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Spatial distribution, resource utilisation and intraspecific competition in the dung beetle Aphodius ater

Abstract Competitive interactions in northern temperate dung beetles are poorly understood. This investigation therefore comprises a series of field and experimental work on a dung beetle species common in northern Europe, Aphodius ater, with special focus on intraspecific competitive interactions. The between-pat distribution of adult A. ater in relation to the age of sheep dung pats was studied in the field. The distribution of both sexes was contagious in the fresh pats but became more regular with increasing pat age. The successional occurrence of males and females did not differ, but immature females tended to occur in fresh pats while mature females were mainly found in older pats. With increasing age of pats, the egg load of females also increased. Egg-laying behaviour of the beetles was studied in laboratory experiments. The mean number of eggs laid per female per dung pat decreased with increasing beetle density. Thus, density-dependent processes seem to regulate resource utilisation with regard to breeding behaviour, resulting in equal exploitation of the available pats. Survival and weight of recently hatched beetles decreased with increasing initial density of eggs. Hence, in A. ater, competition between larvae for food within pats does occur.

Key words Aggregation · Density dependence · Dung beetles · Egg-laying behaviour · Scarabaeidae

Introduction

Dung pats are resource patches of high nutritional value but short durational stability that attract many species and individuals of coprophagous animals. The dung beetle community in northern temperate regions is dominated by Aphodius Illiger species, so-called dwellers. The adult beetles occur in fresh dung, mainly of herbivorous mammals. The larvae, in contrast, either occur in older dung pats or, in some species, are saprophagous and feed on decaying matter or even on plant roots (White 1960). In Aphodius species with both adults and larvae occurring in dung, the eggs are simply laid in the dung itself or beneath the dung in the soil, from where the larvae invade the dung pat after hatching (White 1960). As adults and their larvae live freely within the pat, there is a potential for competition for both food and space in larvae and adults (Cambefort and Hanski 1991).

Since field investigations with artificial identical cattle dung pats spaced evenly over the pasture have shown that adult Aphodius tend to aggregate in certain pats while other pats of same size and age contain only relatively few individuals (Holter 1982; Hanski and Kusela 1983; Hanski 1991a), it has been suggested that competition between and within species of the Aphodius dung beetle community is not very intense (Hanski 1991b). In fact, the contagious between-pat distribution of the adults led to the supposition that intraspecific aggregation within certain pats occurs because it facilitates mate finding at low population densities (Holter 1982).

Studies on the spatial pattern of insect communities in other ephemeral, patchy habitats such as carrion (Hanski 1987, 1990; Ives 1991; Kouki and Hanski 1995), fallen fruits (Atkinson and Shorrocks 1984; Rosewell et al. 1990) and mushrooms (Rosewell et al. 1990) have shown that the individuals are usually contagiously distributed among the single resource patches if the species are relatively small in relation to the available resource, and if they cannot monopolise it. According to Hanski (1986, 1987, 1991a) these communities are structured by variance-covariance dynamics. In such communities, the coexistence of competing species is supposed to be facilitated by independent aggregation of
different species in different pats, reducing the level of interspecific interactions. The *Aphodius* dung beetle community could well be structured by such variance-covariance dynamics. The beetles are relatively small in relation to the pat and a few individuals cannot dominate a single cattle dung pat.

However, during certain times of the year adult *Aphodius* of a single species can be extremely abundant so that they disintegrate whole dung pats within a day. This has been reported both for the species with saprophagous larvae and for true dung species with both adults and larvae living in dung pats (Schmidt 1935). Competition could therefore occur for both food and space in adults and in larvae of these species. There is experimental evidence for intraspecific competitive interactions in *Aphodius*. The experiments of Landin (1961) indicated that emigration from cattle dung pats in *Aphodius* was density-dependent, and Holter (1979) found that eggs of *A. ruﬁpes* in cattle dung pats in the ﬁeld were less contagiously distributed than the adult beetles. In a laboratory experiment, the oviposition rate of females of *A. ruﬁpes* decreased with increasing beetle density.

The relatively even distribution of eggs and the density-dependent oviposition rate could reduce possible competitive interactions between *Aphodius* larvae. The larvae are “bulk feeders”, consuming large amounts of the remaining plant material in the dung (Holter 1974, 1975). They depend entirely on the dung pat in which the females have laid their eggs. Resource depletion due to large numbers of conspeciﬁcs or other dung feeding competitors could result in reduced survival rates of the larvae or reduced weight in the adult stage.

