

Spatial ecology of dung beetles

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Academic dissertation

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The thesis is based on the following articles:

- I** Roslin, T. 1999. Dung beetle movements at two spatial scales. Submitted.
- II** Roslin, T. 1999. Population genetic structure of the patchily distributed dung beetle *Aphodius fossor*. Submitted.
- III** Roslin, T. and A. Koivunen. 1999. Distribution and abundance of dung beetles in fragmented landscapes. Submitted.
- IV** Roslin, T. 1999. Large-scale spatial ecology of dung beetles. Submitted.

These are referred to by their Roman numerals in the text.

Contributions

In chapter **III**, my co-author, Miss Anne Koivunen, contributed to the design of the study and the gathering of empirical data. Although he was not included as an author, my supervisor Prof. Ilkka Hanski made a substantial contribution both to the original idea and the study design of chapters **I–IV**.

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Introduction

During the past two decades, ecologists have increasingly recognised the importance of the spatial context in their studies of individuals, populations and communities (Kareiva and Wennergren 1995, Tilman and Kareiva 1997, Hanski and Gilpin 1997, Hanski 1998). A rapidly expanding literature demonstrates how the spatial distribution of habitats can affect all aspects of ecology, from population genetics (e.g., Whitlock 1992; Dias et al. 1994, 1996; Giles and Goudet 1997, Hedrick and Gilpin 1997) and single-species dynamics (e.g., Kareiva 1990, Hastings and Higgins 1994, Hanski 1997, 1998, 1999) to community composition (e.g., Danielson 1991, 1992; Caswell and Cohen 1993; Holt 1993, 1997) and evolutionary change (e.g., Brown and Pavlovic 1992, Holt and Gaines 1992, Kawecki and Stearns 1993, Barton and Whitlock 1997, Thomas et al. 1998, Travis and Dytham 1998). Some authors regard the recent emphasis on space as a whole paradigm shift in ecology. Whether they are right or not, spatial ecology is certainly “one of the most visible developments in ecology and population biology in recent years” (Hanski 1999, p. 261).

The metapopulation concept, sprouting from the seminal work of Richard Levins (1969, 1970), has been of high heuristic value in the development of spatial ecology. The general notion of “populations” formed by many local populations connected by migration has been widely accepted among ecologists, perhaps because it conceptually resembles the well-rooted idea of populations formed by interacting individuals (Hanski and Simberloff 1997, Hanski 1999). Most fruitfully, it has led ecologists to compare the importance of within-population processes to spatially structured interactions at the “metapopulation level”, between local populations. Yet, in the classic model of Levins (1969, 1970), the spatial setting is merely implicit. The dynamics of the system depends solely on local extinction and (re)colonisation events, which occur with the same probability in each habitat patch. Thus, although habitat

patches and local populations are discrete units in space, they are all of the same size, and equally connected to each other.

Much recent theoretical work has been focused on developing more realistic models of spatially structured populations, in which habitat patches vary in size and each patch occupies a unique spatial location (as recently reviewed by Hanski 1997, 1998, 1999). Lately, some authors have begun to address the consequences of spatial variation in habitat quality for populations inhabiting mosaic landscapes (e.g., Pulliam 1988, 1996, Pulliam and Danielson 1991), and others have modelled the effects of interspecific differences in habitat specificity on the composition of “metacommunities” in patchy environments (Holt 1993, 1997). At the same time, empirical studies have widened our view of spatial population structures in natural populations (as reviewed in Harrison 1991, 1994; Hastings and Harrison 1994; Harrison and Taylor 1997). Although the evidence is still scanty, it suggests that natural populations form a continuum in terms of the discreteness of local populations, the level of movement between patches and the relative importance of particular local populations to the persistence of the whole metapopulation (Harrison and Taylor 1997, Thomas and Hanski 1997). Even within one and the same species, metapopulations in different areas, and in different parts of the same patch network, can display dissimilar dynamics depending on the spatial distribution of habitat patch sizes and inter-patch distances (Thomas and Harrison 1992, Hill et al. 1996, Sutcliffe et al. 1997, Thomas and Hanski 1997).

An increase in realism and empirical detail is a salutary development within any field of science. Yet, the diversity of spatial population structures and dynamics that is being uncovered accentuates the importance of system-specific studies. A satisfactory understanding of a spatially structured population can only be reached through quantification of key features such as local population sizes and turnover rates, as well as the amount of migration between local populations (Harrison 1991, Thomas and Harrison 1992, Harri-

son 1994, Harrison et al. 1995, Harrison and Taylor 1997). In the absence of evidence, related or otherwise similar species are sometimes assumed to show similar spatial population structures and dynamics (Murphy et al. 1990, Wahlberg et al. 1996). However, the data are simply not there to support such sweeping generalisations (Hanski and Simberloff 1997). Well-studied systems are relatively few (for reviews see Harrison and Taylor 1997, Thomas and Hanski 1997, Hanski 1999), and much more empirical work is needed before we can say something about the prevalence of particular spatial structures in nature, or their potential affinities to particular taxa (but see Hanski and Kuussaari 1995).

In this thesis, I analyse the spatial ecology of dung beetles in the genus *Aphodius*. My main objectives are twofold: 1) to compare spatial population structures among several closely related species co-occurring on a common resource, and 2) to relate the spatial population structures of individual species, and groups of ecologically similar species, to their abundance, distribution and dynamics at several spatial and temporal scales.

The study system

Aphodius are small to medium-sized beetles, 3–13 mm in length (Landin 1957). In Finland, and in the rest of northern Europe, they dominate the communities of dung-feeding beetles, both in numbers and in biomass (Hanski 1987a, Hanski and Cambefort 1991). The genus *Aphodius* is of considerable ecological importance, since the majority of its more than 1,000 species contribute to the decomposition of dung pats world-wide (Holter 1979, 1983; Gittings et al. 1994; Hirschberger and Bauer 1994). Several species have recently been introduced to Australia as part of an apparently successful effort to control the accumulation of cattle dung in pastures (Doube et al. 1991). In Finland, thirty-six *Aphodius* species have been recorded to date (Silfverberg 1992). As a group, they offer at least three dis-

tinct advantages for studies in spatial ecology.

