

A PEDOBIOLOGICAL STUDY OF THE DUNG BEETLE

TYPHAEUS TYPHOEUS (COLEOPTERA, GEOTRUPIDAE)

CENTRALE LANDBOUWCATALOGUS



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A PEDOBIOLOGICAL STUDY OF THE DUNG BEETLE

TYPHAEUS TYPHOEUS (COLEOPTERA, GEOTRUPIDAE)

(Een bodembologisch onderzoek over de mestkever

Typhaeus typhoeus (Coleoptera, Geotrupidae))

Proefschrift

ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C.C. Oosterlee,
in het openbaar te verdedigen
op vrijdag 1 november 1985
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van de Landbouwhogeschool te Wageningen

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LANGUAGES
WAGNER

1. De in vakkringen ingeburgerde aanduiding "vingers van Hoeksema" voor de sporen in de bodem die de aanleiding vormden tot dit proefschrift, wijst er reeds op dat aan deze structuren een biogene oorsprong wordt toegedacht.
2. Inzicht in de genese en dynamiek van biogene poriënstelsels vereist onderzoek naar de populatiedynamiek van de organismen die de poriën vormen.

Dit proefschrift.

3. De in Nederland aangetroffen niet recente sporen van mestkeveractiviteit in zandgronden zijn hoofdzakelijk gevormd tijdens de overgangsperiode van de koude, Pleistocene Jonge Dryas-tijd naar het milde, Holocene Preboreaal.

Dit proefschrift.

4. Driehoornmestkevers bevorderen de bewortelbaarheid van zandgronden.

Dit proefschrift.

5. De betekenis van de ichnologie, dat is de leer der gefossiliseerde sporen van activiteit van planten en dieren, voor de vakgebieden der bodemkunde en terrestrische geologie, wordt onderschat.

Dit proefschrift.

Valiachmedov B. Pedobiologia 17: 60-69 (1969).

Miller M F et al. Trace fossils and paleoenvironments. J Paleontology 58: 283-598 (1984) (Special issue).

6. De verstoring van gelaagde structuren in de bodem onder invloed van flora en fauna kan niet worden omschreven als biologische homogenisatie.

Hoeksema K J, Edelman C H. Trans 7th Int Cong Soil Sci IV: 402-404 (1960).

Slager S. Morphological studies of some cultivated soils. Thesis, Wageningen, 111 pp (1966).

7. Mestkevers die in de bodem graven en er mest in brengen, hebben een onderschatte invloed op de concurrentieverhouding tussen heideachtigen en grassen.

Sheikh K H, Rutter A J. J Ecology 57: 713-726 (1969).

Berendse F. Oikos 44: 35-39 (1985).

De Jager A. Response of plants to a localized nutrient supply. Thesis, Utrecht, 137 pp (1985).

8. Dat in achtereenvolgende mestpropfen een slechts weinig variabel aantal konijnekeutels wordt verwerkt, betekent niet dat de driehoornmestkever kan tellen.

9. Entomologen die de driehoornmestkever als zeldzaam beschouwen, komen in het winterhalfjaar niet veel in het veld.

10. Kalisz en Stone gaan ten onrechte voorbij aan de mogelijkheid dat de opmerkelijke en scherp begrensde verschillen in vegetatie tussen de "eilanden" van *Pinus palustris* en de "zee" van *Pinus clausa* in Florida (USA) in stand blijven onder invloed van de door henzelf geconstateerde aanzienlijke verschillen in menging van de grond door de bodemfauna.

Kalisz P J, Stone E L. Ecology 65: 1743-1754 (1984).

Kalisz P J, Stone E L. Soil Sci Soc Am J 48: 169-172 (1984).

11. De keuze van de mestworm *Eisenia fetida* als toets-organisme voor het evalueren van oecologische effecten van milieubelastende stoffen is een van de slechtst denkbare keuzen uit de in NW Europa voorkomende wormen.

EEC. Guideline for testing of chemicals. Proposed protocol for testing the toxicity of chemicals to earthworms (1981).

Ma W. RIN-rapport 84/10, 17 pp (1984).

FAO. Guidelines on environmental criteria for the registration of pesticides (1985).

12. Zowel in een landbouwkundige als in een milieukundige context vormt kwantificering van de rol van de bodemfauna in opslag, omzetting, transport en vrijmaking van plantevoedende en van milieubelastende stoffen een van de meest urgente terreinen van onderzoek in de bodembioëologie.

13. Het grote maatschappelijke belang van alternatieven voor de chemische bestrijding van ziekten en plagen in de land- en tuinbouw rechtvaardigt een veel grotere inspanning aan fundamenteel populatiebiologisch onderzoek dan thans in Nederland wordt geleverd.

Ministerie van Landbouw en Visserij. Gewasbescherming in Nederland, 18 pp (1983).

Van Lenteren J C. Plaagbestrijding anders: meer dan kunst- en vliegwerk? Inaugurele rede, 37 pp, Wageningen (1985).

14. Het drastisch verminderen van de nadelige gevolgen van de hedendaagse land- en tuinbouw levert een grotere bijdrage aan de bescherming van natuur, milieu en gezondheid dan de eveneens noodzakelijke instandhouding en uitbreiding van natuurreservaten.
15. Dat zoveel gelovigen door de gebroken wereld geen heil zien in het gebroken geweer is niet geloof-waardig.
16. Om van *star wars* af te komen moeten we de *war stars* de laan uit sturen.
17. Het is wenselijk dat bij de adressen in de telefoongids ook de postcodes worden vermeld.
18. Dat de stellingen losbladig voorafgaan aan het proefschrift duidt erop dat ze *hors d' oeuvre* zijn.

Proefschrift van Lijbert Brussaard.

A pedobiological study of the dung beetle

Typhaeus typhoeus (Coleoptera, Geotrupidae).

Wageningen, 1 november 1985.

"Onder het lopen droomde hij ervan ooit ergens één kubieke meter van de aarde net zolang te onderzoeken tot deze geen geheimen meer voor hem had. Te weten wat de samenstelling van de grond was, waar de verschillende planten en beestjes zich mee voedden, hoeveel en wat ze precies nodig hadden, wat er gebeurde als de grond bevroor, hoe trillingen van voetstappen zich voortplantten door de aarde, hoe oud de grond was, wat nu precies leven was en wat dood, of werkelijk alles volgens wetten ging ... Hij wist dat het onmogelijk was, maar zijn verlangen was altijd sterker dan dit besef van onmogelijkheid".

Oek de Jong, Opwaaiende zomerjurken.

VOORWOORD

Het is niet teveel gezegd dat het onderzoek, waarvan dit proefschrift het resultaat is, heel wat bescheidener van opzet en uitvoering zou zijn geweest zonder de medewerking van de studenten die een deel van hun opleiding aan de mestkevers hebben gewijd: Jo Antonides, Ton Baltissen, Hans Hurkens, Robbert Hijdra, Ria Loonen, Ad Olsthoorn, Hans Outhuis, Lex Runia, Hans Tinkelenberg en Wilma Visser. Hun aandeel was van grote waarde. De kundige supervisie van mijn promotor, Prof. Dr. Ir. L.J. Pons, de intensieve begeleiding door Dr. S. Slager en Dr. P.J. den Boer en de talrijke discussies met Ir. K.J. Hoeksema zijn voor mij een voortdurende stimulans geweest. Dr. Th. S. van Dijk bleek steeds bereid mijn manuscripten mede te beoordelen. Ook de bemoeienis van wijlen Prof. Dr. H. Klomp in de korte periode tussen zijn terugkeer aan de Landbouwhogeschool en het openbaar worden van zijn ziekte is van invloed geweest op het onderzoek.

Mijn collega's bij de vakgroep Bodemkunde en Geologie complimenteer ik ermee dat zij een bioloog in hun midden hebben geduld. Ik heb veel van hen geleerd.

Het onderzoek heeft grote inzet gevergd van het technisch en administratief personeel. Ik heb nooit tevergeefs een beroep gedaan op de volgende personen: Mw. G. van Dinter-Deuring en haar voorgangster, Mw. G.J. Bruinsma, en hun medewerksters, wijlen de heer G.J. van de Waal, de heren P. Looijen, G. Buurman, P.G.M. Versteeg en Z. van Druuten (vakgroep Bodemkunde en Geologie), de heer B. Kroesbergen (vakgroep Grondbewerking), Mw. J. Molenaar en de heren H. Snellen, R. de Fluiter en P.W.T. Huisman (destijds vakgroep

Dieroecologie) en de heren T.H.P. van Huizen en A.J. Spee (Biologisch Station, Wijster).

Het is de verdienste van Mw. J. Burrough-Boenisch dat ik niet alleen mijn Engels heb kunnen verbeteren, maar ook mijn teksten beter heb leren redigeren.

De heer A. van der Meijden ben ik erkentelijk voor het vervaardigen van de omslagtekening.

Dit proefschrift is afgerond terwijl ik al in dienst was bij mijn huidige werkgever. De directie van het Instituut voor Bodemvruchtbaarheid en het hoofd van de afdeling waar ik werkzaam ben,

Dr. H. van Dijk, ben ik erkentelijk voor de toestemming om een deel van de werktijd aan het proefschrift te besteden.

Van Abram de Swaan, socioloog te Amsterdam, is de uitspraak dat rond elk artikel een stukje terreur zit tegen je medemensen die geprobeerd hebben je van je werk te houden. Deze uitspraak is ten dele waar. Dat van die terreur heb ik het meest betreurd ten opzichte van mijn twee zoons Bob en Frits, vooral jegens de eerste, die oud genoeg is om te accepteren dat zijn vader zo vaak op zolder zat, maar te jong om het te kunnen rationaliseren. Dat mijn medemensen me van mijn werk wilden houden, geldt in elk geval niet voor mijn vrouw Cineke, die steeds, en vooral tijdens de afronding van het proefschrift, een geïnteresseerde en deskundige steun is geweest.

Tenslotte wil ik bij de totstandkoming van dit proefschrift mijn ouders bedanken. Zij hebben mij altijd de gelegenheid geboden me te ontplooien in de richting die ik maar wilde.

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ABSTRACT

Brussaard, L., 1985. A pedobiological study of the dung beetle *Typhaeus typhoeus* (Coleoptera, Geotrupidae). Doctoral thesis, Wageningen, x+ 168 pp., Eng. and Dutch summ.

From a study of the reproductive behaviour of the dung beetle *Typhaeus typhoeus* it is concluded that cylindrical structures filled with soil material in sandy soils of The Netherlands are the result of the back-filling of burrows by scarab beetles.

Apparently ancient structures of this type were dated using data on fossil beetle remains and on clay illuviation. The microstructures of the infillings of back-filled burrows and of the undisturbed matrix were quantified and compared.

To develop a method to predict the beetles' contribution to the genesis of sandy soils, the habitat selection of *T. typhoeus* was studied, as influenced by soil temperature, soil bulk density, soil moisture and the availability of dung.

Key words: *Typhaeus typhoeus*, dung, scarab beetles, traces, back-filling, soil mixing, disturbance of stratification, sandy soil genesis, soil microstructure, habitat selection, soil temperature, soil bulk density, soil moisture, food exploitation, foraging.

CHAPTER 1

GENERAL INTRODUCTION

During the past few years, interest in soil biology research has been growing both in the soil sciences and in the biological sciences. This thesis is one of the products of that interest. Although Kubišna recognized as early as 1948 that "principally, the driving force of any soil forming process is biological", the modern soil sciences are still predominantly focussed on physical and chemical rather than on biological processes in the soil. Only very recently has the important role of soil organisms in converting plant litter and promoting nutrient cycling, in buffering the movement of water and air in the soil and in influencing soil formation and erosion enjoyed renewed interest (e.g. Hole 1981, Bal 1982). As regards the genesis of soils, three groups of invertebrates can be considered instrumental, viz. earthworms (e.g. Hoogerkamp et al. 1983), termites (Wielemaker 1984) and scarab beetles* (this thesis).

This thesis deals with cylindrical structures filled with soil material in sandy soils of The Netherlands and with the organisms, i.e. scarab beetles, that are considered to be responsible for their formation. In ichnology, a sub-discipline of paleontology, such

* Scarab beetles are beetles belonging to the superfamily Scarabaeoidea, which includes, besides dung beetles, beetles living on carrion or plant material. The larvae and/or adults of many of these species burrow into the soil.

structures are called traces or trace fossils, and to judge from a recent paper by Bracken and Picard (1984), the structures dealt with in this thesis can be classified in the ichnogenus *Muensteria* von Sternberg, 1833. After having been described by Hijszeler (1957) these structures were observed by soil scientists at numerous places in The Netherlands and the surrounding countries. This raised the following questions, which will be dealt with in this thesis:

- (1) how and when did/do these structures originate?
- (2) how much do they affect the soil and can their effect on the soil be predicted?

Because of their meniscate infillings and their small range in size, the structures were considered to be traces of animal activity. Our working hypothesis was that they could well originate from scarab beetle activities because the individuals of species that are of the right size to have been able to form such structures, are known to burrow into sandy soils. One of these, the dung beetle *Typhaeus typhoeus* (Linnaeus, 1758) was chosen as a model species for this study, because it is known to burrow 1 m or even deeper into the soil (Kuijten 1960) and it is locally abundant in heathland areas in The Netherlands. In order to understand how the above-mentioned traces were formed, the behaviour of the beetles in the soil had to be studied (chapter 2). The traces they made by back-filling their burrows were compared with the above-mentioned structures (chapter 3). In chapter 3 the ages of apparently ancient structures are determined with the help of fossil beetle remains and by interpreting clay illuviation phenomena in and around the traces. Because not all aspects of the ancient structures could be unquestionably explained

from the traces made by our model species, *T. typhoeus*, additional evidence that scarab beetles are indeed responsible for the genesis of the structures was derived from the study of another species (chapter 4).

The question of how much the traces actually do and can be predicted to affect the soil has two aspects. Firstly, how different is the microstructure within the traces from that of the surrounding matrix? This aspect is treated in chapter 5. Secondly, how many traces are there and can be predicted to be formed and at what rate? To get to grips with this aspect it was thought necessary to start a study of the population biology of *T. typhoeus*.

At this point it seems justified to digress a little to discuss soil biology as a division of the biological sciences, as discernable from soil biology in the soil sciences. In the biological sciences, the overwhelming diversity of soil organisms and the complexity of soil ecosystems has led to three types of study: firstly, autecological and population studies of single species; secondly, community studies resulting in frequencies of the occurrence of species in different soil macrohabitats; thirdly, ecosystem studies, in which the emphasis shifts from the soil organisms to the soil processes resulting from their activities, such as energy flow and storage and transport of nutrients. The results of the first two types of study are often difficult to extrapolate to the level of the ecosystem and this is perhaps one of the reasons, together with the tendency to avoid the studies of populations of organisms, that "pedobiologists" and

"biopedologists" are showing increasing interest in collaborating in the third type of study (see the proceedings of the meeting on Biological Processes and Soil Fertility, Tinsley and Darbyshire 1984). Although in the third type of study ample data are collected on soil processes, such studies shed little light on the causal structure of these processes. For certain practical purposes such causal analyses are, indeed, often considered unnecessary. Yet, if we wish to predict how a soil will develop or if we wish to manipulate soil processes in which soil organisms play an important part, e.g. in connection with nature management and agriculture, we need to understand "how the local system works". Perhaps the only way to reach this goal is (1) to restrict ourselves for the time being to relatively simple environments and (2) to restrict ourselves to those species that seem to play a crucial role in the relevant processes and (3) to derive the contributions of these species to the relevant soil processes from studying their population dynamics. The latter requires knowledge about habitat selection, about the effects of the organisms on the environment inhabited and about individual contributions to population processes.

The dung beetle *Typhaeus typhoeus* occupies a relatively simple environment, dry heathland, where it is at least locally abundant and can be considered to play an important and direct role by reworking the soil (chapters 2-5) and by transporting and converting organic matter (dung) (Brussaard 1983). It also plays an indirect part by facilitating root development (chapter 5). Therefore, there appeared to be every reason to study the influence of *T. typhoeus* on the soil by the approach indicated above, i.e. by studying its habitat

selection and reproductive performance (chapters 2, 6 and 7).

From the very beginning of the study, however, it was clear that this line of research could not be followed as far as extrapolating the outcomes of individual behaviour to population processes, because the time allowed for the study was very short (less than four years) given the generation time of the beetles (two years or more). Therefore, it is hoped that this study will be continued as a study of population dynamics, so that it will become more than just another one-species study and the point of integration of "biopedology" and "pedobiology" can actually be reached.

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CHAPTER 2

"Certes il ne nous révélera pas l'origine des instincts; il laissera le problème aussi ténébreux que jamais; du moins il pourra projeter quelque lueur en un petit recoin, et tout lumignon, si vacillant soit-il, doit être la bienvenue dans la noire caverne où nous conduit la bête".

J.H. Fabre, 1914.

Souvenirs entomologiques X: 1-73.

REPRODUCTIVE BEHAVIOUR AND DEVELOPMENT OF THE DUNG BEETLE *TYPHAEUS TYPHOEUS* (COLEOPTERA, GEOTRUPIDAE)

by

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ABSTRACT

This paper is part of a study of the contribution of dung beetles to soil formation in sandy soils. *Typhaeus typhoeus* (Linnaeus) has been selected because it makes deep burrows and is locally abundant. The beetles are active from autumn until spring, reproduction takes place from February to April. Sex pheromones probably influence pair formation. The sexes co-operate in excavating a burrow (up to 0.7 m below surface) and in provisioning the burrow with dung as food for the larvae. Co-operation is reset by scraping each other across the thorax or elytra. Dung sausages, appr. 12.5 cm long and 15 mm in diameter, are manufactured above each other. Development is rapid at 13–17 °C. The life cycle is accelerated by a cold period in the third larval stage. These requirements are met by soil temperatures up to 15 °C in summer and down to 5 °C in winter. The life cycle lasts two years, but longer under certain conditions. Newly hatched beetles make their way to the surface through the soil, but do not follow the old shaft. Adults reproduce only once. Differential rate of completion of the life cycle and occasional flying probably reduce the risk of local extinction. The study is thought to be relevant for behavioural ecology and soil science.

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INTRODUCTION

There were two main reasons for this study of dung beetles. First, ancient traces of former activity by small burrowing or crawling animals, presumed to be dung beetles, can be found today in sandy soils. By studying the behaviour of dung beetles it should be possible to ascertain whether these are indeed the relics of dung beetle activity.

Second, in areas where dung beetles are abundant nowadays, recent traces of their activity are present in the soil and this raises the ques-

tion of how much dung beetles contribute to soil formation today.

These topics will be discussed in subsequent articles. The ancient traces (with an account of their age) will be described in a forthcoming paper and will be compared with the traces resulting from recent dung beetle activity. It will be shown that dung beetles may indeed be responsible for the ancient traces.

Knowledge about the reproductive behaviour of the dung beetles is required for a proper understanding of their influence on soil morphology, and therefore this is discussed in the present paper. After a brief introduction to dung beetles as a group, the general biology of the species selected for study, i.e. *Typhaeus typhoeus* (Linnaeus, 1758), is described and its geographical range is discussed.

In order to quantify the beetles' contribution to soil formation it will eventually be necessary to explain and predict their population dynamics. This considerable task was reduced to two basic investigations in the present study. The first pertains to the development of life stages during the season and to phenological phenomena that seem to be related to the persistence of

the species in time and space. As this constitutes part of the biology of the species it has been included in the present paper. The second basic investigation pertains to the environmental conditions (including soil conditions) with which the beetles have to cope during the season of adult activity. These conditions may affect the beetles' burrowing and reproduction. This will be treated in another paper. It will be shown that the number of dung targets and their distribution in the field is of paramount importance for the population ecology of *T. typhoeus* and its impact on soil.

In its impact on soil *Typhaeus typhoeus* should serve as a model species for all Geotrupini found in the temperate Holarctic and, to some extent, also for other dung beetle species of the paracoprid type in other parts of the world.

Consequently, in this paper about *T. typhoeus*, the emphasis will be on aspects of behaviour that may help to explain the impact on soil formation caused by this kind of dung beetle. Aspects of the reproductive behaviour of *T. typhoeus* that have been published elsewhere will be re-described in terms of their relevance to soil formation. Furthermore, useful new information about behaviour and the development of life stages will be presented.

DUNG BEETLES AND THEIR ASSOCIATION WITH SOIL

Representatives of several coleopteran families are regularly found inhabiting dung, e.g., Hydrophilidae and Histeridae. The term "dung beetle", however, is usually restricted to a number of species belonging to the superfamily Scarabaeoidea. Scarab beetles, whether dung beetles or not, show a close connection with soil. The larvae of most species live underground on a food-stock of dung or plant remains, prepared by their parents, or they show a free-living, root-sucking habit. Adults of most species forage above-ground on fungi, dead organic matter or fresh leaves and burrow into the soil to prepare food-stocks for their larvae, to lay eggs or to hibernate or aestivate.

Living on dung may have evolved from living on dead organic matter and fungi (Iablokoff-Khnzorian, 1977; Crowson, 1981). In the family Geotrupidae, to which *Typhaeus typhoeus* belongs, all these habits occur and this family has been placed near the base of the scarabaeoid evolutionary tree by the authors mentioned above. Dung-feeding beetles may have devel-

oped the practice of digging into the soil as a result of searching for truffle-like fungi that adopted a subterranean life history during times of warming climate. The habit of making food-stocks out of dead organic matter or dung instead of searching for fungi is presumed to have developed subsequently.

Dung beetles spread all over the world from the Jurassic/Cretaceous periods onwards (Iablokoff-Khnzorian, 1977; Crowson, 1981). The Geotrupini tribe probably radiated out from the area of the Tertiary Tethys Sea (Krikken, 1980) and now shows a predominantly temperate, Holarctic distribution.

In addition to the Geotrupidae, one other family of scarab beetles is important for our study, viz., the Scarabaeidae. This family not only contains dung beetles (e.g. Scarabaeinae and Aphodiinae), but also beetles of the cockchafer type (Melolonthinae), which, as adults, live on fresh leaves and, as larvae, show a root-sucking way of live. Cockchafers will be discussed in a subsequent paper.

CHOICE OF *TYPHAEUS TYPHOEUS* AS AN OBJECT OF STUDY

The impact of dung beetles on soil may be two-fold: enrichment with dung or plant remains, and physical disturbance. On the basis of their impact on soil, dung beetles may be divided into three ecological groups, as proposed by Bornemissza (1969) in a different context.

First, the endocoprids, which pass their life cycle from egg to adult in the dung on the surface, or spend part of their life cycle a few centimetres deep in the soil, e.g. Scarabaeidae-Aphodiinae. Second, the telecoprids, which make a ball out of the dung, roll it some distance away and bury it superficially as a food source for the larva, e.g. Scarabaeidae-Scarabaeinae. And, third, the paracoprids, which burrow a fairly deep shaft under or close to the dung patch; part of the burrow is filled with food for the larvae and part of it is back-filled with soil, e.g. Geotrupidae.

Because of the depth of the shafts and the amount of dung transported below the ground, dung beetles of the paracoprid type, especially the larger species, may be considered to have the greatest impact on soil. In the temperate regions, paracoprid dung beetles of the Geotrupini tribe are the most important in this respect, as has been shown by the studies of Fabre (\pm 1910), Schreiner (1906), Spaney (1910), Von Lengerken (1954), Howden (1955, 1964, 1974),

Table 1. Depth of shafts in Geotrupidae.

faunal region	species	depth of shaft (cm)	source
Palearctic	<i>Geotrupes mutator</i> *	≅ 30	Teichert, 1955
	<i>G. spiniger</i> *	25— 30	Lumaret, 1980
	<i>G. stercorarius</i> *	≅ 50	Teichert, 1955
		35— 60	Spaney, 1911
	<i>G. stercorosus</i> *	35— 60	Spaney, 1910
	<i>G. vernalis</i> *	12— 68	Teichert, 1959a
	<i>Lethrus apterus</i>	60—100	Frantsevich et al., 1977
		75—100	Teichert, 1959b
		50— 65	Schreiner, 1906
	<i>Typhaeus momus</i>	10— 15	Baraud, 1977
	<i>T. typhoeus</i> *	29—100	present study
		60—100 (150)	Kuyten, 1960
		48—130	Teichert, 1959b
		70—140	Spaney, 1910
		≅ 150	Fabre, ca. 1910
Nearctic	<i>T. biostius</i>	60—160	Crovetti, 1971
	<i>Geotrupes egeriei</i>	20— 75 (90)	Howden, 1955
	<i>G. hornii</i>	40— 75	id.
	<i>Bolboceras farctum</i>	57	id.
	<i>Bradycinetulus ferrugineus</i>	35—105	id.
	<i>Mycotrupes retusus</i>	45— 90	Olson, Hubbell & Howden, 1954
	<i>M. gaigei</i>	≅ 205	id.
	<i>Pelotrupes youngi</i>	140—270	Howden, 1952

* occurring in The Netherlands.

Teichert (1955, 1956, 1957, 1959a), Kuijten (1960), Croveti (1971) and Klemperer (1978, 1979). There are differences between geotrupid species in, for example, geographical range, habitat, (use of) flight capability, reproductive season, depth of the shaft (table 1) and number of eggs laid (table 2).

In northwest Europe, *Typhaeus typhoeus* (fig. 1) is one of the most obvious species to study. The beetles are locally abundant with a

maximum of 1—2 pairs per m² and they make very deep burrows (tables 1 and 3). Occasionally I have found them as deep as 1 m and they may go even deeper, up to 1.50 m (Fabre, ± 1910; Spaney, 1910; Teichert, 1959b; Kuijten, 1960). Moreover, they transport a fair amount of dung below the ground, as reflected by the number of dung sausages produced (= number of eggs laid; tables 2 and 4).

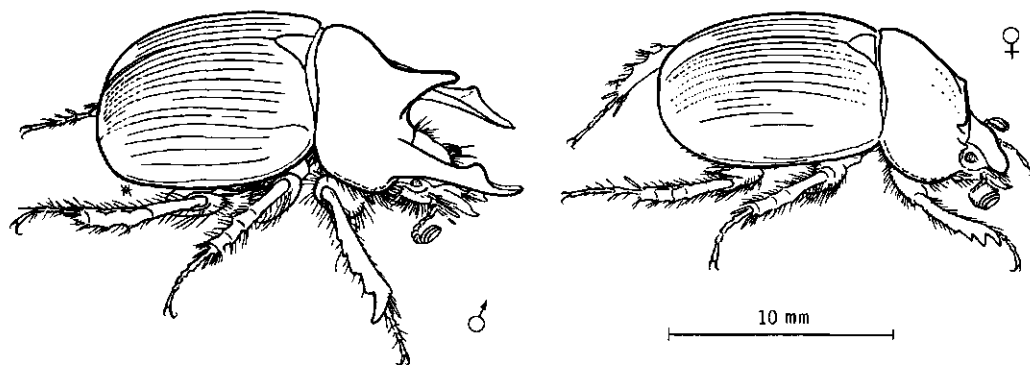


Fig. 1. *Typhaeus typhoeus* (Linnaeus, 1758). Left, male, and right, female.

