = 7; *A. rufus* n = 3; *A. granarius* n = 1.

Table 6. Comparison of species frequencies in pitfall traps and dung pad samples. Analysed by randomised block analysis of variance (see text). All data were log (x+1) transformed. Significance of F-values are indicated as follows: † $p > 0.1$; * $p < 0.05$, ** $p < 0.01$ *** $p < 0.005$; **** $p < 0.001$.

	C 1	C 2	C 3
A. ater	$F_{3,\,39} = 0.48^{ns}$	$F_{2,\,29} = 13.29^{****}$	$F_{2,\,29} = 0.75^{ns}$
A. depressus	$F_{3,\,39} = 19.2^{****}$	$F_{2,\,29} = 1.72^{ns}$	$F_{2,\,29} = 1.6^{ns}$
A. erraticus	$F_{3,\,39} = 9.48^{****}$	$F_{2,\,29} = 1.51^{ns}$	$F_{2,\,29} = 0.58^{ns}$
A. fimetarius	$F_{3,\,39} = 1.26^{ns}$	$F_{2,\,29} = 2.29^{ns}$	$F_{2,\,29} = 2.94^{\dagger}$
A. fossor	$F_{3,\,39} = 5.39^{**}$	$F_{2,\,29} = 2.16^{ns}$	$F_{2,\,29} = 3.68^{*}$
A. prodromus	$F_{3,\,39} = 1.04^{ns}$	$F_{2,\,29} = 2.73^{\dagger}$	-
A. rufipes	$F_{3,\,39} = 2.34^{\dagger}$	$F_{2,\,29} = 16.88^{****}$	$F_{2,\,29} = 3.15^{\dagger}$
A. rufus	-	-	$F_{2,\,29} = 2.11^{ns}$
A. sphacelatus	$F_{3,\,39} = 2.00^{ns}$	-	-
S. lunatum	$F_{3,\,39} = 4.72^{**}$	$F_{2,\,29} = 1.74^{ns}$	$F_{2,\,29} = 2.11^{ns}$
S.scarabaeoides	$F_{3,\,39} = 5.08^{**}$	$F_{2,\,29} = 12.31^{****}$	$F_{2,\,29} = 0.30^{ns}$

Table 7. Effect of dung type on species richness and Simpson's diversity of the *Aphodious* taxocenes. Analysed by randomised block analysis of variance (see text). Data were untransformed. Significance of F-values are indicated as follows: † $p < 0.1$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.005$, ****$p < 0.001$.

Experiment	Type	Day	Type*Day
***Aphodius* species richness**			
Expt. C1	$F_{3,\,59} = 45.3^{****}$	$F_{2,\,59} = 57.5^{****}$	$F_{6,\,59} = 5.3^{****}$
Expt. C2	$F_{2,\,44} = 34.4^{****}$	$F_{2,\,44} = 6.6^{***}$	$F_{4,\,44} = 6.4^{***}$
Expt. C3	$F_{2,\,44} = 30.3^{****}$	$F_{2,\,44} = 4.5^{*}$	$F_{4,\,44} = 1.33$ns
Expt. C4	$F_{4,\,49} = 3.2^{*}$	$F_{4,\,49} = 0.7$ns	$F_{4,\,49} = 2.1$ns
Simpson's diversity			
Expt. C1	$F_{3,\,59} = 26.5^{****}$	$F_{3,\,59} = 3.1^{\dagger}$	$F_{3,\,59} = 10.7^{****}$
Expt. C2	$F_{2,\,44} = 11.3^{****}$	$F_{2,\,44} = 1.4$ns	$F_{2,\,44} = 2.1$ns
Expt. C3	$F_{2,\,44} = 18.5^{****}$	$F_{2,\,44} = 3.0^{\dagger}$	$F_{4,\,44} = 3.0^{ns}$
Expt. C4	$F_{4,\,49} = 3.74^{*}$	$F_{4,\,49} = 0.2$ns	$F_{4,\,49} = 1.2$ns

that, based on pitfall captures, the relative findability of hor (imp) appeared to decrease over experiments C1- C3. In all three experiments, sheep dung generally had the highest pitfall captures of dung beetle biomass, and remained the most 'findable' over a longer duration. In between-dung type comparisons of colonisation between pitfall trap and pad samples, the relative species frequencies tended to be similar (17 out of 28 comparisons; Table 6). Of the nine cases where species had significantly different between-dung type distributions in pitfall and pad samples, five cases had species that were significantly more frequent in dung pads, while species were more frequent in pitfall samples in two examples.

Species diversities of *Aphodius* within dung types showed no consistent patterns over time in experiments C1-C3 (Fig. 3); however, there were significant differences among the dung types (Table 7). *Aphodius* species richness (Fig. 4) typically decreased or showed no significant change over time in the various dung types in experiments C1-C4. There were significant differences in levels of *Aphodius* species richness and diversity among the dung types (Table 7), with sheep dung having consistently higher species richness.

Laboratory experiments

In experiment A1, there were significant differences among dung types in the production of eggs and larvae by *A. ater* (Anova: $F = 12.47$, $p = 0.003$, square-root transformed; Table 8), with sheep dung having significantly greater production than horse and cow dung (Fig. 5). There were very low emigration rates from any of the dung types, and pad residence times (PRT) were not statistically analysed. In experiment A2, there were significant differences in the pat residence times of *A. depressus* among all three dung types (Anova: $F = 23.42$, $p < 0.001$, untransformed, Table 8). Individuals in sheep and cow dung had the highest and lowest PRT respectively (Fig. 5). Comparing numbers of progeny (the combined number of eggs and larvae), there were significant differences between sheep and cow dung only (Anova: $F = 5.2$, $p < 0.05$, log-transformed; Table 8, Fig. 5). In experiment A3, pat residence times of *A. rufipes* were significantly lower in cow dung than in sheep or horse dung (Anova: $F = 17.2$, $p < 0.001$, untransformed). Comparing numbers of progeny (the number of eggs and larvae combined), cow dung produced significantly lower numbers of eggs and larvae than sheep and horse dung (Anova: $F = 17.2$, $p < 0.001$, log-transformed; Table 8, Fig. 5). In experiment A4, there were significant differences in emigration rates of *A. prodromus* (Anova: $F = 6.37$, $p < 0.001$, untransformed).

Table 8. Reproductive performance of *Aphodius* species in laboratory experiments employing pads of sheep, horse and cow dung (using dung from experiment C2). Experiments A1 (*A. ater*, 12 days) and A2 (*A. depressus*, 11 days) employed 0.5 L pad sizes (n = 4), and for each dung type the numbers of produced eggs and larvae in different stages are indicated. Experiment A3 (*A. rufipes*, 9 days), employed 0.6 L pad sizes (n = 5). Indicated are the numbers (mean ± s.e.) of broods, eggs and larvae observed at the end of a period of 9 days. Adult emigration was allowed in all three experiments.

Expt.	Type	eggs	LI	LII	LIII	Total
A1	**Sheep**	30.0 ± 9.3	32.3 ±15.7	49.3 ± 41.9	1.0 ± 2.0	112.5 ± 63.8
	Horse	4.5 ± 5.9	3.0 ± 4.8	3.8 ± 5.7	0.0 ± 0.0	11.3 ± 8.7
	Cow	0.3 ± 0.5	7.8 ± 10.3	5.0 ± 4.4	1.5 ± 2.4	14.5 ± 16.5
A2	**Sheep**	39.3 ± 24.6	22.3 ± 23.8	37.0 ± 14.5	36.0 ± 25.1	144.8 ± 71.7
	Horse	31.5 ± 22.1	16.8 ± 9.6	26.0 ± 8.8	35.3 ± 25.1	109.5 ± 45.7
	Cow	3.8 ± 5.2	3.5 ± 4.5	10.0 ± 5.0	38.0 ± 18.0	55.3 ± 18.4
			broods	**eggs**	**larvae**	**Eggs + larvae**
A3	**Sheep**		3 ± 2.0	25.4 ± 19.6	9.6 ± 5.2	35.0 ± 18.2
	Horse		5.2 ± 1.5	41.4 ± 11.1	6.2 ± 5.4	47.6 ± 8.1
	Cow		0.0 ± 0.0	0.0 ± 0.0	4.8 ± 5.2	4.8 ± 5.2

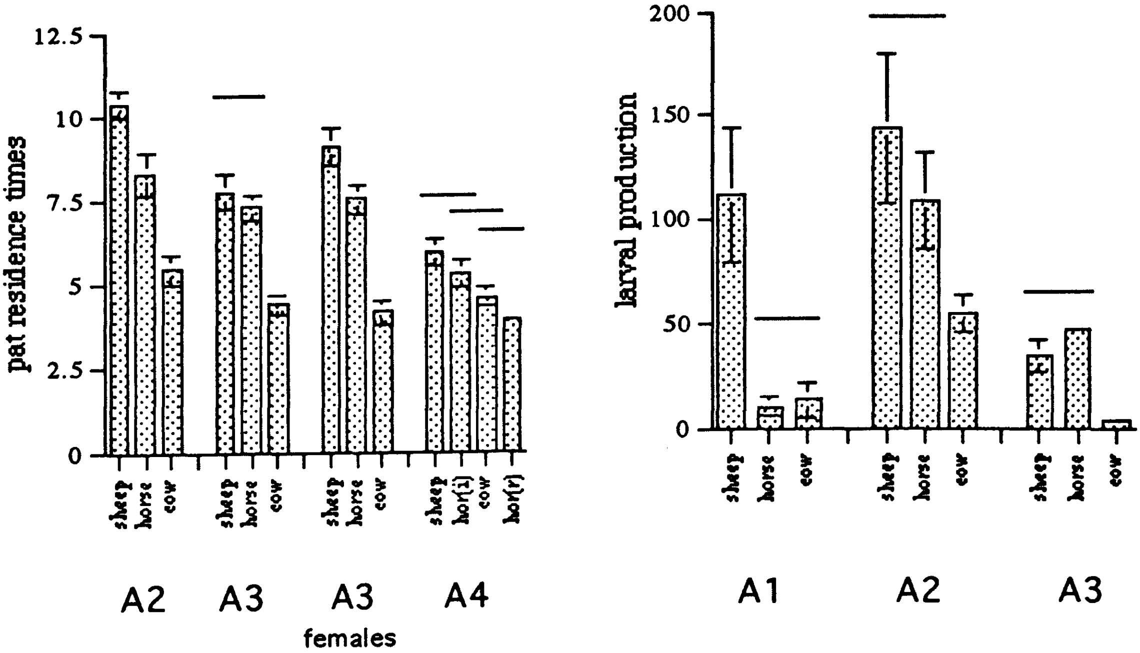


Fig. 5. Pat residence times and total larval (and egg) production (mean ± s.e.) in laboratory experiments with sheep, horse and cow dung types from experiment C2. Within experiments, treatments connected by lines are not significantly different. Experiments A1, A2, A3 and A4 used *A. ater*, *A. depressus*, *A. rufipes* and *A. prodromus*, respectively. In experiment A3, pat residence times are indicated for all beetles, and for females only. Horizontal bars connect treatments that did not significantly differ.

Table 9. Summary of the canonical correspondence analysis ordinations for experiments C1-C3 using day and dung type (a) as well day, size and dung type (b) as environmental variables. The ordination summary of experiment C4 (c) included day, dung type and selected dung chemistry parameters as environmental variables. See Methods for details of the forward selection procedure. Environmental variables in italics (below dotted line) did not contribute any significant extra fit to the ordination model. Note that none of the environmental variables in (c) contributed any significant extra fit. Monte Carlo permutation tests on the overall ordination were significant ($p < 0.02$) for (a; F= 4.97) and (b; F= 5.55) only.

a. Experiments C1 - C3, day and dung type environmental variables

	Forward selection	Axis 1 Canonical coefficients	Axis 2 Canonical coefficients	Axis 3 Canonical coefficients	Axis 1 Inter set correlations	Axis 2 Inter set correlations	Axis 3 Inter set correlations
day	0.18	1.05	0.26	-0.24	0.81	0.09	-0.17
hor (i)	0.06	-0.41	0.53	-1.08	-0.27	0.52	-0.29
sheep	0.05	-0.22	-0.70	-1.09	0.092	-0.55	-0.29
hor(r)	*0.01*				*0.073*	*0.123*	*-0.114*
cow					*0.125*	*0.136*	*0.610*
eigenvalues		0.195	0.056	0.036			

b. Experiments C1 - C3; day, dung type and size as environmental variables

	Forward selection	Axis 1 Canonical coefficients	Axis 2 Canonical coefficients	Axis 3 Canonical coefficients	Axis 1 Inter set correlations	Axis 2 Inter set correlations	Axis 3 Inter set correlations
day	0.17	1.04	0.26	-0.22	0.80	0.10	-0.17
hor (i)	0.06	-0.25	1.06	-0.22	-0.26	0.53	-0.27
cow	0.05	0.17	0.53	0.91	0.13	0.15	0.60
size	*0.02*				*-0.013*	*0.206*	*0.171*
sheep					*0.079*	*-0.554*	*-0.287*
hor(r)					*0.015*	*0.102*	*-0.14*
eigenvalues		0.187	0.058	0.038			

c. Experiment C4; day, dung type and dung chemistry parameters as environmental variables

	Forward selection	Axis 1 Canonical coefficients	Axis 2 Canonical coefficients	Axis 3 Canonical coefficients	Axis 1 Inter set correlations	Axis 2 Inter set correlations	Axis 3 Inter set correlations
cow 2	*0.07*						
moisture	*0.06*						
cow 1	*0.05*						
day	*0.03*						
organic matter	*0.02*						
cow 4	*0.02*						
cow 3	*0.01*						
cow5	*0.01*						
eigenvalues		0.157	0.086	0.049			

