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Brood care in the dung beetle *Onthophagus vacca* (Coleoptera: Scarabaeidae): the effect of soil moisture on time budget, nest structure, and reproductive success

Peter Sowig

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Under laboratory conditions brood care behaviour, nest structure and weight of dung supply in brood chambers of the dung beetle *Onthophagus vacca* proved to depend on water content of the soil beneath the dung. The substrate in a bucket beneath the dung pat was dry sand (4% water content) or moist sand (8% water content). Emigrating beetles were trapped and counted at 12 h intervals. In a total of 109 replicates one pair was released on an artificial 1000 g dung pat. From 95 replicates in which brood chambers were built the following results were derived: 1) Breeding females and resident males which helped the female stayed longer in dung pats on dry sand than in those on moist sand. 2) Nest architecture was influenced by substrate moisture: length of main tunnels did not differ between nests in dry and moist sand, but total length of side tunnels was shorter in dry sand. 3) Numbers of brood chambers were equal in both substrate types, weight of the dung supplies was larger in dry sand. 4) Offspring size was not only influenced by dung provision in the brood chambers. Beetles emerging from chambers in dry sand were smaller than those emerging from moist sand even if the amount of dung supply was equal.

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Samples from dung pats can be regarded as “snapshots” of a dung beetle community at the smallest scale at a certain place and time. Abundances of species in a dung pat are the result of a steady-state between immigrating and emigrating individuals. From the exact abundances of each species in all examined droppings one can try to conclude to the reason why a certain individual inhabits a certain patch. The decision to stay or to leave a pat may be influenced not only by foraging for food resources, but also by reproductive strategies like mating, egg laying (Otronen and Hanski 1983), and brood care behaviour (Sowig 1996). Only detailed studies on the behavioural ecology of single species can result in a better understanding of the structure of ecological communities as a whole.

Within coprophagous scarabaeid beetles most species which care for their brood are called “paracoprid”. Beneath a dung pat they dig a more or less branched system of tunnels which are terminated by a brood chamber. Each brood chamber is filled up with dung as provision for one larva, which hatch from an egg at the top of the chamber. While females dig tunnels and brood chambers in the soil, males are active mostly on the surface moving portions of dung to the entrance of the tunnel system. This mode of co-operation has been observed in different paracoprid dung beetles (Main 1916, Burmeister 1930, Goidanich 1961, Rommel 1961, Teichert 1961, Halffter and López 1977, Klemperer 1982, Brussaard 1983). In general, it is assumed that brood care behaviour in coprophagous beetles evolved

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in order to protect the offspring from competition and desiccation.

Many field studies indicate that the distribution of brood caring Scarabaeidae depends on soil quality (Doube 1983, Avila and Pascual 1986, Brussaard and Slager 1986, Lumaret and Kirk 1987, Cambefort 1991, Hanski and Cambefort 1991), and substrate preferences have been observed in laboratory experiments (Sowig 1995) or under seminatural conditions (Fincher 1973).

Most Palaearctic paracoprid Scarabaeidae belong to genus *Onthophagus*. Details of brood care behaviour and co-operation between sexes in *Onthophagus*-species has been described by Burmeister (1930). More recent studies dealt with the influence of parental size on offspring size (Lee and Peng 1981), modification of nest structure influenced by soil moisture (Barkhouse and Ridsdill-Smith 1986), mating strategies (Cook 1990), and benefits of biparental brood care (Sowig 1996).

As reproduction of *Onthophagus*-dung beetles takes place in a discrete patch, brood care activities like sex-specific time consumption (i.e. time between immigration to and emigration from the dung pat), resource allocation (number of brood chambers and weight of dung supply), and nest structure can be studied quantitatively. As pointed out in a previous paper (Sowig 1995) soil parameters like loam content and moisture may influence habitat selection and time budgets in *Onthophagus*-species via time consumption for tunnelling, but detailed studies about sex-specific time budgets and nest architecture in relation to soil parameters are lacking. The aim of this paper is to improve our knowledge about the influence of soil moisture on the brood care activities of *O. vacca*.

Material and methods

Onthophagus vacca (Linné) was collected near Schelingen (Kaiserstuhl; southwestern Germany). The beetles were separated according to sex, kept in 20 × 20 cm plastic boxes at 23°C and provided with surplus amounts of fresh dung twice a week. Since *O. vacca* shows an extreme variation in body size (unpubl.) and parental size has been shown to influence weight of dung supply and offspring size in *O. gazella* (Lee and Peng 1981), only large individuals (pronotum width ≥ 5.5 mm) were used in the following tests.