First, all species co-occur in the same patchily distributed resource: cattle dung. Their habitat is thus distinctly structured at several spatial scales. The primary resource (dung) is divided into discrete units (droppings), whereas droppings occur within well-defined habitat patches (pastures on cattle farms). Cattle farms form patch networks at the landscape level, which combine to a huge network of cattle farms at the national scale (Fig. 1). Most fortunately, both the past and present configuration of this system are exceptionally well known. A data base of all Finnish farms, their locations and cattle stocks is continuously updated by agricultural officials (Anonymous 1996). Temporal changes are documented in official agricultural statistics spanning this century (National Board of Agriculture 1920–1985, Information Centre of the Ministry of Agriculture and Forestry 1986–1996). Such data allow for studies across spatial and temporal scales which have rarely been accessible to ecological research (II, IV).

Second, drastic loss of pasture habitats allows for efficient tests of hypotheses regarding spatial processes in *Aphodius*. As a result of changing agricultural policies, the density of Finnish cattle farms has rapidly dwindled during the 20th century (Fig. 2; see also IV, Fig. 1). A previously dense network of cattle farms in southern and central Finland has been split into regions with considerable differences in pasture density. The removal of cattle farms through time, and the creation of regional differences in farm densities can be thought of as large-scale experimental treatments applied to the system. In III and IV, I make use of this “experiment” by analysing temporal changes and regional differences in the abundance and distribution of *Aphodius*.

Last but not least, the basic biology of most species is well known (e.g., Madle 1934; Schmidt 1935; Horion 1958; White 1960; Landin 1957, 1961; Balthasar 1964; Rainio 1966; Christensen and Dobson 1976, 1977; Rojewski 1983, Yoshida and Katakura 1985, Gittings and Giller 1997). This knowl-

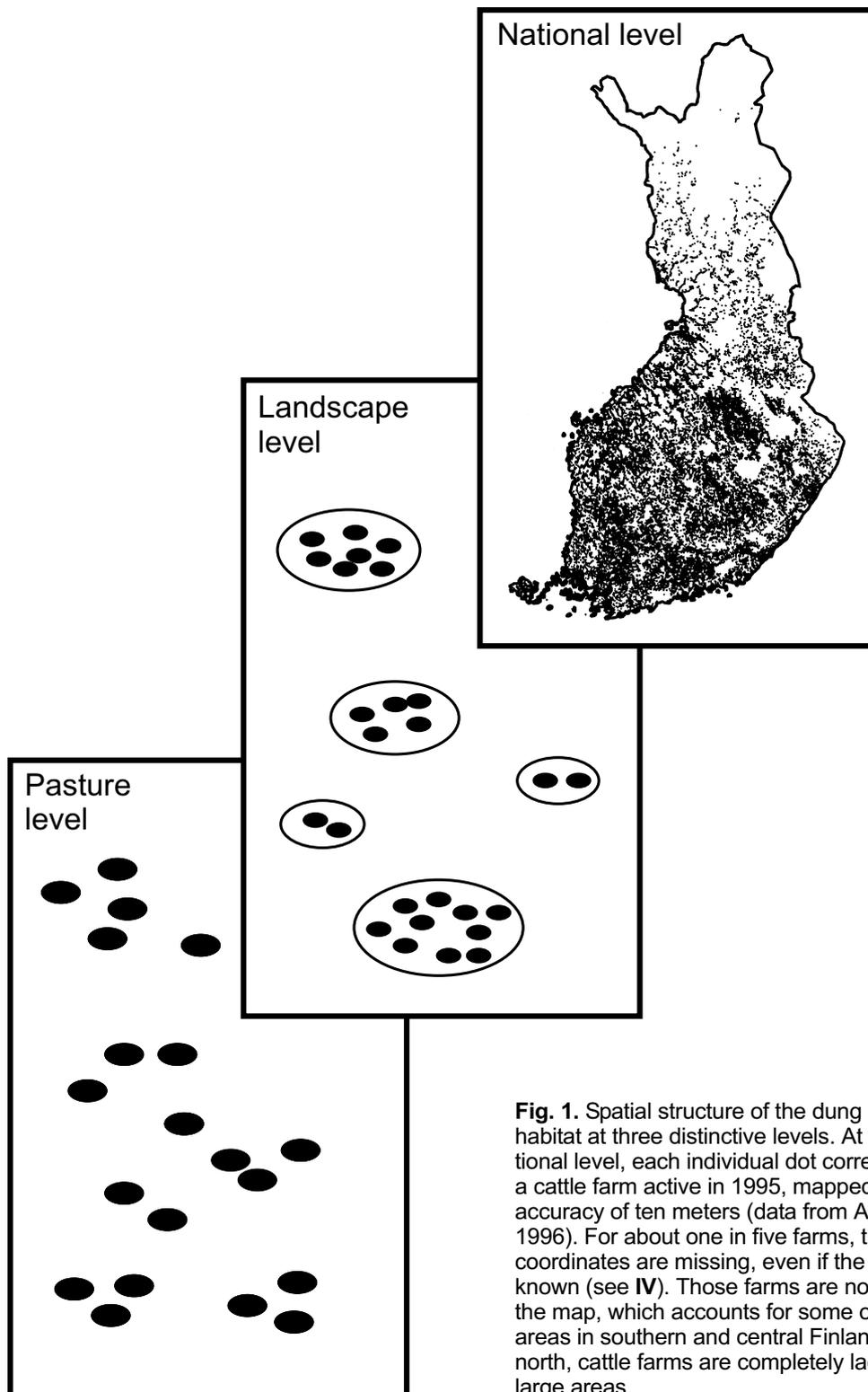


Fig. 1. Spatial structure of the dung beetles' habitat at three distinctive levels. At the national level, each individual dot corresponds to a cattle farm active in 1995, mapped with an accuracy of ten meters (data from Anonymous 1996). For about one in five farms, the exact coordinates are missing, even if the county is known (see **IV**). Those farms are not plotted in the map, which accounts for some of the white areas in southern and central Finland. In the north, cattle farms are completely lacking from large areas.