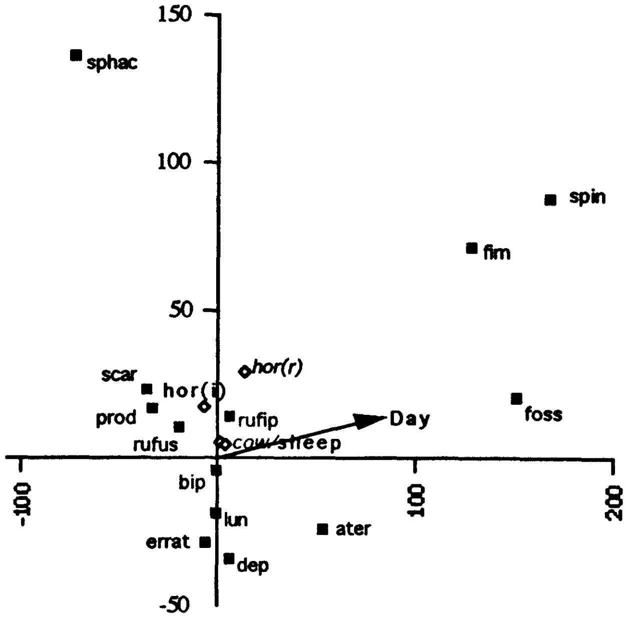


Fig. 6. CCA ordination biplot of species arrangements in relation to dung types in experiments C1-C3. Corresponds to ordination summary in Table 9a. The environmental variable 'Day' and the centroid for each dung type are shown. Environmenatl variables in bold type were included in the ordination model by the forward selection procedure. Key to species codes: ater = *Aphodius ater*, bip = *Sphaeridium bipustulatum*, dep = *A. depressus*, errat = *A. erraticus*, fim = *A. fimetarius*, foss = *A. fossor*, lun = *S. lunatum*, prod = *A. prodromus*, rufip = *A. rufipes*, rufus = *A. rufus*, scar = *S. scarabaeoides*, sphac = *A. sphacelatus*, spin = *Geotrupes spiniger*.

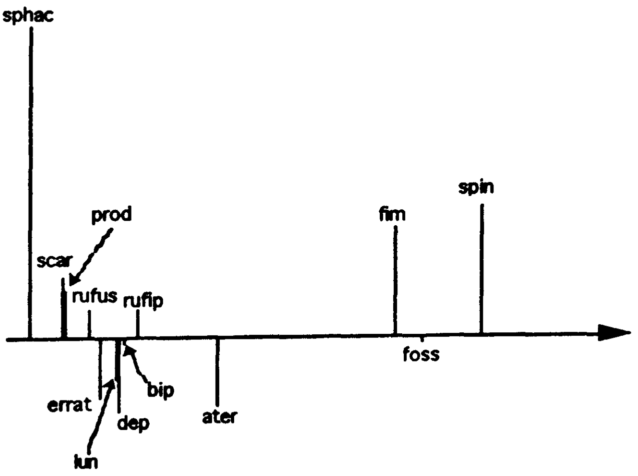


Fig. 7. Relative successional occurrence of various dung beetle species. The figure illustrates the positions of species along the 'day' vector in the ordination which included experiments C1-C3. See Fig. 6 for species codes.

CCA Ordinations

In the ordination of the dung type colonisation experiments (C1-C3), using day and dung type parameters, 'day' was identified as explaining most of the variation in the species data, and the first axis ordered species along a successional gradient (Table 9a, Figs. 6 and 7). The second axis corresponded to dung type (Fig. 6). The variable 'size' was included as an additional environmental variable in a second ordination, but did not contribute any significant extra fit to the ordination model (Table 9b). The ordination diagrams produced by the omission and inclusion of the variable size were virtually identical, and the former only is presented here. Note, however that the selection of the sheep and cow dung types by the forward selection procedure is reversed between the two ordinations (Table 9). Both of these ordinations were significant (Monte Carlo permutation, $p < 0.02$).

The ordination of the different cow types in experiment C4 used day, dung type and two chemical parameters (moisture content and organic matter) as environmental parameters. The forward selection procedure did not select any of the environmental variables; thus, none of these variables explained a significant amount of the species variation. The inclusion or exclusion of the dung chemistry parameters in experiment C4 did not qualitatively affect the ordination, and the former example only is presented here.

Comparisons of sheep, horse and cow assemblages in the literature

Re-analysis of the data in Rainio (1966) indicated that, per unit weight of dung, dung beetles preferentially occurred in sheep, then horse and then cow dung (Table 10). However, this order of preference was probably biased by the preferences of the most abundant species, and some species of beetles occurred in obviously higher numbers in horse dung, e.g. *S. bipustulatum*, *A. conspurcatus*, *A. rufipes* and *A. sordidus*. Apart from *S. lunatum*, no dung beetle species had a preference for cow dung, and of 12 of the 23 species, cow dung was the least preferred dung type. These data also indicate that most species can be found in all three of the dung types; those species that only occurred in one or two of the three dung types did not appear to be abundant at the time of the experiment. Thus, their absence from a dung type allows no reliable conclusion to be drawn about their dung type preferences. The rank abundance correlations between dung type data were all significant, but the cow and sheep dung combination was most similar. Nevertheless, comparisons of the relative abundances indicated distinct preferences for dung types by many of the beetle species, and, per unit dung size, sheep dung attracted over twice as many beetles as horse or cow dung. From additional data in Table 5 of Rainio (1966), seven species were sufficiently abundant ($n > 10$; Table 11) to be included in pairwise correlations of the rank abundance of species among the four types of dung (Table 12). Two of the six correlations were significant; these were the horse/pig and sheep/cow combinations. Note that this was the only example in which sheep dung was not the most preferred dung type (per unit weight of dung).

Table 13 indicates the *Sphaeridium* and scarabaeid species collected in sheep and cow dung by Kessler *et al.* (1974). Spearman correlation of the rank abundance of species in both dung types was significant ($r_s = 0.731$, n= 17, $p < 0.001$); however, when the five (uncommon) species that were found in cow dung only were omitted from the analysis, there was no significant correlation ($r_s = 0.329$, n= 12, n.s.). Note that despite the fact that there was a 700-fold difference between the two dung types in the amount of dung examined, there was only a 5-fold difference in the numbers of individuals collected (Table 13) and some species were of similar or greater abundance in the sheep dung data.

Data in Breymeyer and Zacharieva-Stoilova (1975) indicated that although approximately 70 times more cow dung than sheep was sampled, the total number of dung beetles sampled was only 2.3 times greater in the cow dung. Twenty-six and thirty-eight species of scarab were found in sheep and cow dung, respectively. A correlation of the rank abundance of the most abundant species between the two dung types (see Methods) was not significant ($r_s = 0.278$, n = 17, $p > 0.1$). The three most abundant species in cow dung were *A. fimetarius* (25%), *Onthophagous furcatus* (18%) and *Oniticellus fulvus* (12%), while the three most abundant species in sheep dung were *Onthophagous ruficapilus* (58%), *Onthophagous furcatus* (11%) and *Caccobius schreberi* (8%).

In experiments C1 - C3 of this study, there generally were significant correlations of species rank abundances among the dung types (Table 14). The obvious exception was horse (rgh) in experiment C1. This dung type had low numbers of captures, and nine of the species included in the analysis were represented by fewer than 8 individuals in this dung type (see Table 1, Chapter 1). The low abundances in the horse (rgh) dung probably make this type of analysis unsuitable in this instance, where differences of only a few individuals can dramatically alter the rank abundance. Thus, the low correlations between horse (rgh) and the other dung types is most likely to be a reflection of the low numbers captured. Similar correlations of the cow dung types in experiment C4 were all significant (Table 14), and typically had higher correlation coefficients than those obtained for experiments C1-C3.

Table 10. Numbers of beetles per unit dung weight sheep, cow and horse dung (from Table 3, Rainio 1966). Numbers are based on thirteen sampling events between 1 June and 16 October, 1961 and the total weight of deposited dung for the sheep, cow and horse dung was 13 kg, 26kg, and 26 kg respectively. Also indicated are pairwise correlations of the rank abundance of the species in the dung types, with all species included, and with 4 of the least abundant species omitted.

	number of beetles per kg of dung		
	sheep	cow	horse
Sphaeridium bipustulatum	5.6	1.7	10.5
S. lunatum	0.5	1.8	1.7
S. scarabaeoides	10.8	9.7	5.6
Aphodius ater	6.1	0.5	0.1
A. borealis	0.8	-	0.1
A. conspurcatus	0.7	0.1	5.8
A. depressus	3.1	0.6	0.1
A. distinctus	0.1	-	-
A. erraticus	11.3	2.3	1.4
A. fasciatus	2.3	0.7	0.04
A. fimetarius	93.3	26.4	30.7
A. foetens	0.1	0.1	0.7
A. fossor	1.0	2.4	0.1
A. haemorrhoidalis	2.5	1.3	-
A. merdarius	10.2	1.1	5.7
A. prodromus	59.0	46.7	53.8
A. pusillus	4.8	0.8	0.3
A. rufipes	5.5	6.3	8.3
A. rufus	47.0	15.5	4.5
A. sordidus	0.2	0.2	3.7
Onthophagous gibbulus	-	0.1	-
Geotrupes stercorarius	0.5	0.3	1.5
G. stercorosus	0.2	0.1	0.3
Total per kg dung	256.5	118.5	135.5
Correlations (r_s)	cow / sheep	horse/sheep	cow/horse
All 23 species	0.814^{***}	0.541^{**}	0.582^{**}
omitting rarer species , n = 19	0.753^{***}	0.433^{*}	0.437^{*}

Table 11. Number of individuals of the seven most abundant species in pig, cow, horse and sheep dung in Table 5 in Rainio (1966). Sampling was conducted from July to August 1960, and employed dung types of equivalent sizes, with a weight of 200 g at deposition.

	pig	cow	horse	sheep
Aphodius erraticus	4	8	0	3
A. fimetarius	234	228	150	72
A. merdarius	43	4	33	4
A. rufipes	114	147	117	48
A. rufus	29	137	7	216
Geotrupes stercorosus	14	9	10	9
Sphaeridium scarabaeoides	4	15	7	12
Total	442	548	324	364

Table 12. Pairwise correlations (Spearman) of the rank abundance of species in pig, cow, horse and sheep dung (re-analysis of data from Table 5 in Rainio 1966). Significance of correlations are indicated as follows: ^{ns} = $p > 0.1$, * = $p < 0.05$, ** = $p < 0.01$. See Table 11.

	pig	cow	horse
cow	0.577^{ns}		
horse	0.918**	0.523^{ns}	
sheep	0.523^{ns}	0.857*	0.378^{ns}

Table 13. Abundances of *Sphaeridium* and scarabaeid beetles collected in cow and sheep dung in South Dakota, USA in 1969 (from Table 1, Kessler *et al.*, 1974). See text for details.

	cow	sheep
Sphaeridium bipustulatum	294	9
S. lunatum	521	22
S. scarabaeoides	428	28
Aphodius haemorrhoidalis	824	47
A. granarius	297	356
A. fimetarius	139	6
A. vittatus	45	13
A. distinctus	18	18
A. ruricola	24	60
A. coloradensis	19	0
A. stercorosa	11	0
A. fossor	10	0
A. prodromus	1	0
Ataenis spretulus	103	18
Copris tulluis	7	0
Onthophagus hecate	315	45
Onthophagus pennsylvanicus	43	10
Amount of dung sampled	207 litre	0.296 litre
Total number of beetles	3099	632
Number of species	17	12

Table 14. Spearman correlation of the rank abundance of *Sphaeridium* and scarabaeid species collected in different dung types in experiments C1 - C4. Significance of analyses indicated as follows: ^{ns} = p > 0.1, † = p < 0.1, * = p < 0.05, ** = p < 0.01.

	sheep	horse (imp)	cow
C1 (n = 10)			
horse (imp)	0.654*		
cow	0.869**	0.506†	
horse (rgh)	0.243^{ns}	-0.007^{ns}	0.164^{ns}
C2 (n = 9)			
cow	0.717*	0.812**	
horse	0.745*		
C3 (n = 9)			
cow	0.866**	0.812**	
horse	0.712*		

C4 (n = 10)	Gr	F	Sp	Sil
F	0.750*			
Sp	0.939**	0.841**		
Sil	0.906**	0.853**	0.954**	
Sum	0.976**	0.841**	0.976**	0.936**

Due to their low numbers, some species were excluded from the analyses:
C1- *S. bipustulatum*, C2- *S. bipustulatum*, C3- *A. ater* and *G. spiniger*

Discussion

Colonisation preferences of different herbivore dung types

Gittings and Giller (1998) pointed out that between dung of different types and ages, there are at least three factors of potential importance in processes involving dung beetle colonisation and reproduction. For example, these include the findability of the dung, regardless of the suitability of that dung type as a microhabitat. Secondly, the relative suitability of the pad as a microhabitat may vary for the different life stages of dung beetles (eggs, larvae and adults). Thirdly, the chemical and physical qualities of the dung may affect both the nutritional quality of the dung pad as a food resource and resource availability for the larval and adult stages. In field and lab experiments which employed a range of dung types (cow, giraffe, zebra, guanaco, ostrich and red lechwe), Gittings (1994) found that colonisation preferences of dung beetles in field experiments (based on dung chemical parameters and age) corresponded to their oviposition behaviour. In addition, reproductive performance (oviposition rates and larval development) of several *Aphodius* species tended to be higher on those dung types in which the beetles showed colonisation preferences in the field.