The idea was to release one pair of *O. vacca* in fresh dung and to record emigration behaviour and number, depth and size of brood chambers at two different moisture contents of the sand beneath the dung pat. I conducted two series of experiments with dry (4% water content) or moist (8% water content) sand respectively. The experiments were carried out at 12 h/12 h day/night phase and 22–25°C in sand-filled buckets 20 cm deep and 30 cm in diam. as described by Sowig (1995).

Round sheets of filter paper separated the substrate into four 5 cm thick horizontal layers. Each bucket was surrounded by a groove and covered by a removable cage made of transparent plastic and gauze which fitted tightly against the outer limit of the groove. At the beginning of each replicate 1000 g of fresh cow dung was deposited on the surface of the soil. A jar containing one male and one female of *O. vacca* was placed upside down in the middle of the dung pat. This set-up forced the beetles to dig themselves into the dung to leave the jar. The plastic cage prevented emigrating beetles from escape and the groove served as pitfall trap. Trapped beetles were counted at 12 h intervals.

After all beetles had emigrated, the dung pat was discarded and holes in the soil were filled with melted paraffin to conserve the structure of the upper parts of the tunnel system. As the deeper parts of the tunnels are refilled with substrate from secondary tunnels which branch off from the main tunnel (Burmeister 1930), the further course of these tunnels could be reconstructed only from the position of holes in the filter paper. The soaked sheets of filter paper were dried with a hair-drier and carefully removed. The result was a three-dimensional model of the tunnel system from which the length of the main tunnel and the side tunnels could be obtained. I carefully inspected each layer of the substrate for dung-filled brood chambers. Their numbers, depths and weights were recorded.

The brood chambers containing dung supply and eggs were buried in plastic boxes filled up with sand of 4 or 8% water content, as proscribed by the particular experiment. The boxes were stored at a constant 23°C. Twice a week I weighed each box to measure the amount of water lost as a result of desiccation. The substrate was moistened again until the whole box reached its original weight. This procedure guaranteed a little variation in water content of the substrate until the larvae had undergone metamorphosis.

Experiments were conducted from late spring to early summer, a period which corresponds to the natural breeding season of *Onthophagus* in Europe. Since the portion of individuals which have no intention to breed may vary within one breeding season, replicates from both experiments were conducted in a random sequence in order to exclude any influence of seasonal variation in reproductive disposition.

A total of 59 and 50 replicates were conducted on moist and dry sand, respectively. Since eleven females on moist sand and three females on dry sand left the pat without any intention to breed, results from 48 resp. 47 replicates were evaluated. While females started to build brood chambers in all 95 replicates, breeding pairs were formed in 66 replicates only, while in 29 cases the male left the dung pat leaving the breeding female alone. Unless mentioned otherwise below all significance levels of differences between mean values are derived from Mann–Whitney tests.

Results

Mean emigration times of males did not depend on soil moisture when all males were taken into consideration (Mann–Whitney test; NS). Distributions of emigration times proved to be bimodal (Fig. 1) with a minimum at 60 resp. 72 h. As shown in a previous study (Sowig 1996) resident from non-resident males can be distinguished in *O. vacca*. While resident males stay longer than 60 h in the dung pat to help a breeding female, non-resident males leave the pat within the first 60 h although a breeding female is present. The portions of resident males (32 from 48 on moist sand and 34 from 47 on dry sand) did not differ between both experimental groups (χ -square test in a 2×2 contingency table; NS). Mean emigration times of resident males, however, depended significantly on soil moisture ($p < 0.05$). Resident males stayed ca 12 h longer in dung pats on dry sand (125.65 ± 23.31 h) than in dung pats on moist sand (113.63 ± 19.98 h).

Time budget of breeding females was strongly influenced by soil moisture. Females left dung pats on moist sand after 115.00 ± 19.31 h, while females breeding in dry sand stayed ca 21 h longer (136.09 ± 24.04 h; Fig. 2). This difference between the mean values was highly significant ($p < 0.001$). The difference of mean numbers of brood chambers (4.54 ± 1.41 in dry sand and 5.17 ± 1.63 in moist sand), however, was not significant according to the Mann–Whitney test.