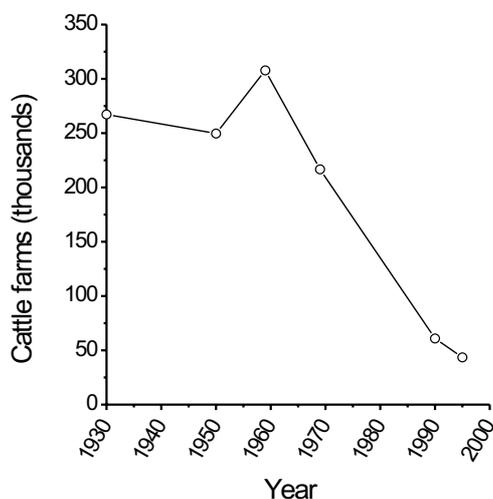


Fig. 2. Changes in the number of Finnish cattle farms between 1930 and 1995. Data source: National Board of Agriculture (1920–1985), Information Centre of the Ministry of Agriculture and Forestry (1986–1996).

edge permits me to relate the characteristics of each species to its spatial population structure and associated dynamics (I–IV), and to identify subgroups of ecologically similar species within dung beetle assemblages (III, IV).

Outline of this study

This thesis consists of four papers, each of which focuses on spatial structures and processes at a different level of organisation, and at a different spatial scale.

In the first paper (I), I set the stage by exploring how dung beetles move at two small spatial scales: between dung pats within pastures, and between pastures. I ask questions such as: What distances do dung beetles typically move, and how are these movement distances distributed? How frequently do individuals of different species move between dung pats and pastures? Can more or less discrete local populations be distinguished, and if so, in which species and at what spatial scale?

In paper (II), I refine the picture of migration in one particular species, *Aphodius fossor*. I do that by using an indirect approach – I analyse patterns of genetic variation at the national scale, and ask what those patterns can tell us about current rates of gene flow between local populations. I then compare these indirect estimates of gene flow with direct estimates of migration rates.

In paper (III), I explore how the spatial population structures of different dung beetle species relate to their abundance, distribution and dynamics at the landscape level. I compare the regional distributions and local abundances of *Aphodius* species within two landscapes with different cattle farm densities. Within one of these areas, I examine temporal changes in the local dung beetle fauna during 15 years of rapidly declining farm density.

In the last paper (IV), I move on to a large scale, and ask whether my previous results (I–III) can help to explain the composition of local dung beetle communities at individual farms across Finland, and changes in these communities during this century?

Material and methods

Throughout the thesis, I have strived to use several complementary approaches to illuminate the role of space for *Aphodius*. In this section, I will provide a brief overview of the general methods and the types of data that I have used, and how the different approaches relate to each other. For details, I refer the reader to the original papers (I–IV).

To study how dung beetles move in space, I used two different designs (I). First, I marked more than 3,000 *Aphodius* representing 12 species, and studied their movements within and between artificial pastures consisting of baited traps. Second, I placed the same traps at fixed distances from six replicate natural pastures, and analysed how the density of migrants declined with increasing distance from the pasture. In combination, these two approaches allowed me to quantify movements at two spatial scales, and to identify