Table 2. Number of eggs laid per nest or per female (if reported) in Geotrupidae.

species	number of eggs laid per nest or per female	source
<i>Geotrupes mutator</i> *	4—16 per ♀	Teichert, 1955
<i>G. spiniger</i> *	9—10 per ♀	Lumaret, 1980
<i>G. stercorarius</i> *	4—17 per ♀	Teichert, 1955
	(2) 3—6 (8)	Spaney, 1910
<i>G. vernalis</i> *	5—10 per ♀	Teichert, 1959a
<i>Lethrus apterus</i>	5—7	Frantsevich et al., 1977
	6—11 per ♀	Schreiner, 1906
<i>Typhaeus typhoeus</i> *	(1) 4—16 (21) per ♀	present study
	1—6 per nest (field)	id.
	≤ 10 per nest	Palmer, 1978
	≤ 15 per ♀	Kuyten, 1960
	3—6 (8)	Spaney, 1910
<i>T. biostius</i>	2—8 per nest (field)	Crovetti, 1971

* occurring in The Netherlands.

GENERAL BIOLOGY

Nesting

The reproductive behaviour consists of burrowing a branching shaft, provisioning the branches with food for the larvae and sealing the remaining burrow partly or completely with soil. Though the female, once fertilized, can perform the whole process on her own, the beetles normally operate in pairs. Some aspects of the reproductive behaviour have been outlined previously by Fabre (\pm 1910), Kuyten (1960) and Palmer (1978).

Habitat

The habitat is open to half open heathland, and the beetles are most abundant in bare areas surrounded by *Nardus stricta*, *Cladonia* spp. and *Calluna vulgaris*, and along paths. They also occur in open pine woods, predominantly along paths and in small clearings. A vital prerequisite is the presence of dung. The beetles are found only on herbivore dung, mostly that of rabbits, as the rabbit is the most abundant herbivore in the habitat of *T. typhoeus*. They will also use dung from sheep, deer and roe.

Seasonal and diurnal incidence

From the second half of September onwards and throughout the winter, *T. typhoeus* is active whenever the temperature is above zero and there is no snow. Intense activity occurs in October and November, which is the main period of maturation feeding, and from February to April, which is the main period of reproduction. From May onwards the reproductive activity

declines rapidly and from June to the latter half of September there is no adult activity at the soil surface (fig. 2). Contrary to the common assumption that the beetles only reproduce after the turn of the year (Fabre, \pm 1910; Main, 1917; Kuijten, 1960) I have established from field observations that pair formation, oviposition and provisioning with dung is not exceptional as early as the third week of October. On the other hand, unpaired beetles can be found in shallow burrows as late as March, where they are apparently still involved in maturation feeding.

Although in overcast and humid weather activity on the surface by day is not exceptional, *T. typhoeus* is usually active above-ground at dusk and at night.

DISTRIBUTION

The genus *Typhaeus*

The genus *Typhaeus* Leach, 1815, contains six species of about the same size: 14—22 mm long and 8—11 mm wide. Five of these are restricted to the Mediterranean area: *T. biostius* (Gené, 1836), *T. momus* (Olivier, 1789), *T. fossor* (Walzl, 1838), *T. lateridens* (Guérin, 1838) and *T. typhoeoides* Fairmaire, 1852. The first of these is endemic to Sardinia. The sixth species, *T. typhoeus* has the largest geographical range: from Morocco to South Sweden, westwards to Ireland and eastwards to Poland (Horion, 1958; Lindroth, 1960) and Yugoslavia (Miksič, 1956), but it is absent in Hungary (pers. obs. and Endrödi, pers. comm., 1981). A preliminary map of the distribution in Europe is given in fig. 3.

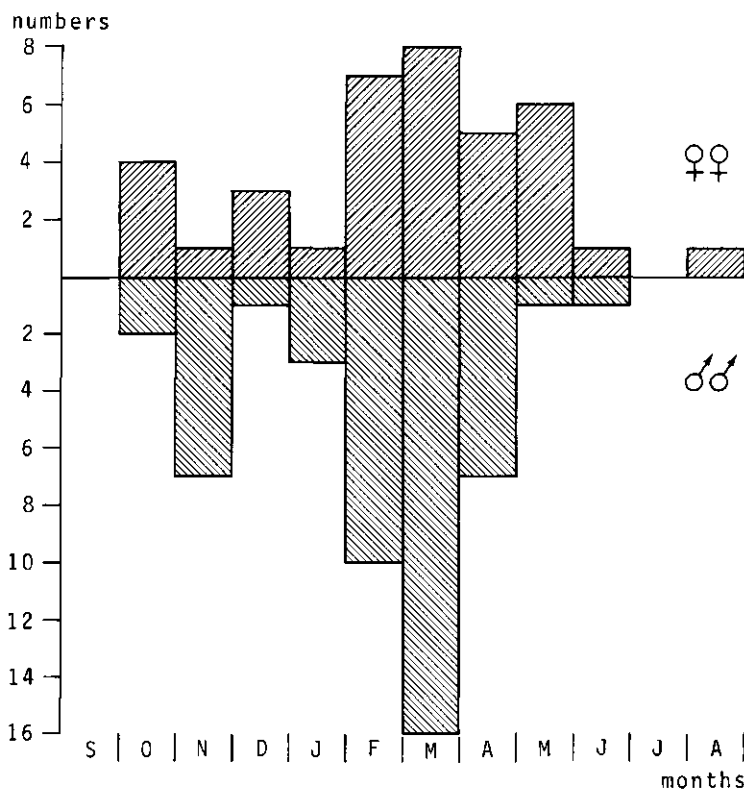


Fig. 2. Number of *Typhaeus typhoeus* captured in standard pitfalls in various heathlands in the Dutch province of Drenthe during the years 1959–1967. (Courtesy of P. J. den Boer.)

Typhaeus typhoeus in The Netherlands

In The Netherlands, *T. typhoeus* is found in sandy areas, even in isolated spots surrounded by peat, clay or loam soils (Gaasterland, Betuwe, South Limburg) but, remarkably, it is not present in the dunes along the west coast and on the Wadden islands in the north of the country. Fig. 4 is a preliminary map of the distribution of *T. typhoeus* in The Netherlands.

Absence from the dune region

In a preliminary experiment to ascertain the reasons for the absence of *T. typhoeus* from the dunes, it was found that under laboratory conditions two pairs of beetles reproduced quite normally when supplied with pellets of rabbit dung from the Wadden island of Vlieland. The trial was stopped when the larvae were in their final instar. Under field conditions in enclosures in the dunes of North Holland near Castricum, beetles made normal burrows in which they

provisioned dung for their offspring, whether supplied with pellets of rabbit dung from the dunes (two pairs) or from the inland (two pairs). When the burrows were excavated six months later, it appeared, however, that only one of the 22 dung sausages contained a live larva, whereas in most of the other cases the larva had died and in some cases the egg had evidently not hatched. This work needs to be continued to yield conclusive results.

METHODS

To study the behaviour of *T. typhoeus* in the laboratory, the beetles were kept in cages (1 m high and 0.60 m wide), similar to the one described by Main (1916/17): a wooden frame in which two windows (4 mm thick) were kept a distance of 15 mm (sometimes 12 mm) apart. The space between the windows was filled from above with tamped down portions of sand that came from a field at Wijster, in the Dutch prov-

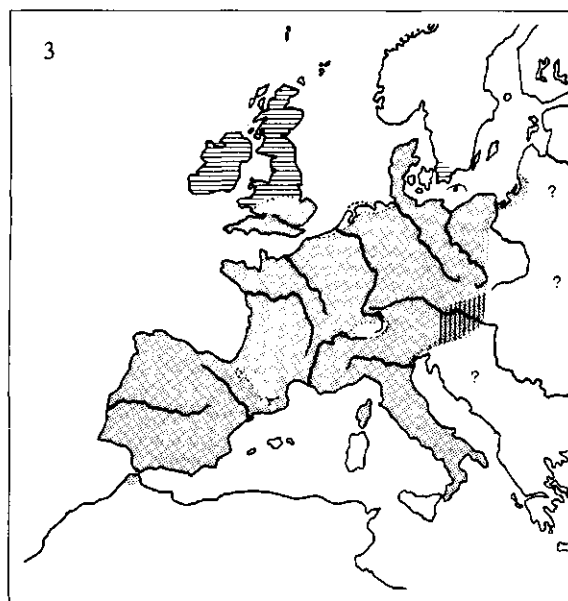


Fig. 3. Geographical range of *Typhaeus typhoeus*. Grey area: after Pijpers (1981). Striped area: *typhoeus* present according to Horion (1958), Lindroth (1960) and Sinclair (1977). Barred area: *typhoeus* not occurring according to Endrödi (pers. comm., 1981).

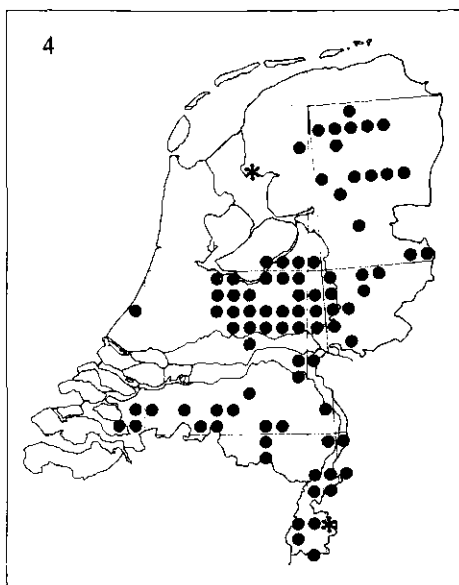


Fig. 4. Distribution of *Typhaeus typhoeus* in The Netherlands. After Pijpers (1981). Each dot indicates at least one specimen. Stars constitute additional occurrences, assessed by present author. The dot near the west coast pertains to two specimens, captured around the turn of the century.

ince of Drenthe, where *T. typhoeus* occurs naturally. The soil there is coversand to a depth of 1.40 m, in which a podzol has developed (Van Heuveln, 1965). The predominant particle size was 0.1–0.2 mm and particles larger than 0.6 mm were scarce. The organic matter content of the sub-soil was 0.6%. The sand was air-dried and subsequently moistened to a water content of 10% (by mass) to approximate field conditions in September at a depth of about 0.50 m below the surface. The tamping resulted in a bulk density of approximately 1.50 g/cm³, which was similar to the field situation at about 0.50 m below the soil surface.

The beetles made their burrows in the sand between the windows. The light/dark regime in the rooms with the cages was the same as in nature. Daylight conditions were simulated with TL-33 tubes supplemented with normal bulbs. To prevent light affecting the beetles in the soil, the windows of the cages were covered with sheets of black plastic. A horizontal walking-surface (0.50 × 0.60 m²) on which dung could

be offered was mounted on top of the glass cage and covered with 0.8 mm mesh wire-netting to prevent the beetles from flying away. Observations were usually carried out under dim red light, after the plastic sheets had been removed.

For the rearing 60 cages were used. To compare the laboratory results with the field situation, five cages were dug into the soil in the field at Wijster. In addition, the experimental equipment in the field included five 1 × 1 m² and six 2 × 2 m² enclosures consisting of 0.50 m wide stainless steel plates which were inserted to a depth of 0.20 m in the soil. These enclosures were also spanned with the wire-netting.

Almost all beetles used in the experiments were captured at the same site near Havelte in the province of Drenthe. Newly hatched adults can easily be collected in autumn from under the small hummocks of soil, where they have retired with some dung for their maturation feeding. Prior to experiments the beetles were kept in sand-filled plastic jars, 13 cm high and 10 cm in diameter, for a least six weeks at 5 °C.

Further details about the experimental methods will be given in the appropriate sections below.

REPRODUCTIVE BEHAVIOUR

Emergence and maturation feeding

The first newly hatched adults of *T. typhoeus* appear on the surface in the second half of September, usually after heavy rain. They immediately go in search of dung.

As soon as a beetle has found a small collection of dung it excavates a J-shaped feeding burrow approximately 15–20 cm deep (in the case of females sometimes deeper) and 13–16 mm in diameter. The beetle carries a number of dung pellets (in the case of rabbit dung mostly 10–20) down into its burrow and starts its maturation feeding. Given that reproduction was observed as early as the third week of October, the maturation feeding time in *T. typhoeus* is probably approximately four weeks, at a temperature of 13–16 °C.

Flying

To judge from the many beetles I found crawling around on the surface and the relatively few flying, it would seem that the beetles mostly move by walking and less so on the wing. Nonetheless, flying was observed in the field at a temperature of about 12 °C in the second week of October at dusk, in foggy weather with little wind. The beetles emerged from their burrows with their hind wings already unfolded and pumped up and flew off immediately. They flew low, zigzagging over the vegetation and the maximum distance I saw covered in one

flight did not exceed an estimated 50 m. Attempts to fly were also observed at the same time of the day in the laboratory in the plastic jars in which the beetles were kept prior to experiments. Blut (1938) encountered *T. typhoeus* flying at dusk in late May. Flying is possible even at very low temperatures, since in one of my laboratory experiments a female flew around in the walking area of a glass cage at 5 °C, although she had been subjected to that temperature for over six weeks.

To study flight movements in *T. typhoeus* more closely, two window traps and a mist-net trap were placed in a study plot at Wijster, in the Dutch province of Drenthe. The window of the window trap measures 100 × 50 cm² and it catches beetles flying at a height of 150–200 cm above the ground. The mist-net trap measures 100 × 50 cm², catching beetles flying 20–70 cm above the ground. After colliding with a trap the beetle falls down into a reservoir containing 4% formaline. The two window traps were in operation from 29 September 1978 and the mist-net trap from 8 November 1978 until the summer of 1980. In all, 19 beetles were trapped: eight males and eleven females (fig. 5). Fifteen beetles were captured in the single mist-net trap and only four in the two window traps, which confirms that the beetles fly low. Of the eleven females, ten were relatively unimpaired when the trap was inspected; two (captured on 27 September and 1 October, respectively) showed developing ovaries and had not yet mated; eight contained eggs and had mated, to judge from the presence of sperm cells. This shows that although no flying beetles were captured during peak reproduction in March, *T. typhoeus* can be

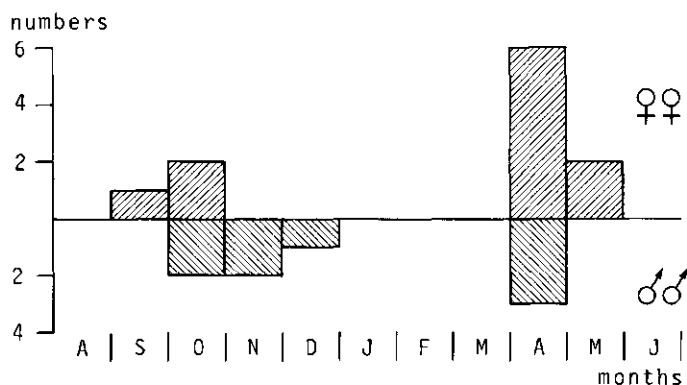


Fig. 5. Number of beetles trapped in flight at a study plot at Wijster (province of Drenthe, The Netherlands) during 1978/79 and 1979/80.

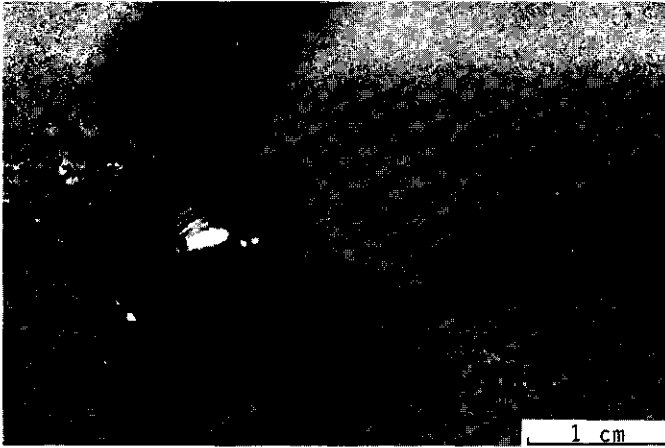


Fig. 6. Stance adopted by male *Typhaeus typhoeus* for supposed pheromone release during defecation. (Photo of beetle in nest entrance on walking surface of glass cage.)

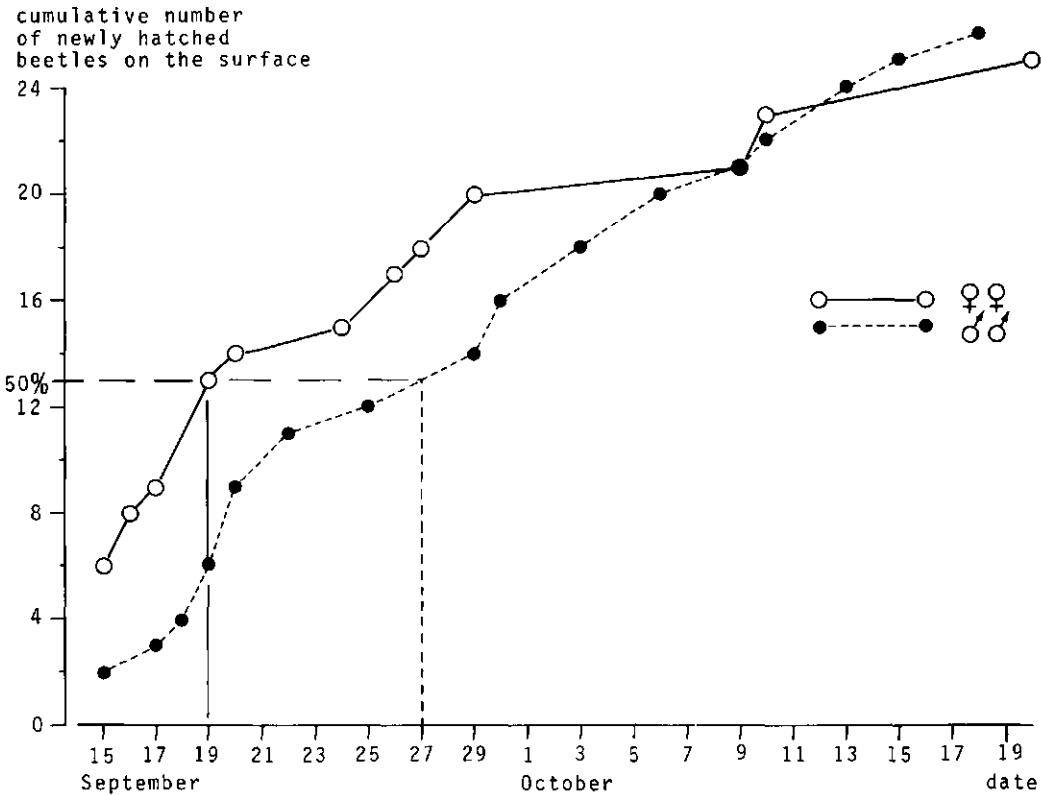


Fig. 7. Cumulative number of newly hatched male and female beetles appearing at the surface in September and October 1980 in a rearing trial started in late winter 1979.

added to the list of species not obeying the oogenesis-flight syndrome of Johnson (1969).

The gut content of 14 of the trapped beetles was qualitatively estimated. In five beetles the gut was half filled or less, in nine the gut was more than half full. From these findings it cannot be concluded that a shortage of dung is the reason for flight.

Settlement and pair formation

Croveti (1971) states that in *Typhaeus bios-tius* the male penetrates the feeding burrow of a female after maturation feeding. In *T. typhoeus* I have observed behaviour that strongly suggests that pheromones may play a role, at least

in some stage of adult life, in pair formation: under laboratory conditions I have repeatedly observed that a male who has abandoned a nest with a female, then digs a shallow burrow near a food source, similar to the J-shaped feeding burrow. Next to this the male can be observed defecating in a characteristic stance, his body tilted at an angle of about 45° to the surface with his head above the entrance of the burrow and his abdomen lifted (fig. 6). This stance suggests that a pheromone is released with the excrement. Although the hypothesis of pheromone release needs experimental confirmation, it is significant that this stance was invariably adopted around the time that the light in the ex-

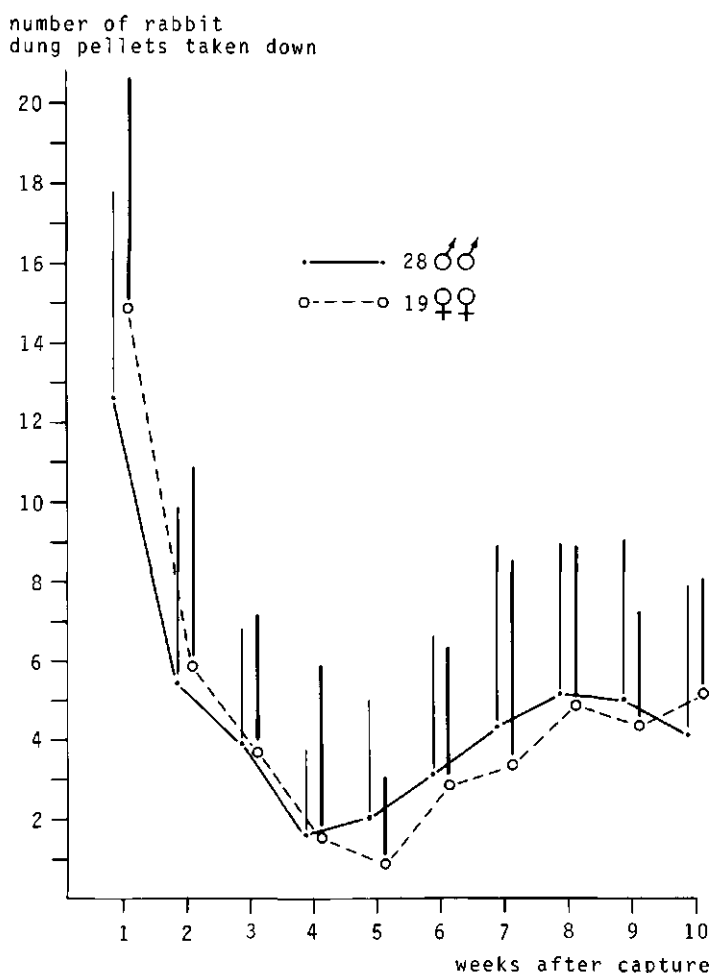


Fig. 8. Mean number of rabbit dung pellets carried down by beetles kept in plastic jars at 13–16 °C for ten weeks after their capture on 29 September and 4 October 1978. Vertical lines indicate upper half of standard deviation.

perimental room was automatically switched on or off, i.e., around dawn or dusk. At those times the weather is usually favourable for odour communication because of high air humidity and moderate wind velocity.

Crovetti's (1971) observation that the male joins the female after maturation feeding and my observation that males appear to be trying to attract females after the pair has split up, suggests that the former behaviour changes to the latter in the course of the season (assuming the two *Typhaeus* spp. behave similarly). There is some evidence to support this. In the rearing trials I carried out, the females usually appeared on the surface and started maturation feeding before the males: the median of the total number of females on the surface was reached eight days before that of males (fig. 7). Furthermore, in a cohort of beetles captured in the field, females carried down the same quantity of dung for maturation feeding as did the males (fig. 8). If the duration of maturation feeding is the same for both sexes then it seems probable that females mature sexually earlier than the males. For a female, the prerequisites for reproduction are a male and an adequate amount of dung, as a food source for the future larvae, and therefore her most profitable strategy seems to be not to go and search for one of the few males available for mating, but rather to settle near a spot rich in dung, make a shallow burrow and wait there for a male. This needs to be confirmed by additional research.

During the reproductive season the pattern changes: whenever a pair of beetles abandons a nest it is usually the male who leaves first, as will be reported in greater detail in another paper. Several days may pass before the female appears outside the burrow. By the time the male leaves the burrow most females will be paired and involved in breeding, so that it is unprofitable for him to search for one of the few burrows with an unpaired female. Instead, he seeks a spot with plenty of food, near which a new nest can be made, and tries to attract one of the females that will appear above-ground after abandoning a nest.

Copulation

On the first encounter, which usually takes place in a shallow feeding burrow, the male vigorously sweeps his front tibiae across the female's thorax, the female turns around and then the male sweeps across her elytra while half

mounted on her back. Finally, the female lifts her abdomen and copulation follows, lasting from 3 to 20 min. The female terminates the copulation by stepping forwards a few cm, turning around and pushing the male back.

Burrowing

Having paired and copulated the beetles make a nest that finally consists of a shaft that may or may not divide into tunnels, from which a number of brood chambers branch off, provisioned with dung for the progeny and sealed by back-filling with soil (fig. 9). The female excavates by scraping the sand under her body with her front tibiae and then using her middle and hind legs to move it further back. As the sternites are densely covered with backward-pointing hairs, the sand does not fall down past the beetle when she is in a vertical position. While excavating, the beetle intermittently turns around its length axis. Every time the beetle has excavated 0.5–1.0 cm of the shaft she moves several mm backwards, and by doing this tamps down the moist sand behind her into a plug. Then she turns around and pushes the plug into the shaft with her head and thorax, again intermittently turning around her length axis. This turning enables her to apply force to a different point and thus facilitates the transport of the plug. The upper part of the shaft, within a depth of 30 cm from the surface, is made horizontal for some 10–15 cm (fig. 9). Here the female always leaves her sand plug before returning down the burrow to continue excavating. The male then burrows through the sand plug. Since the female has left the plug in a horizontal part of the passage, the sand does not fall down the shaft. Once past the small plug, the male turns around and shovels it to the exit, transporting it in the same way as the female. In this way a sand heap gradually accumulates on the surface, finally achieving a height of some 5 cm and a diameter of 10–15 cm.

In one of the glass cages the excavation of the shaft was closely monitored. Fig. 10 clearly shows that the beetles may continue to excavate for four days without pausing.