Soil moisture also influenced the architecture of the subterranean tunnel system, depth of brood chambers, and weights of the dung supplies. In dry, as in moist sand, a more or less vertical main tunnel to the first brood chamber was built almost to the bottom of the bucket. Consecutive chambers were built at the terminal ends of secondary tunnels which branch off from the main tunnel. In dry sand these branches were

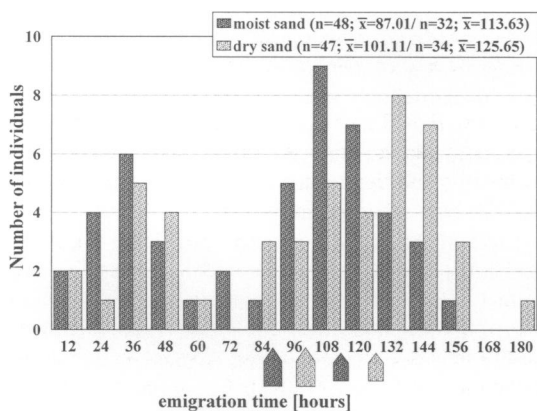


Fig. 1. Frequency distribution of emigration times of males from 1000 g dung pats on moist sand resp. dry sand. Large arrows beneath the x-axis indicate mean values of the whole data sets, small arrows refer to mean values of the emigration times of resident males.

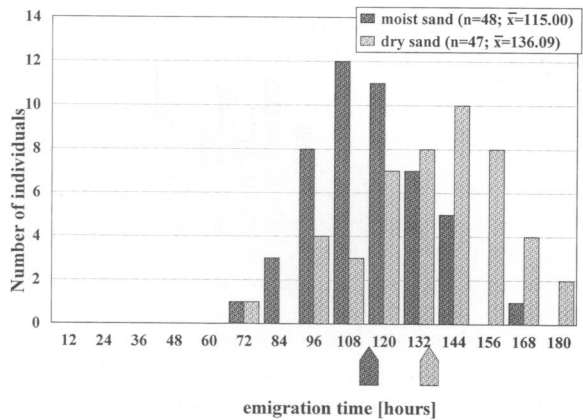


Fig. 2. Frequency distribution of emigration times of breeding females from 1000 g dung pats on moist sand resp. dry sand. Arrows beneath the x-axis indicate mean values.

constructed close together near the bottom of the bucket. In moist sand secondary tunnels and brood chambers were nearly evenly scattered over all four levels (Fig. 3). Both distributions differ significantly from each other (χ^2 -test of homogeneity; $p < 0.001$). Mean of total tunnel lengths was lower in dry sand (53 ± 9.6 cm) than in moist sand (81 ± 13.5 cm; $p < 0.001$). This difference is due to significant differences regarding total side tunnel lengths only (31 ± 4.7 cm in dry sand; resp. 64 ± 9.7 cm in moist sand; $p < 0.001$), since the first brood chamber was situated nearly always at the bottom of the bucket and thus length of main tunnels did not differ significantly between both set-ups. Tunnel walls in dry sand were totally covered with dung while in moist sand dung was attached to the tunnel walls only near the entrance to brood chambers. The mean mass of dung supplied to brood chambers in dry sand was significantly greater (7.71 ± 1.35 g) than

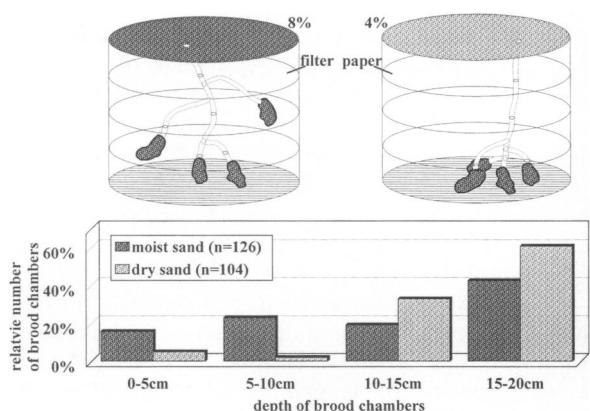


Fig. 3. Nest architecture and depth of brood chambers in moist and dry sand. The upper drawings show two examples of tunnel systems in moist and dry sand respectively. The substrate is divided into 5 cm thick layers by sheets of filter paper, which are penetrated by the tunnel-digging beetles.

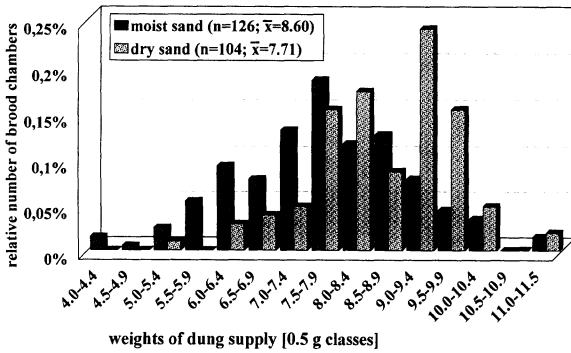


Fig. 4. Distribution of weights of dung supplies in brood chambers buried in moist and dry sand respectively.

that supplied in moist sand (8.60 ± 1.41 g; $p < 0.01$; Fig. 4).