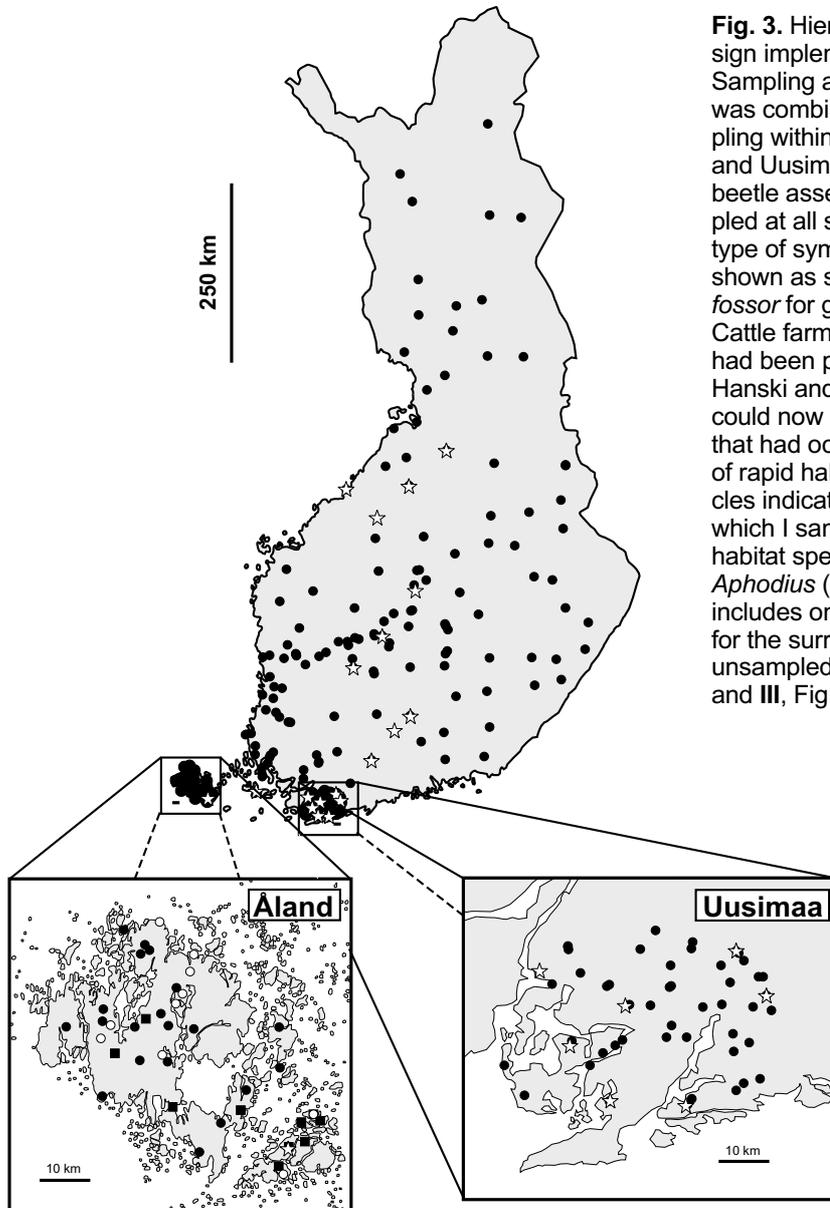


Fig. 3. Hierarchical sampling design implemented in this study. Sampling at the national scale (IV) was combined with intensive sampling within two landscapes: Åland and Uusimaa (III). Local dung beetle assemblages were sampled at all sites marked with any type of symbol. At cattle farms shown as stars, I preserved *A. fossor* for genetic analyses (II). Cattle farms shown by squares had been previously sampled by Hanski and Kuusela (1983), and I could now assess the changes that had occurred during 15 years of rapid habitat loss (III). White circles indicate cattle-free sites, which I sampled to evaluate the habitat specificity and mobility of *Aphodius* (III). (Note that this map includes only the sampling sites; for the surrounding network of unsampled cattle farms see Fig. 1 and III, Fig. 1.)

interspecific differences in movement rates and patterns.

To evaluate the discreteness of local *Aphodius* populations in pastures, I combined the movement data obtained in (I) with samples from cattle-free sites at different levels of isolation from cattle farms (III; Fig. 3) and with information on each species' habitat selection gathered from the literature (see III

and references therein). Together with estimates of local population densities (II, III, IV) and population turnover rates (III), these data allowed me to probe into the spatial population structures of *Aphodius*.

To compare the spatial population structure of *Aphodius fossor* with its genetic population structure, I sampled the whole Finnish range of the species (Fig. 3), and used two dif-

ferent classes of genetic markers (allozymes and mitochondrial DNA sequences) to measure levels of genetic subdivision (III). Estimates of Wright's (1931, 1940, 1951) *F*-statistics were converted to indirect estimates of gene flow (*sensu* Slatkin 1994), assuming that migration has reached an equilibrium with genetic drift and mutation. Contrasting different types of data with each other (II versus I, III, IV) gave me a rare opportunity to evaluate the validity of this assumption.

To relate the spatial population structures of *Aphodius* to their abundance, distribution and dynamics at several spatial scales, I implemented a hierarchical sampling design (III, IV). At the landscape level, I sampled local dung beetle assemblages on 86 cattle farms of different size and isolation within two areas approximately $50 \times 50 \text{ km}^2$ in size (III; Fig. 3). At the national scale, I sampled 131 cattle farms throughout Finland (IV; Fig. 3). The latter sampling was made possible by the co-operation of a large youth organisation, the Finnish 4H Federation.

Finally, to assess how temporal changes in the spatial distribution of cattle farms affect *Aphodius*, I used historical data provided by Biström et al. (1991) and Hanski and Kuusela (1983). At the landscape level, I compared the abundance and distribution of dung beetles at ten farms before and after 15 years of rapid cattle farm loss (III; Fig. 3). At the national scale, I analysed changes in the distribution of *Aphodius* species during eight decades of decreasing cattle farm density (IV).

Results and discussion

In this section, I summarise the main results of my study on spatial patterns and processes in *Aphodius*, and their general implications.

1. Dung beetles form “patchy populations” within pastures

This thesis demonstrates that dung beetles occurring in different dung pats within the same

pasture form a “patchy” population (Harrison 1991, Harrison and Taylor 1997) with much movement among individual pats. Only one generation of *Aphodius* larvae develop in any particular pat (Landin 1961), and thus each generation, individuals emerging from an old dung pat will leave it to feed on and reproduce in a new set of pats. In the mark-release-recapture studies (I), I found that the time for which an adult beetle stays in a given pat is so short (median 8 days across species) that each female is likely to oviposit in several different pats during her life time. As a result, progeny is mixed among dung pats, and *Aphodius* populations within pastures are effectively unsubdivided (I). This observation supports the view of Harrison and Taylor (1997) that invertebrates which specialise on ephemeral resources are so mobile that local populations will typically extend over large arrays of resource patches (cf. Kitching 1971, Hanski 1987b, Kaitala 1987).

2. Migration rates between pastures depend on species' body size and habitat specificity

Cattle pastures add significant spatial structure to *Aphodius* populations. In every *Aphodius* species covered by my mark-release-recapture studies, only a minority (0–50%) of individuals moved between pastures (I). Nevertheless, there were considerable interspecific differences in migration rates (I). Movements between pastures were more frequent the larger the species, the more specific its occurrence in relation to pat age, and the more specialised it is on cow dung and open pasture habitats (I). Apparently, the effect of body size reflect ecophysiological constraints on insect flight (Roff 1977, Casey and Joos 1983, Utrio 1995), whereas the relationship between migration rate and pat age-specificity is an adaptive response. Species which only utilise dung pats of a certain age depend on a very unpredictable resource, for which they compensate by increased mobility (Southwood 1962, 1977). Increasing habitat specificity is, by definition (I, Appen-

dix A), associated with stronger attraction to pasture habitats. This association results in higher migration rates among pastures in more specialised species, as fewer individuals disappear into the matrix habitat surrounding the pastures (I).