In the present study, dung beetles had significantly different abundances in dung pads and pitfall traps of different dung types, and CCA analyses identified at least some dung type preferences by dung beetles. In addition, data from the laboratory experiments conducted indicate that both larval production and pat residence times were higher in those dung types which were preferred in the colonisation experiments. It is interesting that data from both this study and that of Gittings (1994) indicated that *Aphodius rufipes* dung beetles have both relatively low abundances and poor reproductive performance in cow dung. Nevertheless, *Aphodius rufipes* is quite abundant in areas where there is only cow dung available (see Chapters 2 and 5).

Overall, the ordinations in the present study did not provide as conclusive evidence of dung type preferences as those in Gittings and Giller (1998). Contrary to the situation in Gittings and Giller (1998), the present ordinations did not group species according to their breeding behaviour, and the ordination of experiment C4 was not significant. This may be due to a number of reasons. Firstly, dung chemistry values of the dung types in the present study may have had relatively low variability, compared to the variability among dung types in Gittings and Giller (1998) (see below). Thus, if chemical cues are important in colonisation, there would have been less opportunity for beetle preferences to be expressed. Secondly, in the CCA ordination for experiment C4, only two dung chemistry variables were included, and these may not have been the most appropriate parameters which correspond to colonisation preferences of dung beetles. No dung chemistry parameters were included in the ordination of data from experimetns C1- C3.

Comparisons of the organic matter and moisture content values between the present study and those in Gittings and Giller (1998) indicated that there was greater variation in dung chemistry values among dung types in Gittings and Giller (1998) (cf. Tables 3 and 15) than in the present study. For example, one can determine the standard deviations about the mean of selected dung chemistry parameters, across a number of dung types within a colonisation experiment. Thus, standard deviations of the organic matter content in C1 of the present study, and those of experiments C1 and C3 of Gittings and Giller (1998), were 2.0, 10.2 and 12.3 respectively; standard deviations in the moisture contents were 3.6, 5.9 and 6.6 respectively (cf. Tables 3 and 15). Greater variation in dung chemistry among available dung types probably facilitates the finding of a more pronounced colonisation preference or dislike by dung beetles for a dung type.

Table 15. Mean dung chemistry values of organic matter and moisture content in a number of dung types from exotic herbivores in four field experiments (C1-C4). Note that standard errors of these means never exceeded± 0.3; from Table 3 in Chapter 4 of Gittings (1994).

	cow	gu	gi	ost	redl	zeb
C1						
organic matter	80.93	75.25	-	55.85	80.60	73.72
moisture content	89.33	73.78	-	77.72	80.96	83.85
C2						
organic matter	85.51	-	-	53.55	84.34	83.85
moisture content	88.19	-	-	75.52	76.84	82.64
C3						
organic matter	79.37	-	86.87	56.28	83.17	82.68
moisture content	90.17	-	75.37	73.71	78.89	82.69
C4						
organic matter	83.06	-	83.28	56.07	81.26	72.22
moisture content	89.17	-	71.52	75.01	81.14	82.60

Note that Gittings (1994) found that while chemical parameters of dung types explained significant amounts of variation in species colonisation data, CCA ordinations based on dung quality (as continuous variables) were quite similar to CCA ordinations based on dung types (as categorical variables). In addition, CCA ordinations using the initial values (Day 0) of the dung chemical parameters were very similar to those ordinations which used the sampling day values. This would indicate that, using CCA ordinations at least, successional changes in dung quality parameters did not appear to be very important.

Comparisons of sheep, horse and cow dung in published literature

Differences in the methods of comparison among published studies require some caution in the interpretation of the data. In particular, differences among dung types in pad size may present the greatest confounding factor, although this depends on the objective of the study. Recent data (Chapter 3) show that beetle number, biomass and density are positively correlated with dung pad size, and that differences in dung pad size can affect pat residence times. The chemical quality of pads may differentially vary with pad size, possibly through the greater resilience of larger dung pads to environmental effects, particularly dessication (for an example from studies on mycophagous diptera, see Worthen *et al.*, 1998). Thus, the suitability of different-sized pads as microhabitats for dung beetles may also be affected. Pitfall trapping data using dung baits of different sizes indicated that dung size profoundly affects the immigration rate of beetles (Chapter 3). Therefore, attempts to experimentally discover the role of dung quality as a causal effect of differences in colonisation, pat residence times, dung chemistry etc. must first standardise dung size among the dung types. Otherwise, comparisons of naturally-dropped pads of different dung types (e.g. sheep and cow dung) will reflect natural field conditions, in which pads incorporate both differences in dung size and dung quality among dung types.

From the four examples from data collected in Finland, USA, Bulgaria and Ireland, it appears that most dung beetle species can usually be found in all available dung types, i.e. species composition is very similar (although relative abundances could vary). In those situations where several species occurred in some dung types and not in others, those species were usually (but not always, see Rainio 1966) of low abundance at the time of the experiment. Alternatively, different dung sizes were employed (e.g. Kessler *et al.*, 1974; Breymeyer and Zacharieva-Stoilova, 1975; see above) and there was a huge disparity among the dung types in the amount of dung sampled. In the latter case, differences in species composition and/or species numbers were most likely to be sampling artifacts resulting from the different sample sizes of beetles in the dung types. In either case, the dung type preferences of at least some species are rendered inconclusive.

The need to clarify 'dung beetle preferences for dung types'

Differences in assemblage structure among dung types may be expected to arise through differences in (1) species composition (2) absolute abundances (3) relative abundances or (4) combinations of these. Data indicate that there is generally considerable overlap in dung beetle species composition among dung types in a local sampling area (Rainio, 1966; Breymeyer and Zacharieva-Stoilova, 1975; Sowig and Wassmer, 1994; Himmelsbach, 1993; this study). This is particularly true if the uncommon and rare species are not considered, and when dung size is standardised (e.g. Rainio, 1966; this study). However, despite comparable dung beetle species composition among dung types, there can be very considerable differences in absolute and relative abundances of colonising beetles (Rainio, 1966; Heijerman, 1990; Himmelsbach, 1993; Sowig and Wassmer, 1994; this study). This was also evident in dung beetle assemblages in more southerly European regions (Breymeyer and Zacharieva-Stoilova, 1975; Lumerat *et al.*, 1992). In the present study, dung types of similar pad size differed significantly in the absolute number of colonising beetles. Within any experiment, different species could show preferences for different dung types e.g. in experiment C1 of the present study, *A. ater* preferred sheep dung, *A. prodromus* preferred horse (imp) dung and *A. erraticus* preferred cow dung (see Table 1, Chapter 1).

To answer the question whether there are dung type preferences displayed by north temperate dung beetles or not, it appears that there is no consesus about whether the first two of the above four scenarios constitutes a preference by dung beetles for some dung type over another. This is indicated by the terminology employed by Hanski (1991) 'most species...use the dung of domestic mammals- cattle, horses, and sheep- without much discrimination', and Rainio (1966) who indicates that while species did have dung type preferences, 'none of the beetle species is wholly specialised to any particular kind of dung'. Thus, it may be that a distinction should be made between beetles which have a dung type preference (occurring in several dung types, but having higher absolute or relative abundances in some dung types) and beetles which are dung type specialists (occurring in that dung type only).

References

Aschenborn, A.A., Loughnan, M.L. and Edwards, P.B. (1989) A simple assay to determine the nutritional suitability of cattle dung for coprophagous beetles. *Entomologia Experimentalis et Applicata*, **53**, 73-79.

Breymeyer, A. and Zacharieva-Stoilova, B. (1975) Scarabaeidae in two mountain pastures in Poland and Bulgaria. *Bulletin de l'Académie Polonaise des Sciences (Série des Sciences Biologiques)*, **23**, 173-180.

Davis, A.L.V. (1989) Nesting of Afrotropical *Oniticellus* (Coleoptera, Scarabaeidae) and its evolutionary trend from soil to dung. *Ecological Entomology*, **14**, 11-21.

Desière, M. and Thome, J.P. (1977) Variations qualitatives et quantitatives de quelques populations de coléoptères coprophiles associés aux excréments de 3 types d'herbivores. *Revue d'Écologie et de Biologie du Sol*, **14**, 583-591.

Edwards, P.B. (1991) Seasonal variation in the dung of African grazing mammals, and its consequences for coprophagous insects. *Functional Ecology*, **5**, 617-628.

Fincher, G.T., Stewart, T.B., and Davis, R. (1977) Attraction of coprophagous beetles to feces of various animals. *Journal of Parasitology*, **56**, 378-383.

Finn, J.A., Gittings, T. and Giller, P.S. (1998a) *Aphodius* dung beetle assemblage stability at different spatial and temporal scales. *Applied Soil Ecology*, **241**, in press.

Finn, J.A., Gittings, T. and Giller, P.S. (1998b) Spatial and temporal variation in species composition of dung beetle assemblages in southern Ireland. *Ecological Entomology*, **23**, in press.

Gittings, T. (1994) *The community ecology of* Aphodius *dung beetles.* Unpublished Ph.D. thesis. National University of Ireland.

Gittings, T. and Giller, P.S. (1997) Life history traits and resource utilisation in an assemblage of north temperate *Aphodius* dung beetles (Coleoptera: Scarabaeidae). *Ecography*, **20**, 55-66.

Gittings, T. and Giller, P.S. (1998) Resource quality and the colonisation and succession of coprophagous dung beetles. *Ecography.* In press.

Greenham, P.M. (1972) The effects of variability of cattle dung on the multiplication of the bushfly (*Musca vetustissima* Walk.). *Journal of Animal Ecology*, **41**, 153-165.

Hanski, I. (1991) North temperate dung beetles. *Dung Beetle Ecology* (ed. by I. Hanski and Y.Cambefort), pp. 75-96, Princeton University Press.

Hanski, I. and Kuusela, S. (1983) Dung beetle communities in the Åland archipelago. *Acta Entomologici Fennici*, **45**, 1-12.

Heijerman, T. (1990) Seasonal changes in the relative abundance of some dung beetle species in faeces of the wild boar and mufflon (Coleoptera: Scarabaeoidea). *Entomologische Berichten (Amsterdam)*, **50**, 81-86.

Himmelsbach, W. (1993) Einfluß einiger abiotischer Faktoren auf die Besiedlung von drei bzw. vier Tage altem Rinderdung durch ausgewahlte Arten der Diptera und Coleoptera. Diplomarb. i. Br.

Horgan, F.G. (1989) *Dung Beetle (Scarabaeoidea, Hydrophilidae, Coleoptera) Assemblages at Fota Island Wildlife Park, Republic of Ireland.* Unpublished BSc thesis, Department of Zoology, University College Cork.

Kessler, H. and Balsbaugh, E.U. (1972) Succession of adult coleoptera in bovine manure in east central South Dakota. *Annals of the Entomological Society of America*, **65**, 1333-1336.

Kessler, H., Balsbaugh Jr., E.U. and McDaniel, B. (1974). Faunistic comparison of adult Coleoptera recovered from cattle and sheep manure in east-central South Dakota. *Entomological News*, **85**, 67-71.

Krikken, J. (1978) Interessante *Aphodius*-soorten (Colepotera: Scarabaeidae) uit mest van Nederlands grofwild. *Zool. Bijdr.*, **23**, 137-147.

Kunz, S.E. (1980). Horn fly production as affected by seasonal changes in rangeland forage conditions. *The Southwestern Entomologist*, **5**, 80-83.

Landin, B.-O. (1961) Ecological studies on dung beetles. *Opuscula Entomologica (Supplementum)*, **19**, 1-228.

Lumaret, J.P., Kadiri, N. and Bertrand, M. (1992) Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology*, **29**, 349-356.

Macqueen, A., Wallace, M.M.H. and Doube, B.M. (1986) Seasonal changes in favourability of cattle dung in central Queensland for three species of dung-breeding insects. *Journal of the Australian Entomological Society*, **25**, 23-29.

Matthiessen, J.N. and Hayles, L. (1983) Seasonal changes in the characteristics of cattle dung as a resource for an insect in southwestern Australia. *Australian Journal of Ecology*, **8**, 9-16.

Palmer, W.A. and Bay, D.E. (1983) Effects of intraspecific competition and nitrogen content of manure on pupal weight, survival and reproductive potential of the horn fly, *Haematobia irritans irritans* (L.). *Protection Ecology*, **5**, 153-160.

Peck, S.B. and Howden, H.F. (1984) Response of a dung beetle guild to different sizes of dung bait in a Panamanian rainforest. *Biotropica*, **16(3)**, 235 - 238.

Raino, M. (1966) Abundance and phenology of some coprophagous beetles in different kinds of dung. *Annales Zoologici Fennici*, **3**, 88-98.

Ridsdill-Smith, T.J. (1986) The effect of seasonal changes in cattle dung on egg production by two species of dung beetles (Coleoptera: Scarabaeidae) in south-western Australia. *Bulletin of Entomological Research*, **76**, 63-68.

Sowig, P. and Wassmer, T. (1994) Resource partitioning in coprophagous beetles from sheep dung: Phenology and microhabitat preferences. *Zool. Jb. Syst.*, **121**, 171-192.

ter Braak, C.J.F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167-1179.

ter Braak, C.J.F. (1988) *CANOCO-a FORTRAN program for canonical community ordination by [partial} [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (Version 2.1).* Technical report LWA-88-02, Agricultural Mathematics Group, Wageningen, The Netherlands.

ter Braak, C.J.F. (1990) *Update notes: CANOCO version 3.10.* Agricultural Mathematics Group, Wageningen, The Netherlands.

Tyndale-Biscoe, M., Wallace, M.M.H. and Walker, J.M. (1981) An ecological study of an Australian dung beetle, *Onthophagus granulatus* Boheman (Coleoptera: Scarabaeidae), using physiological age-grading techniques. *Bulletin of Entomological Research*, **71**, 137-152.