On four successive days, during periods indicated in fig. 10, I recorded the intervals during which the female was involved in sand excavation and transport, respectively. On the first three days the duration of the periods of excavation was the same, on the fourth day the duration was much longer, presumably indicating that the female was about to terminate the bur-

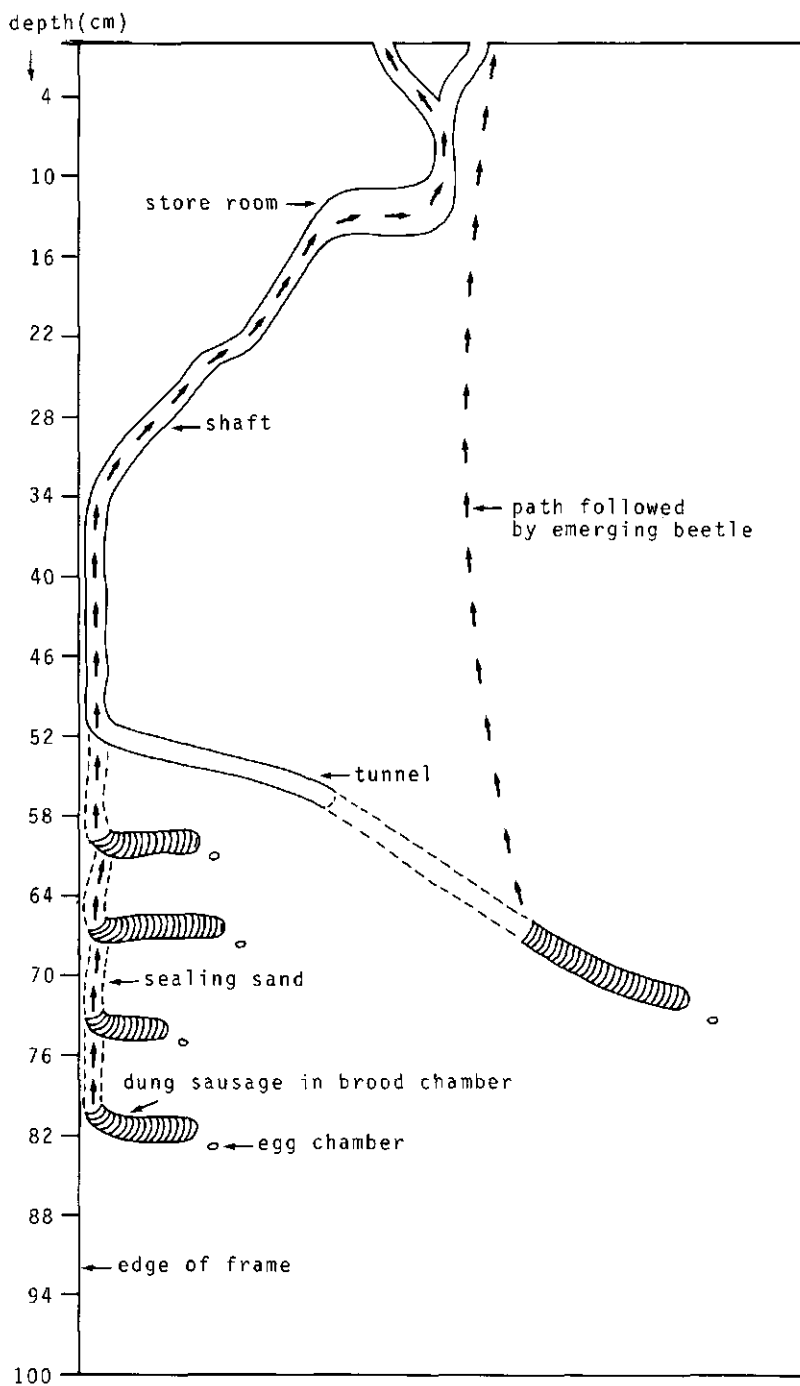


Fig. 9. Nest of *Typhaeus typhoeus* in one of the glass cages.

rowing. The duration of sand transport steadily increased to half an hour per plug. The cage had been filled and the sand tamped down under water. This resulted in a bulk density of 1.70 g/cm³, which is the maximum a beetle may generally encounter in the field. The temperature in the room with the cage was 5 °C throughout the reproduction of the beetles. This approximates the soil temperature up to a depth of 1 m, measured in the field at the beginning of March, following the severe winter of 1978/79. This temperature was, therefore, near the lowest the beetles may encounter underground in the field in The Netherlands. Even so the beetles progressed fairly rapidly (fig. 10). In a total of 60 cages filled with less densely packed sand (not exceeding 1.55 g/cm³) and at temperatures of 5–17 °C the shaft was excavated within 1–3 days.

The morphology of the shaft was very variable. However, a horizontal part was invariably present within a depth of 30 cm. During the process of excavation the female often made another horizontal or slightly sloping gallery where she left the sand plug while continuing deeper. The shaft terminated in an oblique or horizontal gallery 6–15 cm long; the future first brood chamber (fig. 9). The depth of the shaft varied considerably, as can be seen from table 3.

The diameter of the shaft is determined by the size of the larger of the two beetles. In the field, casts of twelve shafts were made using liquid paraffin wax that solidified on cooling, enabling the diameter of the shafts to be measured. The mean diameters of all shafts were then averaged: the overall mean was 14.2 ± 0.7 mm (S.E.).

Oviposition and behaviour prior to and following it

As soon as the female has terminated the burrowing she begins to make a small cavity (diameter about 0.5 cm) for the future egg by moving her head and fore legs in the blind end

of the almost horizontal terminal part of the burrow, alternately scraping some sand away and pushing part of it back. When she has finished she walks up and down the passage until the male arrives. The male joins the female, sometimes before she has finished the egg chamber, when he no longer encounters a sand plug to transport upwards. Then the beetles usually mate, as described before.

Copulation at this stage, i.e. prior to oviposition, is not obligatory but it is seldom omitted. After copulation the male starts scraping sand over a distance of about 10–15 cm from the bottom of the future first brood chamber. He may do this several times, so that a sand plug is formed. Then he turns around and transports the plug upwards. The female continues to prepare the egg chamber, breaking off to walk through the future brood chamber, with her abdomen pulsating. These pulsating movements are probably connected with the transport of an egg into the oviduct. Finally she moves her abdomen into the egg room and oviposits, making gentle pumping movements. Oviposition may last 10–25 minutes. After oviposition the female shows the backward scraping behaviour, just like the male, over a distance of some 10–15 cm, but in the opposite direction. Then she turns around and pushes the sand into the end of the burrow, thus sealing the egg chamber. The wall that thus separates the egg chamber from the future brood chamber becomes 10–15 mm thick (compare fig. 9). As a consequence of the scraping of sand by male and female the diameter of the brood chamber is slightly larger than that of the rest of the burrow: 15.0 ± 0.7 mm (S.E.), $n = 12$.

While the female is completing the egg chamber and preparing the brood chamber, the male is involved in widening the shallow horizontal part of the burrow, which is to become a store room for dung pellets. The diameter of the store room becomes 2–4 cm.

Table 3. Depth of shaft in *Typhaeus typhoeus* under laboratory and field conditions. [Temperature in the lab 5° or 9 °C; bulk density in glass cages and casks about 1.55 g/cm³ to match field conditions. Enclosures 1 × 1 m²; casks 0.5 × 0.5 × 1 m³. Ample supplies of dung were provided in all experiments.]

year	experimental set-up			n	depth (cm)	range (cm)
1979	glass cages	lab	(2-dim.)	12	67 ± 22	29–100
1979	enclosures	field	(3-dim.)	5	69 ± 6	63–80
1980	glass cages	field	(2-dim.)	5	68 ± 9	52–78
1980	casks	lab	(3-dim.)	4	58 ± 13	46–78

Dung provisioning

When she has finished preparing the brood chamber the female walks up the burrow to meet the male in the store room or, alternatively, if he is ready first, the male walks down after enlarging the store room. When they meet, the female pushes the male upwards firmly and vigorously sweeps his elytra with her fore legs. This continues, until the male finally makes for the surface to fetch dung, the female waiting for him in the store room or in the brood chamber.

When he has found a fecal pellet, the male usually takes it between his front tibiae and walks backwards with it to the nest entrance. Sometimes he holds the pellet between his mandibles, but I have never observed the pellet being carried on the horns as described by Fabre (± 1910). The male drags the dung pellet into the direction of the nest entrance in a straight line, however tortuous his searching path may have been. If the dung pellet is found within about 40 cm from the nest entrance the male usually enters the hole at once. If the fecal pellet is found further away, however, the beetle drops it within 5–10 cm from the entrance and then moves directly to the entrance, walking forwards, puts his head into the entrance for a few seconds, turns around, picks up the dung pellet and carries it down without further delay. Whenever the beetle misses the entrance he finds it after an area-restricted search. This behaviour of searching for the entrance in the vicinity of the nest shows that the beetle is capable of roughly estimating the distance from the place where the dung was found. During the procedure of dragging a dung pellet from a fair distance away, the behaviour of leaving it behind and walking forwards to the nest entrance may occur more than once.

As soon as the male, dragging the dung pellet backwards into the nest, appears in front of the female below, she immediately begins to sweep his elytra. Then the male pushes the dung pellet underneath himself and walks up the shaft again to fetch more dung. The number of rabbit dung

pellets dragged in successively by the male does not usually exceed 30; it depends on the ease with which he can find them and the distance to be covered. The time needed to collect them also varies, but seldom exceeds two hours. After this bout of dragging dung pellets, the male stays below-ground for some hours.

The female takes a dung pellet from the store room and, holding it in her fore legs, lets herself fall down the shaft by drawing in her middle and hind legs close along the body. In the brood chamber she tears the pellet to pieces with the help of her mandibles and fore legs and then firmly presses the pieces into the blind end of the brood chamber with her head and thorax, intermittently turning around her length axis. This firm pressing causes a meniscate layering within the dung sausage that is going to fill the brood chamber. The female walks up the shaft to collect every dung pellet. Alternatively, the male may supply her with dung by carrying down a number of fecal pellets. Sometimes the male kicks the dung pellets out of the store room with his hind legs. As a consequence the lowest part of the burrow behind the female becomes filled with fecal pellets.

Often, the male walks down the shaft to the female. If the female progresses too slowly he may stimulate her and he often tries to copulate. When the female goes up to fetch more dung to provision the brood chamber and encounters the male before she reaches one of the pellets in the store room, she invariably stimulates him by sweeping his elytra. It thus appears that the co-operation of male and female in the stage of dung provisioning is often reset by interaction.

The number of rabbit dung pellets processed per dung sausage varies between 30 and 65, averaging about 40. The number of dung sausages manufactured varies between 4 and 21, averaging about 10 (table 4).

Sealing the dung sausage and excavating the next brood chamber

When the dung sausage is finished the female

Table 4. Number of eggs laid (= dung sausages manufactured) in *Typhaeus typhoeus* under laboratory and field conditions. [Experimental conditions as mentioned in table 3.]

year	experimental set-up		n	number	range
1979	glass cages	lab	(2-dim.)	11	9.9 ± 4.3 5–21
1979	enclosures	field	(3-dim.)	5	10.6 ± 4.9 6–19
1980	glass cages	field	(2-dim.)	5	7.8 ± 2.9 4–12
1980	casks	lab	(3-dim.)	4	10.5 ± 1.7 8–12

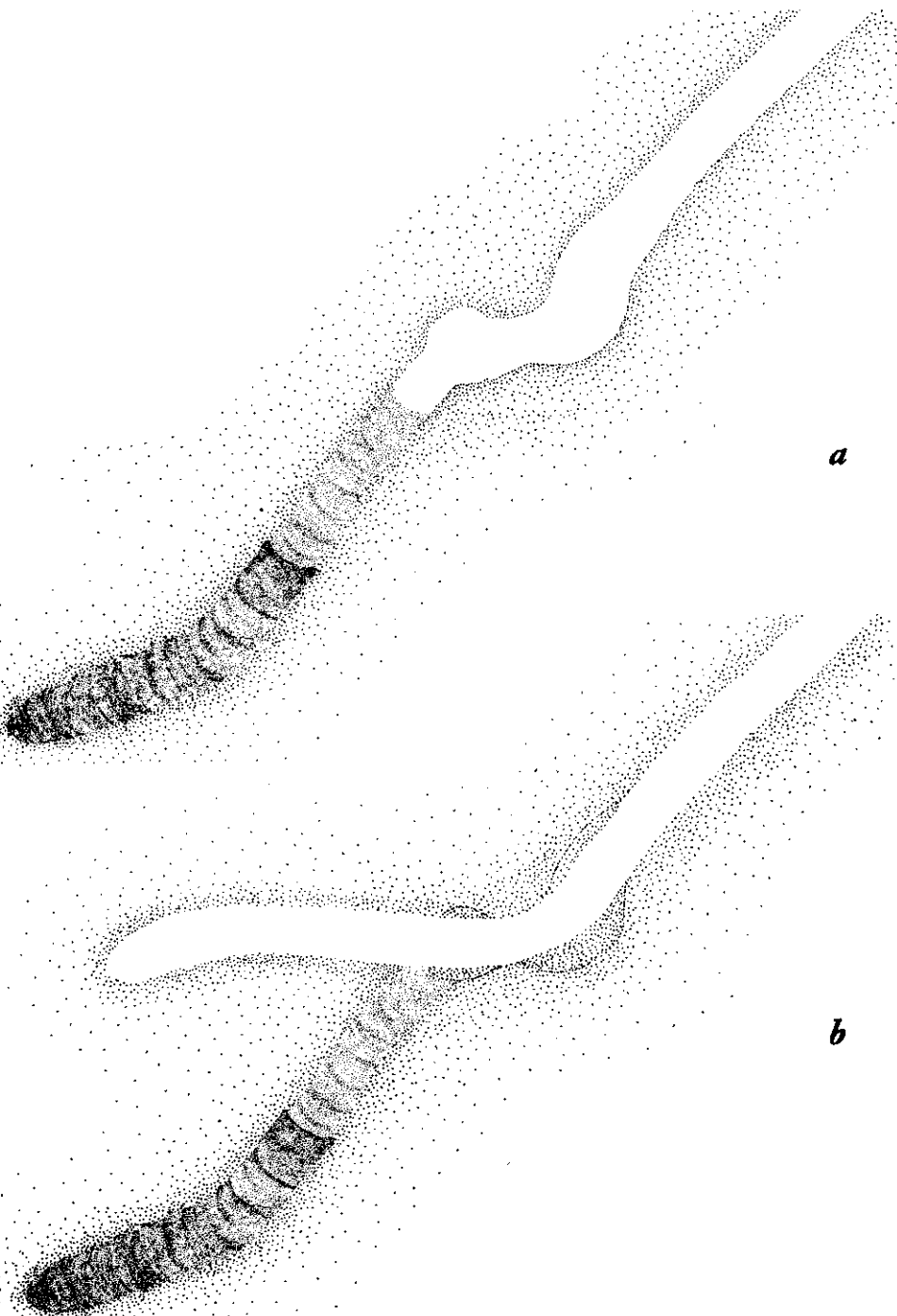


Fig. 11a. Dung sausage being sealed over a predetermined stretch with sand from the shaft walls. Fig. 11b. The widening is plastered with sand from the new brood chamber.

seals it with soil, using sand scraped from the wall of the shaft. Interestingly, this wall-scraping starts some cm above the proximal end of the dung sausage and in this way the amount of the shaft to be filled with sand is determined (fig. 11a). Only half way or later in the stage of sealing is the next brood chamber excavated. The widened part of the shaft above the sand plug that seals the former dung sausage is inadvertently plastered by the beetle with sand that it drops as it is carrying it upwards (fig. 11b). The next brood chamber is excavated above the former one (fig. 12).

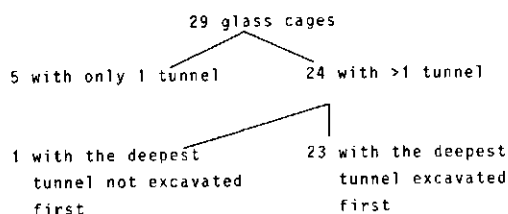


Fig. 12. Brood chambers are excavated above each other, beginning with the deepest.

Fig. 15 shows that the first tunnel excavated is usually the deepest. A tunnel is that part of the burrow from which one or more brood chambers branch off. This may be equivalent to a shaft, but more than one tunnel may be found branching off from the same shaft (fig. 9). A new tunnel is usually branched off when the latest brood chamber is relatively shallow. In the present study, the uppermost dung sausage in 22 cases with more than one tunnel was, on average, about 40 cm deep (table 5). While excavating the subsequent brood chambers the same behavioural sequence of transporting sand, copulation, oviposition and dung provisioning is shown.

As long as the male is present the female always excavates a new brood chamber, at times preceded by a new tunnel, irrespective of the availability of dung or the number of eggs already laid. If the male is no longer there, the be-

haviour of the female varies. If there is still a supply of dung she may continue the whole process of excavating a brood chamber, egg-laying, gathering dung and manufacturing dung sausages on her own. She may even excavate the next brood chamber with no male present and no dung around. If she has laid the next egg although there is no supply of dung, she may fill the newly excavated brood chamber with sand from the walls of the burrow, which shows that the behaviour after oviposition is fixed upon provisioning with whatever material there is around. Alternatively, the female may abandon the nest, invariably after finishing and sealing the last dung sausage, and continue reproduction elsewhere.

Behaviour of larvae and newly hatched adults

As soon as the egg has hatched the larva makes its way through the 1—1.5 cm thick sand wall that separates it from the dung sausage and moves into the dung in a somersaulting motion by which it displaces material from in front of it to behind it. As a consequence, after the larva has passed through, a small wad of dung, several mm long and wide, remains at the distal end of the dung sausage. The larva eats its way through the dung sausage, back-filling the space behind it with its excrement (fig. 13), so that the cavity surrounding the larva becomes only 2—3 cm long. It may eat its way through the dung sausage several times. There are three larval stages. Finally the larva III moves out of the dung sausage at the distal end and makes a cavity at the site of the former egg chamber: the pupal chamber. As a consequence, the distal end of the dung sausage becomes filled with sand displaced by the larva. The pupal chamber is plastered with excrement by the larva, which finally lies on its back to pupate (fig. 14).

After pupation the newly hatched adult often remains days or weeks in the pupal chamber before going to the surface. In my rearing trials, 45 out of 51 emerged adults passed through the partly eaten dung sausage, which thus appeared to be the rule. The other 6 immediately bur-

Table 5. Depth of uppermost dung sausage in shafts with more than one tunnel. [Experimental conditions as mentioned in table 3.]

year	experimental set-up		n	depth (cm)	range (cm)
1979	glass cages	lab	(2-dim.) 10	36 ± 10	20—48
1979	enclosures	field	(3-dim.) 5	42 ± 12	35—54
1980	glass cages	field	(2-dim.) 3	38 ± 10	25—50
1980	casks	lab	(3-dim.) 4	32 ± 8	20.5—40.5

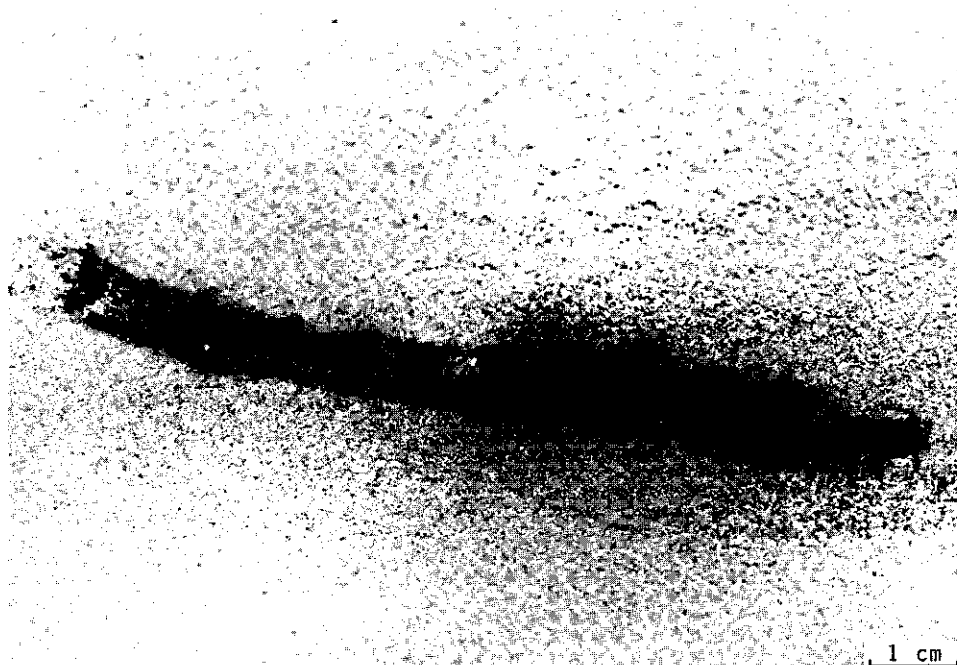


Fig. 13. Larva of *Typhaeus typhoeus* eating its way from the distal end (right) to the proximal end (left) of a dung sausage and back-filling it with its own excrement. (Photo of dung sausage and larva in glass cage.)

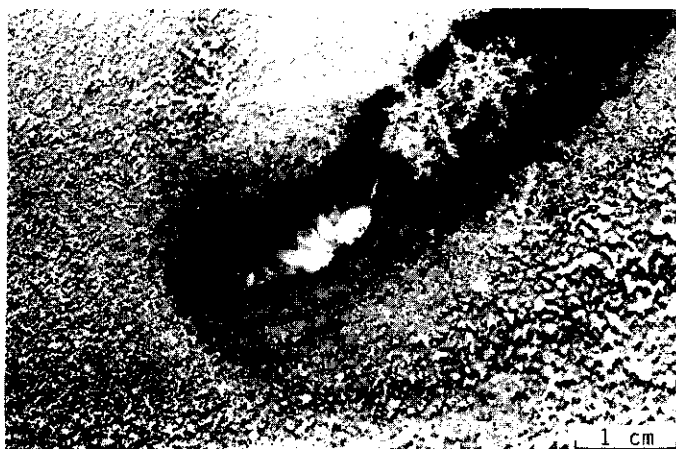


Fig. 14. Pupa of *Typhaeus typhoeus* in pupal chamber made outside the distal end of the dung sausage. The horn (right upper part of pupa) shows that this specimen will become a male. (Photo of pupa in glass cage.)

rowed their own way upwards from the pupal chamber. At least 23 out of the 45 passing through the old dung sausage subsequently also burrowed their own way upwards. I believe this to be the normal behaviour because after passing through the old dung sausage, the remaining

22 broke through the sealing sand and subsequently followed the old shaft, but they were most probably forced to do so by the cages, so this should be regarded as abnormal behaviour (see the arrows in fig. 9).

A beetle burrowing its way upwards scrapes

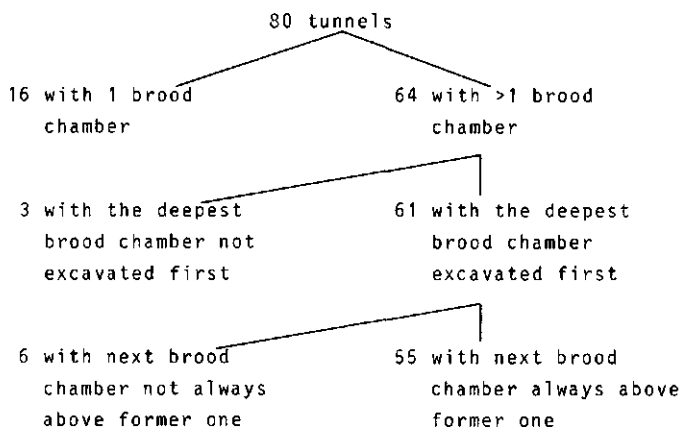


Fig. 15. The tunnel excavated first is usually the deepest.

the sand away above itself, turns around and firmly presses it behind. Consequently, at the beginning of this behaviour the space in the old dung sausage or in the pupal chamber is filled with sand. Subsequently, a corridor about 8 cm long steadily extends upwards through the soil, the beetle scraping sand away above and pressing it beneath itself. An emerging beetle reaches the surface within a few hours, depending on the depth from which it starts. On arrival at the surface the animal shows the behaviour as described in the section on emergence and maturation feeding.

DEVELOPMENT

Development of eggs and larvae

To study the (rate of) development of the different stages of *T. typhoeus*, beetles were reared in cages as described in the section on methods. The results of the rearing trials, which lasted almost three years, are given in tables 6 & 7, which cover the rearing period from winter 1979 to autumn 1980 and from autumn 1980 to autumn 1981, respectively. In the rearing trials the effect of administering cold winter periods was most noticeable. These cold periods were administered because soil temperature had been found to drop from 13 °C in August to 3 °C in February at a depth of 1 m in the field. At 0.20 m from the surface the fall in temperature was greater (from 16° to 1 °C).

After presenting the results of the rearing trials in the laboratory, the development of larvae in the field will be described. To facilitate com-

prehension, the course of development is briefly outlined in fig. 16.

Rearing trials (1979—1980)

The rearing trials were carried out in rooms with constant temperatures of 1°, 5°, 9°, 13° and 17 °C, respectively. These temperatures were chosen because soil temperatures measured in 1979 in the study plot at Wijster (where *T. typhoeus* occurs naturally) ranged from 3—10 °C in the reproductive period and increased to 13—16 °C during summer, when the larvae develop. At all the temperatures they were subjected to, the beetles showed their reproductive behaviour.

At 1 °C only very few eggs were laid, however, and the dung sausages were abnormal, consisting partly or completely of whole dung pellets. The eggs did not hatch. Therefore the rearing trials carried out at 1 °C will not be discussed further. At 5 °C reproductive behaviour was normal, but the eggs did not hatch either, not even after 20 months. At a temperature at or exceeding 9 °C the eggs did hatch. The time eggs laid at 5 °C took to hatch at 9°, 13°, 17° and 20 °C was estimated (table 8). Though the number of observations is small in some groups (because this trial was not solely intended to study the hatching time of the eggs) it is quite clear that at 9 °C development is relatively slow. At the start of the rearing trials there were four cages at each temperature. However, three of the cages kept at 9 °C soon had to be discarded because in one cage the female died without reproducing and although

Table 6. Results of rearing pairs of *Typhaeus typhoeus* in glass cages at four different temperatures.

temp- era- ture (°C)	ADULTS			EGGS			LARVAE			(PRE) PUPAE					ADULTS				
	number of pairs	number of beetles	date of start rearing trial	number of eggs	number of eggs present	first date with eggs present	number of eggs present	number of pupae present	first date with pupae present	number of pupae present	number of pupae present	number of pupae present	number of pupae present	number of pupae present	number of pupae present	number of pupae present	number of pupae present	number of pupae present	number of pupae present
5°	28/29.III.1979	4	41	8	11	1.5	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
9°	28/29.III.1979	2	21	16	19	2.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
13°	28/29.III.1979	2	21	4	19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19
17°	28/29.III.1979	2	20	17	17	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19	4.19
without winter period	4	42	38	32	33	14	14	14	14	14	14	14	14	14	14	14	14	14	14
with winter period	4	42	38	32	33	14	14	14	14	14	14	14	14	14	14	14	14	14	14

1) Stopped in November 1980, i.e. 20 months after the start.