The differences in movement patterns observed among dung beetle species contribute to a mixture of different spatial population structures in different species (see Main result 5 below). Whereas some species have a “closed” population structure with relatively sedentary local populations in pastures, others display an “open” structure with extensive movement among pastures (cf. Ford 1945, J.A. Thomas 1984, Warren 1992a,b). Although the current data set is rather small ($n = 9$ species), it is exciting to notice how the observed differences in movement patterns can be linked to particular ecological traits. Nieminen and co-workers (Nieminen 1996a, Nieminen et al. 1999) have observed similar correlations among a large number of moth species occupying a set of small islands. In these moths, the migration rate varied with body size, host plant specificity and local abundance. The accumulation of more such data sets may allow for wider generalisations across species in the future.

3. Migration rates do not decay exponentially with distance

Many recent models of spatially structured populations assume that the probability of an individual moving between habitat patches decreases exponentially with distance (e.g. Harrison et al. 1988, Hanski 1994, Hanski and Thomas 1994, Hanski et al. 1994). For the dung beetle *Aphodius pusillus*, I found sufficient evidence to reject this assumption (I). In traps placed outside pastures, the distribution of migration distances was leptokurtic, with more individuals moving short and long distances than expected on the basis of an exponential function (I). The most likely explanation is that dung beetle movements include an element of non-randomness not captured by the exponential model. Mechanistically, the

exponential distribution follows if individuals move away from the starting point at a constant speed and settle with a constant probability in unit time. Thus, individuals should *not* be able to locate patches of suitable habitat from a distance, and their movement behaviour should *not* be modified by the structure of the landscape through which they move. These assumptions seem rather unrealistic for insects specialised on highly ephemeral resources. Such organisms are likely to have well-developed senses, and to be able to locate the scattered resources from some distance (K. Donner and B. Hansson, personal communication). It remains a challenge for ecologists to incorporate more realistic assumptions about migration in models of spatially structured populations (Hanski and Thomas 1997, Ims and Yoccoz 1997, Wiens 1997, Sjögren Gulve 1998).

Given the demonstrated misfit of the exponential model to empirical data in (I), it may come as a surprise that I have still used it to describe the effect of distance on dung beetle movements in subsequent chapters (II, III, IV). This is justified, as the fit of the model is close enough *for the current purpose*, which is only to scale physical distances between pastures to the approximate scale of dung beetle movements (II, III, IV). As discussed in (I), the exact distribution of migration distances is not expected to be critical in established metapopulations (Hanski 1999), although it will clearly make a difference during phases of population spread (Kot et al. 1996, Lewis 1997, Clark et al. 1998, Turchin 1998).

4. Extensive gene flow leads to large-scale genetic homogeneity in *Aphodius fossor*

Direct studies on animal migration – such as (I) – have the disadvantage that they are necessarily limited in time and space (Slatkin 1994). However, in *Aphodius fossor*, high rates of migration observed at a small spatial scale (I) were fully consistent with patterns of genetic variation at a large spatial scale (II).

Both allozyme markers and mtDNA sequences revealed striking genetic homogeneity across the Finnish mainland, suggesting that gene flow between neighbouring local populations is strong enough to homogenise the gene pool within large areas. That the dispersal capacity of *A. fossor* still has its limits was shown by genetic differentiation between local populations on the Finnish mainland and on Åland – a group of islands some tens of kilometres from the mainland. Even here, significant differences were only found in mtDNA haplotype frequencies, which are more sensitive to restrictions of gene flow than are allozyme markers (Avisé 1994). Thus, the results of this thesis (I, II) consistently depict *A. fossor* as an insect with considerable dispersive powers, which allow for frequent movements between neighbouring cattle farms. High migration rates go some way to explain the wide-spread occurrence of the species at high local abundances across large parts of Finland (III, IV). Moreover, the population genetic structure observed in *A. fossor* contradicts the belief that species living in patchy environments would automatically exhibit less gene flow among different localities than species utilising continuous habitats (Shoemaker and Jaenike 1997).

5. Species-specific traits lead to dissimilar population structures and dynamics among *Aphodius* species

Related species utilising similar resources are often assumed to show similar spatial population structures and dynamics (Murphy et al. 1990, Hanski and Kuussaari 1995, Wahlberg et al. 1996). In this thesis, I found considerable ecological variation within a set of closely related dung beetle species co-occurring on cattle dung. Interspecific variation in ecological specialisation and habitat selection (I, III, IV), in migration rates and movement patterns (I, II), in the distribution of local population sizes (II, III, IV), and in the likely rate of population turnover (III) all contribute to differences in spatial population structures among *Aphodius*. That these differ-

ences are large enough to cause dissimilar spatial dynamics among *Aphodius* was evident as interspecific differences in the response to contemporary landscape composition, and as variation in species' responses to habitat loss over time (III, IV). During the 20th century, idiosyncrasies among species have resulted in considerable changes in Finnish dung beetle assemblages, with at least four species becoming increasingly rare, and one species expanding its distribution (IV; Biström et al. 1991).

These results from dung beetles add to a growing body of evidence from other taxa showing that there is a wide variety of spatial population structures in nature (Harrison 1994, Harrison and Taylor 1997, Thomas and Hanski 1997) and that natural populations form a continuum regarding the relative importance of within-population processes compared to interactions at the metapopulation level (Hanski 1999). The wealth of structural diversity that is being uncovered in natural populations provides a stimulating challenge for ecologists striving to develop a mechanistic understanding of spatial population dynamics.

6. Metapopulation structure in *Aphodius pusillus*

Throughout my thesis, *A. pusillus* emerges as the one species most sensitive to the spatial distribution of pasture habitats. At the level of individual farms, the incidence of the species increased with farm size, and small populations seem to be prone to extinction (III). At the regional scale, *A. pusillus* was more widespread and occurred at higher local densities in a landscape with a dense network of cattle farms than in a sparse networks of farms (III). This result was essentially replicated at a national scale, where the incidence of the species increased with regional farm density (IV). Over time, loss of pasture habitats caused a decline in the distribution of the species, both during 15 years at a regional scale (III), and during this century at the national scale (IV).