Worthen, W.B., Jones, M.T. and Jetton, R.M. (1998) Community structure and environmental stress: dessication promotes nestedness in mycophagous fly communities. *Oikos*, **81**, 45-54.

Chapter 5

Aphodius dung beetle assemblage stability at different spatial and temporal scales

John A. Finn, Tom Gittings and Paul S. Giller
Department of Zoology and Animal Ecology, University College Cork,
Lee Maltings, Prospect Row, Ireland.

Accepted by Journal of Applied Soil Ecology, February 1998.

Abstract

1. The stability of north temperate *Aphodius* assemblages was analysed at four spatial scales: geographical, regional, local and between-field and three temporal scales: inter-annual, seasonal and between-day.

2. Greatest variability in assemblage composition occurred at the geographical scale. The similar level of variability at the regional, local and between-field spatial scales and the inter-annual temporal scale, inferred some degree of spatio-temporal stability at these scales. DCA analyses indicated that assemblage composition was as variable at the smaller between-field scale as at the regional scale.

3. The marked seasonal variability in assemblage structure over the year exceeded variability from one year to the next. At the daily scale, species abundances within a field displayed high variability, but there was relatively little variability in assemblage structure.

1. Introduction

European north temperate dung beetle assemblages are typically dominated by *Aphodius* species. *Aphodius* dung beetles are generally small to medium sized (4-20 mm elytral length) endocoprids or 'dwellers' that are active and lay eggs within the dung pad. To date, studies of these assemblages have concentrated on the colonisation and succession of *Aphodius* beetles in dung pads, habitat preferences and seasonal activity patterns (see Hanski, 1991). Most of this research has been set in relatively small spatial and temporal scales (but see Hanski, 1980a, 1986), yet dung beetle assemblages can be studied over a range of nested scales. These may range from the smaller within-pad, between-pad and between-field scales to the local regional and geographical spatial scales. Temporally, scales of analysis may vary from hours, days and weeks to seasons, years and decades or greater. Our aim in the present paper is to examine how the *Aphodius* assemblage structure varies across a greater range of scales than has hitherto been attempted, and in so doing, explore the degree of stability of the assemblages in time and space.

There are differing concepts of stability but here we are concerned with 'variability', defined as "the degree to which a variable changes over time .... measured by such statistics as the standard deviation or coefficient of variation of consecutive measurements of those things that interest us," (Pimm, 1984). In the present context, variability refers to the degree to which *Aphodius* assemblage structure (species composition and relative abundance distribution) changes over space and time. Low variability between samples indicates stability of assemblage structure at that scale of analysis. We thus address the following questions:
i) How does assemblage structure vary over time and space?
ii) Can we identify at what scale(s) major changes in assemblage structure occur?
iii) What are the implications of these changes for the study of *Aphodius* assemblages?

2. Methods

In the present study, we concentrate on the geographical, regional, local and between-field spatial scales, and the inter-annual, seasonal and daily temporal scales.

2.1. *Macroscales (geographical spatial and inter-annual temporal scales)*

Nineteen data sets have been obtained from 11 geographical areas across Europe (Table 1) based on *Aphodius* assemblages from cow and/or sheep dung from open pasture habitat. The seasonal sampling of the data sets encompassed at least the majority of the period from April to October. This period covers the majority of the active period of the *Aphodius* assemblage, and includes those periods during which maximum species richness would be expected to occur. Most sites were 380 to 2500 km apart, the Finnish sites were 100 km apart. As the data varies in quality and detail, samples from individual sites were pooled across the duration of the *Aphodius* adult flight period (annual assemblage). The Finland B data set pooled *Aphodius* abundances sampled from open pasture, half-open pine forest and closed spruce forest. Where possible, data sets were analysed to determine species richness of *Aphodius*, total sample sizes, the dominant *Aphodius* species (abundance and biomass) and the number of other scarabaeid dung beetle species in the annual assemblage (Table 1).

Comparison of such data sets requires caution due to the variation in sampling methods (light-trapping in one study, but typically pitfall trapping and dung pad sampling) and year of sampling across studies. Studies have shown that although dung pad and pitfall samples of the same assemblage may differ in the absolute number of captured individuals, they produce similar rank order of abundances (Doube and Giller, 1990; Gittings, 1994). *Aphodius* assemblage structure was therefore compared across all the sites using Mountford average linkage cluster analysis of community similarity based on rank correlations of data sets.

Inter-annual data sets for Ireland were collected in 1991, 1992 and 1995 using pitfall traps baited with cattle dung located in rotationally-grazed pastures at Fota, County Cork, southern Ireland (see Gittings, 1994). Trapping was conducted from mid-March to mid-November using the methodology of Gittings and Giller (1997). Other inter-annual data were available from the literature (Table 1).

2.2. Mesoscales (between-field (0-1km), local (2-10km) and regional (50-85km) spatial scales and seasonal temporal scales)

Using pitfall trapping data from Fota during 1990-1992, the duration of the adult flight period of *Aphodius* species was calculated as the period during which 90% of the total catch occurred.

To allow cross-scale comparison, we combined the analysis for the inter-annual temporal scale and the between-field, local and regional spatial scales. This analysis included the above data from Fota and additional rotationally-grazed sites which had been studied using a similar methodology. Seven sites were sampled at Fermoy, Co. Cork (50 km from Fota) in 1991; two lowland (40-50 m a.s.l.) within-farm pairs (0.6 km apart), MA/MB and BA/BB, (approximately 2 km apart); and three (U1-U3) upland (190-230 m a.s.l.) sites. U1 and U2 were 1 km apart and approximately 14 km from U3. The upland and lowland sites were 6-11 km apart. Another site was studied in 1995 at Killarney, County Kerry (70-80 m a.s.l.), approximately 85 km from Fota and Fermoy.

Due to considerable seasonal variation in assemblage composition (see Gittings and Giller, 1997), analyses of catches summed across the whole year can be confounded by very large abundances of one species at one time of the year. For example, large catches of autumn species will depress percentage values of early summer species in the pooled catch. Yet, early summer and autumn species are unlikely to interact and comparisons of their relative abundances may not be biologically meaningful. Furthermore, dung beetle flight activity and hence pitfall captures are strongly related to weather conditions (see below). This confounding factor may be exaggerated when data sets are pooled over a year during which large parts of the year experienced greatly contrasting weather conditions. We have therefore identified three periods (spring, early and late summer) during which species composition is relatively constant, and between which distinct breaks in species composition may be identified. For each of these subsets of the annual assemblage, we have conducted a detrended correspondence analysis (DCA) on log transformed abundance data in which rare species were down-weighted to examine the degree of similarity in *Aphodius* assemblages amongst samples.

2.3. Microscale (Daily temporal scale)

Between-day differences in *Aphodius* community structure were investigated at Fermoy in June 1993. Over nine consecutive days, ten pitfall traps were baited daily with one litre of fresh dung and the contents collected one day later. Temperature and rainfall data for each 24-hour period were obtained from a weather station located within 1 km. The mean daily total catches were then compared. The assemblages on individual days, pooled across the ten traps, were compared using a Mountford average linkage cluster analysis, based on Bray and Curtis coefficients of similarity between the nine samples.

2.4 Cross-scale measure of variability

Despite differences in sampling methodology and scale across the data sets, it is possible to compare the variability between data sets across the different scales using a method based on correlation of rank order of abundance of species. Unless otherwise stated, these analyses are based on pairwise correlations of the rank order of abundance of the annual catch of each species. This method is most appropriate due to some of the problems with pitfall trapping (see above). *Aphodius* assemblage structure at the geographical scale was based on rank correlations of the data, after data sets from the same geographical area (see Table 1) were pooled. Note that due to the considerable distance between them, the Germany A and Germany B data sets were not pooled. Between-year correlations were based on the Fota 1991, 1992 and 1995 data sets and between-region correlations were based on the Fota, Fermoy (MA site only) and Killarney data sets, respectively. To obtain data on the degree of variability between seasons within any one year, correlations were conducted on the rank order of abundance of species between the three subseasonal data sets, for each of nine of the sites and years (excluding one of a between-field pair). For each of the between-field pairs (here we consider U1 and U2 as such), correlations of rank abundance of species in nearby/adjacent fields were conducted. Variability at the local scale was based on the data collected around Fermoy in 1991. Each of the three between-field pairs were pooled, and pairwise correlations of rank abundance of species in each of the local sites (MA/MB, BA/BB, U1/U2 and U3) were conducted. Some of the sites at the local scale differed in altitude. To investigate any effect of altitude, we combined data from each of the between-field pairs and conducted pairwise correlations on the rank order of abundance of species between the resulting four local sites (MA/MB, BA/BB, U1/U2 and U3). This analysis was conducted separately for each of the subseasonal data sets of these local sites.

3. Results

3.1. Macroscale

The combined geographical data sets yielded a total of 40 *Aphodius* species, a fraction of which were present at any one site (Table 1). *Aphodius* species richness varied across sites and the central European sites had more of the other scarabaeid species. The large differences in sample sizes mean that patterns in species richness should be interpreted with caution. However, taking into account these differences, the low species richness of the Irish *Aphodius* assemblage becomes more striking.

The dominant species and its relative abundance also varied (Table 1). For example, in England 1977, *A. equestris* (Panz.) was dominant, yet only comprised 13% of the total annual catch. In contrast, *A. prodromus* (Brahm) was dominant in Germany B in 1991 with a percentage contribution of 79%. At a single site, the dominant species was generally consistent over time (e.g. *A. rufipes* (L.) in Ireland and *A. lapponum* (Gyllen) in N. England) but not always so (e.g. Polish data). Sampling from different types of dung in the same year can also yield different dominant species (Bulgarian data). A more consistent pattern emerges in terms of biomass in cow dung

Table 1. Comparison of *Aphodius* assemblage characteristics of the different study sites used at the geographical scale.

Study site	Year	Altitude (m a.s.l.)	Dung type	Sample size	No. of *Aphodius* species	Other scarabaeid species	Dominant species (abundance)	Dominant species (biomass)
[1]Copenhagen, Denmark	1972-77	25	cow	17836	15	1	*A. rufus* 30%	*A. rufipes* 58%
[1]Copenhagen,Denmark	1978-80	25	cow	18537	15	2	*A. contaminatus* 78%	*A. contaminatus* 78%
[2]Oxford, England	1977	60-165	cow	24255	21	3	*A. equestris* 13%	*A. rufipes* 40%
[3]Cork, Ireland	1991	20	cow	17411	11	1	*A. rufipes* 62%	*A. rufipes* 90%
[3]Cork, Ireland	1992	20	cow	5430	10	1	*A. rufipes* 41%	*A. rufipes* 77%
[4]Cork, Ireland	1995	20	cow	9407	9	1	*A. rufipes* 50%	*A. rufipes* 86%
[5]S. Finland A	1970-74	?	cow	3141	>11	≥1	*A. fimetarius* 28%	*A. rufipes* 44%
[6]S. Finland B	1966-67	?	cow	4380	18	1	*A. prodromus/rufipes* 29%	*A. rufipes* 67%
[7]Liège, Belgium	1972	?	cow	1456	12	3	*A. rufipes* 35%	*A. rufipes* 74%
[8]Pennines, N. England	1955	upland	sheep	3430	13	?	*A. lapponum* 52%	*A. lapponum* 42%
[8]Pennines, N. England	1956	upland	sheep	1707	12	?	*A. lapponum* 51%	*A. lapponum* 44%
[9]Jaworki, S. East Poland	1970	700	sheep	?	10	6	*A. pusillus* 36%	*A. ater* 32%
[9]Jaworki, S. East Poland	1971	700	sheep	?	10	6	*A. fimetarius* 32%	*A. fimetarius* 43%
[10]Sofia, Bulgaria	1970	700	cow	?	15	12	*A. fimetarius* 71%	*A. fimetarius* 75%
[10]Sofia, Bulgaria	1970	700	sheep	?	14	9	*A. distinctus* 34%	*A. erraticus* 38%
[11]Bayreuth, Germany A	1991	500	sheep	1288	10	6	*A. fimetarius* 63%	*A. fimetarius* 76%
[12]Freiburg, Germany B	1990	400	sheep	1787	16	5	*A. pusillus* 41%	*A. luridus* 29%
[13]Freiburg, Germany B	1991	430	cow	6460	13	7	*A. prodromus* 79%	*A. prodromus* 72%
[14]Freiburg, Germany B	1993	~ 400	cow+sheep	6972	14	11	*A. pusillus* 32%	*A. fimetarius* 20%

Sources: [1] Holter, (1982); [2] Hanski, (1980); [3] Gittings, (1994); [4] Finn (unpublished); [5] Koskela, (1979); [6] Hanski and Koskela, (1977); [7] Desière, (1983); [8] White, (1960); [9] Breymeyer, (1974); [10] Breymeyer and Zacharieva-Stoilova, (1975); [11] Hirschberger, (1991); [12] Wassmer and Sowig, (1994); [13] Himmelsbach, (1993); [14] Wahl, (1995). For details, consult original studies. Corrections to the data sets were as follows: for England 1977, columns 2, 7, 18, 24 and 36 in appendix of Hanski (1980) were pooled. In the original Bulgarian data set, 23 species (with non-specified value of less than 0.75%) were pooled at 4.95% of the sample before back-calculation of percentage composition of *Aphodius* assemblage only. Values of the species *A. varians* and *A. varians* ab. *fabrici* were combined, as were those of the synonymous species *A. conspututs* F. and *A. prodromus*. In the Belgian study, the rare species (not enumerated in the original study) were assigned a total contribution of 1%. Absolute abundances were back-calculated from biomasses and converted to percentage composition. Monthly abundances of *Aphodius* are corrected for weight of dung collected in the following data sets; [12] dry weight; [13] wet weight; [14] wet weight. In [5], abundances were corrected to account for the variable trapping effort; note that the published data set only included species with >15 specimens.