2) Initially 4 pairs of beetles, soon declining to 1 pair, see text.

3) Artificial winter period at 5°C from 5 XI 1980 to 23 I 1981, i.e. 11 weeks.

4) Stopped in September 1981, i.e. 20 months after the start.

Data from pairs subjected to a cold period from 30 October 1979 to 28 February 1980 are presented on the right side of the relevant columns; data from pairs not subjected to a cold spell are given on the left side. Totals at the bottom of the table pertain to data from rearing trials at 13° at 17°C only (see text), hence the break in the table between the 9° and 13°C rows. There was a significant difference between the number of beetles that emerged from the cages receiving a cold treatment and those that emerged from the cages that did not receive a cold treatment: $\chi^2 = 21.85^{***}$.

Table 7. Results of ongoing rearing trials in glass cages from November 1980 until October 1981 in rooms kept at a temperature of 13° or 17 °C.

winter periods offered at 5°C as indicated in Fig. 12	number of beetles	5 November 1980 number of pairs	1 July 1981 number of pupal chambers on	number of pupal emerged in 1981	number of beetles that pupated not pupating	larvae remaining in a cold period	number of living and cages not given cold treatment	difference in number of beetles emerging from (females : males)	sex ratio of emerging beetles
-	+	7	27	27	23	0			
+	+	7	2	+4 = 6	5	0		$\chi^2 = 20.12^{***}$	18 : 15
+	-	6	6	+1 = 7	0	2		$(P < 0.005)$	
-	-	7	11	+3 = 14	5	8			

five dung sausages were made in each of the other two cages they were very superficial and the larvae soon died, probably because the fluctuations in moisture were too great.

On 30 October 1979, by which time virtually all the larvae had emerged, the cages were divided into two groups, one group remaining at the temperature it had been subjected to so far, the second group receiving a five-month cold spell at 5 °C until 28 February 1980, after which the cages were once again subjected to their former temperatures. The single cage remaining at 9 °C was assigned by chance not to receive a cold spell. One year later, rearing at 9 °C was repeated with one cage that was given a cold period (see table 6). The number of pupal chambers and the time that elapsed until they appeared can be read from table 6. At 9 °C the median number of pupal chambers was reached much later in the cage without a cold period than in the cages at 13 °C and 17 °C, whether or not the latter received the five-month cold spell. This

again indicates that development is very slow at 9 °C.

At 13 °C and 17 °C pupal chambers were made by the larvae of all groups. This proves that a cold period is not a prerequisite for making a pupal chamber. At 13 °C and 17 °C, in the groups receiving a cold period, the median number of pupal chambers was achieved after a similar period from the start of the trials: 55 and 52 weeks, respectively. The date by which half the beetles had emerged was also very similar for these two groups. Therefore, I felt justified in combining the data on the different stages in the cages kept at 13 °C and 17 °C (bottom of table 6). This resulted in a very significant difference between the proportions of beetles emerging from cages which had and those emerging from cages which had not been subjected to a cold period: only one beetle emerged from 19 pupal chambers in the latter, compared with twelve beetles out of 14 pupal chambers in the former ($\chi^2 = 21.85^{***}$, $P < 0.005$). Thus a

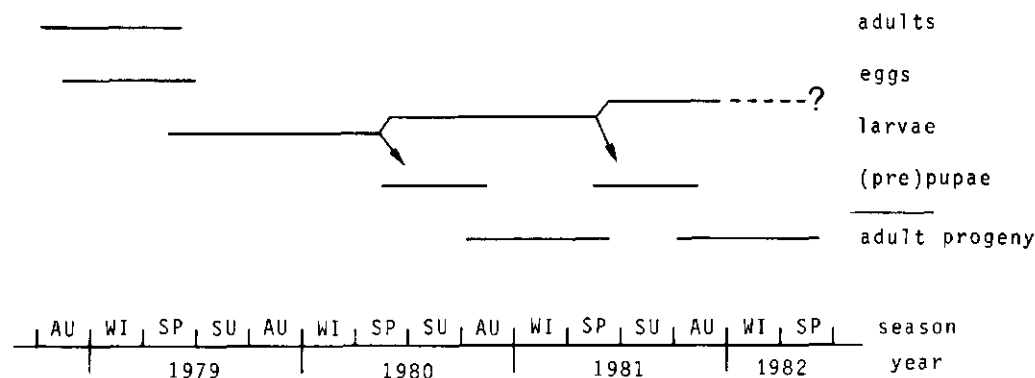


Fig. 16. Outline of development of life stages in *Typhaeus typhaeus*. At the bifurcations arrows indicate larvae changing into the pupal stage, while the continuous line indicates remaining in the larval stage.

Table 8. Numbers of eggs hatching and median time that elapsed before hatching in a rearing trial in glass tubes.

temper- ature (°C)	number of weeks that elapsed until eggs had hatched	number of eggs that hatched	number of glass tubes with egg and dung sausage at start on 28 August 1980
9°	3	5	7 - 8
13°	3½	44	39
17°	2½-3	5	3
20°	2 - 2½	5	3

cold period, although not a prerequisite, certainly favours the completion of the life cycle. The single beetle that emerged from a cage without a cold spell appeared in the same period as those from the cages subjected to a cold interlude (table 6).

Of the 13 beetles that emerged, six were females and seven were males: a 1:1 sex ratio.

From these results it can be inferred that soil temperatures in the field ranging from 3–10 °C in early spring to 13–16 °C in summer, favour reproduction and the development of the larvae.

Two other experiments in cages were carried out in early spring 1979, one at 5 °C and one at 9 °C. These will be reported in another paper. In June 1979, when reproduction in these experiments was over, the cages were taken to rooms in which constant temperatures of 13 °C or 17 °C, respectively, were maintained. Thenceforth these cages were exposed to the same treatments as those in the above-mentioned rearing trials, including the division into groups that did or did not receive the cold period. Data on pupal chambers and the beetles that

emerged are given in table 9. The results clearly confirm the conclusions already reached regarding sex ratio and effect of a cold spell on rearing results.

Rearing trials continued (1980–1981)

As mentioned before, in cages at 5 °C, the eggs had not hatched after 20 months. The two cages at 9 °C, one of which had received a cold winter period, were kept at 9 °C until 20 months had elapsed from the start of the rearing trials. By that time they contained three and one live larvae in pupal chambers, respectively. It may thus be surmised that even at such a low temperature adult beetles might have emerged after a (new) cold period.

Since the results of the 13 °C and 17 °C treatments of the three trials were similar and, moreover, the beetles emerged in the same period (tables 6 & 9), those cages that apparently still contained life after the period of emergence of the beetles, were pooled and subsequently divided into four groups for continued rearing. Two of the groups were subjected to a cold period at 5 °C from 5 November 1980 to 23 January 1981. This was done in such a way that after the rearing trials were completed all four combinations of 0 to 2 cold periods had been realized, as outlined in fig. 17. The results are given in table 7.

A beetle emerged from almost all pupal chambers in cages subjected to a cold period for the first time (23 beetles out of 27 pupal chambers). In cages that had already received a cold period during the 1979–1980 part of the rearing trials, only two pupal chambers remained in which the larva had not pupated. During the 1980–1981 part of the rearing trials this small number rose to six and, when subjected to a second cold period, a beetle emerged from five of

Table 9. Rearing results from two additional experiments. Data on left of columns pertain to glass cages that had not received a cold period. Data on right of columns pertain to glass cages that did receive a cold period.

additional experiment (13°C)	15	0	-	30 IX 1980	} $\chi^2 = 42.00^{***}$ ($P < 0.005$)	}	14 : 13
additional experiment (17°C)	8	2	25 IX 1980				} $\chi^2 = 10.43^{***}$ ($P < 0.005$)
	9	9	25 IX 1980				

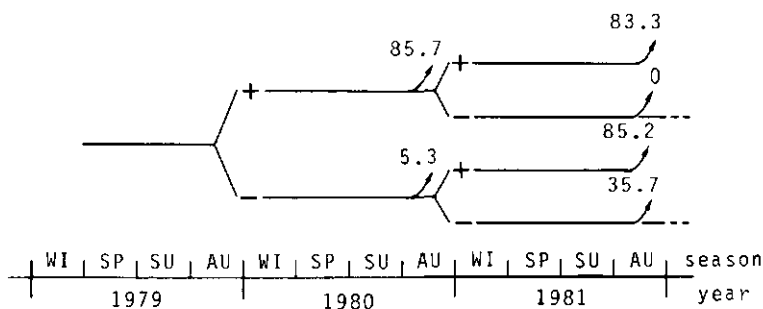


Fig. 17. Cold spell at 5 °C (+) or no cold spell (-; constant temperature of 13 °C or 17 °C) administered in rearing trials during 1979—1981 and percentages of adults emerging. Percentages pertain to numbers mentioned in Table 6, columns 8 and 12, and Table 7, columns 4 and 5.

these six pupal chambers. But in the cages not subjected to a second cold period no beetles emerged from the seven pupal chambers. Few beetles emerged from cages that received no cold treatments (five beetles from 14 pupal chambers). As in 1979—1980, the number of beetles that emerged after a cold period during the 1980—1981 part of the rearing trials differed very significantly from the number that emerged from cages not subjected to a cold period ($\chi^2 = 20.12^{***}$, $P < 0.005$).

Of the 33 beetles emerging from the cages in 1981, 18 were males and 15 females, which confirms the 1 : 1 sex ratio found the previous year. All twelve larvae remaining after the 1980—1981 part of the rearing trials were in their third instar (head capsules 4.6—5.2 mm).

Development of larvae in the field

Evidently, the quantity of cold that larvae of a given generation experience in the field during winter will differ because of the differing depths at which eggs are laid in the soil and because some winters are more severe than others. In general, the larvae occurring closest to the surface will experience more cold in winter and more heat in summer, which may accelerate their development vis-à-vis that of deeper larvae. To test this, five cages were dug into the soil in the study plot at Wijster in November 1979, in such a way that their upper edges just reached the surface.

At the beginning of March 1980 a pair of dung beetles and ample dung were introduced into each cage. The beetles were prevented from exchanging with the surrounding field population by wire-netting placed over the cages' walking surface. The cages were dug out at the

beginning of September 1981, by which time larvae that had completed their life cycle could be found as newly hatched but not yet emerged beetles; in addition, this was also the right time to check whether, as expected, some of the larvae had not yet completed their life cycle. The five cages proved to contain 39 dung sausages. In eleven of these a living larva was found, one of which was in a pupal chamber. All larvae were in the third instar (head capsules 4.5—5.0 mm). In addition, one newly hatched beetle was found. Though this is minimal evidence, the trial does demonstrate that under field conditions larvae of the same generation may give rise to adult beetles in different years, assuming, of course, that some of the remaining larvae would complete their life cycle in the future, as occurred in the laboratory rearing trials. Interestingly, the cage with the adult beetle also contained a larva in the pupal chamber and some other larvae, still in dung, which shows that different rates of development may occur in the offspring of one pair of beetles.

The results of another field trial, executed in the same period, enable a judgement to be made about whether the poor survival obtained in the above-mentioned field trial (life in 12 out of 39 cases = 31%) was somehow induced by the glass cages. In this trial five pairs of beetles were released in enclosures measuring 2 × 2 m², at the beginning of March 1980. Their nests were dug up in May and June 1981, i.e. about three months earlier than the cages. There proved to be 32 dung sausages, 14 of which (i.e. 44%) contained a living larva; three of them had already made a pupal chamber. Assuming some mortality in the enclosures between May/June and September, the data suggest that there was

no difference in survival between the enclosures and the cages. Thus there is no evidence that the cages have a detrimental effect on survival.

Conclusions on rearing

The results from the rearing trials imply that the development of the larvae is very slow at 9 °C as compared with that at 13° and 17 °C. The latter temperatures closely approximate those in soil during summer. Some larvae pass through the life cycle at constant high temperature (17 °C). But the proportion of larvae that develop into adults is greatly improved by a cold period in the third larval stage. This condition matches to a varying degree the low soil temperature during winter. Depending on the experience of a cold winter period, larvae of the same generation and even from the same pair of beetles may give rise to adults in different years. So the life cycle may last three instead of two years and perhaps even longer. This variation in the duration of the life cycle enables genetic exchange between reproductive pools to be passively achieved in successive years.

Longevity of adults

Genetic exchange between reproductive pools in successive years might also be achieved if adult beetles reproduced more than once. This is unlikely to be the case in *T. typhoeus*, since in all laboratory trials executed at a temperature above 5 °C and in all the field trials, the beetles died shortly after reproduction. In many insect species, the dissection of females starting repeated reproduction reveals the presence of yellow bodies (corpora lutea) at the terminal ends of the ovarioles; these are the remnants of the follicular epithelium, which degenerates after egg release (Krehan, 1970; Vlijm & Van Dijk, 1967). To investigate whether yellow bodies are formed and can be found in *T. typhoeus*, adult females were collected in the course of their active period and subsequently dissected. Moreover, females from several experiments that died after reproduction were dissected. Of 14 females that died after reproduction, three proved to possess corpora lutea. This indicates that in *T. typhoeus* yellow bodies are not always formed to an extent that they can be recognized. Of 52 females, captured in the field in the course of the season, eight possessed distinct corpora lutea and three only a vague indication of these. These eight females were captured late in the season (May and June). Obviously, it was not known whether these females were on their

way to aestivate or to die.

Clearly, the absence of yellow bodies does not allow conclusions to be drawn about repeated reproduction, and only if their presence is established at the onset of the reproductive period can these bodies be used as indicators of repeated reproduction.

Therefore, an experimental approach was followed. A trial to have beetles aestivated and let them reproduce in the following activity period was executed twice. From May 1979 onwards, 60 beetles, captured when newly emerged in October and November 1978, were kept in plastic jars (13 cm deep, 10 cm in diameter; one beetle per jar) containing moist sand at a temperature equal to that measured in the study plot at Wijster 20 cm below the surface. Natural daylength was applied. The beetles were regularly supplied with fresh rabbit dung. Of the 60 beetles, 25 had survived after reproduction (13 males and 12 females) before May at a constant temperature of 5 °C. The other 35 (23 males and 12 females) had been kept at 5 °C in the jars since their capture. By 2 August 1979 all the beetles had died except for two males (one male from each group). Shortly thereafter the temperature-regulating equipment in the laboratory broke down and the beetles died from heat.

In 1980, 25 beetles that had not reproduced but that had been kept in plastic jars at 5 °C since their capture in autumn 1979 were used in a trial. No beetles that had already reproduced were available. In mid-March 1980 these 25 beetles were divided into four groups: staying at 5 °C (three males, one female); 9 °C (six males, three females); 13 °C (five males, one female); and 17 °C (five males, one female). By 1 July all the beetles kept at 9°, 13° and 17 °C had died; two males at 5 °C were still alive. These two males survived and were given the chance to pair with two fresh females in glass cages on 27/28 November 1980. One male died on 2 December without having reproduced, the other died on 15 December after the female had laid a few eggs.

From the results of the dissection and of the trials, it can be concluded that aestivation of adult beetles and repeated reproduction in *T. typhoeus* is very exceptional, if indeed it occurs. Most of the beetles die after the first reproductive season. Thus the contribution to genetic exchange between reproductive pools in successive years by means of survival of adults is virtually non-existent.

DISCUSSION

Influence of glass cages on behaviour
and results of rearing

Although the behaviour of the beetles seemed normal, the narrow space in which they were confined may have influenced their behaviour. Tables 3 & 4 show that there were no major differences in the depth of the shaft and number of dung sausages between beetles kept in the laboratory and those kept or found in the field. Moreover, the number of dung sausages produced in the present trials was very comparable with figures reported in the literature (tables 2 & 4). As reported in the section on the development of eggs and larvae, the survival of larvae kept in glass cages dug into the soil and kept in enclosures in the field was similar. This confirms that glass cages do not adversely affect the behaviour of the beetles.

Pheromones

There are few data on settlement and pair formation in the literature. Halffter & Matthews (1966), in their extensive review of the biology of Scarabaeidae, assume that the sexes meet by chance near the dung patch. In addition to the case of *Typhaeus biostius* mentioned earlier (Crovetti, 1971), the intrusion of a male into a female's feeding burrow and joint feeding until sexual maturity, is also reported by Rommel (1961) in *Copris hispanus* and by Halffter & Lopez (1977) in *Phanaeus daphnis*. The hypothesis of pheromone communication in *T. typhoeus*, tentatively suggested in the present paper, is supported by reports that in Scarabaeidae some dung patches are densely populated with beetles, whereas others are not, and that the densely populated dung patches often differ from each other in the taxon that is most represented (e.g. Halffter & Matthews, 1966; Paschalidis, 1974). A similar clustered distribution is known in bark beetles (Scolytidae), and this is known to be caused by aggregation pheromones (Blight et al., 1980). By analogy, pheromones may be important in dung beetles, too. Moreover, the stance adopted by the male *T. typhoeus* during the supposed pheromone release is virtually the same as that described by Paschalidis (1974) in three scarabaeid *Sisyphus* spp. and by Tribe (1975) in *Kheper nigroaeneus*. In the latter case pheromone release was proved. In *Kheper* the pheromone is released from a depression on either side of the first abdominal sternite, with the help of paraffin tubules as a

carrier. This is very different from the way the pheromone is supposed to be released by *T. typhoeus*, i.e. along with the excrement. The latter mechanism is also known for other groups, e.g. in bark beetles, boll weevils and some Orthoptera (Jacobson, 1972). If properly supported by additional research, pheromone release by *T. typhoeus* would constitute the first known example of pheromone communication in Geotrupidae. The conformity in releasing stance and the difference in releasing mechanism point to a convergent development and may be added to arguments in favour of the modern view of classifying scarabaeids and geotrupids in distinct families (Crowson, 1967, 1981) instead of in subfamilies (Halffter & Matthews, 1966).

In all cases the pheromone release stance has so far only been described in male dung beetles. The possibility should not be excluded, however, that after maturation feeding the male is also attracted to his first female by means of pheromones. Fabre (\pm 1910) had already noticed that at times two or three males of *T. typhoeus* can be found in a burrow with only one female. Teichert (1955) observed the same in *G. mutator* and from this he inferred that males were attracted by pheromones released by the female. This would certainly improve the female's chances of mating. It has been stated by Halffter & Matthews (1966) that the similar size of the antennal clubs in almost all male and female dung beetle species is a sign of the unimportance of pheromone communication in these beetles. But this argument does not hold if both sexes respond to pheromones.

Burrowing

One may wonder how much faster the female progresses in the burrowing stage thanks to help from the male. The gain is estimated by Teichert (1957) to be one-fourth to one-third of the excavation time.

Co-operation between male and female in the burrowing phase is not so close in some species as it is in *T. typhoeus*. It is marked in the relatively deep burrowing species *Geotrupes vernalis*, *Lethrus apterus* and *Typhaeus biostius*, whereas in the shallow burrowing species *G. mutator*, *G. stercorarius* and *G. spiniger* the male does little more than remove some soil from the entrance (Teichert, 1955, 1959a, 1959b; Crovetti, 1971).

According to Klemperer (1979), in *G. spiniger* the female stops excavating the shaft and the brood chamber as a response to their length.

Behaviour preceding and following oviposition

Oviposition in *T. typhoeus* is almost always preceded by copulation. According to Weaver & Pratt (1977) repeated copulation has a stimulating influence on the reproductive effort in the cockroach *Periplaneta americana*. This is probably why a female of *T. typhoeus* that has lost the male continues reproduction much more slowly.

During the backward scraping activity that follows oviposition, the beetle presses its head and thorax hard against the walls of the brood chamber, possibly to make the walls resist the pressure they will be subjected to when being provisioned with dung. Although he did not observe the pressing behaviour, Fabre (\pm 1910) noticed that the walls of the brood chamber were smoother than those of the shaft.

Dung provisioning

One may wonder how the male orients himself on the surface, when dragging a dung pellet to the nest entrance. Kuyten carried out some unpublished experiments in 1961/62 from which he concluded that the position of a light source provides the beetle with a directional cue. The same conclusion was independently reached by Frantsevich et al. (1977) after some very similar experiments with *Lethrus apterus*. But it has not yet been explained how *typhoeus* takes its bearings by night or on cloudy days, when most of the excursions for dung are made.

Sealing and excavating brood chambers

Klemperer (1979) states that in *Geotrupes spiniger* sealing a dung sausage is a side-effect of excavating the next brood chamber. In *Typhaeus typhoeus*, however, at the start of sealing the sand is scraped from the wall and firmly pressed into the shaft above the dung sausage. Moreover, the last dung sausage is invariably sealed; this is also evidence of a distinct behavioural phase.

In the endemic Sardinian species *Typhaeus biostius*, which closely resembles *typhoeus* both in its biology and in the reproductive season, the sequence of excavation of brood chambers is remarkably different. Contrary to *typhoeus*, *biostius* constructs the uppermost dung sausage first, at about 60–70 cm below the surface, and every subsequent sausage is 10–15 cm deeper, the completed burrow generally reaching a depth of 1.30–1.60 m. As a result, under field conditions some weeks after the nest has been

completed the uppermost dung sausage already contains a larva III, whereas the egg belonging to the lowest dung sausage has not yet hatched (Crovetti, 1971). This behavioural sequence may well be related to soil moisture conditions (Crovetti, pers. comm., 1981), the female beginning to lay eggs approximately at ground-water level and then deeper as the water table falls. The ultimate function of this sequence may be to ensure that eggs and larvae do not dry out during the hot summer.

In *T. typhoeus*, however, the risk of drying out may be considerably lower. In this species, laying the first egg approximately at ground-water level and thenceforth more shallowly may ensure that the larvae and their dung sausages do not become waterlogged during the next winter. In this context it would be interesting to study the behavioural sequence in *typhoeus* in the southern part of its geographical range.

Emergence through soil

The way the beetle moves to the surface is seldom mentioned in the literature. Sano (1915/16) reports that *Geotrupes stercorarius* does not always use the original tube made by the parents, but makes its own route, as described for *Typhaeus typhoeus* in this paper. Crovetti (1971) reports that *T. biostius* breaks through the partly eaten dung sausage and the sand that seals it and follows the shaft made by the parents. The evidence available for *T. typhoeus* (this paper) and for *T. biostius*, suggests that the newly hatched beetle starts moving upwards at a place where the resistance from soil is least, i.e. through the remnants of the dung sausage. However, it seems to be luck, rather than strategy, whenever the beetle finds the open part of the parental shaft. Emergence through soil thus seems to be the rule.

Behaviour as a reaction chain

According to Klemperer (1979) the nesting behaviour of *Geotrupes spiniger* can be described as a reaction chain in which each action generates its own terminating stimulus and initiates the subsequent response. Although experimental analysis is beyond the scope of the present paper, the nesting behaviour of *T. typhoeus* is in many respects very similar to that of *G. spiniger*. In addition, the way in which the stretch of the burrow that is to be filled with sealing sand is determined in *T. typhoeus* (fig. 11) is an example of an action that generates its own terminating stimulus. So it may well

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CHAPTER 3

"Unfortunately, our understanding of biogenic structures in modern and ancient (...) nonmarine deposits lags far behind".

M.F. Miller et al., 1984.

Journal of Paleontology 58: 283-598.

RECENT AND ANCIENT TRACES OF SCARAB BEETLE ACTIVITY IN SANDY SOILS OF THE NETHERLANDS

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ABSTRACT

Brussaard, L. and Runia, L.T., 1984. Recent and ancient traces of scarab beetle activity in sandy soils of The Netherlands. *Geoderma*, 34: 229–250.

Traces of burrowing activity by the scarab beetle *Typhaeus typhoeus* in sandy soils of The Netherlands are described. These traces include mounds of sand deposited on the surface and open and back-filled burrows in the soil. Other back-filling traces are described from two types of sandy soil in The Netherlands. By analogy with the traces from *T. typhoeus* these are interpreted as resulting from scarab beetle activity.

Preliminary measurements have been made of the amounts of soil deposited on the surface by *T. typhoeus*. In favourable habitats the quantities are as high as 450 kg ha⁻¹ annually.

The disturbance of sandy soil profiles by scarab beetles is calibrated by their back-filling traces with the help of literature data on fossil beetle remains and original data on clay illuviation. The disturbance is shown to be mainly of Preboreal and post-Atlantic age.

Clay configurations in back-filling traces associated with lamellae support the contention that the lamellae were formed by clay illuviation.

INTRODUCTION

This paper describes traces of activity from scarab beetles living in sandy soils of The Netherlands. To date no mention has been made of the conspicuous, locally abundant and probably most persistent of those traces, viz. the traces of back-filling of burrows by the beetles. We will utilize the back-filled burrows to calibrate the disturbance of the soil by the beetles.

Biological homogenization, i.e. the reworking of soil by animals resulting in the disruption or obliteration of soil lamination was described as an

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important process in soil formation by Hoeksema and Edelman (1960). Recently, interest in the effects of animals on soil has been growing (Hole, 1981; Bal, 1982; Hoogerkamp et al., 1983). Scarab beetles or their larvae, however, have only rarely been mentioned. For example, traces from the June beetle, not specified in detail, are mentioned by Ahlbrandt et al. (1978) as common and abundant, respectively, in two out of eleven inland dune fields in the U.S.A. Valiachmedov (1977) mentioned scarab pupal chambers as traces in Sierozem soils in the Soviet republic of Tadzhikistan, and Ratcliffe and Fagerstrom (1980) report the open burrows of scarabs as traces.

Finally, Kalisz and Stone (1984) measured the mixing of sandy soils of north-central Florida (USA) by scarab beetles.

This paper is the second of a series evaluating the contribution of scarab beetles to the past and present genesis of sandy soils.

TRACES OF ACTIVITY FROM THE DUNG BEETLE *TYPHAEUS TYPHOEUS*

We have chosen the dung beetle *Typhaeus typhoeus* (Linnaeus, 1758) as a model trace-making scarab beetle, because it burrows down to 1 m and in some cases even deeper. *T. typhoeus* is associated with sandy soils, as are most scarab beetles of its kind.

Fig. 1 schematically shows the results of the activity of a pair of dung beetles in the soil. The behaviour of the beetles has been described by Brussaard (1983).

A "trace" has been defined as "an individually distinctive biogenic structure, especially one that is related more or less directly to the morphology of the organisms that made it: tracks, trails, burrows, coprolites, fecal castings and similar features, fossil or recent" (Frey, 1973). Among the most conspicuous, though ephemeral, traces of activity are the sand mounds on the soil surface, measuring approximately 5 cm in height and 10–15 cm in diameter. They arise when the beetles push up the sand while excavating a burrow for nesting. If the soil profile is known, the composition of the mound gives a rough indication of the depth the beetles have reached.

The number of mounds in 37 plots measuring 25 m² each in heathland with a sparse and low vegetation near Maarheeze (southern part of The Netherlands) was found to be as high as 40 but commonly around 7 per 25 m² in 1975. Extrapolation yields a number of 2800 mounds ha⁻¹.