All of these results suggest that *A. pusillus* persists regionally as a metapopulation (*sensu* Hanski and Kuussaari 1995, Hanski et al. 1995a), and that habitat loss alters the dynamic equilibrium between local colonisation and extinction rates, and between immigration to and emigration from existing local populations (III, IV). However, to demonstrate that the long-term persistence of a species is really due to processes at the metapopulation-level, one should show that 1) the species has local breeding populations in relatively discrete habitat patches; 2) that patches of suitable habitat are not too isolated to prevent recolonisation; 3) that no single population is large enough to have a long expected lifetime in comparison with the expected lifetime of the metapopulation; and 4) that local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely (Hanski and Kuussaari 1995, Hanski et al. 1995a, Hanski 1997).

Of these criteria, the first three are clearly met by *A. pusillus*. The species has well-defined local populations in pastures, as it is never encountered far from such habitats (III). In the mark-release-recapture studies, *A. pusillus* proved to be among the most sedentary *Aphodius*, with ca 90% of individuals staying within the pasture of release (I). Nevertheless, a nontrivial proportion of individuals are likely to move over the distances which typically separate Finnish cattle farms, thus allowing for recolonisation of empty habitat (I). Local populations are generally small. Based on the approach outlined in (II), I estimate that the median size of local *A. pusillus* populations in Finland is around 150 individuals, or only a tenth of the average population size in *A. fossor* (II). Local populations of this size seem to be subject to frequent population turnover, although the current data are clearly limited on this point (III). The fourth criterion cannot yet be evaluated.

I conclude that the long-term persistence of *A. pusillus* in Finland depends on metapopulation-level processes. "Classical" metapopulation persistence has previously been demonstrated in several other insects,

but these are mostly Lepidoptera (e.g., Hanski and Kuussaari 1995; Hanski et al. 1995a; Nieminen 1996b; Lewis et al. 1997; reviewed in Thomas and Hanski 1997) or parasites of Lepidoptera (Lei and Hanski 1997, but see Kindvall and Ahlen 1992, Kindvall 1996, Appelt and Poethke 1997, Gonzalez et al. 1997). Whether other small dung beetles with a strong preference for pasture habitats, such as *A. merdarius*, also conform to a metapopulation structure remains an open question. Due to a recent population crash (III, IV), *A. merdarius* is currently too rare to be studied. The potential that metapopulation dynamics caused the abrupt crash remains a fascinating if yet unproven possibility (III).

7. Landscape structure affects local community composition

Historically, analyses of local community composition rarely took any notice of the existence of other communities in the surrounding landscape. This thesis shows how the spatial structure of the landscape leaves its distinct imprint on local communities. Although all *Aphodius* species studied here co-occur on the same resource, cattle dung, the presence or absence of individual species at a particular site and their local abundances are critically dependent on the spatial context. Such effects were evident at all spatial and temporal scales that I studied. At the scale of individual dung pats, pasture specialist species grew increasingly rare with increasing isolation from neighbouring cattle farms (III). At the scale of individual cattle farms within landscapes, forest specialist species had a relatively high incidence at particularly isolated farms, which were mainly surrounded by forest (III). At the regional scale, the relative abundance and distribution of several species differed between a landscape with a dense network of cattle farms and a sparse network of farms (III). At the national scale, a larger proportion of the regional pool of pasture specialist species was found locally on each farm with increasing density of cattle farms in the landscape (IV). Over time, a decrease in the

density of cattle farms was associated with considerable changes in the composition of local dung beetle communities at the regional level (III) and throughout Finland (IV; Biström et al. 1991).

These observations support the prediction of Holt (1993, 1997) that the frequency and spatial distribution of a habitat type will influence the composition of local communities within it (cf. Harrison 1997, 1999). Thus, analyses of local community composition without any consideration of the surrounding landscape may be misleading.

Open questions

In scientific endeavours, the search for an answer to some questions frequently leads to new ones. In this section, I identify and briefly discuss three questions which I have touched upon in my thesis work, but which are left essentially unanswered.

1. Given extensive migration and gene flow in many *Aphodius* species (I, II), is there potential for local adaptation?

Several studies have shown how insects may adapt to their local environment despite what appears to be strong gene flow between local populations. Recent examples include local differentiation in host plant preferences within a metapopulation of the butterfly *Melitaea cinxia* (Kuussaari 1998) and adaptations to individual host trees in the leaf miner *Stilbosis quadricustatella* (Mopper et al. 1995).

To uncover possible local adaptations in *Aphodius*, I made an experiment with *A. ater*. This species occurs in three types of habitats. It is most abundant on sheep pastures and frequent on cow pastures, but it also maintains sparse populations on deer and elk dung in forests (Horion 1958, Landin 1961). To explore whether local populations from different habitats vary in their habitat selection and

migration behaviour, I collected *A. ater* on three isolated sheep pastures, five remote forest sites, and four isolated cow pastures in the Åland islands. After one generation of laboratory rearing, 1,121 marked individuals were released in a set of artificial pastures. Half of the individuals from each replicate population were released in the experimental pastures described in (I), whereas the other half were released some 20 m inside a low birch forest next to the open field (Fig. 1 in I).

In this experiment, I found no significant differences between populations from different habitats. A similar proportion of the individuals released inside the forest (10–30%) was later recaptured in the pastures, regardless of the source habitat (change in deviance when habitat of origin added to a logistic regression model $D = 1.58$, $df = 2$, $P = 0.45$), and movements between pastures were equally rare in populations from all habitats (0–10% of the recaptured individuals; logistic regression, $D = 1.22$, $df = 2$, $P = 0.54$). In the Åland islands, gene flow between *A. ater* in different habitats may thus be sufficiently strong to prevent local differentiation in the traits that I studied. This does not, however, exclude local adaptations in traits subject to stronger selection pressures. Hanski and Kuusela (1983) have previously described differences in the flight period of *A. ater* on two neighbouring islands on Åland, and attributed these differences to local adaptation. Future studies would thus be needed to establish at what spatial scale, and in which traits, local adaptations may emerge in such mobile insects as dung beetles.