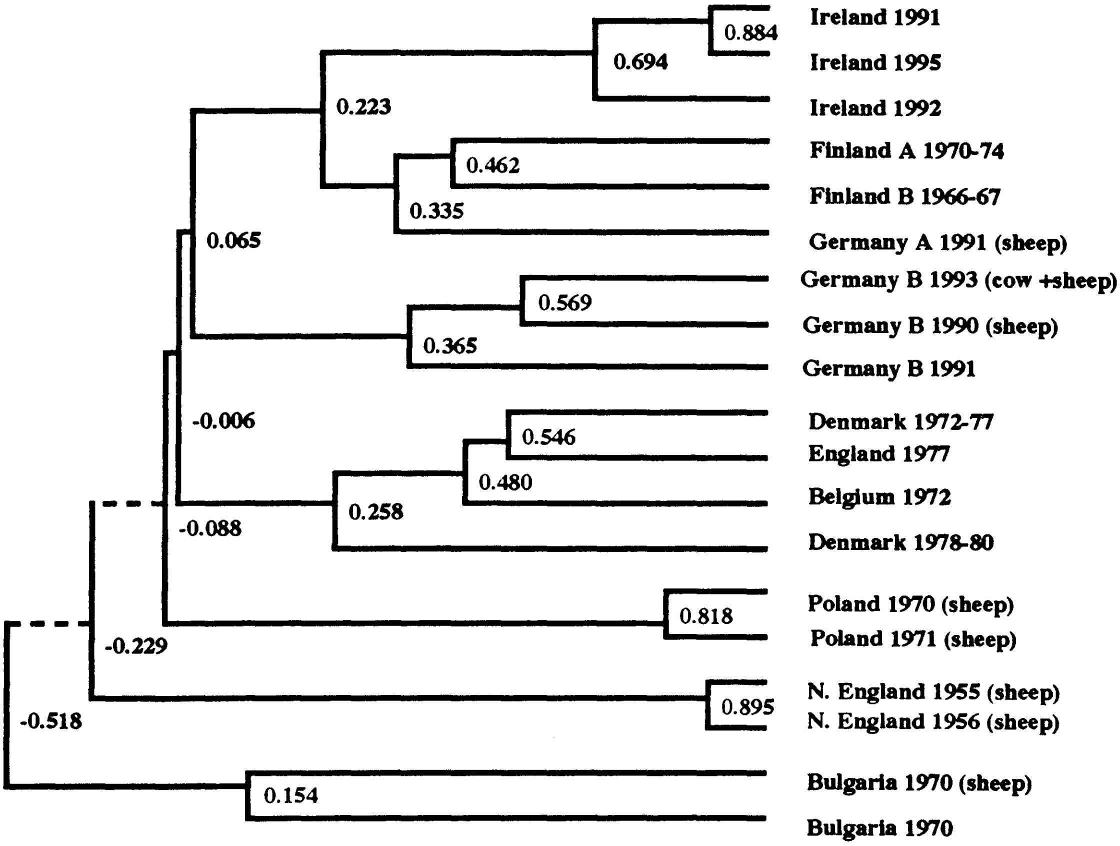


Fig. 1. Similarity of *Aphodius* assemblages across northern and central Europe. Assemblage similarity was compared by Spearman's rank correlation coefficient. The dendrogram was constructed by Mountford average linkage cluster analysis. For sources of data see Table 1.

assemblages, which tend to be dominated by *A. rufipes*. In contrast, there is greater variation in the dominant species of sheep dung assemblages.

Generally, there was low similarity between sites in different geographical areas for both sheep and cow dung assemblages (Fig. 1). This indicates a considerable turnover of species between sites at this geographical scale. However, there is an indication of a cluster of lowland sites in north-west Europe (Belgium/Denmark/England). There was generally greater similarity in assemblage structure within sites over the inter-annual temporal scale of a few years than over the geographical spatial scale (i.e. Ireland, Germany B, Poland and N. England, Fig. 1) . The Danish data sets differed in this respect. However, the Denmark 1978-80 data set included a few anomalous dung pads each of which contained thousands of *A. contaminatus* (Herbst) (Holter, 1982). Between-year samples on a single dung type at one site (cow or sheep only e.g. Ireland, Poland, N. England) seem less variable than between-dung type samples within one year (sheep and cow e.g. Bulgaria).

3.2. Mesoscale.

At the seasonal scale, there was a relatively predictable turnover in the species composition of the *Aphodius* assemblage as one progressed through the year (Fig. 2). This is a direct reflection of the consistency in the occurrence and duration of the flight activity period of *Aphodius* species.

In the interpretation of the DCA analyses (Fig. 3), the relative similarity of the assemblage structure in the various data sets is negatively related to their degree of separation in the ordination biplots. In the three ordinations, the upland and lowland Fermoy sites consistently separate. This is possibly related to environmental differences (e.g. temperature). The Killarney site tends to cluster with the Fermoy upland sites. Depending upon the season, some or all of the Fota data sets show affinity with the Fermoy lowland sites. Axis 2 tends to separate sites within these clusters. Within each cluster, the relative similarity of the assemblages changes across the seasons.

In the interpretation of the DCA analyses (Fig. 3), the relative similarity of the assemblage structure in the various data sets is negatively related to their degree of separation in the ordination biplots. In the three ordinations, the upland and lowland Fermoy sites consistently separate. This is possibly related to environmental differences (e.g. temperature). The Killarney site tends to cluster with the Fermoy upland sites. Depending upon the season, some or all of the Fota data sets show affinity with the Fermoy lowland sites. Axis 2 tends to separate sites within these clusters. Within each cluster, the relative similarity of the assemblages changes across the seasons.

Overall, the variability in assemblage structure at the regional scale between Killarney and the Fermoy upland sites is similar to that at the local scale within the Fermoy upland sites. Moreover, in each ordination, the variability between at least one of the Fota and Fermoy lowland data sets (local scale) is similar to the variability at the between-field scale in the Fermoy lowland sites. The between-year variability at Fota is of the same order as the variability between Fota and Fermoy or between Fota and Killarney. To summarise, these ordinations indicate that variability in assemblage structure can be of a similar order of magnitude at the between-field, local and regional spatial scales and the inter-annual temporal scale.

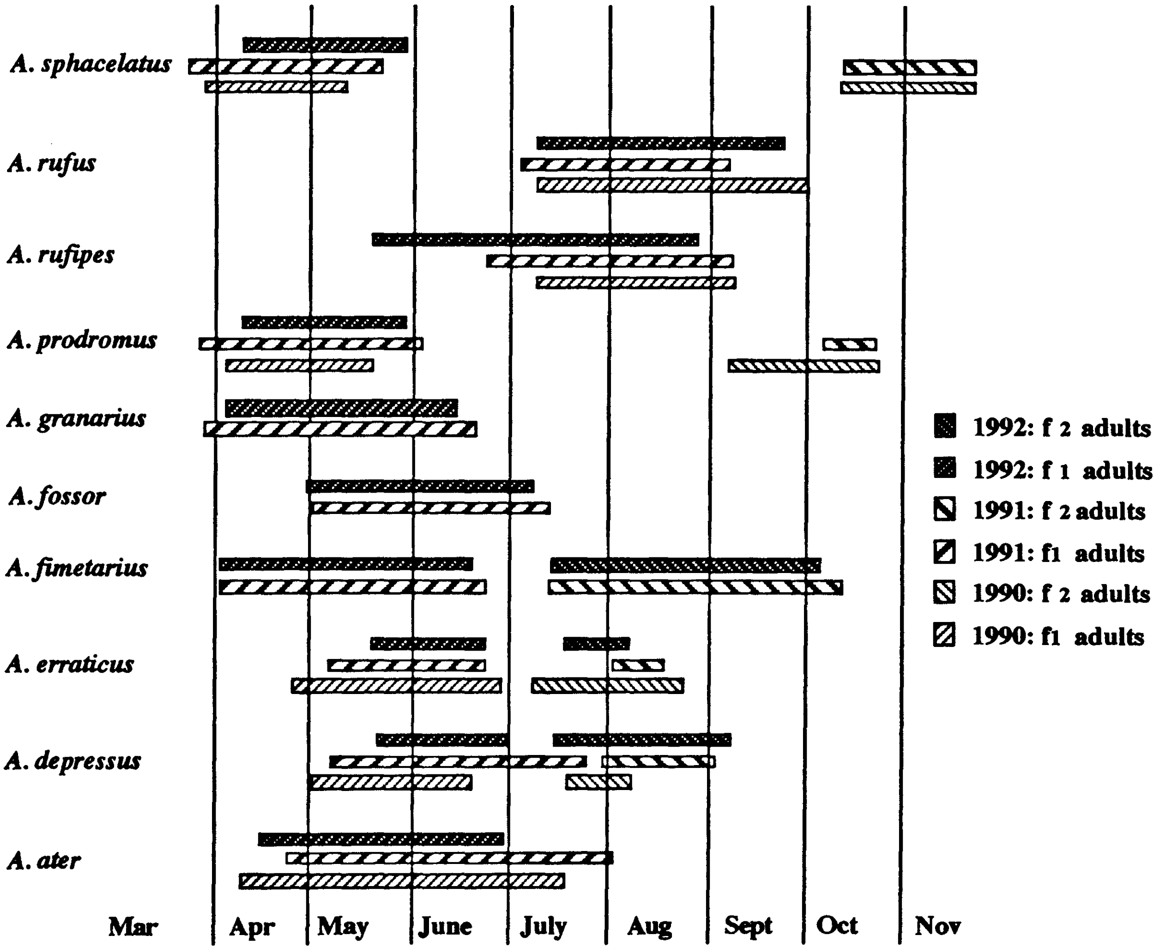


Fig. 2. Adult flight periods of *Aphodius* species at Fota during 1990-1992. The bars show the seasonal range of occurrences of 90% of the total pitfall catch. In 1990, some species had insufficient pitfall captures for inclusion, and early termination of pitfall trapping in 1992 prevented calculation of autumn flight periods of *A. prodromus* and *A. sphacelatus*.

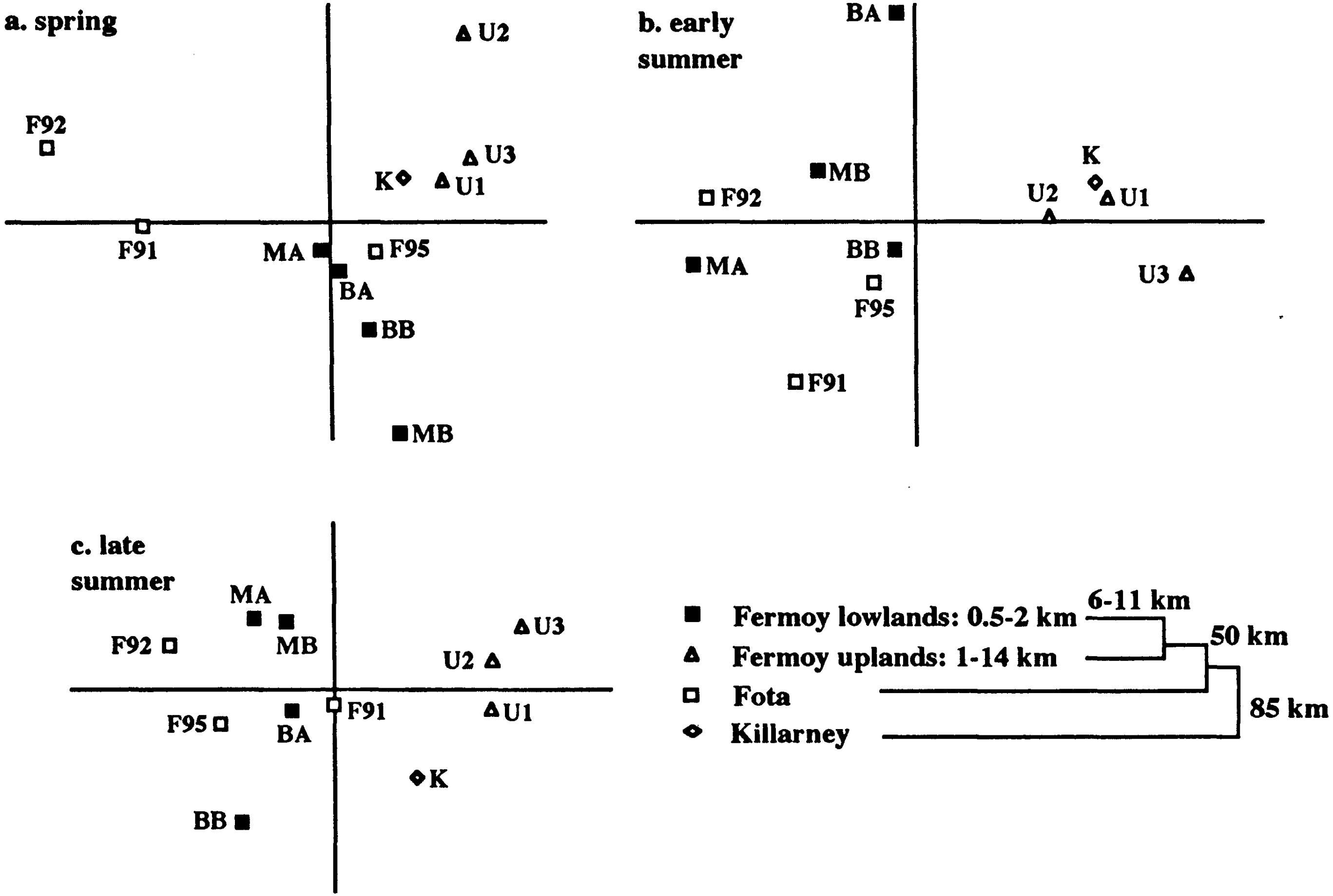


Fig. 3. Detrended Correspondence Analysis ordinations of Aphodius assemblages in southern Ireland. Separate analyses have been carried out for three seasonal assemblages (see text). The ordinations include nine different sites and data from three different years. The Fermoy lowland sites were paired; (BA/BB and MA/MB). The pairs were 2 km apart and within each pair the sites were 0.6 km from each other. There were three Fermoy upland sites; U1, U2 and U3 (U1 and U2 were 1 km apart and 13-14 km apart from U3). All the Fermoy sites were sampled in 1991. The Fota site was sampled in three years (F91, F92 and F95). Killarney (K) was sampled in 1995. The sums of eigenvalues for each analysis were 0.230 (spring), 0.176 (early summer) and 0.271 (late summer). The analyses were carried out on ln (x+1) transformed data. Ordinations are drawn to same scale.