The amount of sand transported to the surface was 120 ± 22 g per dung beetle nest ($n = 14$) in a 36.75-m² plot near Wijster (northern part of The Netherlands) in 1979 and 163 ± 83 ($n = 8$) in another 49-m² plot near Wijster in 1980. Extrapolation yields amounts of sand deposited on the surface of 457 and 266 g ha⁻¹, respectively.

After the burrow is made, dung is transported from the surface into the soil to provision the brood chamber with food for the larvae. The parent beetles seal in each dung sausage by back-filling the burrow leading to the

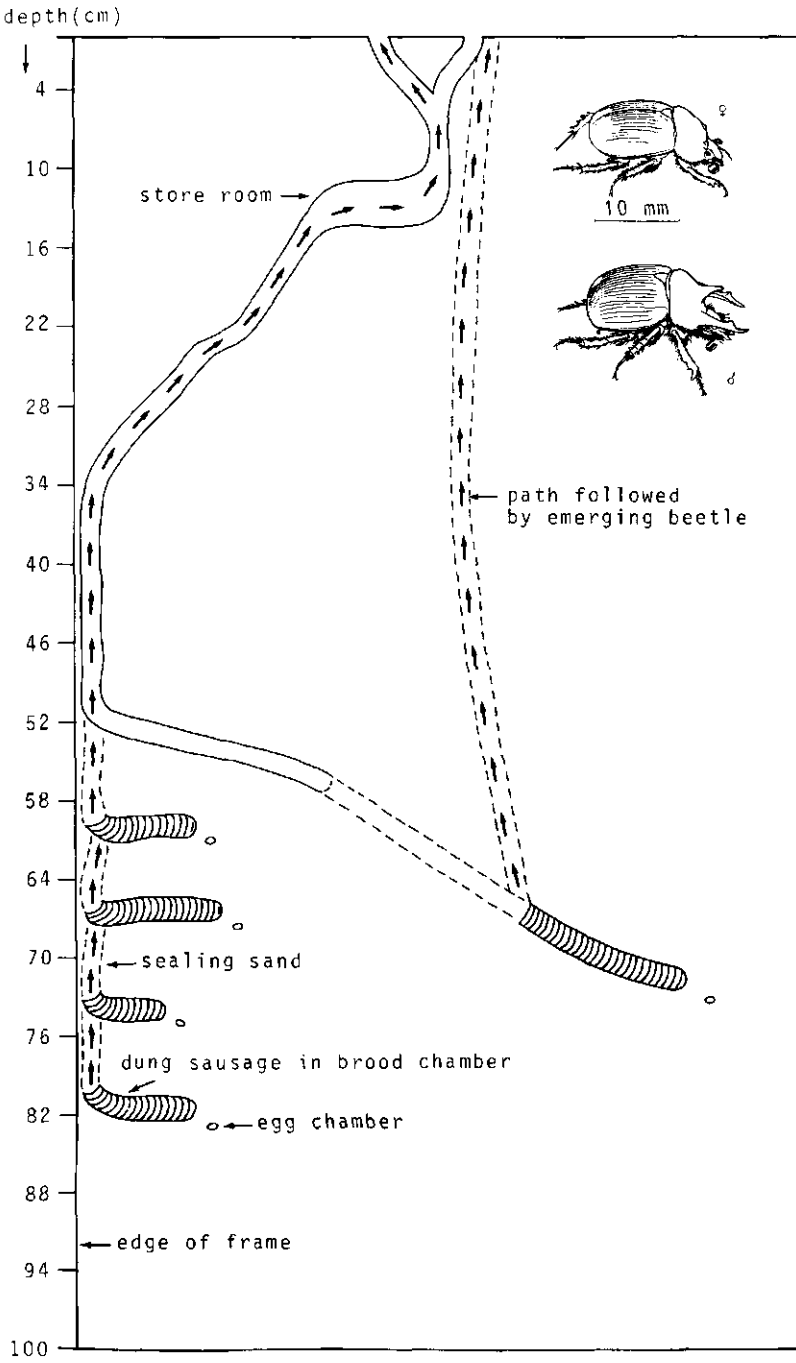


Fig. 1. Nest of *Typhaeus typhoeus*.

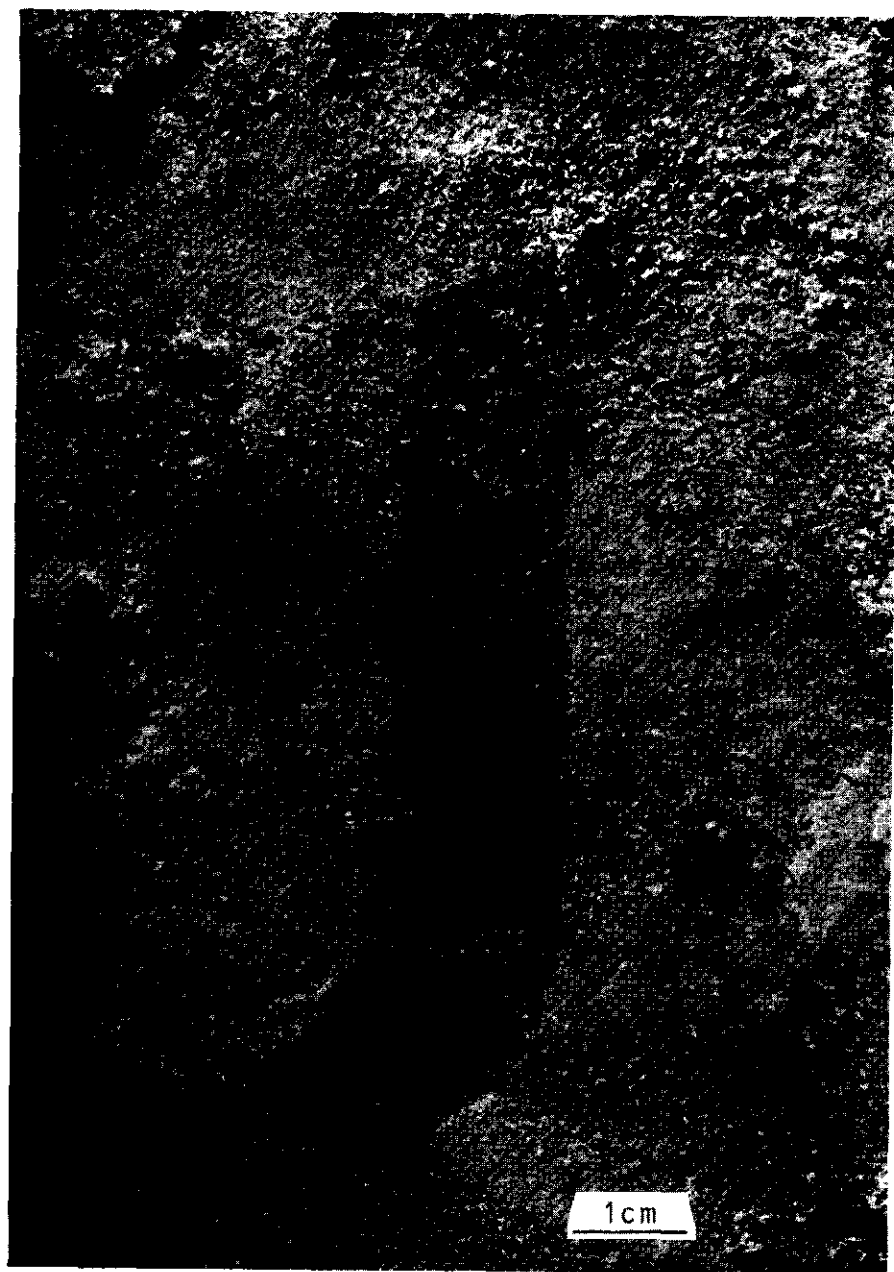


Fig. 2. Back-filled part of a burrow leading to a dung sausage (not visible) of *Typhaeus typhoeus* in a sandy subsoil. In this case the back-filling sand was scraped away from differently coloured horizons higher in the profile, thus accentuating the meniscate infilling.

dung with sand for a distance of several centimetres. A meniscate layering results from the firm packing movements of the beetles (meniscate = resembling a crescent-shaped body). The meniscate layering is accentuated when the sealing sand is alternately scraped away from differently coloured horizons nearer the soil surface (Fig. 2). Back-filling traces also come about when the newly hatched adults make their way to the surface through the soil. This has been observed in rearing cages with glass walls in the laboratory (Brussaard, 1983).

After sealing the uppermost dung sausage the beetles leave the remaining part of the shaft open for a distance averaging 40 cm. The number of open burrows at a depth of 15 cm may be as high as 50 m^{-2} (Fig. 3) and is thus considerably higher than the number of sand mounds at the surface.

In contrast to the sand mounds, the back-filled burrows and, presumably to a lesser degree, the open burrows, persist in the soil as traces.

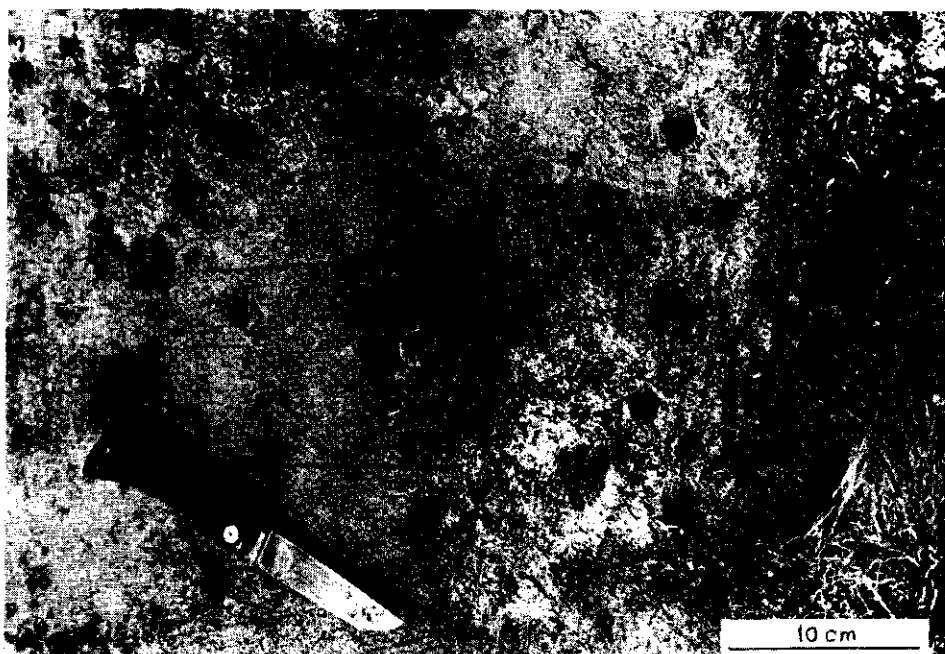


Fig. 3. Open *Typhaeus typhoeus* shafts at a depth of 15 cm below the surface.

ORIGIN OF BACK-FILLING TRACES IN SANDY SOILS

The stratification in sandy soils is often disturbed below 70 cm by finger-wide streaks, usually vertical, but sometimes oblique or horizontal. Evidence that these are back-filling traces from scarab beetles will be presented, following some details about the soils in which we have found the traces.

The features are most conspicuous in two types of sandy soil. Firstly, the

profile shown in Fig. 4. This is a Humic Podzol (FAO, 1974), overlain by a thin layer of drift sand.

The parent material is aeolian Cover Sand. From the lower part of the profile to approximately 125 cm below the surface this is Younger Cover Sand I, deposited during the Earlier Dryas, a Late Weichselian stadial lasting

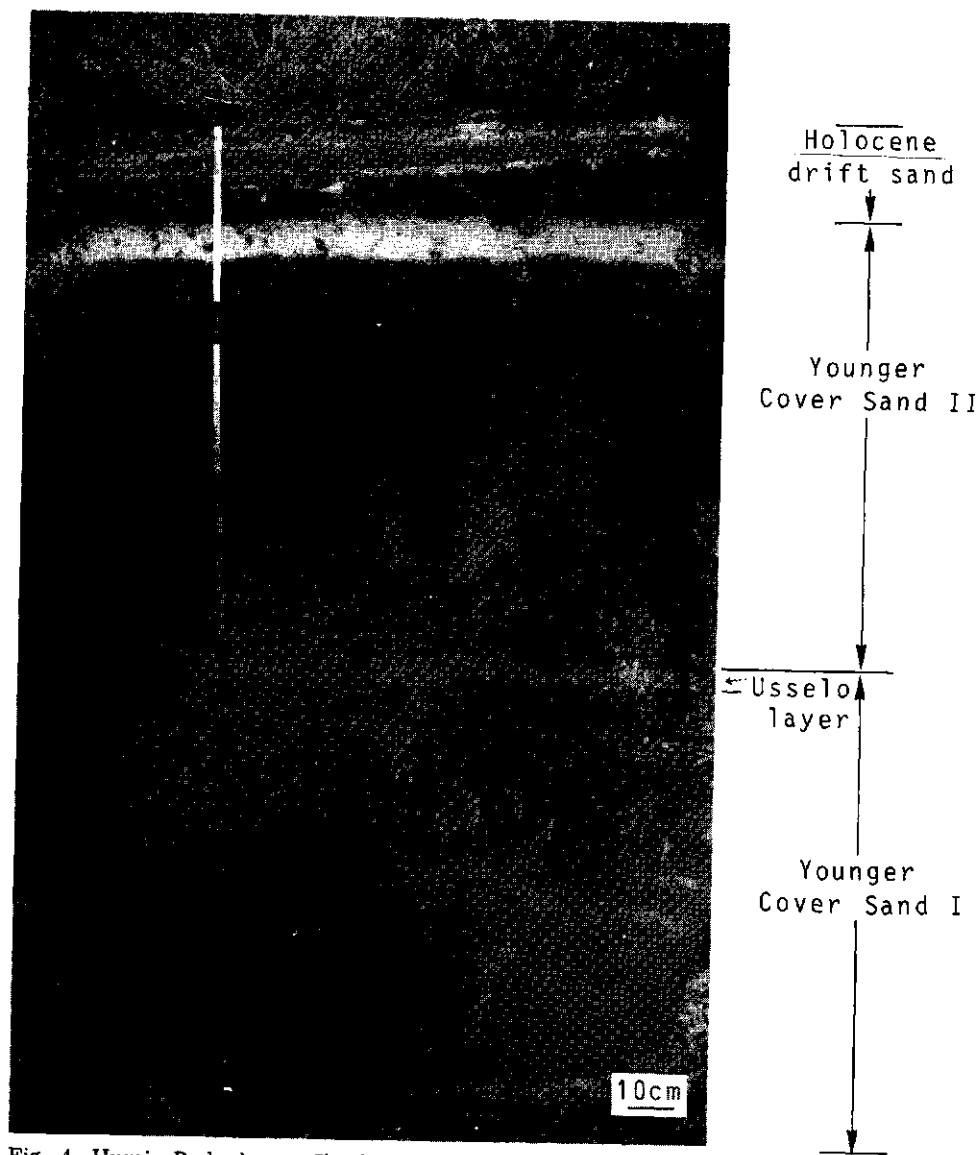


Fig. 4. Humic Podzol near IJsselstein, The Netherlands (coordinates topographical map 386,500/190,900). The vertical or oblique whitish streaks are back-filled scarab beetle burrows. For further explanation see text.

from 12,000 to 11,800 BP (Zagwijn, 1975). Between 125 and 25 cm below the surface is the Younger Cover Sand II, deposited during the Younger Dryas, a Late Weichselian stadial lasting from 11,000 to 10,000 BP (Zagwijn, 1975). Up to 25 cm below the surface the sand is humic Holocene drift sand. The Podzol that developed in the Younger Cover Sand II is of Holocene age.

Approximately 125–130 cm below the surface is a pallid layer, the so-called Usselo layer, which developed during the Alleröd period (11,800 to 11,000 BP), an interstadial phase of no sedimentation (Van der Hammen, 1951; Hipszeler, 1957).

The Cover Sands were deposited with a horizontal or, in some places, a criss-cross stratification (Van der Hammen, 1951; and pers. comm., 1984). The stratification below 70–110 cm is locally disturbed by the finger-wide streaks, which we studied (whitish in Fig. 4). Three lines of evidence indicate that these are back-filling burrows from scarab beetles. Firstly, their diameters ($14.0 \text{ mm} \pm 1.5$, $n = 50$) are virtually the same as those of recent traces made by *Typhaeus typhoeus* (14.2 ± 0.7 , $n = 12$) (Brussaard, 1983). Secondly, their infillings are clearly meniscate (Fig. 5).

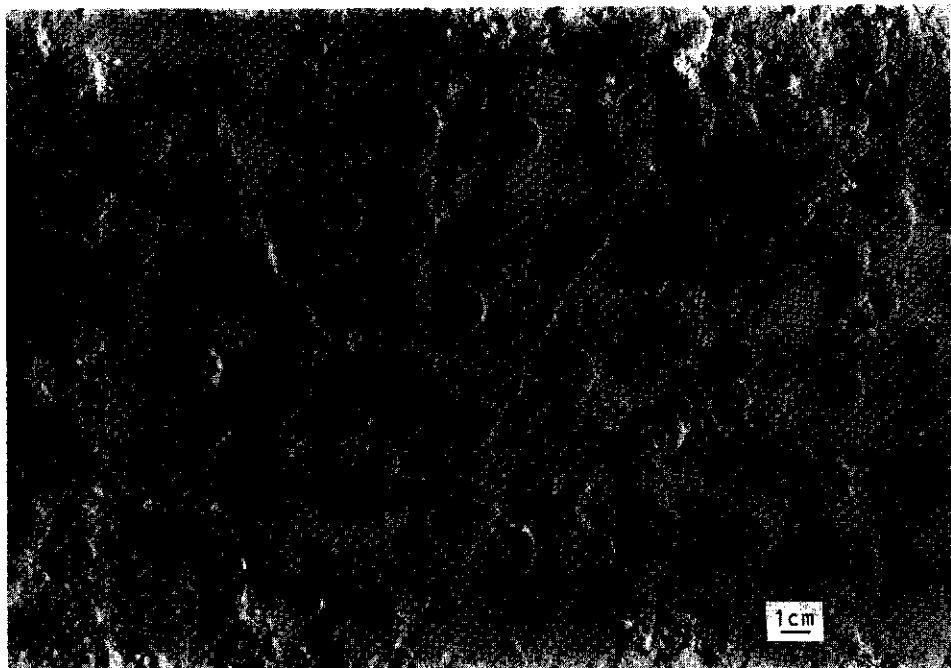
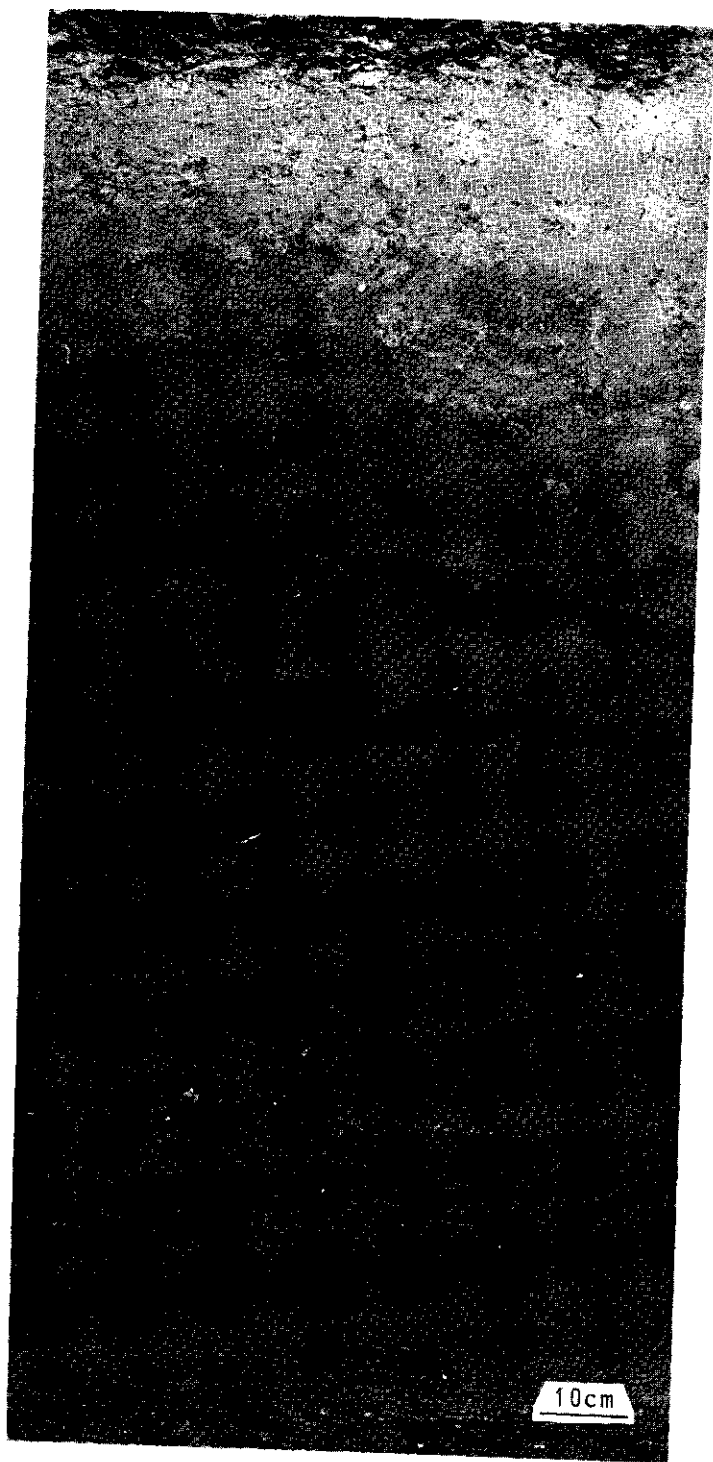


Fig. 5. Horizontal cross-section at 1.20 m below the surface through a profile similar to that in Fig. 4. Near Venray, The Netherlands, coordinates topographical map 396,275/194,500. Note meniscate layering within the burrow and uniform diameter of burrows. (The contrast with the soil matrix has been accentuated by fixation in the soil peel.)



Thirdly, they only rarely branch. The Usselo layer is characterized by various amounts of small pieces of charcoal. Charcoal is also present in the traces above and below the Usselo layer, indicating that they are filled with translocated Usselo sand. The Usselo layer with the traces has been observed from Denmark south to Belgium and eastwards to Poland (Chmielewska and Chmielewski, 1960, cited in Van der Sluijs and Maarleveld, 1963) wherever the overlying Younger Cover Sand II is thick enough to have prevented the Usselo layer from being obliterated during Holocene pedogenesis. Where the Usselo layer is present the traces are seldom absent. The traces can be inferred by analogy from photos in several publications showing the Usselo layer: Van der Hammen (1951), Hijzeler (1957), Maarleveld and Van der Schans (1961).

The second profile showing the features considered to be back-filling traces is developed in sands of the rivers Rhine and Meuse (Fig. 6). It has been classified as a Leptic Podzol (FAO, 1974). It consists of cross-bedded, stratified, fluvial sand with gravel lenses, overlain from 1.05 m upwards by terrace sand, reworked by wind during the Late Weichselian. In this type of soil lamellae are much in evidence. Lamellae are "subsoil layers which contain more clay than the layers above or below them" (Dijkerman et al., 1967). The lamellae are disturbed by predominantly vertical finger-wide streaks. Here again, their diameters ($14.2 \text{ mm} \pm 1.3$, $n = 12$) are virtually the same as those of *Typhaeus* back-filling traces, their infillings are clearly meniscate and they only rarely branch.

We have also observed such traces in The Netherlands near Lochem (coordinates topographical map 462,100/220,000) where lamellae have developed in the aeolian Cover Sands. One of us (LB) also observed the traces in sandy soils with lamellae in the Nyirseg region in eastern Hungary in 1981. Similar traces can be inferred by analogy from photos published by Tüxen (1964) of profiles with lamellae in West Germany.

Lamellae are well known from various parts of the U.S.A. (Dijkerman et al., 1967) but to date we have not seen any reports of back-filling traces left by scarab beetles in sandy soils of the U.S.A. Such traces can be inferred by analogy, however, from figs. 6 and 7 in Dijkerman (1965), which are photos of profiles developed in very fine sandy loam and loamy fine sand in Orleans County, New York. We also suspect that Plate 4A, an Alfic Udipsamment, in Soil Survey Staff (1975) shows the traces.

AGES OF BACK-FILLING TRACES IN SANDY SOILS

In this section we shall try to date the traces and calibrate the disturbance of the sandy soils by the beetles.

Fig. 6. Leptic Podzol in river terrace sand near Geysteren, The Netherlands, coordinates topographical map 395,000/201,600. Note lamellae, disturbed by back-filled scarab beetle burrows. For explanation see text.

Circumstantial evidence indicates that most of the traces described in the preceding section are ancient. Firstly, in the profile of Fig. 4, with traces below the Podzol, the Podzol itself is largely intact, whereas it could be expected to be disturbed by back-filling traces if the scarab beetle activity were recent. Secondly, the vegetation on soils with traces is often too dense for scarab beetle activity nowadays.

More conclusive results on the ages of the back-filling traces follow from two more lines of evidence, which will be discussed below.