2. What causes a large-scale cline in the frequency of two colour morphs of *A. depressus*?

Aphodius depressus has two discrete colour morphs, one with a dark head and pronotum contrasting with red elytra, and another one which is uniformly dark (var. “*caminarius*”, Faldermann 1835). The sampling of dung beetle assemblages across Finland (IV) revealed an interesting pattern in the distribu-

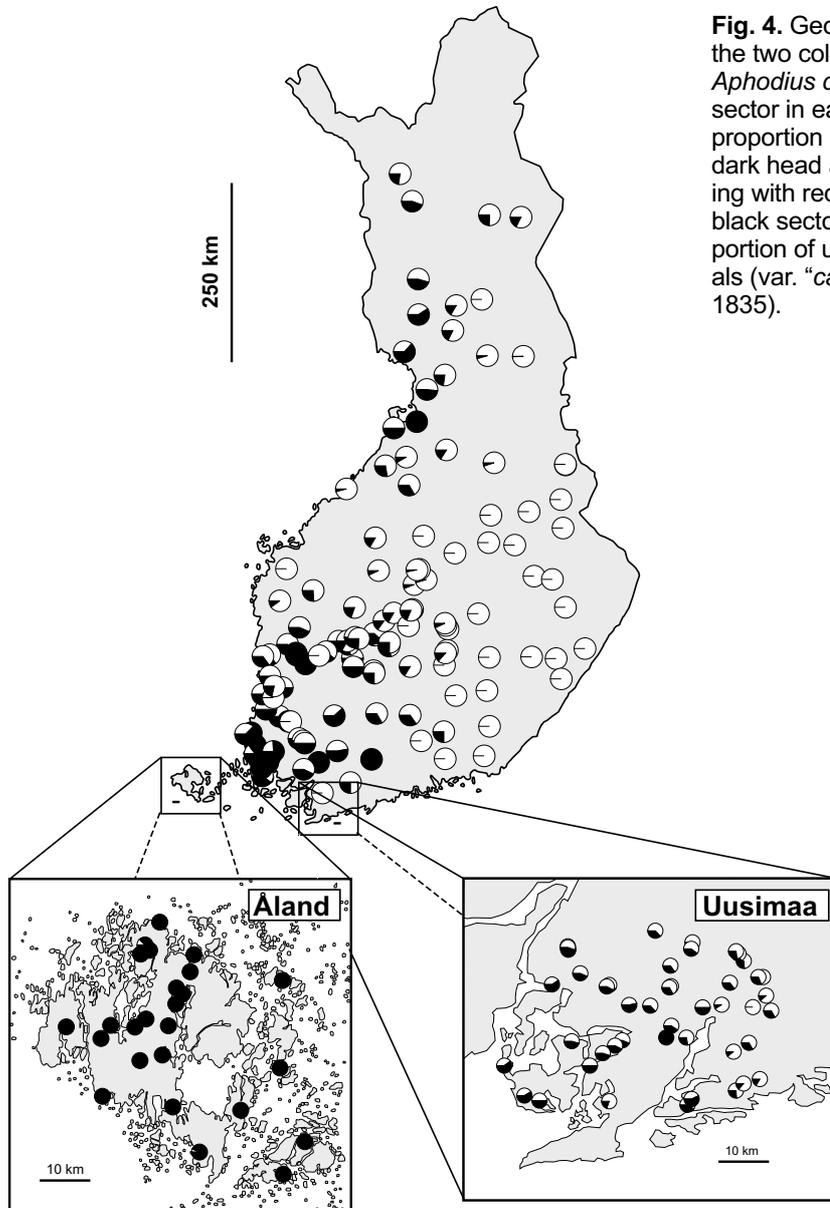


Fig. 4. Geographic distribution of the two colour morphs of *Aphodius depressus*. The white sector in each pie chart shows the proportion of individuals with a dark head and pronotum contrasting with red elytra, whereas the black sector represents the proportion of uniformly dark individuals (var. “*caminarius*”, Faldermann 1835).

tion of the morphs: the frequency of var. *caminarius* uniformly decreases towards the east (Fig. 4). On closer examination, this pattern was evident even at a landscape level, within Uusimaa (Fig. 4). Anecdotal accounts from Sweden suggest a similar pattern; here, *caminarius* is said to be rare in the northern parts of the country (Landin 1957). Whether the observed pattern reflects some events in

the history of the species, whether it is a response to geographical variation in selection pressures, or whether it is a sign of current population viscosity at a large spatial scale is not known. The genetic basis of the colour dimorphism deserves closer scrutiny, as the two morphs frequently occur side-by-side in local populations (Roslin, personal observation). Perhaps the frequency of the two morphs

could be used as a marker to infer spatial population processes in *A. depressus*?

3. What mechanisms generate the relationship between abundance and distribution in *Aphodius*?

Over the past 20 years, a positive relationship between the regional distribution of a species and its local abundance has been well documented across a wide range of taxa and habitats (e.g., Hanski 1982, Brown 1984, Gaston and Lawton 1990a, Hanski et al. 1993, Gonzalez et al. 1997). Among *Aphodius*, this relationship was evident at several spatial scales (III, IV) and across a time span of fifteen years (III), even though the ranking order of species in abundance and distribution varied in time and space (III, IV).