3.3. Microscale

The significant variation in abundances of *Aphodius* beetles captured over the nine day period (Fig. 4) may be partly explained by local weather conditions. For example, the dramatic decline in numbers captured on day 4 correlates with the heavy rainfall on that date. The only apparent major change in environmental conditions on day 3, when numbers increased, was the removal of a herd of cattle from the pasture immediately adjacent to the field containing the pitfall traps. This would have decreased the number of nearby fresh colonisation sites compared to the situation on days 1 and 2 and hence a greater number of *Aphodius* were captured by the pitfall traps than on the previous two days when resource availability was higher. These patterns are representative of other similar experiments (see Gittings, 1994). Although *Aphodius* abundance varied over time, between-day assemblage similarity values were all fairly high, although highest values were generally between consecutive days (Fig. 5). The results indicate a relatively high degree of stability in assemblage structure in fresh dung at this small temporal scale, which is impressive given the high degree of variability in the abundances of beetles.

3.4 Cross-scale measure of similarity

Employing our single measure of similarity across the various scales (Table 2), the greatest temporal similarity in *Aphodius* assemblages occurred at the between-day scale, while the least temporal similarity was between seasons in any year. There was a comparable level of similarity at the local and regional spatial scales, and assemblage comparisons at the between-field temporal scale showed the greatest similarity (but see Discussion). However, the relatively lower level of similarity in data sets from the geographical scale was very pronounced, and this corresponds to the pattern evident from Fig. 1. Note that comparisons between assemblages from different altitudes at the local scale (Table 2) indicated that assemblages at similar altitudes were more similar than assemblages from different altitudes.

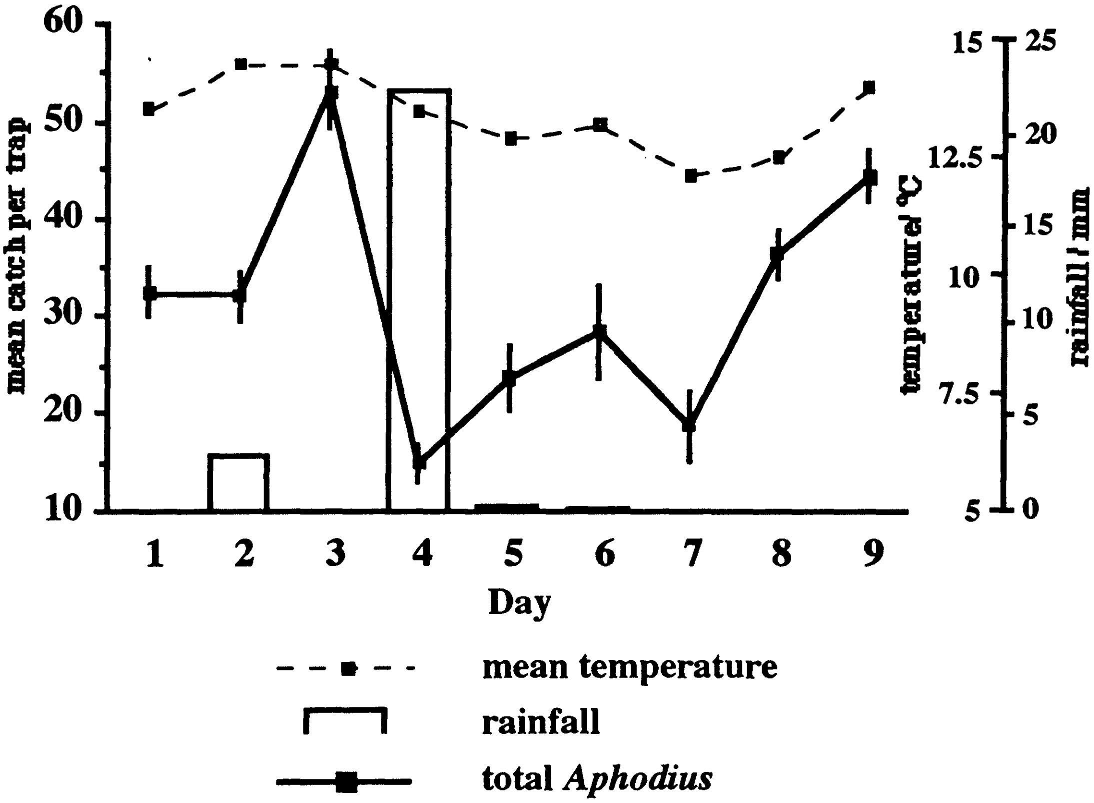


Fig. 4. Daily variation in *Aphodius* flight activity in relation to weather conditions. The graph shows variation in temperature, rainfall and mean (± 1 SE) numbers of *Aphodius* per pitfall trap (n = 10). From Gittings (1994).

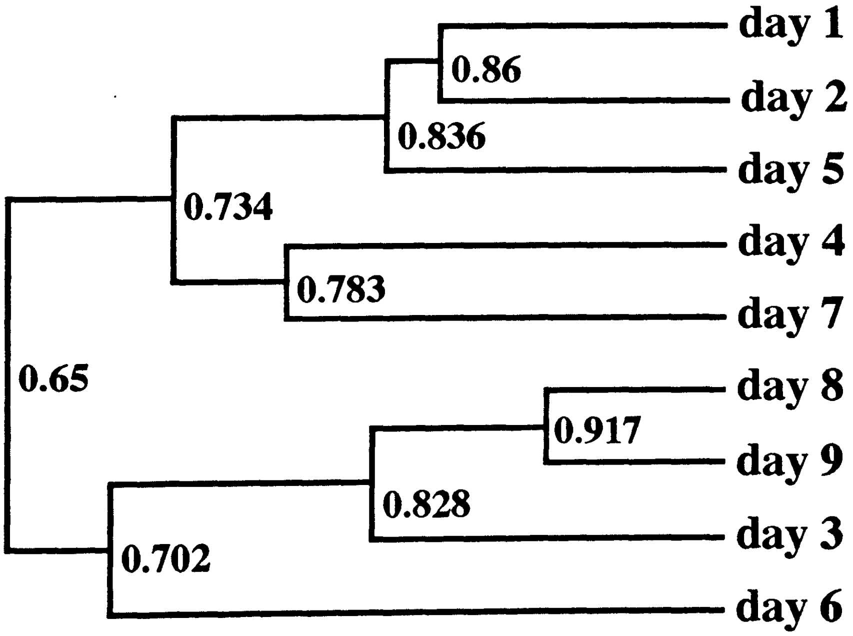


Fig. 5. Between-day similarity of *Aphodius* assemblages captured by dung-baited pitfall trapping compared by Mountford average linkage cluster analysis on Bray and Curtis coefficients of similarity.

Table 2. Mean (±S.D.) coefficient of correlation of rank abundance of species from data sets at different spatial and temporal scales. We also indicate assemblage comparisons conducted on assemblages from different altitudes and assemblages at the same altitude at the local scale, as well as the number and direction (+/-) of significant correlations ($p < 0.05$) in the analyses. See text for details.

Spatio-temporal scale	Mean	S.D.	n	$p < 0.05$
Between days at one site	0.839	0.102	36	36+
Between seasons at any one site	0.406	0.358	27	7+
Between years at one site	0.650	0.165	3	2+
Between fields	0.991	0.005	3	3+
Between local sites	0.806	0.106	6	6+
Between regions	0.809	0.056	3	3+
Geographical scale	-0.007	0.305	45	7+/10-
Comparisons between altitudes	0.718	0.121	12	11+
Comparisons within altitudes	0.884	0.081	6	6+

Note that the geographical data set involved a pool of 40 species, whereas data at all the other scales are derived from a pool of 12 species.

4. Discussion

The limitations of the study should be acknowledged. Because of the different biases inherent in the various sampling methods used in the published work, our analysis at the geographical scale was limited to the relatively coarse resolution of comparisons of rank abundances. Use of correlation coefficients as community similarity indices can be problematic but appears to be reasonably reliable in low-diversity data sets with high sample sizes (Krebs, 1989). However, we are confident that we have chosen a robust method for analysis that overcomes the small-scale differences in sampling between studies, and indicates that greatest variability occurs at this scale, due to species turnover. The geographical scale includes data sets over a 30 year period. Comparisons at this scale could be confounded by long-term changes in assemblage structure, especially if trends such as the severe declines in three species of *Aphodius* recently reported from Finland (Biström et al, 1991) have also occurred elsewhere. Comparisons at the other scales are largely restricted to southern Ireland. The Irish *Aphodius* fauna is depauperate (see Gittings, 1994) and it is possible that the richness of the geographical species pool may influence the degree of species turnover at the finer spatial scales. For example, Hanski (1980b) conducted a similar trapping effort in England to our Fermoy lowland study. The species turnover between five fields in Oxford was higher with a mean proportion of 0.78 (SE = 0.03) of species shared between pastures compared with a mean of 0.95 (SE = 0.02) shared species in the Fermoy sites. Finally, the analyses have been limited to data from cattle- or sheep-grazed open pastures. However, throughout much of northern Europe these are by far the dominant dung beetle habitats. Data sets were sampled from a range of altitudes, and some previous research has indicated that abundance of individuals of *Aphodius* species can change in relation to altitude (Key, 1982; Gittings, 1994). In this study, there was greater variability between assemblage comparisons from different altitudes than between assemblage comparisons from similar altitudes, but this may be confounded by changes in soil types between the lowland and upland sites in our study (Gittings, 1994).

4.1 Multiscale comparisons of assemblage variation

The structure of *Aphodius* assemblages can change through species turnover (loss or gain of species) and changes in relative and actual abundances. The latter factor has only been considered here at the daily scale. Reliable estimates of north temperate dung beetle population densities are difficult to obtain (Gittings, 1994), although the numbers colonising individual dung pads can be measured.

At the geographical scale of 300-2500 kilometres, less than 50% of the species are shared between each pair of neighbouring sites and correlations of rank abundances are usually low. However, at the regional scale of 50-100 km within Ireland, assemblages shared 90% of their species and generally had highly correlated rank orders of abundance. Hanski (1986) has suggested that species composition of abundant species may be relatively stable at scales of tens of thousands of years but turnover of rare species may be high at the scale of 50 years. We are not aware of any complete data sets on dung beetles available at the scale of decades or greater. However, analysis of data in De Graef and Desiére (1984) show that the rank order of abundances of the eight commonest species changed dramatically between 1972 and 1982-83 ($r_s = -0.5$). At the scale of 1-4 years, however, assemblages appear to be relatively stable. Note that when variability was based on annual total captures of species (Table 2), variability at the between-field scale was distinctly less than that of the local and regional scales. However, at these scales of analysis, the DCA ordinations provide a more informative and refined method of comparison, being based on the subseasonal data sets. Thus, ordinations indicate that variations in assemblage structure are of similar magnitude at the regional, local, between-field and between-year scales. Therefore, major changes in assemblage structure appear to occur at spatial scales greater than 100 km.

At the finest scales, abundances are highly variable but species frequencies of beetles colonising fresh dung are very similar at the between-day scale. Variability in abundances are likely to be caused by variation in weather conditions and by rotational grazing (Gittings, 1994). In rotational grazing, cattle are rotated through a series of pastures over 20-30 days. Therefore, in any one pasture, fresh dung will only be available for a few days each month. If beetle populations, and early successional ones in particular, follow cattle movements through the rotation, this will cause short term variability in abundances in any one field. Moreover, in practice, the changing age-composition of the dung-pats should cause larger variability in assemblage structure at the between-day scale than was apparent from the fresh dung used in our study. At one of the finest spatial scales, i.e. between-pads, the reported high levels of aggregation indicate high variation in abundances (Holter, 1982; Hanski, 1986).

4.2 Implications for further studies

The apparent equivalence of assemblage variation over a range of spatial scales illustrates the problem for community ecologists in defining the unit of study. Dung beetle assemblages 100km apart separated by mountain ranges (Fota/Fermoy and Killarney) obviously cannot be regarded as part of the same community. However, neither is the assemblage within a single field an entire community. Indeed in rotationally-grazed pastures, adult assemblages only persist within a field for a few days until the early successional species are forced to leave in search of fresh dung. The usual method of studying dung beetle assemblages has been fixed point sampling. However, if the community covers tens of square kilometres, this method clearly risks biased sampling and cannot uncover the complex spatio-temporal dynamics which occur in rotationally-grazed pastures. While a dependence on a single sampling site at a local scale may not provide adequate description of the community, once the local assemblage has been defined (from a number of sites) it may be representative up to the regional scale.