Evidence from fossil beetle remains

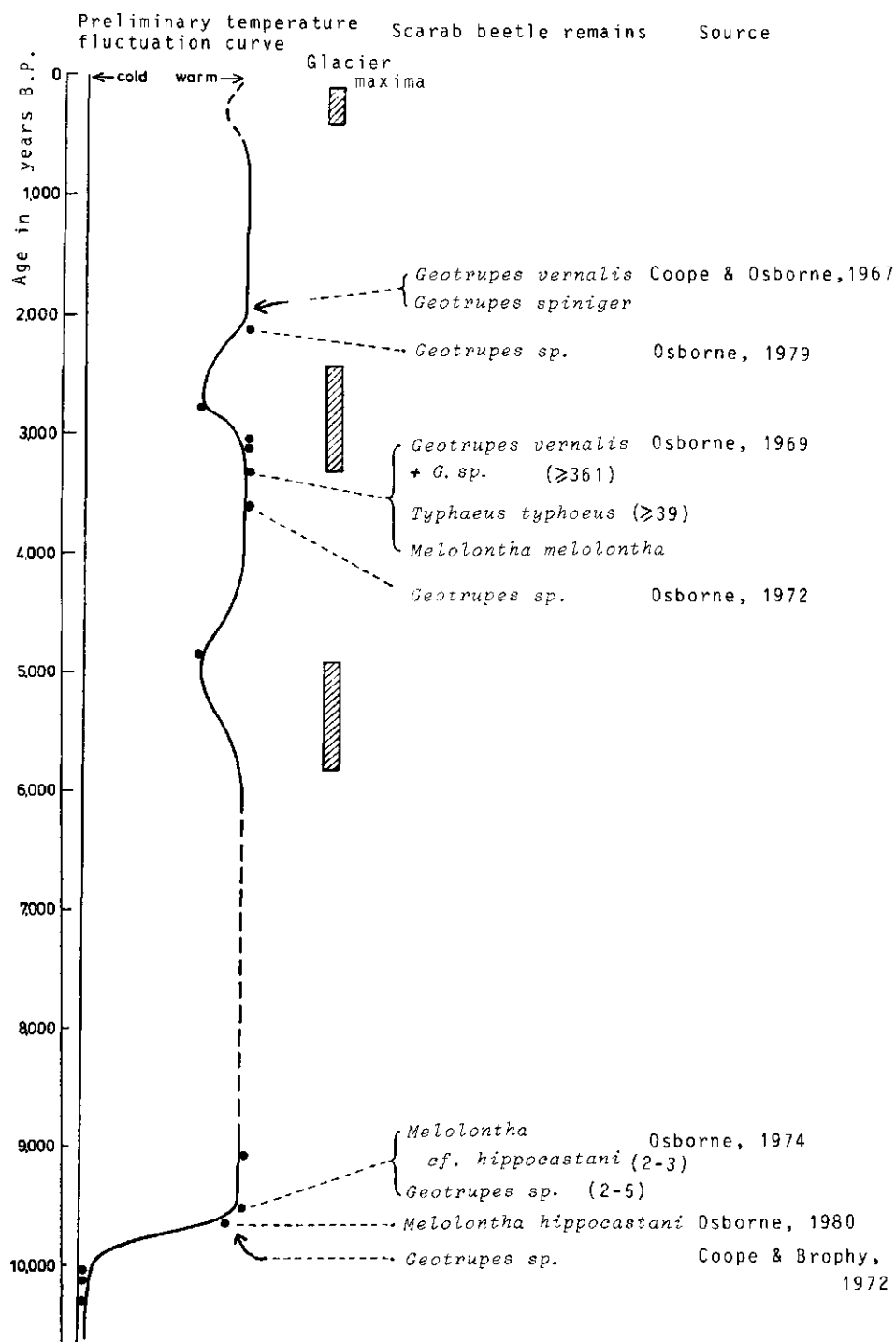
A suitable environment for larger herbivores, on which dung beetles of the size of *Typhaeus* or *Geotrupes* are dependent, has been present in northwest Europe since at least c. 5000 BP, i.e. from the Atlantic onwards. From that time increasing areas were becoming less densely forested, park-like or even open (e.g. Van der Hammen and Bakker, 1971). Finds of beetle remains in ¹⁴C-dated soil samples from several places in Britain support the hypothesis that dung beetles were present during most of this period (Fig. 7). No remains of beetles the size of geotrupids were found from the preceding ages with a forested landscape, the Boreal and the Atlantic (8800–5000 BP) (Osborne, 1972). One of the reasons may be that in general the ground cover was too dense. This is unfavourable for most of the dung beetles (Landin, 1955; Brussaard, 1983; Kalisz & Stone, 1984). The dwindling of populations of larger herbivores during the afforestation of the landscape (Kurtén, 1968) may also have played a role.

In contrast with the Boreal and the Atlantic, remains of scarab beetles the size of geotrupids have been found from the first Holocene period, the Preboreal (Fig. 7), which was initially treeless. One of us (LTR) has observed back-filling traces in a Bronze Age barrow and in postholes in archaeological excavations, suggesting that they were formed in the Subboreal or Subatlantic.

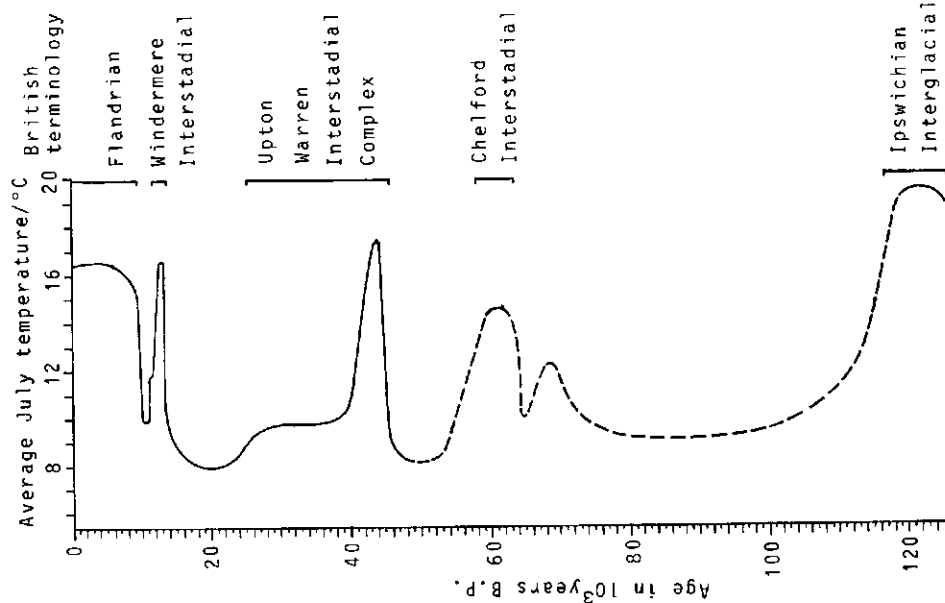
One observation supporting the contention that a number of the traces originated in historical time can be added to Fig. 7. De Bakker (1979) described an anthropogenic soil with an A₁ horizon thickened by age-long use of manure-impregnated sods. Back-filling traces disturb the boundary between the (A₁ + A₂) pb horizon and the underlying horizon. The agricultural practice of gradually raising the A₁ horizon only began some 800–1000 years ago and therefore this type of trace cannot be any older.

In conclusion we infer from the available data that the back-filling traces

Fig. 7. Climatic variation during the Holocene and finds of remains of large scarab beetles. Each dot indicates a ¹⁴C-dated sample. Arrows refer to samples not indicated by dots, which could only be dated approximately. Number of specimens of beetles indicated in brackets, if exceeding 1. Temperature curve from Osborne (1976).



A G E



Fossil scarab beetle remains

European terminology

Source

= Holocene

= Bölling+Alleröd

Geotrupes sp.

Osborne, 1972

= Denekamp

= Hengelo

Geotrupes sp.

Coope, Shotton & Strachan, 1961

Geotrupes sp.

Morgan, 1973

Geotrupes sp.

Coope & Angus, 1975

+ *Geotrupes spiniger**Geotrupes spiniger*
or *G. stercorarius*

Coope, 1959

= Amersfoort

= Eemien ----- *Melolontha melolontha*

Coope, 1974

may well have come about during the Preboreal and from the closing of the Atlantic onwards.

All the back-filling traces we observed were in Weichselian deposits and we now turn to the question of if and when traces were formed during the period preceding the Holocene.

Remains of geotrupid dung beetles have only been found in samples from the relatively warm interstadials (Fig. 8), although the stadials were sampled to the same extent (G.R. Coope, pers. comm., 1981). This fits in well with the rapid decrease towards the present subarctic zone in the number of dung beetle taxa and in the number of places from which they have been recorded (Lindroth, 1960).

Part of the traces described from Fig. 4 protrude upwards from the Usselo layer and, consequently, date from a period later than the Alleröd, i.e. after c. 11,000 BP.

As indicated above, scarab beetles the size of geotrupids probably could not stand the climate during the Younger Dryas stadial, c. 11,000–10,000 BP, which was temperate subarctic and probably had a permafrost (Van der Hammen et al., 1967; Zagwijn, 1975). As corroboration, a soil sample taken in The Netherlands at the type locality of the Usselo layer yielded no sign of geotrupid-like or similarly sized scarabs from the Younger Dryas period (G.R. Coope, pers. comm., 1981). Hence, the traces disturbing the Usselo layer do not pre-date the Holocene Preboreal.

We conclude from the available evidence that the traces of back-filling by scarabs were not formed during the Pleistocene stadials. The traces penetrating the Usselo layer were probably formed during the early Preboreal transitional period to a warmer climate.

Evidence from clay illuviation phenomena

In this section we offer further support for the conclusions reached in the former section by dating the clay illuviation in and around the back-filling traces that are associated with lamellae (Fig. 6).

To discriminate between the relative ages of the back-filling traces associated with the lamellae, we shall distinguish three cases, which, for the sake of convenience, are classified in terms of interpretation:

(1) Traces formed *during* clay illuviation. Under micromorphological examination these traces show plasma with reworked clay (encircled in Fig. 9) plus in-situ (this means without disturbance after deposition) clay (bridge cutans, arrowed in Fig. 9) whereas in the undisturbed lamella only in-situ clay is found (Fig. 10). Reworking is attributed to scarab beetle activity.

Fig. 8. Variations in the average July temperatures in lowland areas of the southern and central British Isles since the Eemian interglacial, in relation to finds of large scarab beetle remains. Some 25 samples were studied from deposits covering the whole Weichsel. Temperature curve from Coope (1977).



Fig. 9. Detail from within a back-filled scarab beetle burrow disturbing a lamella, with skeleton grains, plasma with reworked clay (e.g. encircled part of photo) and illuviated clay in situ (bridge cutans, arrowed). Samples for micromorphological inspection were taken in the vicinity of the profile shown in Fig. 6. Coordinates topographical map 201,425/395,125. Thin section, half-polarized light.

(2) Traces formed *before* the onset of clay illuviation. In the absence of other diagnostic characteristics these are the traces that show no reworked clay when examined micromorphologically. When examined macroscopically, the traces contain an in-situ layer of illuviated clay, distinguishable from the adjacent lamella by being thinner (arrowed in Fig. 6), or by partly or wholly following the meniscate infilling within the trace (Fig. 11, middle and right, respectively).

(3) Traces formed *after* termination of clay illuviation. Under micromorphological examination the clay in these traces shows up as reworked clay only.

In the discussion we shall return to the assumption of a pedogenetic origin of the lamellae.

Our macroscopic and micromorphological inspection of traces associated with lamellae showed that case 1 (beetle activity during clay illuviation) was the most common, followed by case 3 (beetle activity after clay illuviation). Case 2 (beetle activity preceding clay illuviation) was by far the least common.

Since the Eemian interglacial, two climate regimes conducive to clay migration in sandy soils have prevailed at the latitude of northwest Europe

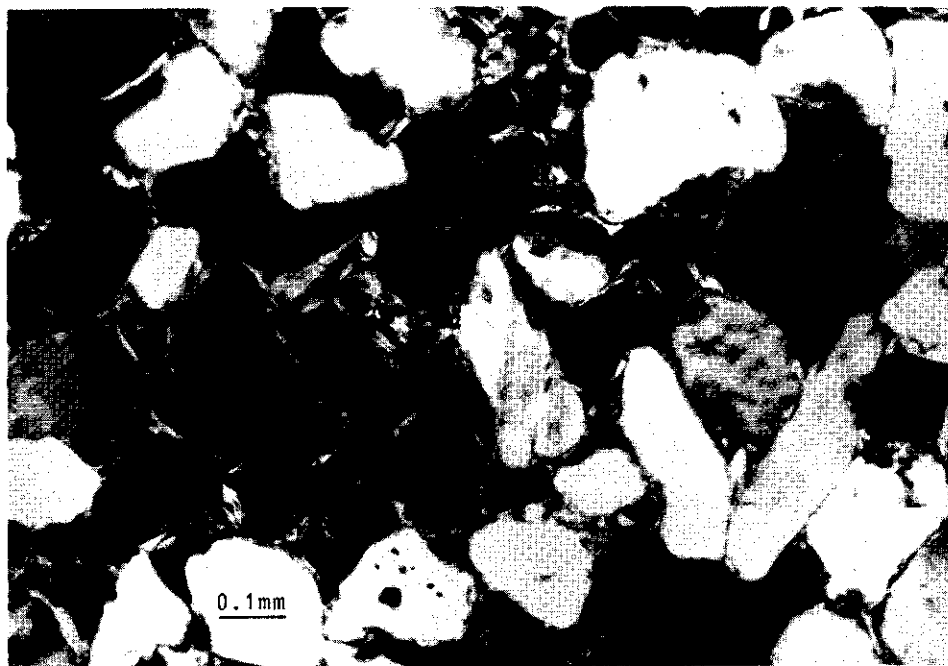


Fig. 10. Detail from within an undisturbed lamella with illuviated clay in situ, not reworked. Compare with Fig. 9. Thin section, half polarized light.

(literature overview in Schröder, 1979). The first, temperate climatic conditions with a forested vegetation during the Boreal and Atlantic, will not have favoured scarab beetle activity, as witnessed by the lack of fossilized beetle remains from those periods (Fig. 7). Hence, coincidence of scarab beetle activity and clay illuviation during those periods seems unlikely. Secondly, clay migration may have occurred in soils under the frigid or cryic temperature regime with periods of sudden snow melt that prevailed during the Alleröd, Bolling and possibly in earlier Weichselian interstadials and during the early Preboreal, whenever the frost or permafrost disappeared from the soil. A reasonable number of fossilized scarab beetle remains has been reported from these periods (see pp. 238 and 241; Figs. 7 and 8).

To conclude, the available evidence points to concomitant clay illuviation and scarab beetle activity during the interstadials of the Late Weichselian and during the early Preboreal. On p. 239 we concluded from the evidence of disturbance of the Usselo layer that scarab beetle activity may well have occurred during the early Preboreal. Further evidence that scarab beetle activity was important in the Preboreal is presented by the profile near Lochem, mentioned earlier on p. 237. It shows Younger Cover Sands I and II, separated by the Usselo layer at a depth of 1.50 m and, moreover, this soil contains lamellae. The uppermost lamella, which had traces in



Fig. 11. Lamella in sandy soil near Horst, The Netherlands; coordinates topographical map 200,100/388,250. Within the extreme right burrow the illuviated clay follows the meniscate layering just below the lamella (see arrow); within the burrow in the centre of the photo part of the clay follows the layering within the burrow (see arrow) and part of it links up with the lamella (see dashed arrow). Scale in cm. For further explanation see text.

this profile, was observed in and slightly above or below the Usselo layer. This clearly points to a post-Alleröd, and hence presumably Preboreal period, of clay illuviation and concurrent scarab beetle activity.

Conclusions

The back-filling traces preserved in sandy soils probably originate from scarab beetle activity. Most of the evidence strongly suggests that scarab beetles were absent during the Late Weichselian stadials and that scarab beetle activity and clay illuviation occurred concurrently during the early Preboreal period of ameliorating climate and possibly also during the Late Weichselian interstadials. Scarab beetles seem to have been absent or at least less common during the Boreal and Atlantic, because of unsuitable habitat, but reappear from the Subboreal onwards. These periods of scarab beetle activity determine the ages of their back-filling traces.

DISCUSSION

In our attempt to describe and explain traces from scarab beetles in sandy soils we have touched upon such divergent disciplines as zoology and pedology. The effort seemed worthwhile, because there is a great need for scientists from these disciplines to co-operate to achieve a better understanding of soil-forming processes. Some of the issues likely to arise from those fields are anticipated below.

(1) There are some organisms that are of similar size to the scarabs mentioned and which also burrow into the soil, e.g. wolf spiders (Lycosidae), mole-crickets (Gryllotalpidae) and the larger tiger beetles (Cicindelidae). Back-filling of burrows has not been described in these groups, however, as far as we are aware. It has been described in cockchafer larvae (Scarabaeidae—Melolontinae) (Schwerdtfeger, 1939), but if the traces did originate from those organisms, their diameters would range between 5 and 15 mm, because the larvae of different stages differ considerably in girth. No such range occurred in the traces we described. Back-filling of burrows has also been described in cicada nymphs (Cicadidae) by Hugie and Passey (1963) in soils formed in loess in the U.S.A. Here again, considerable ranges in the diameters of the back-filled burrows (7.5–20 mm) occurred, depending on the stages of the nymphs. No such range was present in the traces we described and, moreover, a European equivalent of such cicadas is not known to us.

(2) We expect back-filling traces of species other than those mentioned in the present paper to be found in the future and in different types of soil. Judging from their way of life, scarabaeid dung beetles from the Phanaeini tribe, widely distributed in the southern and central parts of the U.S.A. (Fincher, 1973), are likely to back-fill parts of their burrows in sandy soil, as the numerous geotrupids in that part of the world probably do, although Kalisz and Stone (1984) make no mention of back-filling traces from *Pelotrupes*. Likewise, the many species of scarabs whose pupal chambers Valiachmedov (1977) found up to 1.20 m below the surface in light Sierozem soils will form back-filling traces.

(3) In densely packed sandy soils plant roots often cannot penetrate the soil below 25 cm. The disturbance of the soil stratification by scarab beetles might enable plant roots to penetrate considerably deeper.

(4) Extrapolation of the data mentioned on the amounts of soil deposited annually on the surface by *T. typhoeus* to amounts per hectare suggests that up to 500 kg ha⁻¹ is not exceptional in favourable habitats. The figure for *Pelotrupes youngi* is 3–7 times higher in favourable habitats in Florida (Kalisz and Stone, 1984). Because the latter species burrows up to 5 times as deep as *T. typhoeus* the mixing of the upper 1 m of the soil seems fairly comparable in both species. Additional data are required to check this possibility.

(5) If, as we argue, many of the observed back-filling traces were made by

scarabs during the early Preboreal, they must have been started from the present-day surface in soils that have not been covered by Holocene drift sands. There is a marked difference, however, between the depths to which scarabs in The Netherlands usually burrow nowadays (up to c. 80 cm below the surface) and the depths at which we observed most of the ancient traces: 70–135 cm below the surface and some even deeper. We suggest that the reason for this difference could be that we only observe the ancient traces from the rare specimens that burrowed to extreme depths. Their traces have been preserved, whereas the traces from beetles that burrowed to more usual depths have been reworked by successive scarabs or through biological homogenization by other animals or roots.

(6) Our observations that in-situ clay follows the meniscate layering within back-filled burrows or links up with the adjacent lamella as a layer thinner than the lamella itself support the pedogenetic origin of the lamellae.

Recent micromorphological evidence of clay migration in northwest European river terraces during the Late Weichselian is given by Miedema et al. (1983). Schröder (1979) has also shown that clay illuviation is present in Late Weichselian and Preboreal soils in northwest Europe, but is virtually absent in the younger soils. As a corroboration, Van Vliet and Langohr (1983) conclude that clay illuviation occurred before the Holocene in the soils they studied. The authors cited above also note that under forest, currently active drainage pores lack recent illuvial bodies of well-oriented fine clay.

As regards the periods of concurrent operation of clay illuviation and scarab beetle activity, the evidence from these studies supports the Late Weichselian interstadials and early Preboreal rather than the Atlantic.

A pedogenetic rather than a geogenetic origin of the lamellae can be inferred from the morphology, both macroscopic and microscopic, of the lamellae: in Fig. 6 the course of the lamellae is largely horizontal wherever the bedding of the sand is criss-cross. In thin sections of the lamellae many ferri-argillans (some bridge-forming) are visible, pointing to clay illuviation as the process of formation.

(7) Van Geel and Kolstrup (1978) propose that there has been a steady increase in the emission of solar energy since the Upper Pleniglacial or that at any rate the emission of solar energy has not been limiting for the amelioration of the climate. The Late Weichselian and early Holocene oscillations in climate would then have arisen from retarded changes and varying intensities in west–east air circulation. Van Geel et al. (1981) give a different interpretation for one of these phases, as an alternative to a climatic oscillation, viz. the Rammelbeek phase of Van der Hammen (1971) (9,850–9,700 BP). This phase is an interlude between the first Preboreal phase (Friesland phase of Behre (1966) (10,150–9,850 BP)) and the Preboreal proper. The Rammelbeek phase is characterized by a sharp decline in the ratio of arboreal:non-arboreal pollen. This may point to a dry period, but the alternative proposed is that large numbers of mammals were driven to the north in front of the advancing tree line.

In spite of any such advance the herbivores would have retarded the pace of afforestation by grazing. As long as most of the trees were kept away, herbs and grasses were favoured by the ameliorating climate. Herbivores therefore became abundant. Finally, the herbivores lost more and more terrain to the trees and were driven further northwards and most of the species were even driven to extinction (Kurtén, 1968). The abundance of dung is supported by the high percentage of nettle (*Urtica*) in the pollen record from the Rammelbeek phase (Van Geel et al., 1981). Nettle is known to have high nutrient requirements. The interpretation of Van Geel et al. (1981) is attractive in the context of our study because it would account for an associated great abundance of dung beetles in the early Preboreal.

It is tempting to extend the speculations made by Van Geel et al. (1981) to the point where the abundant dung beetles, by reworking the soil, helped prepare the way for tree roots to penetrate the deeper layers, so that the pace of reafforestation was considerably accelerated. This would mean that the Late Glacial herbivores ultimately helped dig their own graves by means of the dung beetles! But even if we forgo the speculation, there is still much evidence available for our conclusion that the ancient back-filling traces were formed by scarabs during the relatively warm periods precluding the Holocene and again after the Atlantic.

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Drs. A.D. Verlinde (Amersfoort) kindly allowed us to open up the type locality of the Usselo layer, which is normally inaccessible. Special mention should be made of the visit one of us (LB) made to Dr. G.R. Coope and Mr. P.J. Osborne (Birmingham). They provided us with all the data on fossil beetle remains. Their willingness and hospitality are gratefully acknowledged.

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CHAPTER 4

"Since the essence of the soil consists in its being a biological system, soil science will remain incomplete without biological knowledge".

W.L. Kubišna, 1964.

In: A. Jongerius (ed.), Soil micromorphology: 1-13.

Back-filling of burrows by the scarab beetles

Lethrus apterus and *Typhaeus typhoeus*

(Coleoptera, Geotrupidae)

by

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INTRODUCTION

In an earlier paper (Brussaard & Runia, 1984), traces of bioturbation in sandy soils were interpreted as being burrows back-filled by scarab beetles, presumably geotrupids. The traces were approximately 14 mm in diameter and up to 20 cm long. They were found up to 2 m deep in some sandy soils in The Netherlands and the surrounding countries. Some traces had been filled with material replaced downwards by animals crawling upwards, resulting in "concave" infillings of the burrows. In contrast, there were also traces that had been filled with material replaced upwards by animals crawling downwards, resulting in "convex" infillings of the burrows.

It was hypothesized that geotrupid beetles belonging to an array of species could have been responsible for producing the traces of bioturbation and the earlier paper (Brussaard & Runia, 1984) focused on the geotrupid dung beetle *Typhaeus typhoeus* (Linnaeus, 1758). Beetles of this species do produce burrows with concave infillings, but in this paper I will show that convexly filled burrows do not result from the behaviour of beetles of this particular species. The aim of the present paper is to show that other geotrupid beetles, in particular *Lethrus apterus* (Laxmann, 1770), do produce such convexly filled burrows.

This paper is one of a series evaluating the contribution of scarab beetles to the past and present genesis of certain sandy soils.

The objects of study

Lethrus apterus and *Typhaeus typhoeus* are remarkably similar in size, reproductive behaviour and ecology (Schreiner, 1906; Brussaard, 1983). Beetles of both species reproduce in spring. The reproductive behaviour

includes burrowing a branching shaft, up to 1 m deep and sometimes deeper, provisioning the branches with food for the larvae and partly sealing the remaining burrow with soil. Males of both species defend the nest against intruders. The habitat consists of bare to half open areas, preferably with a sandy soil (*T. typhoeus*) or sandy to loamy soil (*L. apterus*). The most important differences between the two species are:

- Distributional range: *L. apterus* occurs in Slovakia, South Poland, Hungary, Rumania and the southwestern part of the Soviet Union, eastwards as far as the river Don and south of the line Kiev-Oriol-Woronez but not on the Krim peninsula (Schreiner, 1906; Horion, 1958); *T. typhoeus* is found throughout Western Europe from Morocco to South Sweden (see map in Brussaard, 1983).
- Food: *L. apterus* cuts fresh leaves from grasses, herbs and shrubs, both to feed on and to provision the future larvae with; *T. typhoeus* uses herbivore dung for the same purposes.
- Generation time: In *Lethrus* the generation time is uniform and always one year (Schreiner, 1906; Nikolayev, 1966). The generation time is two or more years in *T. typhoeus* (Brussaard, 1983). The life cycle of a single generation of *L. apterus* and of *T. typhoeus* is shown in Figure 1 (the adults were assumed to have reproduced in the spring of 1979).

Back-filling of burrows

A *concave* infilling of a burrow comes about when the beetles seal in the food provision for the larvae with soil, and also when a young adult makes its way from the pupal cell to the soil surface. A *convex* infilling might come about when beetles dig down the soil profile when

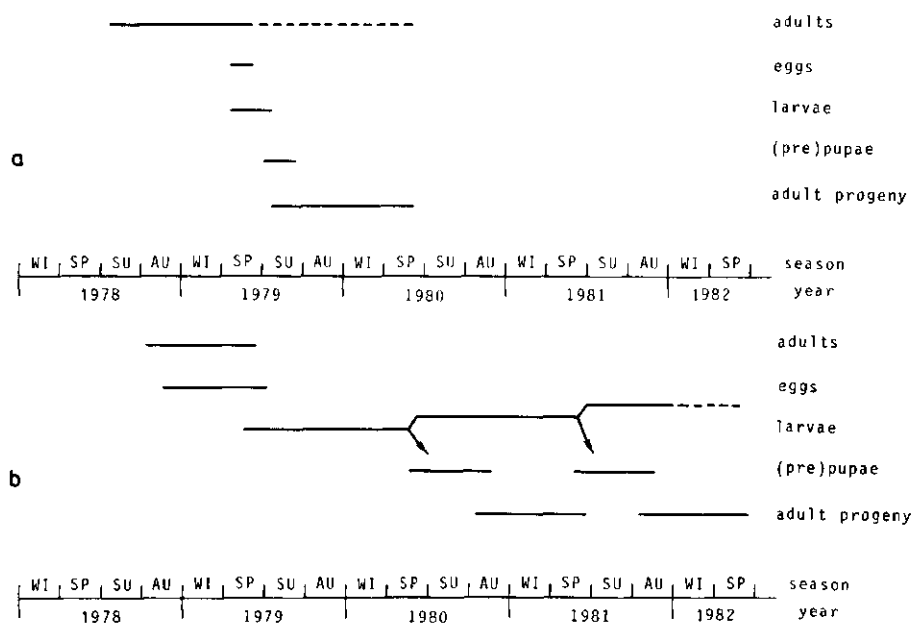


Figure 1.