Offspring size, measured as pronotum width, showed a significant correlation with weight of dung supply of the brood chambers the beetles emerged from (t-test; $p < 0.005$ resp. $p < 0.001$; Fig. 5). As regression lines of both experimental groups differed from each other, offspring size is influenced by soil moisture, too. Beetles emerging from brood chambers in dry sand were significantly smaller than those emerging from brood chambers in moist sand, after adjusting for weight of dung supply as a covariate (ANCOVA, $F_{1,57} = 22.17$, $p < 0.001$).

Discussion

Since most middle European *Onthophagus*-species prefer sandy to humous soils with the exception of *O. coenobita* which prefers loamy soils (Burmeister 1930), experiments with pure sand refer to a natural situation. Especially *O. vacca* breeds well in the two substrates used in these experiments (Sowig 1995). The influence

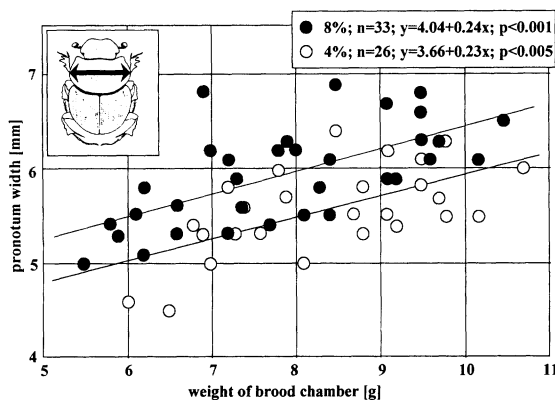


Fig. 5. Correlation between weight of dung supplies in brood chambers and body size of the emerging offspring.

of moisture of dry desert soils on nest architecture has been described by Rougon and Rougon (1983) and Barkhouse and Ridsdill-Smith (1986) in *Euoniticellus intermedius*. In this species brood chambers are arranged to dense clusters in dry soils but in moist soils they are placed apart from each other. This grouping of brood chambers has been interpreted as an adaptation to delay desiccation of the dung supplies by minimizing the surface between the brood chambers in extremely dry soil with 1–2% moisture content. This explanation does not apply to *O. vacca*, since even in dry sand, brood chambers were still widely spaced. Under humid conditions in Middle Europe, soil moisture mostly increases with increasing depth. Especially in dry soils, it seems adaptive to place brood chambers as deep as possible. The maximum depth is limited by the ground water level and/or the time required to build the nest. Especially dry sand is not sufficiently compact for tunnelling and the beetles have to attach dung to the tunnel walls (Barkhouse and Ridsdill-Smith 1986). Brussaard and Slager (1986) showed that in loosely packed soils *Typhaeus typhoeus* spent more time in preparing brood chambers than in dense soils. It seems reasonable in this context, that beetles invest much time and energy in a vertical main tunnel to reach a sufficient depth. In dry sand, secondary branching tunnels are short and ramify near the terminal end of the main tunnel.

Offspring size was not only related to the amount of dung provided. Moreover, larvae have to be provisioned with more dung in dry sand than in moist sand to reach the same body size. Females breeding in loose dry sand have to spend more time in one dung pat and have to provision larger amounts of dung but do not achieve more offspring and gain less in terms of offspring size.

As maximum depth of brood chambers was limited to 20 cm by the experimental set-up additional experiments with deeper buckets and artificial depth-dependent moisture gradients are required to explain substrate dependent modifications of nest structure.

The time that single individuals spend in a certain patch determine the structure of an ecological community since the species composition of a community at a certain place and time can be considered as the result of an equilibrium between immigration and emigration of individuals from discrete patches. The results from this paper indicate that environmental factors like water content of the soil may influence the time budget of a paracoprid dung beetle. Such studies on the behaviour of single species can serve as stepping stones towards a better understanding of the structure of ecological communities in a patchy environment (MacArthur and Pianka 1966). In this study interactions between individuals were limited to encounters between one male and one female of the same species, while interspecific relationships like competition or predation were totally

excluded by the experimental design. On a pasture cow dung pats can be considered as discrete patches. We are able to investigate the exact abundances of each species in each dung pat, but a causal analysis of the species composition is based on the information about the reason why and for how long a certain individual inhabits a certain patch.

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