One could envisage a spectrum of community types from small, relatively isolated assemblages in well-wooded landscapes with small permanently-grazed pastures, to large inter-connected assemblages in open landscapes of large rotationally-grazed pastures.The differences in the spatial dynamics of these 'macro-community' types would be likely to influence the structure of their constituent assemblages. For example, the overall species richness might be greater in the former type, with greater spatial variation between assemblages. Furthermore, the effects of rotational grazing on spatial dynamics are likely to differ between early and late successional species which may result in interspecific variation in the spatial resolution of *Aphodius* populations. There would then be no spatial scale at which a single self-contained *Aphodius* community occurs. Research is required to better define the spatial structure and landscape relationships of *Aphodius* assemblages.

Between-year variability is similar to variability at a spatial scale of 50-100 km, indicating that comparisons across these spatial scales should include data from several years. The degree of inter-annual variability relates to changes in relative abundances of individual species. For example, 1845 specimens of *A. rufus* were caught at Fota in 1991, but only 42 were caught the following year. However, much greater variability in *Aphodius* assemblages occurs between-seasons than between-years and broad seasonal groupings of species can be defined (Gittings and Giller, 1996). Whether the annual assemblage comprises seasonal sub-assemblages with little interaction between them remains to be seen. In practise, some degree of overlap occurs between all species (e.g. *A. rufipes* can be dominant throughout most of the summer). The issue to be resolved is whether the seasonal limits of the seasonal sub-assemblages arose and/or are being maintained by interactions across the sub-assemblage boundaries (see Gittings, 1994). Nevertheless, we suggest that the appropriate method of assemblage comparisons in *Aphodius* are between the seasonal sub-assemblages rather than between the annual assemblages.

Acknowledgements

We thank Eileen Finn, Kathleen Hawes and staff at Moorepark Research Station and Fota Wildlife Park for assistance with fieldwork and are grateful to Peter Holter and Peter Sowig for providing unpublished information. We are also grateful to two anonymous referees for helpful comments on the manuscript.

References

Biström, O., Silfverberg, H., Rutanen, I., 1991. Abundance and distribution of coprophilous Histrini (Histeridae), *Onthophagus* and *Aphodius* (Scarabaeidae) in Finland (Coleoptera). Entomologica Fennica 2, 53-66.

Breymeyer, A., 1974. Analysis of a sheep pasture ecosystem in the Pieniny mountains (The Carpathians). XI. The role of coprophagous beetles (Coleoptera: Scarabaeidae) in the utilisation of sheep dung. Ekologia Polska 22, 617-634.

Breymeyer, A., Zacharieva-Stoilova, B., 1975. Scarabaeidae in two mountain pastures in Poland and Bulgaria. Bulletin de L'Académie Polonaise des Sciences (Série des Sciences Biologiques) 23, 173-180.

Desière, M., 1983. Écologie des coléoptères coprophiles en prairie permanente pâturée. 1.-Caractéristiques des populations de Coléoptères adultes coprophiles. Phénologie et dynamique saisonnière. Bulletin d'Écologie 14, 99-117.

De Graef, F., Desière, M., 1984. Écologie des coléoptères coprophiles en prairie permanente pâturée. III. Dynamique et phénologie des guildes d'Hydrophilidae de Scarabaeidae et de Geotrupidae. Bulletin de la Société Royale des Sciences de Liège 53, 158-172.

Doube, B.M., Giller, P.S., 1990. A comparison of two types of trap for sampling dung beetle populations. Bulletin of Entomological Research 80, 259-263.

Gittings, T., 1994. The Community Ecology of *Aphodius* Dung Beetles. Unpublished PhD thesis, National University of Ireland.

Gittings, T., Giller, P.S., 1997. Life history traits and resource utilisation in an assemblage of north temperate *Aphodius* dung beetles (Coleoptera, Scarabaeidea). Ecography 20, 55-66.

Hanski, I., 1980a. The community of coprophagous beetles (Coleoptera, Scarabaeidae and Hydrophilidae) in northern Europe. Annales Entomologici Fennici 46, 57-73.

Hanski, I., 1980b. Spatial patterns and movements in coprophagous beetles. Oikos 34, 293-310.

Hanski, I., 1986. Individual behaviour, population dynamics and community structure of *Aphodius* (Scarabaeidae) in Europe. Acta Œcologia, Œcologia Generalis 7, 171-187.

Hanski, I., 1991. North temperate dung beetles. In: I. Hanski and Y. Cambefort (Eds.), Dung Beetle Ecology. Princeton University Press. pp. 75-96.

Hanski, I., Koskela, H., 1977. Niche relations among dung-inhabiting beetles. Oecologia (Berl.) 28, 203-231.

Himmelsbach, W., 1993. Einfluß einiger abiotischer Faktoren auf die Besiedlung von drei bzw. vier Tage altem Rinderdung durch ausgewahlte Arten der Diptera und Coleoptera. Diplomarb. i. Br.

Hirschberger, P., Bauer, T., 1994. The coprophagous insect fauna and its influence on dung disappearance. Pedobiologia 38, 375-384.

Holter, P., 1982. Resource utilisation and local coexistence in a guild of scarabaeid dung beetles (*Aphodius* spp.). Oikos 39, 213-227.

Key, R.S., 1982. Cluster analysis of dung inhabiting beetle communities from different altitudes in Jostedalen, South-West Norway. Fauna Norvegica Series B 29, 24-33.

Koskela, H., 1979. Patterns of diel flight activity in dung-inhabiting beetles: An ecological analysis. Oikos 33, 419-439.

Krebs, C.J., 1989. Ecological Methodology. HarperCollins, New York.

Pimm, S.L., 1984. The complexity and stability of ecosystems. Nature 307, 321-326.

Wahl, P., 1995. Die Lebensgemeinschaft dungbewohnender Käfer (Familien Scarabaeidae und Hydrophilidae) auf der Schelinger Viehweide im Kaiserstuhl. Diplomarb., Freiburg i. Br.

Wassmer, T., Sowig, P., 1994. Die coprophagen Käfer der Schafweide "Flachsland" am Schönberg bei Freiburg. Veröff. Naturschutz Landschaftspfl. Bad-Wurtt. 68/69, 355-376.

White, E., 1960. The natural history of some species of *Aphodius* (Col., Scarabaeidae) in the northern Pennines. Entomologist's Monthly Magazine 96, 25-30.

Chapter 6

Conclusions

Chapter 6

Conclusions

This study has considered the effects of various factors (both extrinsic and intrinsic) on the structure of dung beetle assemblages, at several different spatio-temporal scales. For example, I have compared different sampling techniques and investigated patterns of dung beetle assemblage structure from between-day to inter-annual temporal scales. I have also considered the effects of both dung pad size and quality at the between-pad spatial scale through to differences in assemblage structure at geographical spatial scales. In this final chapter, I discuss the role of scale in affecting observed patterns in dung beetle ecology, present an overview of the main conclusions of this study and indicate possible areas for future research.

Comparisons of pitfall trapping and cohort pad sampling

Despite the variety of methods employed, not much work has previously addressed the effect of sampling method on descriptions of north temperate dung beetle assemblages. In agreement with Gittings (1994), comparisons of pitfall trapping and cohort pad sampling yielded different species frequencies, but correlations of the rank order of species abundance of the two methods were usually significant. Gittings (1994) identified other potentially serious problems in relation to dung-baited pitfall trapping, and these problems were also identified in this study. For example, considerable variations in beetle abundances were closely related to weather conditions, and movements of cattle in rotational grazing regimes. Note that although they may indicate levels of activity (in colonisation rates), these short-term fluctuations in beetle abundances appeared to be independent of absolute changes in actual population abundances of dung beetles.

In addition to the effects of small-scale changes in weather conditions, extended periods of unusually warm and dry, or cool, wet and windy weather will further confound comparisons of dung beetle assemblage structure that are based on annual totals. For this reason, and because of the temporal segregation of dung beetle species between seasons (e.g. White, 1960; Holter, 1982; Hanski, 1986; Palmer, 1995; Gittings and Giller, 1997; see below), comparisons of assemblage structure of north temperate dung beetles are probably best achieved through comparisons of seasonal assemblages (e.g. spring, early summer, late summer and autumn).

Seasonality in dung beetles

The seasonality displayed by the various dung beetle species in this study (Appendix, Chapter 2; Chapter 5) has been well documented. Several authors have demonstrated mathematically the segregation of *Aphodius* species along the seasonal axis (Holter, 1982; Palmer, 1995). Hanski (1980) demonstrated that 'core' species were better spaced out in habitat-season-size niche space than were 'satellite' species. Note, however, that in relation to such overdispersion of niches, Holter (1982) has pointed out that the seasonal distribution of metabolic activity is more uneven than seasonal species frequencies. Thus, at this stage one cannot say whether such differences in the phenology of *Aphodius* arose and/or are being maintained by competition. There are field data which have been proposed to support a competition hypothesis to account for phenological differences in dung beetles (Hanski, 1980; Hanski and Kuusela, 1983). However, data in the present study indicated that the collection of some of these field data (Hanski and Kuusela, 1983) could have been confounded by several factors e.g. local herbivore movements, as well as differences in dung types and dung size.

One of the more important consequences of phenology in the dung beetle community is the need to be aware that analyses employing annual totals will directly compare species which may not interact at all, as they occur in different seasons (e.g. spring and autumn). For this reason, analyses in Chapters 2 and 5 identified time periods over which species composition was very similar, and conducted separate analyses on data collected within these time periods.

Resource utilisation

Dung size

Dung pad size can be related to several critical processes in dung beetle ecology e.g. colonisation, pat residence times and larval development, as well as measures of crowding in both adults and larvae (Chapter 3). Evidence appeared to support a working hypothesis that the importance of dung pad size is provided not by an increase in resource quantity *per se*, but by a relative increase in utilisable resource. For example, smaller pads may be expected to dessicate at a faster rate than larger pads, and this may be important for the fluid-feeding adult *Aphodius* (although it is not known if the levels of fluid required for dung beetle feeding actually deplete to a limiting level in the smaller pads). In addition, size-dependent dessication of the pad is probably very important for the suitability of the pad both as a habitat and source of nutrition for the larvae, which can suffer mortality due to dessication of the pad. In the one exception where no increase in adult biomass density was found in relation to pad size, non-dung-breeding *A. prodromus* were dominant. It may be that what is most important is not so much the suitability of the pad for adult nutrition, but the suitability of the pad for the future larval development of the eggs of breeding adults. The finding of a positive relationship between larval density and pad size (Chapter 3) may have been dependent on the timing of the experiment, as there was a serious heatwave occurring at the time of the experiment. It would be desirable to replicate the larval field experiments and to assess how often conditions arise that sufficiently promote dessication of the pads to an extent that results in larval mortality.

Examples from previously published literature have illustrated the considerable range of dung sizes which have been employed between studies (Chapter 3). In the present study, data on the effect of dung pad size suggested that the use of different pad sizes within studies may confound descriptions of assemblage structure between treatments. For example, comparisons of assemblage structure (rank abundance of species) between dung types across studies generally appeared to be more similar when the pad sizes of the dung types were equivalent (Rainio, 1966; Kessler *et al.* 1974; Breymer and Zacharieva-Stoilova, 1975; this study, Chapter 4). In addition, ecological patterns observed in one dung pad size may not necessarily scale to another size of pad. Hirschberger and Degro (1996) have documented differences in the oviposition behaviour of *A. ater* in response to to the abundance of *Scatophaga* larvae; generally, *A. ater* lays fewer eggs in 50 g sheep pads with *Scatophaga* larvae than in pads without *Scatophaga* larvae. It would be extremely interesting to investigate whether those patterns that were observed with 50 g pads would be observed if dung sizes of 250 g or 500 g were used.

Dung types

Field experiments were used to investigate the colonisation of dung from native herbivore species (cow, horse and sheep), and five different types of cow dung in another experiment. There were typically significant differences between dung types in moisture content and organic matter. There were also significant differences in the biomass, species richness and diversity of dung beetles colonising cow, horse and sheep pads. In experiment C4, there were significant differences among cow dung types in the number of colonising beetles. Laboratory experiments provided evidence that adult emigration and larval production were highest on sheep dung, which was colonised by the highest abundances of beetles in field experiments.

Data from this study, and reanalysis of previously published data, indicated that dung beetle species composition and species richness was usually quite similar among dung types. However, absolute abundances and the rank order of species composition between seasons, and, within-seasons, from differences in the relative abundance of smaller subsets of species which were typically common to all sites. DCA ordinations indicated that there was generally a comparable level of variability between the spatio-temporal scales, but there was some limited evidence that the greatest variability may occur between the more distant (> 50 km) sites. It is difficult to determine what processes promote the variability in the dung beetle assemblages across southern Ireland. Potentially important environmental factors include climate and weather variation, macrohabitat preferences, as well as the amounts and distribution of different macrohabitats; altitude (Key, 1982; Chapter 5); dung quality (Gittings, 1994; Chapter 4) and soil type (Sowig, 1995). Alternatively, asynchronous patterns of inter-annual variation (in assemblage structure) among sites may explain a lot of the variation that was apparent at the local-regional spatial scale (Chapters 2 and 5).