Life-cycle of one generation of *Lethrus apterus* (a; modified after Schreiner, 1906) and *Typhaeus typhoeus* (b; from Brussaard, 1983).

making a shaft for nesting. In that situation, however, the excavated soil is transported to the surface and no burrow with a convex layering will be created. In theory, convexly filled burrows could be produced when beetles dig down into the soil to aestivate or hibernate after the reproductive period. *Typhaeus typhoeus* does not show this behaviour: in rearing trials with tens of pairs of beetles, all adults died after their first reproductive season (Brussaard, 1983). In the present paper it will be demonstrated that back-filling of burrows by beetles moving down the soil profile does occur in *L. apterus*. Some evidence will be given that this behaviour is connected with bridging unfavourable conditions between reproductive seasons.

METHODS

The beetles were kept in glass cages filled with sand so that their burrowing behaviour could be observed. A walking surface on which food was provided was mounted on top of the cage. The cages have been described in detail in an earlier paper (Brussaard, 1983).

A useful method to prove that a beetle has survived from one reproductive season to the next is to demonstrate the presence of yellow bodies (*corpora lutea*) at the terminal ends of the ovarioles. Yellow bodies are the remnants of the follicular epithelium, which degenerates after egg release or egg resorption. They are formed throughout the reproductive season. When present in the still undeveloped ovary at the very beginning of the reproductive season, yellow bodies are conclusive evidence that the beetle is a survivor from the previous reproductive season. Yellow bodies have been used as age indicators in a variety of insects, including ground beetles (Vlijm & Van Dijk, 1967; Krehan, 1970) and dung beetles (Tyndale-Biscoe, 1978). Another useful age indicator is the wear of tibiae and mandibles (Tyndale-Biscoe, 1978; Van Dijk, 1979; Houston, 1981). Wear of tibiae and mandibles will come about throughout the reproductive period and, when assessed at the very beginning of the season, is strongly indicative of survival from the former reproductive season. Tibial wear should be especially pronounced in geotrupid species, given their burrowing habits.

RESULTS

On April 14, 1981 four female and four male specimens of *Lethrus apterus* were collected near Tarján, approximately 10 km NE of Tatabánya in Hungary on one of the first warm and sunny days in spring, at the very

beginning of the reproductive season. The eight beetles were kept in pairs in four glass cages at 17°C and natural daylength. Herbs and grasses were grown on the walking surface on top of the cages to provide the beetles with food. Each of the beetles made a shallow open burrow but they did not form pairs to start reproduction. After a few weeks all beetles had descended into the soil and had back-filled their burrows, thereby bringing about a convex infilling. At that time the females were dissected. The ovaries of all four proved to be still undeveloped. One of them clearly showed corpora lutea (Fig. 2a), the others did not (Fig. 2b). This proves that one of the females had been reproductively active during the preceding season (spring 1980) and had aestivated and hibernated until the present reproductive period. This female also showed pronounced wear of the tibiae (Fig. 3a). In contrast, the tibiae of the other beetles were entirely intact (Fig. 3b). Apparently, the latter had just emerged from their pupal cells when captured and they were at the beginning of their first reproductive season.

DISCUSSION

Although it is not clear why *Lethrus apterus* failed to reproduce in the glass cages, the descent into the soil should be regarded as behaviour associated with bridging an unfavourable time period until reproduction. From the observation of the female with corpora lutea and worn tibiae it may be tentatively inferred that survival between reproductive seasons occurs under natural circumstances in *L. apterus*. Although these observations relate to one of only four beetles, it is difficult to imagine a different explanation. This practice of descending into the soil will result in the regular appearance of back-filled burrows with convex infillings and provides further support to the earlier conclusion

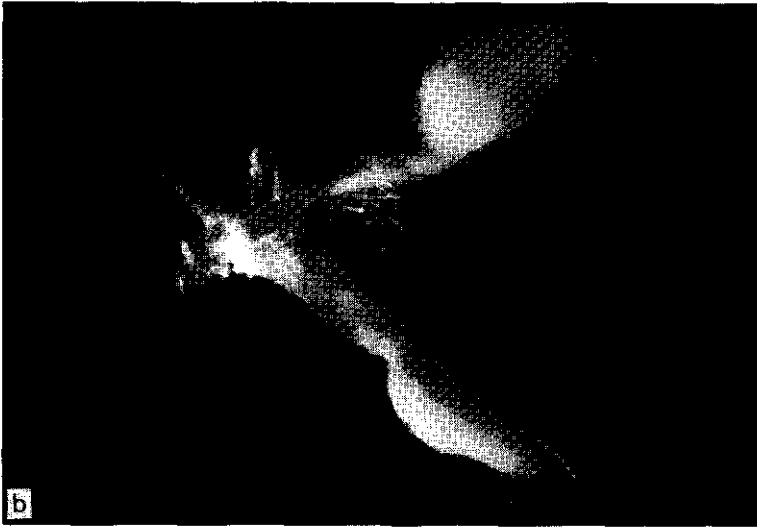
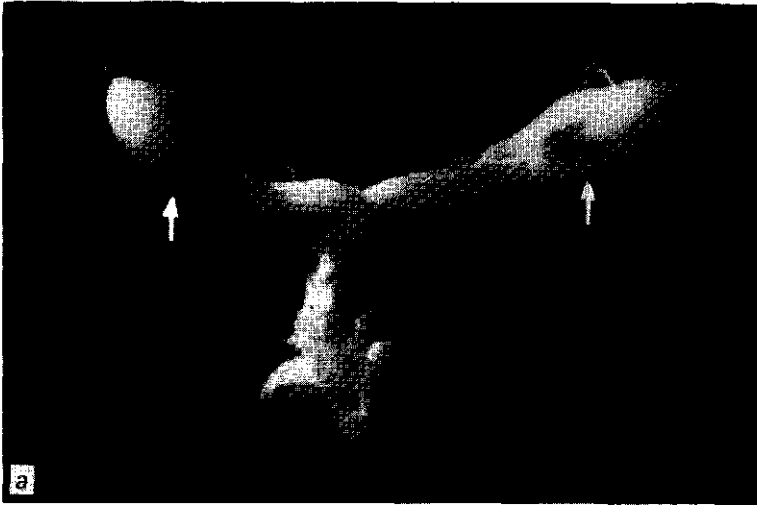


Figure 2.

Undeveloped ovaries with (a) and without (b) corpora lutea in *Lethrus apterus*, indicating the resumption of reproduction (a) and the beginning of reproduction (b).

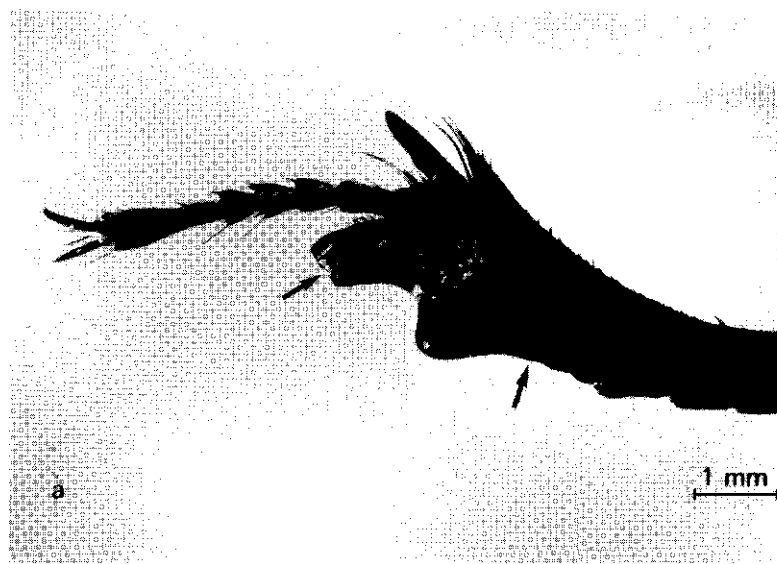


Figure 3.

(a) Distinct wear of tibia of fore-leg of *Lethrus apterus*

(b) Sound tibia of fore-leg of *Lethrus apterus*

(Brussaard & Runia, 1984) that the traces which we described from sandy soils were caused by geotrupid beetles. In addition to the many traces of this type in soil profiles in The Netherlands and the surrounding countries (Brussaard & Runia, 1984), I have observed such traces in several areas in Hungary; particularly in the sandy Nyírség region in the northeast where the traces disturb illuviated clay bands.

Obviously, there is no reason to assume that *Lethrus apterus* is the species which, in the past, produced the back-filling traces in The Netherlands we reported (Brussaard & Runia, 1984). For many of the other geotrupid candidates, it is still not known whether the beetles spend part of their adult life between reproductive seasons in the soil, after producing convexly filled burrows. The behaviour of *L. apterus* merely shows that the phenomenon does occur in Geotrupidae. To my knowledge, the only well-documented cases of long adult life in Geotrupidae so far have been provided by Howden (1954). He kept specimens of *Mycotrupes retusus* J. LeConte, 1866 (which is distributed throughout parts of Georgia and South Carolina in the U.S.A.) alive in a cage for 13 months. Also, he found a few specimens, mainly females, of *M. gagei* Olson & Hubbell, 1954 in Florida, which showed considerable tibial wear at the very beginning of the reproductive season. Howden (1954) mentioned that, in contrast, other North American Geotrupidae he had studied had an adult life of only six to eight months, with a maximum duration of one year. In Europe, the case of *Geotrupes spiniger* (Marsham, 1802) seems interesting. This is an autumn breeder and, apparently, an unknown proportion of adults survive after reproduction and hibernate after descending into the soil to a depth of up to 1 m (Fabre, 1897). Hence, *G. spiniger* would be a most promising species to study, to ascertain whether it makes burrows with a convex infilling.

There is another way that back-filled burrows with a convex layering could come about: *young* adult beetles who have emerged from the soil to start maturation feeding might descend again into the soil to aestivate or hibernate *before* reproducing the following autumn (in autumn breeders) or spring (in spring breeders). No such behaviour occurs in *L. apterus* or *T. typhoeus*, but according to Teichert (1955), the spring-breeding *Geotrupes mutator* (Marshall, 1802), *G. sterconarius* (Linnaeus, 1758) and *G. stercorosus* (Scriba, 1791) do descend into the soil to hibernate at a depth of up to c. 50 cm after their emergence and initial maturation feeding in the autumn. Hence, it would seem to be worth studying this aspect of the biology of Geotrupidae more closely, to shed light on the making of burrows with convex infillings.

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Synopsis: Original scientific paper.

BRUSSAARD, L., 1985. Back-filling of burrows by the scarab beetles *Lethrus apterus* and *Typhaeus typhoeus* (Coleoptera, Geotrupidae). *Pedobiologia*, 28: 327-332.

While emerging from the soil, both *Lethrus apterus* and *Typhaeus typhoeus* back-fill their burrows in the downward direction with material from nearer the surface, resulting in *concave* infillings of the burrows. Unlike *T. typhoeus*, *L. apterus* also back-fills its burrows when descending into the soil, resulting in *convex* infillings of the burrows. This behaviour reinforces the hypothesis that ancient galleries with crescent-shaped infillings in sandy soils are the back-filled burrows of geotrupid beetles.

It is suggested that the movement of the beetles down the soil profile and the associated back-filling of burrows, is connected with aestivation and hibernation of adult beetles until the next reproductive season. Evidence is given for the survival between subsequent reproductive seasons in *L. apterus*.

Key words: back-filling, burrows, *Lethrus apterus*, *Typhaeus typhoeus*, scarab beetles.

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"Zoo zien wij hoe de mijnwerker Driehoorn allerlei veranderingen in de bodemstructuur op zijn geweten kan hebben".

W. Beyerinck, 1938.

De Levende Natuur 40: 358-363.

Effects of back-filling of burrows by
scarab beetles on pores and roots
in some sandy soils of The Netherlands

by

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ABSTRACT

Samples taken from sandy soils at six localities in The Netherlands where back-filled burrows of scarab beetles had been observed were thin-sectioned and subjected to micromorphometric analysis using the Quantimet 720. The volume of pores larger than 0.030 mm was up to 38 % higher in the back-filled burrows than in the undisturbed matrix, as was the volume of pores larger than 0.195 mm; the latter diameter approximates the critical pore diameter for plant roots in densely packed sandy soils. The inference that rooting would be more intensive in the back-filled burrows than in the undisturbed matrix was confirmed by observations. The repercussions of this in heathlands and cultivated areas are discussed.

INTRODUCTION

Recently, interest in the effects of animals on soil has been growing (Hole, 1981; Bal, 1982). Earthworms (Hoogerkamp et al., 1983) and termites (Wielemaker, 1984) have been demonstrated to have clear effects on the structure and physical properties of soil. Also, scarab beetles have been reported to contribute appreciably to the mixing of soil constituents and, in particular, to the disturbance of stratified structures in sandy soil (Brussaard & Runia, 1984; Kalisz & Stone, 1984).

In another area of the literature it has been reported that the size and structural rigidity of pores in sandy soils may mechanically impede root growth wherever other important factors such as aeration and moisture

are not limiting (Wiersum, 1957; Hidding & Van den Berg, 1960; Russell and Goss, 1974). The uptake of nutrients may also be severely affected (Lindberg & Pettersson, 1985). The aim of the present paper is to present quantitative evidence that back-filled burrows of scarab beetles in densely packed sandy soils show a markedly higher pore volume and a marked shift in pore size distribution towards larger pores as compared with the undisturbed matrix. Qualitative evidence will be given that in densely packed sandy soils roots preferentially follow such back-filled burrows.

Details on the back-filling behaviour of one of the locally abundant scarab beetles of The Netherlands, *Typhaeus typhoeus* (Linnaeus, 1753) were given in an earlier paper (Brussaard, 1983).

This paper is one of a series in which the contribution of scarab beetles to the genesis of sandy soils is evaluated.

MATERIALS AND METHODS

Back-filled scarab beetle burrows, approximately 14 mm wide, have been found up to 2 m below the surface in cover sands and river terrace sands in NW Europe (Brussaard & Runia, 1984). We took samples from such sandy soils at six localities in The Netherlands. In the two left-hand columns and the legend of table 1, general information is given on thin sections made from these samples. Cross sections of back-filled burrows were identified by eye on the thin sections. We carried out an electro-optical image analysis of thin section photographs, on which pores show

up black, with a Quantimet 720, as described by Ismail (1975). Using this technique we obtained a quantitative estimate of pore volumes and pore size distributions in the undisturbed matrix and the back-filled burrows in the thin sections.

Given the thickness of the thin sections (0.020-0.025 mm), only pores larger than 0.030 mm in diameter could be measured adequately. The total area of pores larger than 0.030 mm in diameter was measured. We shall henceforth refer to this attribute as "*pore volume*".

Pore size distribution was measured by classifying the pores into two classes, viz. those larger than 0.030 mm in diameter and those larger than 0.195 mm in diameter: 0.030 mm is the equivalent pore diameter at pF 2 ("field capacity") for sandy soils and 0.195 mm approximates the critical pore diameter below which the rooting of plants is seriously hampered in densely packed sandy soils (Wiersum, 1957; Hidding and Van den Berg, 1960; Russell and Goss, 1974).

Finally, back-filled burrows in the field and in soil peels were inspected by eye to see whether they were more intensively penetrated by roots than the undisturbed matrix.

RESULTS

Pore volume and pore size distribution

The results of Quantimet measurements of pore volume and pore size distribution inside and outside the back-filled burrows are listed in

table 1. Of 20 burrows measured, 18 showed a larger pore volume on average than the surrounding matrix. Only the data from Wijster were sufficient in number to enable the comparisons between burrows and matrix to be treated statistically: the pore volumes inside the burrows were significantly larger than in the matrix ($n=7$, $P=0.008$, Wilcoxon's signed-ranks test, one-sided).

Because pores larger than approximately 0.200 mm are essential for roots in densely packed sandy soil (Wiersum, 1957), the test was also carried out for pores measuring over 0.195 mm, with the same result.

Penetration of burrows by roots

At the various places studied we observed many more roots in the back-filled burrows than in the undisturbed matrix (figure 1). Such back-filled burrows with roots predominantly occurred more than 0.30 m below the surface where the soil bulk density increased with depth from approximately 1.30 to 1.70 g/cm³. In several places this was apparently the only way for roots to pass through a compacted B horizon.

DISCUSSION

- (1) Mutual comparison of the measurements of pore volume and pore size distribution in the matrices of the thin sections from the same locality and comparison of such measurements *between* the localities sampled showed a marked scatter. The same applies for such measurements inside the back-filled burrows (table 1). In spite of these scatters, the

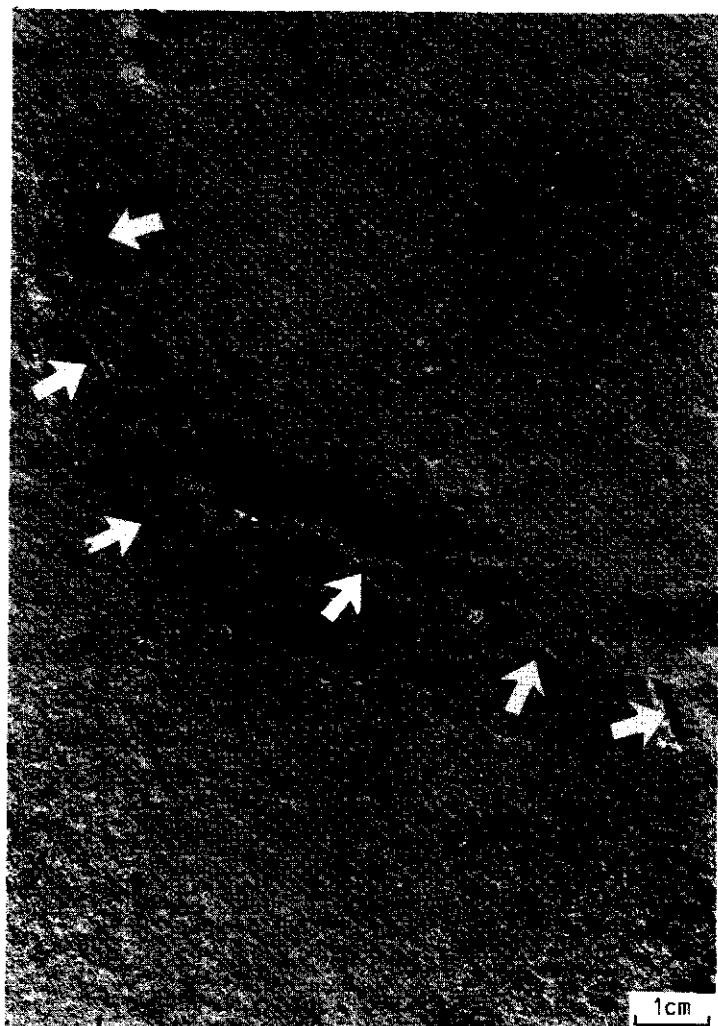


Figure 1.

Back-filled scarab beetle burrow presumably from *Typhaeus typhoeus*, with small root channels inside the burrow (arrowed) but virtually none in the undisturbed matrix.

Photo of soil peel from Wijster, 0.38-0.48 m below the surface.

locality	depth of sample		subject analysed	number of subjects analysed	mean percentage of pore volume	
	below surface (cm)				> 0.030	> 0.195 mm
Wijster	45-60	matrix	8	8.7	4.1	
		burrow	1	39.3		30.2
	50-55	matrix	1	8.1	4.5	
		burrow	1	32.5		22.8
	50-55	matrix	2	7.3	3.7	
		burrow	1	28.1		19.4
	80-85	matrix	6	9.6	4.6	
		burrow	1	22.9		14.9
	90-105	matrix	5	13.2	6.3	
		burrow 1	2	24.5		15.8
Havelte		burrow 2	1	22.8		14.6
		burrow 3	1	25.3		16.4
		matrix	6	9.7	5.5	
	15-30	burrow	2	23.7		18.6
	50	matrix	3	24.5	19.0	
		burrow	3	20.2		15.3
Geysterden	80	matrix	2	15.8	11.9	
		burrow	1	51.9		46.9
	80	matrix	4	15.4	11.2	
		burrow	2	53.6		49.1

Lottum	50	matrix	4	12.2	8.9
		burrow 1	1	21.3	15.4
		burrow 2	1	30.4	24.8
50		matrix	3	10.1	6.7
		burrow 1	1	16.2	10.1
		burrow 2	1	14.1	9.4
		burrow 3	1	7.0	4.2
Ede	150	matrix	3	2.9	1.4
		burrow 1	2	26.3	20.1
		burrow 2	4	14.6	10.3
150		matrix	6	19.7	15.7
		burrow	3	32.0	27.4
Venray	170	matrix	4	16.8	9.6
		burrow	4	18.9	10.1

Table 1. Pore volumes of pores with diameters exceeding 0.030 mm and 0.195 mm respectively, in the undisturbed matrices and inside back-filled scarab beetle burrows in thin sections of soil samples from sandy soils in six locations in The Netherlands. Site characteristics:

Wijster : Orthic Podzol, coordinates topographical map 537,025/229,035

Havelte : Orthic Podzol, coordinates 535,350/212,000

Geysteren: Leptic Podzol, coordinates 395,125/201,425

Lottum : Leptic Podzol, coordinates approximately 386,000/209,000

Ede : Humic Podzol, coordinates 448,800/174,525

Venray : Humic Podzol, coordinates 194,500/396,275

Soil classifications according to FAO (1974).

difference in pore volume and in pore size distribution between the undisturbed matrix and the back-filled burrows was striking in nearly all the thin sections from each of the localities sampled (table 1) and, as mentioned earlier in the text, was statistically significant. This underlines that here we are dealing with a general and important effect of scarab beetle activity in sandy soil.

- (2) Although only qualitatively documented in the present paper, it is clear that roots benefit from the reworking of densely packed sandy soil by scarab beetles whose burrows penetrate the B and C horizons of Spodosols. By exploiting these burrows, the plants will probably be less vulnerable to desiccation and will extract their nutrients from a larger body of soil. Deep tillage has been demonstrated to have similarly beneficial effects on asparagus, carrots, chicory and maize, cultivated on drained Aquods and Psammments in Pleistocene cover sands and Psammments and Orthods in river sands (Reijmerink, 1973; Van Dam, 1973 and personal communication, 1985).

Because *T. typhoeus* and other scarab beetles thrive in these soils if the vegetation is half-open natural heathland, there may even be some scope for employing scarab beetle populations to enhance the suitability for root development wherever densely packed sandy soils are to be reclaimed for cultivation. Employing dung beetles for agronomic purposes has proved to be successful in a different context (Waterhouse, 1974).

- (3) In recent decades the water table over large areas of the Netherlands has fallen considerably. As a consequence, large sandy areas have become an appropriate habitat for rabbits and other mammals. Dung beetles that

live on their droppings, such as *Typhaeus typhoeus*, have probably increased concomitantly in numbers.

What is known about the root development of grasses and Ericaceae suggests that dung beetles may have had and are still having an influence on the vegetation in their heathland habitat. In a comparative study of root development of *Molinia caerulea* and *Erica tetralix* Sheikh and Rutter (1969) found that (1) the grass rooted far more extensively than the heather below 0.20 m under the surface, (2) its total root weight was 6-7 times higher and (3) it penetrated more extensively into pores up to 0.6 mm in diameter. Moreover, *Molinia* is more actively rooting, with a turnover of roots 2-3 times that of *Erica* (F. Berendse, personal communication, 1985), so that all in all the grass appears to be predisposed to benefit much more from those activities of dung beetles that facilitate root development.

Sheikh and Rutter (op. cit.) carried out their study on four wet-heath sites, but recent studies by botanists from Utrecht University indicate that the competition between roots of grasses and Ericaceae in dry heathlands does not differ fundamentally from that in wet heathlands (F. Berendse, personal communication, 1985). During recent decades the latter areas have become considerably more "grassy" in The Netherlands and neighbouring countries because of the increase in *Deschampsia flexuosa* and other grasses, whereas ling, *Calluna vulgaris*, has declined.

Although several explanations for the replacement of Ericaceae by Gramineae in heathlands have been proposed, such as the increase of nutrients in the rain-water, we suggest that the burrowing and back-filling behaviour of scarab beetles has, to a hitherto unknown extent,

contributed to the changing of heathland vegetation by differentially facilitating rooting in densely packed sandy soils. This possibility merits further study so that appropriate nature management can be applied.

- (4) Following a similar line of reasoning we suggest a hypothesis to explain the sustained existence of two contrasting vegetations, viz. "islands" of longleaf pine (*Pinus palustris*) and wire grass (*Aristida stricta*) in a "sea" of sand pine (*P. clausa*) and scrub on well-drained sandy soils along the central ridge of peninsular Florida. In a thorough study, Kalisz and Stone (1984 a) were not able to ascribe the striking contrasts in species composition and the sharp, stable boundaries between the vegetations, to physical or chemical differences in the soil. The only differences were found in the morphology of the upper 0.60 m of soil, where eluviation was the dominant process under sand pine, leading to distinct horizons, whereas active biological homogenization by scarab beetles and pocket gophers inhibited podzolization under longleaf pine. Kalisz and Stone (1984 b) acknowledge that the beetle *Peltotrupes youngi* and other scarabs facilitated rooting in longleaf pine by burrowing more than 3.50 m deep into sand whose bulk density exceeded 1.70 g/cm^3 , whereas no such faunal activity occurred under sand pine. Yet, they did not put forward the hypothesis that these beetles may be the agents that sustain the marked differences in species composition between the two vegetations.

We suggest that this hypothesis should be tested further, by quantifying pore volumes and pore size distributions of the soils where the scarab beetles occur and where they are absent, in combination with a comparative study of the requirements of longleaf pine and sand pine for

rooting and nutrient uptake from the soil below 0.60 m. If our hypothesis is supported by such a study, the extremely low dispersal ability of the deep-burrowing scarab beetles in the area studied by Kalisz and Stone (op. cit.), as reported for *Mycotrupes* by Hubbell (1954) and for *Pelototrupes* by Howden (1955), may well account for the sharp, stable boundaries between longleaf and sand pine vegetations.

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"Indeed the whole principle of determinism is suspect when applied to such a complex and dynamic system as that described by ecology, where so many of the factors affecting the systems involved are stochastic to an extent that even statistical inferences must be regarded as tentative".

F.S. Gilbert, 1980.

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The influence of soil bulk
density and soil moisture on the
habitat selection of the dung beetle
Typhaeus typhoeus (Col., Geotrupidae)
in The Netherlands *)

by

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SUMMARY

In the Netherlands, the dung beetle *Typhaeus typhoeus* is confined to sandy and loamy sandy soils. Experiments were carried out in the laboratory and in the field to ascertain the effects of soil bulk density and soil moisture on various aspects of the reproductive behaviour and development of this dung beetle. Some of the results were validated under natural field conditions.