The aim of the present investigation was to elucidate the intraspeciﬁc competitive interactions in *Aphodius* dung beetles with regard to resource utilisation during egg-laying. The hypothesis underlying the experiments was that the behaviour of adult *Aphodius* females should be selected to ensure optimal development of their offspring by avoiding egg-laying into pats with many competitors. This behaviour should be reﬂected by the spatial distribution of beetles in the ﬁeld. *Aphodius ater* DeGeer was chosen because of the well deﬁned, short temporal occurrence of the adult beetles in northern Germany. The beetles prefer sheep dung, where they lay the eggs in small cavities just below the crust. The study included an investigation of between-pat distribution of adult beetles in the ﬁeld, laboratory experiments on the females’ egg-laying behaviour, and experiments on larval competition.

Suffolk sheep produce large amounts of homogeneous dung pellets, which stick together (even during the hot summers of 1994 and 1995) and do not break up into single pellets. Therefore, the available portions of sheep dung were always relatively large and moist (more than 80% water content) and will be called pats rather than pellets. All sheep dung used during the investigation was collected from the ﬁeld site immediately after defecation was observed so that it had not been invaded by any coprophagous animals. The dung for the laboratory experiments was either used directly or stored at −20°C.

Temporal and spatial patterns in the ﬁeld

To investigate the successional pattern of colonisation and the between-pat distribution of adults of *A. ater*, equally-sized and equally-shaped 50-g dung pats were exposed in the ﬁeld as described in Hirschberger and Bauer (1994). On 9 May 1994, 24 replicates dung pats, 1 m apart, were arranged in a 6 × 4 grid. After each of 1, 2, 4, and 7 days, six dung pats were brought into the laboratory. Adult *A. ater* were collected by hand-sorting. On 1 May 1995, 40 portions of dung were arranged in a 8 × 5 grid, again 1 m apart. After each of 1, 2, 4, 7 and 10 days, eight dung pats were brought into the laboratory where males, females and eggs of *A. ater* were handsorted and counted. Female beetles were dissected to determine whether they were still feeding prior to maturation or had already developed eggs and if so determine the number of eggs present in the ovary.

In order to investigate whether beetles of different sex and maturation state use dung pats of different age, the successional mean occurrence (SMO, after Hanski 1980a) was calculated separately for males, mature and immature females during the exposition in 1995. The SMO value represents the “mean” of the colonisation curve (which gives the numbers of individuals of a species present in dung pats of different ages). SMO is calculated as follows:

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SMO = \frac{1}{n} \sum_{i=1}^{n} p_i (t_i - t_{i-1}) \frac{1}{n} \sum_{j=1}^{n} p_j (t_j - t_{j-1})
\]

where \( p_i \) is the number of individuals extracted from droppings of age \( t_i \) (in days), and \( n \) the number of sampling days along the succession. The unit of SMO is days. The \( \chi^2 \)-test was used to test for signiﬁcant differences in SMO.

To analyse the between-pat distribution of *A. ater* during colonisation, a new method, called spatial analysis by distance indices (SADIE, Perry 1995a, b) was applied to the data. SADIE is especially appropriate for measuring the distribution of counts per sample. It has advantages compared to a simple index of dispersion: it is based on easily understood biological principles instead of a more abstract mathematical approach and the power of tests of randomness are found to be greater than those based on the index of dispersion (Perry and Hewitt 1991). The method is brieﬂy described as follows:

1. The actual sample is compared with a completely regular sample with the same number of individuals within each of the same number of sample units. The distance to regularity \((D_{ad})\) of the actual sample is the least number of moves which individuals must take, from sample unit to sample unit, to achieve complete regularity.
2. Distances to regularity in randomised samples with the same number of individuals within the same number of sample units are calculated 999 times and stored. A frequency distribution of all these distances is established, \( D_{ad} \) being the average distance of regularity of the random rearrangement.
3. The computed value of the distance to regularity of the actual sample is compared to the frequency distribution and the proportion, \( P_s \), of the values in the distribution that are as large or larger than the observed value is noted.

If \( P_s \) is less than 0.05 or greater than 0.95 the null hypothesis that the observed sample came from a spatially random population is rejected at the 5% level in favour of the alternative hypothesis that

**Materials and methods**

**Field site and animals**

The field experiments were carried out on a 60-m² fenced area of a 4-ha pasture west of Kiel (northern Germany, Baltic coast). The pasture had been used for grazing sheep and horses for 8 years prior to the investigation and was grazed by about 30 Suffolk sheep and 5–8 horses from mid-April to October during the investigation.