At least eight different mechanisms have previously been proposed to explain the observed association between abundance and distribution, ranging from sampling artefacts (Wright 1991) to ecological specialisation (Brown 1984) and metapopulation dynamics (Hanski and Gyllenberg 1997; see Hanski et al. 1993, Lawton 1993, Gaston 1994 and Gaston et al. 1997 for overviews). These explanations need not be mutually exclusive (Wright 1991, Gaston and Lawton 1990b). Although the current data are insufficient to resolve between all the proposed hypotheses, they suggest that several different mechanisms contribute to the observed pattern in *Aphodius*. In some pasture specialist species, metapopulation dynamics seem plausible (I, III, IV; see Main result 6 above). Here, correlated changes in abundance and distribution can be generated by the “rescue effect” (Brown and Kodric-Brown 1977): when migration between local populations props up local densities in the smallest populations, and thus decreases their risk of extinction, it creates positive feedback between local abundance and the proportion of occupied patches in the metapopulation (Hanski 1991b, Hanski and Gyllenberg 1993, Stacey et al. 1997, Gonzales et al. 1998). In species not confined to pasture habitats, my scale of

sampling does not coincide with the scale of local breeding populations (III). Here, the relationship between abundance and distribution is probably a sampling artefact. Because locally rare species are difficult to detect (McArdle 1990), the number of samples in which a species is found is an increasing function of the average density of the species (Wright 1991). Explanations based on differences in ecological specialisation seem least likely to account for the observed pattern, as they predict that “species able to exploit a wide range of resources become both widespread and locally abundant” (Gaston and Lawton 1990b). No consistent differences in either abundance or distribution were evident between different functional groups in my data set (see Fig. 3 in III and Table 1 in IV).

Conclusions

Dung beetles in space

In this thesis I have shown how the spatial configuration of the landscape affects *Aphodius* at all levels of organisation. At the level of genes, extensive movement of *A. fossor* individuals over the distances separating Finnish cattle farms homogenises the gene pool over large areas (II). At the population level, the interplay between a species’ movement behaviour and the spatial distribution of pasture habitats affects the regional distribution, local abundance and temporal dynamics of *Aphodius* (III, IV). At the community level, the composition of local *Aphodius* assemblages depends on the spatial structure of the surrounding landscape (III, IV). But above all, this thesis demonstrates that different species perceive the same landscape in a different manner (cf. Levins 1968, Wiens 1989). Even if my work is specifically concerned with a guild of species occurring on the same patchily distributed resource, the spatial population structures of the species turned out to be quite different (I–IV). This finding has two general implications. First, it warns against sweeping generalisations

across groups of similar species (Hanski and Simberloff 1997, Hanski 1999). Even in extrapolating results among closely related species, care has to be taken that relevant ecological features really match. Second, it emphasises the importance of retaining species identity also in analyses of local communities. Only by considering the ecological characteristics of each individual species can we understand its occurrence in a landscape context.

How general are the results?

A fundamental question to address in all ecological research is how far the results can be extended, and how readily they can be generalised to other systems in other areas. Some characteristics of the Finnish countryside suggest that the species-specific results obtained in this thesis should not be uncritically generalised to other countries. In a European context, Finnish cattle farms are comparatively small, as the mean and median size of Finnish cattle farms is only 16 and 19 “effective cow units”, respectively (see **III**, **IV**). Small farm size makes local populations of pasture specialist species relatively small, and perhaps more prone to extinction-colonisation dynamics in Finland than in other European countries (see Main result 6 above). “Classic” metapopulation dynamics (*sensu* Hanski and Simberloff 1997) may also be more likely near the edge of a species range than in the core area of its distribution (Simberloff 1993, 1995).

These corollaries of the present results do not imply that they would constitute local anomalies to some general rule. On the contrary, they strengthen the general notion that the spatial population structure of a species may differ between different parts of its range, with interesting implications for local dynamics (Simberloff 1993, 1995, Thomas and Harrison 1992, Thomas and Hanski 1997). Studies on the spatial dynamics of *Aphodius* species and ensembles in other parts of Europe will provide interesting data for comparison (see Finn et al. 1999a,b).

Implications for conservation

The factors affecting the persistence and large-scale dynamics of dung beetle populations are not merely of academic interest. During the last few decades, the distributions of four *Aphodius* species have rapidly declined (**IV**, see Biström et al. 1991), and of the total of 36 *Aphodius* species recorded in Finland, almost half (15 species) are now regarded as threatened (Rassi et al. 1992). Seven species are thought to be in need of monitoring, one species is considered endangered, whereas six species are already classified as nationally extinct (Rassi et al. 1992, but see Roslin 1998). Quite worryingly, similar declines have recently been reported in other European countries (Zunino 1982, Lumaret 1990). Understanding the spatial ecology of dung beetles may thus be crucial to conserve them for the future.

The results of this thesis indicate that the widespread loss of pasture habitats may have severe effects on dung beetle assemblages. In most *Aphodius* species, large concentrations of dung resources in pastures prop up population densities to levels much higher than in the surrounding habitats, thus creating a potential for source-sink (or source – pseudo-sink) dynamics at the landscape level (**I**; Pulliam 1988, 1996; Watkinson and Sutherland 1995). If the high-productive pastures are removed, populations of many species may collapse regionally (cf. Thomas et al. 1996). Some *Aphodius* appear to persist as metapopulations in a dynamic equilibrium between local colonisation and extinction events (**I**, **III**, **IV**; see Main result 6 above). For such species, it is necessary to conserve sufficiently dense networks of local populations and pasture habitats in order to secure the long-term persistence of the species (Hanski et al. 1996, Hanski 1997, Thomas and Hanski 1997). The rapid disappearance of *A. merdarius* suggests that once the density of pasture habitats falls below a threshold level, a metapopulation may crash quite suddenly (**IV**; cf. Hanski et al. 1995b).

I conclude that if the decline in the cattle stock continues (and there are no reasons why

it would stop), large changes in dung beetle assemblages are likely to occur. Unfortunately, due to their habits and habitat, dung beetles have never been particularly charismatic species for conservation. It remains an important task for the devoted few to communicate their ecological significance (Hanski 1987a, Hanski and Cambefort 1991) and discreet charm (Roslin, unpublished) to the general public.

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