Composition of taxonomic groups in dung beetle assemblages

Although I have concentrated on the *Aphodius* dung beetle assemblage, I have also included data on the spatial and temporal variability of what we consider to be the main taxonomic groups in the dung beetle assemblage, e.g. *Aphodius*, *Sphaeridium*, and *Geotrupes*. There were few differences between the ordinations including the *Aphodius* genus only and those including the *Aphodius*, *Sphaeridium*, and *Geotrupes* genera. This probably reflected the dominance of species composition by *Aphodius* in the dung beetle assemblage at all sites. The pattern of an assemblage dominated by *Aphodius* species, but supplemented by some *Sphaeridium* and a few *Geotrupes* species is, in general, well established for north temperate assemblages (Rainio, 1966; Koskela, 1979; Hanski, 1991; Hirschberger and Bauer, 1994; Sowig and Wassmer, 1994; Heijerman, 1990). Nevertheless, a comparison with other data sets yields some more specific differences. For example, sites at the geographical scale can differ in whether the *Sphaeridium* genus is dominated by *S. lunatum* or *S. scarabaeoides*. For example, where large sample sizes were available, the former species was found to be numerically dominant at sites in Belgium (Heijermann, 1990). *S. scarabaeoides* was numerically dominant at sites in Germany (Sowig and Wassmer, 1994; Himmelsbach, 1993; Wahl, 1995) and Finland (Koskela, 1979). It is unclear what agents are responsible for these patterns. One should also consider the changes in relative abundances of *S. lunatum* and *S. scarabaeoides* at the relatively smaller spatial scales of 50-100 km (this study). This reinforces the need for a measure of variability at regional scales when attempting to interpret data collected from a larger scale. It is noteworthy that in comparison with examples in published literature, few geographical sites were dominated to the same extent by *Sphaeridium* as Fota in 1996. It will be interesting to see how persistent in time this pattern will be. Some geographical sites can have quite large numbers of the typically uncommon *S. marginatum* and *S. bipustulatum* (Himmelsbach, 1993; Wahl, 1995; Rainio, 1966).

Patterns in dung beetle ecology spatio-temporal scales

Community ecology largely seeks to understand how assemblages are organised in space and time. This is most often achieved through the description of patterns of variation in diversity, composition and other characteristics, coupled with attempts to discern what processes are responsible for the patterns. Generally, assemblage composition varies with scale and many ecological processes that are responsible for producing spatio-temporal variation in assemblages can do so in a hierarchical manner (Allen and Starr, 1982; O'Neill *et al.*, 1986). Within such an hierarchy, large scale temporal and spatial processes will be expected to produce wide-ranging and long-lasting effects on assemblage composition, within which other processes will then play their role in influencing assemblage composition.

This study has incorporated sampling at a number of different spatial and temporal scales, and distinct changes in patterns of community structure have been identified across these scales. At the smallest scales, there were highly significant between-day differences in dung beetle abundances (over ca. 9 days), probably due to weather or rotational grazing. However, relative abundance of species was highly correlated between days. Although less similar than comparisons at the between-day scale, there were similar levels of variability between sites at spatial and temporal mesoscales (1-180 km and 6 years, respectively) (see above). At the largest geographical spatial scale considered, there was greatest variability between sites, largely due to differences in species composition, and differences in the relative abundance of species that may have been shared between sites (Finn *et al.*, 1998). Considering the extent of differences in the species composition, relative abundance and absolute abundance of species in north temperate dung beetles assemblages, I would propose the hierarchial relationship indicated in Fig. 1. At different spatio-temporal scales in the hierarchy, I also indicate processes that are probably most important in contributing to variability in patterns of assemblage structure at that scale. In the absence of a single measure of assemblage variability across all the various scales, the proposed hierarchy in Fig. 1 remains tentative. The relative position of the processes is most tentative at the lower end of the hierarchy and it would be interesting to enquire where inherent patterns of aggregation fit in, and what factors are more important in promoting between-pad aggregation when one contrasts the effects of natural variability in pad size, quality and age with natural patterns of aggregation.

Geographical spatial (300-2500km) and
Evolutionary temporal scales (10-100 ky)
- origination, extinction, dispersal

⇓

Ecological Time - local extinction/ immigration
of species populations (metapopulations), fluctuations in abundance

⇓

Regional, Local and Between-field (1-180km) spatial scales and
Between-year (1-6 y) temporal scales
- Regional habitat diversity, local dispersal and extinction

⇓

Between seasons - phenology

⇓

Dung type/size

⇓

Between-day (~9 Days) - weather effects, rotational grazing

⇓

Succession/Aggregation in individual pads

Fig. 1. Proposed hierarchy of scale effects and processes in contributing to variability in *Aphodius* assemblage structure of indiividual pads. Based on relative magnitude of effect on species composition, relative abundance and absolute abundance.

Patterns in north temperate dung beetles at the geographical scale

The analysis of assemblage structure at the geographical scale from published literature has several problems associated with it. Data sets differed to various degrees in sampling methodology and the frequency and extent of sampling over the year, and studies differed in the size and type of dung collected. The lack of quantitative original data in some of the data sets precluded the use of more sophisticated approaches or statistical analyses. However, on a more general point, the pursuit of macro-ecological patterns is almost inevitably subject to the use of data sets collected from a number of small-scale studies, with some differences between studies in sampling protocols. Although more refined analysis will typically be possible when studies are more similar in their methodology, the generality and clarity of trends offered by the identification of large-scale biogeographical patterns can make a significant contribution to ecology, presumably reflecting large scale processes.

In this study, comparisons of assemblage structure at the geographical scale indicated distinct differences between sites. This was primarily due to differences between sites in species composition, and differences in the relative abundance of species that were shared between sites. However, note that when assemblages were examined in terms of their relative biomass, there were similarities between sites in the dominant species. This inspires several questions that may provide fruitful research in the future (see Brown, 1984). For example, among temperate dung beetle assemblages, are there species that are consistently more abundant wherever they occur, and do those species have larger geographical ranges than other species that are typically less abundant?

References

Allen, T.F.H. and Starr, T.B. (1982) *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago.

Breymeyer, A. and Zacharieva-Stoilova, B. (1975) Scarabaeidae in two mountain pastures in Poland and Bulgaria. *Bulletin de l'Académie Polonaise des Sciences (Série des Sciences Biologiques)*, **23**, 173-180.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255-279.

Finn, J., Gittings, T. and Giller, P.S. (1998) *Aphodius* dung beetle assemblage stability at different spatial and temporal scales. *Applied Soil Ecology*, **241**, in press.

Gittings, T. (1994) *The community ecology of* Aphodius *dung beetles*. Unpublished PhD thesis. National University of Ireland.

Gittings, T. and Giller, P.S. (1997) Life history traits and resource utilisation in an assemblage of north temperate *Aphodius* dung beetles (Coleoptera, Scarabaeidea). *Ecography*, **20**, 55-66.

Gittings, T. and Giller, P.S. (1998) Resource quality and the colonisation and succession of coprophagous dung beetles. *Ecography*, in press.

Hanski, I. (1980) The community of coprophagous beetles (Coleoptera, Scarabaeidea and Hydrophilidae) in northern Europe. *Annales Entomologici Fennici*, **46**, 57-73.

Hanski, I. (1986) Individual behaviour, population dynamics and community structure of *Aphodius* (Scarabaeidae) in Europe. *Acta Œcologia, Œcologia Generalis*, **7**, 171-187.

Hanski, I. (1991) North temperate dung beetles. *Dung beetle ecology.* (ed. by I. Hanski, and Y. Cambefort), pp. 305-329. Princeton University Press, Princeton, New Jersey.

Hanski, I., and Kuusela, S. (1983) Dung beetle communities in the Åland archipelago. *Acta Entomologica Fennica*, **42**, 63-42.

Himmelsbach, W. (1993) Einfluß einiger abiotischer Faktoren auf die Besiedlung von drei bzw. vier Tage altem Rinderdung durch ausgewahlte Arten der Diptera und Coleoptera. Diplomarb. i. Br.

Hirschberger, P. and Bauer, T. (1994) The coprophagous insect fauna and its influence on dung disappearance. *Pedobiologia*, **38**, 375-384.

Hirschberger, P. and Degro, H.N. (1996) Oviposition of the dung beetle *Aphodius ater* in relation to the abundance of yellow dungfly larvae (*Scatophaga stercoraria*). *Ecological Entomology*, **21**, 352-357.

Heijerman, T. (1990) Seasonal changes in the relative abundance of some dung beetles in the faeces of the wild boar and mufflon (Coleoptera, Scarabaeoidea). *Entomologische Berichten (Amsterdam)*, **50**, 81-86.

Holter, P. (1982) Resource utilisation and local coexistence in a guild of scarabaeid dung beetles (*Aphodius* spp.). *Oikos*, **39**, 213-227.

Koskela, H. (1979) Patterns of diel flight activity in dung-inhabiting beetles: An ecological analysis. *Oikos*, **33**, 419-439.

Kessler, H., Balsbaugh Jr., E.U. and McDaniel, B. (1974) Faunistic comparison of adult Coleoptera recovered from cattle and sheep manure in east-central South Dakota. *Entomological News*, **85**, 67-71.

Key, R.S. (1982) Cluster analysis of dung inhabiting beetle communities from different altitudes in Jostedelan, South-West Norway. *Fauna Norvegica*, Series B **29**, 24-33.

Lumaret, J.P., Kadiri, N. and Bertrand, M. (1992) Changes in resources: consequences for the dynamics of dung beetle communities. *Journal of Applied Ecology,* **29,** 349-356.

O'Neill, R.V., DeAngelais, D.L., Waide, J.B. and Allen, T.F.H. (1986) *A Hierarchial Concept of Ecosystems*. Princeton University Press, Princeton.

Palmer, M. (1995) Testing for seasonal displacement in a dung beetle guild. *Ecography*, **18**, 173-177.

Raino, M. (1966) Abundance and phenology of some coprophagous beetles in different kinds of dung. *Annales Zoologici Fennici,* **3,** 88-98.

Sowig, P. (1995) Habitat selection and offspring survival in three paracoprid dung beetles: the influence of soil type and soil moisture. *Ecography,* **18**, 147-154.

Sowig, P. and Wassmer, T. (1994) Resource partitioning in coprophagous beetles from sheep dung: Phenology and microhabitat preferences. *Zool. Jb. Syst.,* **121**, 171-192.

Wahl, P. (1995) Die Lebensgemeinschaft dungbewohnender Käfer (Familien Scarabaeidae und Hydrophilidae) auf der Schelinger Viehweide im Kaiserstuhl. Diplomarb., Freiburg i. Br.

White, E. (1960) The natural history of some species of *Aphodius* (Col., Scarabaeidae) in northern Pennines. *Entomologist's Monthly Magazine*, **96,** 25-30.

Acknowledgements

I thank Paul Giller for his supervision of this research and I am extremely grateful for his advice, support and encouragement. I particularly appreciate his willingness to thoroughly discuss progress, problems and aspects of ecology (not necessarily related to dung beetles), apparently regardless of his own workload or the length of the queue outside his office!

I am grateful to Tom Gittings for his endless generosity of time and ideas. His role throughout this study has effectively been that of a second supervisor and on many levels this work has benefitted hugely from his involvement. I am also extremely grateful to him for much helpful discussion, proofreading and permission to use his data.

I would like to thank the staff at Fota Wildlife Park for permission to work at Fota Island, Mr. Barret for permission to work in the cattle pastures at Fota and Gearóid Stakelum for permission to work, and assistance, at Moorepark. I also thank the following for permission to conduct pitfall trapping at various sites; the Finn family at Killarney, Co. Kerry; Noel Culleton and John Murphy at Teagasc, Johnstown Castle, Co. Wexford; Jervis Good, Carrigaline. I am particularly grateful to the Finn family, John Murphy and staff at Moorepark for assisting with pitfall trapping at the Killarney, Wexford and Fermoy sites, respectively. I am grateful to Joe Dwyer for advice and help with chemical analyses at Moorepark, and Imelda Casey, Caroline Plant and Mary Linnane for their help and company at Moorepark. I also thank Kathleen O' Sullivan, Dept. of Statistics, UCC for advice on statistical analyses in Chapter 3.

I wish to thank Tony Brereton and John Murphy for providing meteorological data for the Moorepark and Wexford sites, respectively. I thank Petra Hirschberger, Peter Holter and Peter Sowig for helpful discussion and providing unpublished data. I am particularly grateful to Petra Hirschberger for her generosity of hospitality, ideas and discussion during a visit I made to Kiel at the beginning of this research; the investigation of the role of dung pad size was inspired by discussion during that visit. I am grateful to John Murphy for proofreading, and comments on, Chapter 3.

Many people in the Department of Zoology have provided help during this study. For their assistance in providing help, materials and transport I thank the technical staff; Nora Buttimer, Liam Corby, Sandy O' Driscoll and Bob McNamara. I am grateful to Nora Buttimer for her company and assistance with fieldwork on several occasions. I also thank various other members of the department for help with fieldwork; Derek Casey, Catherine Collins, Brian Duffy, John Murphy, Ken Roche and Susan Steele. I am very grateful to Bob McNamara and Susan Steele for their company and help with fieldwork on the longer journeys to and from the Wexford site. When one considers the medium employed in dung beetle ecology, I reiterate my sincere thanks to all those who assisted with fieldwork!

I particularly wish to acknowledge Paul Giller, Ken Roche, Tom Gittings and Tom Kelly for their instruction and positive influence during what has been a formative period in my scientific training over the past number of years. I am similarly grateful to my postgraduate colleagues and other members of the department, whose depth of friendship and camaraderie over the past few years has made this time a far more fulfilling and enjoyable experience than it would otherwise have been. At the risk of making any omissions I hesitate to list them, but you know who you are. I would also like to thank members of UCC squash club for their friendship (and squash court battles!) since my undergraduate years.

I am particularly grateful to my parents for their extensive support and encouragement throughout my education. I also thank them and my brothers for conducting pitfall trapping in Killarney over a period of two years.

I am especially grateful to Linda Moloney and Gearóid Finn for their continuous support, as well as Linda's assistance with fieldwork. I also thank Linda and Gearóid for their patience and understanding during the many hours that were devoted to this work, but detracted from time that might have been spent with them. Despite Gearóid's frequent and rather insistent offers of his word processing skills, I take full responsibility for any and all errors!