The nesting burrows were shown not to penetrate beyond the upper level of the soil moisture saturation zone. The depth of the burrows was not influenced by the bulk density in moist and free-drained sandy soils.

Lower bulk densities of the soil were shown to result in fewer dung sausages being made, even when sufficient dung was available to provide for the larvae. This phenomenon was attributed to a behavioural response from the dung beetles. The critical bulk density in the field appeared to be approximately $1.40 \times 10^3 \text{ kg/m}^3$.

The survival rate of eggs and larvae was shown to be adversely affected by conditions of high soil moisture (>20% by volume) at the depths where the larvae develop. Evidence is given for a low survival rate of larvae at conditions of low soil moisture ($pF > 2.7$) at these depths.

The impact of certain other soil factors is discussed.

INTRODUCTION

By burrowing in the soil and transporting soil material to the surface, certain scarab beetles contribute appreciably to the mixing of soil constituents and, in particular, to the disturbance of stratified structures in sandy soils (Brussaard & Runia 1984). Traces of back-filling of burrows by scarab beetles, presumably geotrupid dung beetles, have been found up to 2 m below the surface. In some places such traces have been dated back to the early Preboreal (c. 10 000 BP) (Brussaard & Runia 1984); this indicates the persistent nature of the influence of the beetles on the soil.

As a step towards being able to predict the effects of geotrupid dung beetles on the soil, their association with this part of their habitat was analysed. This is the subject of the present paper, which is one of a series in which the contribution of scarab beetles to the genesis of sandy soils is evaluated.

The dung beetle *Typhaeus typhoeus* (Linnaeus, 1758), measuring 12-22 mm in length and 7-12 mm in girth, was chosen as a model species. *T. typhoeus* occurs in open to half open habitats on sandy soils. The beetles are locally abundant with a maximum of 2 pairs/m². Their burrows may reach more than 1 m deep (Brussaard 1983). The beetles provision their nesting burrows with 'dung sausages' as food for the larvae. Parts of their burrows are back-filled with sand: this results in the traces already mentioned. The generation time of the beetles is two years or more (Brussaard 1983). The amount of soil transported to the surface may be as high as 450 kg.ha⁻¹ annually (Brussaard & Runia 1984).

ABOVE-GROUND FACTORS

Above-ground factors, such as shade, vegetation structure and amounts of dung on the surface, probably play a part in the habitat selection of dung beetles before soil characteristics can exert a decisive influence. In regional studies of dung beetle faunae, a clear dichotomy usually emerges between species from shaded habitats versus those from open habitats (see for example Nealis 1977). In the open field, most dung beetle species appear to be more abundant where the vegetation is sparse than where it is dense (Lumaret 1983, Kalisz & Stone 1984). Our observations of *T. typhoeus* at various places confirm these results:

T. typhoeus was virtually absent from shaded places and from densely overgrown open places, in spite of the presence of the main food source, rabbit droppings. We also observed that *T. typhoeus* was more numerous where the amounts of rabbit droppings were relatively high than where they were relatively low.

SOIL FACTORS

Most studies of the effects of environmental factors on the relations between dung beetles and their habitat are concerned with the whole fauna on a regional scale (e.g. Nealis 1977, Lumaret 1983). The insight on the effects of environmental factors on dung beetles at the species level resulting from such studies is at best correlative, not causal. The present study can serve as a test of that part of the correlative work that was done on *T. typhoeus* by Lumaret (1978/79 and unpublished). Sampling 731 sites in an area of 75 000 km² west of the river Rhône, Lumaret (op. cit.) was able to deduce hierarchical values of environmental factors determining the distribution and abundance of single

species. For *T. typhoeus* the hierarchy of soil factors turned out to be as follows: soil temperature, nature of parent rock, soil moisture during the reproductive period, soil bulk density and soil texture. Unfortunately, Lumaret (op cit.) did not circumscribe "nature of the parent rock" (equivalent with soil type?), nor did he make clear in what respect this factor differed from the other factors mentioned. For this reason we could not evaluate its relevance for the habitat selection of *T. typhoeus*.

Soil temperature

The effects of temperature on the reproductive behaviour and development of *T. typhoeus* were reported in an earlier paper (Brussaard, 1983). In the Netherlands the greatest differences in temperature are to be found *within* profiles. Below 0.40 m under the surface, where the larvae develop, the order of magnitude of differences in temperature *between* free-drained soils on sand is only tenths of degrees at the same depths. Hence, studying the effects of soil temperature on the reproduction of *T. typhoeus* on a regional scale was not thought to be worthwhile.

Soil texture

In The Netherlands *T. typhoeus* is confined to soils developed on sand and loamy sand. All soils developed on organic materials or clay, and most soils developed on loam, have high water tables during winter. For this reason they are unfavourable for *T. typhoeus*. Only some small areas in southern Netherlands show free-drained soils developed on silt loam or sandy loam. *T. typhoeus* is not known from these soils. Although soil texture may play a part we suggest that the intensive cultivation or the

luxuriant natural vegetation of these soils contributes more to the absence of the beetles. For these reasons it was decided not to study the effects of soil texture on the reproductive behaviour and development of *T. typhoeus*.

Soil bulk density and soil moisture

We experimentally studied the effects of soil bulk density and soil moisture on various aspects of the reproductive behaviour of the beetles, as listed below. (Later in the text these experiments are referred to by their code, e.g. A(1)).

A. Soil bulk density

- (1) Effects of bulk density on the depth of the nesting burrows
- (2) Effects of bulk density on the number of eggs laid/dung sausages made

B. Excessive soil moisture

- (1) Effects of excessive soil moisture on the depth of the nesting burrows
- (2) Effects of excessive soil moisture on the survival of eggs and larvae

C. Shortage of soil moisture

- (1) Effects of shortage of soil moisture on the survival of eggs and larvae

We did the experiments in the laboratory and in the field and whenever possible we validated the results under natural field conditions.

MATERIALS AND METHODS

Laboratory experiments were carried out at Wageningen in glass cages, consisting of a wooden frame with two window-panes fitted 15 mm apart. The beetles, one pair per cage, burrowed and reproduced in the sand between the windows. On top of the frame a walking surface was mounted, on which more than ample amounts of dung were placed. Field experiments were carried out at various places in $1 \times 1 \text{ m}^2$ enclosures, spanned with fine-mesh wire-netting to prevent the beetles (one pair per enclosure) from flying out or in. More than ample amounts of dung were placed on the surface. Almost all the beetles used in the experiments were captured on a heathland near Havelte in the Dutch province of Drenthe. For more details about the field enclosures and the glass cages see Brussaard (1983).

The following field study sites will be mentioned further in the text:

Wijster I: Orthic Podzol on non loamy to slightly loamy very fine sand (coordinates topographical map of the Netherlands N 537.250, E 229.350)

Wijster III: Orthic Podzol on non loamy to slightly loamy fine sand (coordinates N 538.300, E 228.475)

Castricum: Calcaric Regosol on non loamy moderately fine sand (coordinates N 507.600, E 104.150)

Maarheeze: Orthic Podzol on non loamy moderately fine and very fine and slightly loamy very fine sand; some of the observations mentioned further in the text are from overblown or decapitated variants of this soil type.

These four sites have a similar hydrology: water table permanently below 1.10 m.

Two additional sites, Wijster II (coordinates N 537.550, E 230.150) and Wijster IV (coordinates N 538.600, E 228.850), differed from Wijster I and Wijster III mainly in terms of hydrology, having their highest water table generally within 0.50 m below the surface. The soil classifications are according to FAO (1974). Abridged soil profile descriptions are available from the authors on request.

A. Soil bulk density.

(1) and (2). Effects of soil bulk density on the depth of the nesting burrow and on the number of eggs laid/dung sausages made were studied in a laboratory experiment in 1979 and in a field experiment in 1979 (at Wijster I) and in 1981 (at Castricum). In the laboratory experiment twenty-four glass cages were used, each having one uniform bulk density. The bulk densities ranged from 1.29 to $1.73 \times 10^3 \text{ kg/m}^3$ (exact figures can be read from figure 1) and approximately equalled the range in the field from the surface up to 1 m deep in sandy areas with an undisturbed Orthic Podzol profile where *T. typhoeus* naturally occurs (fig. 2, line Wijster I). The cages were kept under controlled conditions at 5°C and natural daylength from February until April inclusive, in 1979.

In the field experiment five enclosures were used at Wijster I from early March until October 1979. Four such enclosures were used at Castricum from early March until late August 1981. For logistic reasons the field experiment at Wijster I and Castricum could not be carried out during one year.

In order to validate the results of experiment A (1), the depths of 14 dung beetle burrows were determined at the Maarheeze site, all from free-drained soils with similar amounts of dung on the surface. These

soils were classified into four groups, according to the available depth of relatively loose drift-sand. In group I (n=3) the upper boundaries of the densely packed undisturbed C horizons were found up to 0.20 m below the surface, in group II (n=3) at 0.20-0.40 m, in group III (n=5) at 0.40-0.80 m and in group IV (n=3) more than 0.80 m below the surface.

In order to validate the result of experiment A (2), thirty-two free-drained plots at Maarheeze, each measuring 25 m² and having similar amounts of rabbit droppings on the surface, were divided into two groups and the number of *T. typhoeus* mounds in these two groups was compared. Group I (n=21) consisted of plots with an undisturbed Orthic Podzol profile. Most of these plots had been overblown with drift-sand, in some places more than 0.80 m thick. In plots of this group the upper boundaries of the densely packed undisturbed C horizons were found *deeper than* 0.40 m below the surface, which means that part or all of the dung sausages were made in soil with a relatively low bulk density. Group II (n=11) consisted of plots from which the topsoil had been blown away up to the C horizon. Many of these plots had subsequently been covered with a layer of drift-sand less than 0.40 m thick. In plots of this group the upper boundaries of the undisturbed C-horizons were found *within* 0.40 m below the surface, which means that all the dung sausages were made in the densely packed sand.

The field work at Maarheeze was done in 1975, but its results were quantitatively worked out after the termination of the 1979-1981 experiments and, hence, can serve as an independent test of the latter.

B. Excessive soil moisture.

- (1) In a laboratory experiment six glass cages were used with different levels of the water table and upper levels of the saturation zone. The cages were kept under controlled conditions at 10°C and natural daylength from 20 to 27 March 1981.
- (2) In a field experiment from March until October 1979 five enclosures at the free-drained site Wijster I were compared with six such enclosures at the periodically waterlogged site Wijster II.

The conclusions drawn from the latter experiment were validated by daily recording the number of dung beetle mounds from early March until mid-May 1980 in a $7 \times 7 \text{ m}^2$ plot at the free-drained site Wijster III and in a plot of equal size at Wijster IV, less than 100 m away, where the water table was less than 0.75 m below the surface until mid-April. The vegetation at these two sites had developed similarly after a fire in 1976 and the amounts of rabbit droppings were similar.

C. Shortage of soil water.

- (1) In a comparative field experiment five enclosures were used at Wijster I and four such enclosures at Castricum. The sites were chosen as probably having a relatively moist (Wijster I) and dry (Castricum) soil during the development period of the larvae (mid-April until mid-September), because it was known from reports by the Royal Dutch Meteorological Institute that the amount of rainfall at Castricum is 20 % less on average than at Dwingeloo (10 km from Wijster I) during that period. We collected data on the amount of rainfall during the development period of eggs and larvae and the preceding reproductive period of adults (March until mid-April). We

also measured the soil moisture content at each site in late August at the end of a dry and hot period and we collected the necessary data to enable the moisture characteristics of the two sites to be calculated for the C horizons between 0.40 and 0.80 m below the surface.

The burrows that had been made by the beetles were excavated in late August (Castricum) and October (Wijster I). For logistic reasons the field experiment was partly carried out in 1979 (at Wijster I) and partly in 1981 (at Castricum).

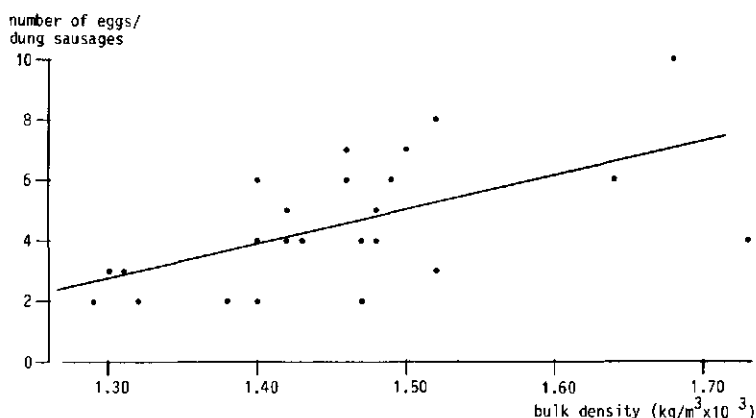


Figure 1.

Regression of soil bulk density on the number of eggs laid (=number of dung sausages made) within four weeks after the start of reproduction; $y = 4.6 + 11.0(x - 1.46)$. Laboratory experiment in 24 glass cages, February to April 1979, Wageningen.

RESULTS

A. Soil bulk density

- (1) a. Laboratory experiment. No effect of the bulk density on the depth of the nesting burrows, which in the cages ranged from 0.42 - 1.00 m deep, could be shown by regression analysis ($P > 0.75$).
 - b. Field experiment. Data from enclosures on the free-drained experimental sites Wijster I and Castricum were compared. The bulk densities were higher at Wijster I than at Castricum (fig. 2). The depths of the nesting burrows are given in table 1. Again, no effect of the bulk density on the depth of the burrows could be shown by Wilcoxon's two-sample test, although there was a tendency for burrows to be shallower in the looser soil ($n=5;4$, $U=18$, $P=0.064$, two-sided).
 - c. Validation. These results were validated with independent field data from Maarheeze. The mean depth of the burrows in group I (upper boundaries of densely packed C horizons up to 0.20 m below the surface) was $0.56 \text{ m} \pm 0.05$; in group II (upper boundaries at 0.20 - 0.40 m) it was $0.49 \text{ m} \pm 0.08$; in group III (upper boundaries at 0.40 - 0.80) it was 0.60 ± 0.03 and in group IV (upper boundaries at more than 0.80 m) it was $0.52 \text{ m} \pm 0.12$. Hence, no effect of the bulk density on the depth of the burrows could be shown (Kruskal - Wallis test, d.f. 3, $H=3.79$, $0.20 < P < 0.30$).
- (2) a. Laboratory experiment. A statistically sound relation was found by regression analysis between the bulk density and the number of eggs laid (=dung sausages made) during the first four weeks of breeding activity in the 24 glass cages ($R^2=0.33$, $F=10.80$, $0.001 < P < 0.005$, one-sided) (fig. 1). After four weeks the number of beetles still laying eggs declined. This is probably why the

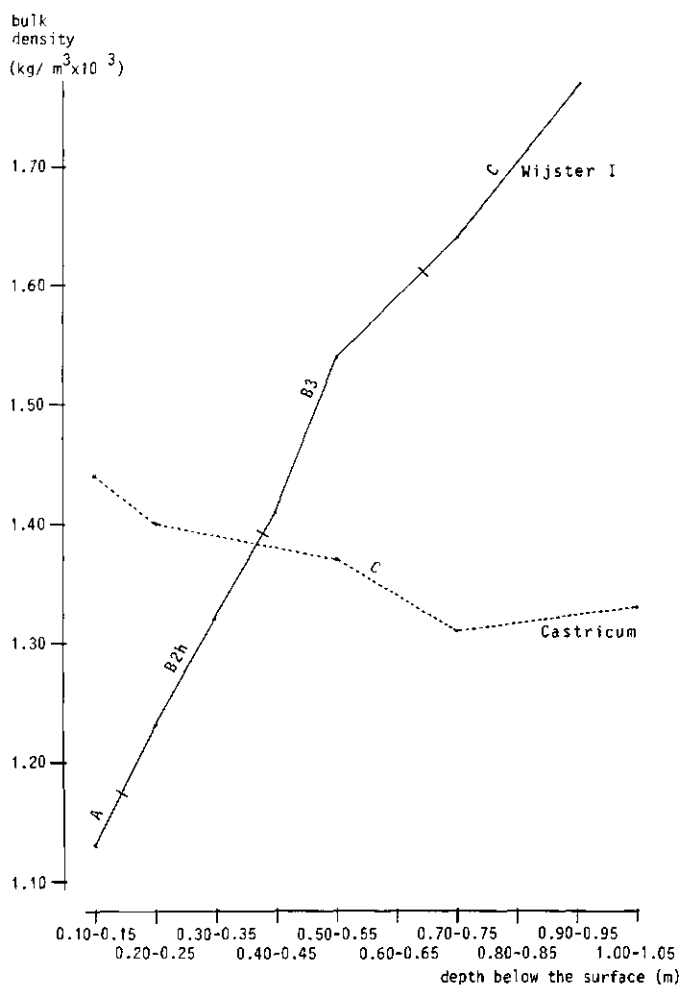


Figure 2.

Soil bulk densities at increasing depths at the study sites
Wijster I and Castricum.

enclosure no.	Wijster I	Wijster II	Castricum
1	0.63	0.57	0.66
2	0.80	0.39	0.58
3	0.64	0.60	0.58
4	0.68	0.42	0.60
5	0.72	0.29	-
6	-	0.43	-

Table 1. Depths of nesting burrows (m below the surface) in enclosures at experimental sites Wijster I and II (1979) and Castricum (1981)

Main site characteristics:

Wijster I: Orthic Podzol in free-drained non loamy to slightly loamy very fine sand

Wijster II: Orthic Podzol in temporarily waterlogged non loamy to slightly loamy very fine sand

Castricum: Calcaric Regosol in free-drained non loamy moderately fine sand.

regression, measured over the whole life-span of all beetles, shows more variance, but it still holds ($n=24$, $R^2=0.24$, $F=6.58$, $0.005 < P < 0.01$, one-sided).

enclosure no	Wijster I	Castricum
1	6	6
2	13	7
3	6	3
4	19	6
5	9	-

Table 2. Number of eggs laid (=number of dung sausages made) in enclosures at experimental sites Wijster I (1979) and Castricum (1981).

- b. Field experiment. Data from enclosures on the free-drained sites Wijster I and Castricum were compared. The data are given in figure 2 (bulk densities) and table 2 (number of eggs laid). No reliable estimate could be made about the period during which all the beetles remained reproductively active, so we had to consider the relationship over the whole life-span. It appeared that the null hypothesis of no relation between soil bulk density and number of dung sausages made could only be statistically rejected at the 10% level (Wilcoxon's two-sample test, $n=5;4$, $U=16$, $P=0.095$, one-sided).
- c. Validation. Comparison of the number of *T. typhoeus* mounds at Maarheeze in plots from group I (upper boundaries of the C horizons deeper than 0.40 m below the surface) with those in plots from group II (upper boundaries within 0.40 m below the surface) showed that there were significantly more dung beetles

glass cage no.	organic matter content of the sand (%)	depth of water table (m)	upper level of saturation zone (m)	depth of deepest egg (m)
1	0.58	0.50	0.35	0.25
2	0.56	0.50	0.35	0.30
3	1.10	0.70	0.42	0.31
4	0.59	0.70	0.54	0.52
5	0.98	0.90	0.68	0.54
6	0.56	0.90	0.82	0.60

Table 3. Greatest depths at which eggs were deposited in glass cages with different levels of water tables and upper levels of saturation zones. Laboratory experiment, March 1981, Wageningen.

in the plots of group II (12.8 ± 10.2 mounds per 25 m^2) than in those of group I (5.4 ± 3.5) (Wilcoxon's two-sample test, $n=21;11$, $t=2.636$, $0.001 < P < 0.01$).

B. Excessive soil moisture.

- (1) a. Laboratory experiment. A statistically sound correlation was found between the depth of the water table or the upper level of the saturation zone and the depth at which the first eggs were deposited (table 3) (Kendall's rank correlation test, $n=6$, $\tau=0.97$, $P < 0.01$).

- b. Field experiment. The water table between 8 March and 23 April 1979, i.e. the main reproductive period, was $1.32 \text{ m} \pm 0.07$ ($n=7$) below the surface at the free-drained site Wijster I and $0.57 \text{ m} \pm 0.13$ ($n=7$) at the periodically waterlogged site Wijster II. Data on the depth of the nesting burrows are given in table 1. The burrows reached significantly deeper at Wijster I (Wilcoxon's two-sample test, $n=6;5$, $U=30$, $P=0.002$, one-sided).
- (2) a. In the same field experiment as mentioned above, the moisture content between 0.40-0.80 m below the surface, i.e. where the larvae developed, varied from 12-20 % (by volume) during the reproductive period at Wijster I ($n=5$; the two extreme values at either side of the range were excluded). At Wijster II the dung sausages were made at shallower depths (0.20-0.60 m below the surface) because the water table was high. In this range of depths the moisture content of the soil varied from 17-31 % (by volume) during the reproductive period ($n=4$; exclusive of the two extreme values). Soil moisture was not measured after April but the soil of Wijster II remained considerably moister than that of Wijster I.

In October 1979, 42 of the 53 dung sausages at Wijster I contained a live larva, whereas at Wijster II only 10 of 43: a very significant difference ($\chi^2 = 27.76$; $P<0.001$).

- b. Validation. At the free-drained site Wijster III fresh mounds were observed from the beginning of the observations but no new mounds were noted after 28 March. In contrast, at the periodically waterlogged site Wijster IV, fresh mounds were not observed before 21 March and continued to appear until early May. These observations are consistent with the hypothesis that dung beetles colonized the Wijster IV site from elsewhere, whereas no

main reprod-											
active period		main period of development of eggs and larvae									
March	April	April	May	June	July	August ^a	September total mid-April to				
(first (second		I		II		III		(first mid-September			
half)		half)		half)		half)		half)			
Wijster I (1979)	86.9	16.1	57.0	86.3	55.0	49.1	33.0	3.3	23.1	21.3	328
Castricum (1981)	124.6	0.0	5.9	90.0	55.7	45.3	16.4	7.9	5.3	11.5	238

^a Roman numerals refer to ten-day periods

Table 4. Rainfall totals (mm) from Wijster I (1979) and Castricum (1981).

dung beetles had emerged from this site itself, probably because the recurrently high water table during winter and early spring precluded survival of the larvae.

C. Shortage of soil moisture.

The amounts of rainfall from March until mid-September are given for Wijster I in 1979 and for Castricum in 1981 in table 4. The humid weather in March was favourable for reproductive activity at both sites. The amounts of rainfall at the two sites were very similar during May, June and July, but measured over the whole development period of eggs and larvae (mid-April to mid-September) the amount at Castricum in 1981 was more than 27 % less than at Wijster I in 1979. This was mainly due to extremely dry weather in April 1981. Mid-August was also very dry both in 1979 and 1981, while during that month the amount of rainfall at Castricum in 1981 was no more than half the amount at Wijster I in 1979. The soil moisture content at 0.40-0.80 m below the surface in late August, i.e. at the end of the period of drought, was 3.5-6.0 % (by volume) at Wijster I and 3.2-5.2 % (by volume) at Castricum. Values for the moisture characteristics of the C horizon of the soils at Wijster I and Castricum were calculated according to Krabbenborg et al. (1983). The values fitted in well in the standard curves for such soils as published by the same authors (fig. 3). By inserting the data on soil moisture contents, the pF values of the soils at Wijster I and Castricum at 0.40-0.80 m below the surface in late August could be read off as follows: Wijster I $2.1 < pF < 2.9$, Castricum $2.7 < pF < 3.8$. Hence, in late August there was almost no overlap in the pF values of the soils at Wijster I and Castricum and the values reached at the latter site

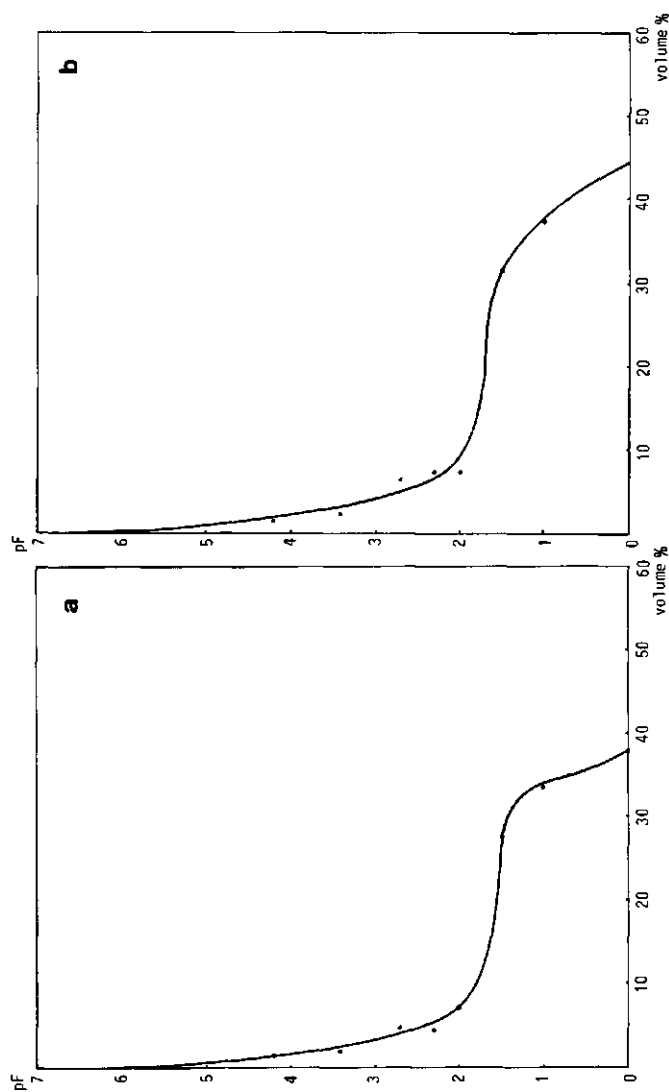


Figure 3a. Standard curve of soil moisture characteristics for C horizons of Orthic Podzols in The Netherlands and pF values for the C horizon of the Wijster I site.

Curve from Krabbenborg et al.(1983); pF values calculated according to the same authors.

Figure 3b. Same as figure 3a for C horizons of Calcaric Regosols and Castricum site.

were very high.

In the comparative field experiment a striking difference in survival rate of larvae since March was shown: 79.3 % in October 1979 in five enclosures at Wijster I (a live larva in 42 of 53 dung sausages) and only 4.6 % in late August 1981 in four enclosures at Castricum (1 of 22) ($\chi^2 = 32.48$, $P < 0.001$).

Assuming that the near absence of rainfall in April 1981 at Castricum indicates that pF values were as high then as in August 1981, there thus appear to have been two periods during which the eggs and larvae may have suffered a shortage of moisture at Castricum. We noticed that 9 of the 22 dung sausages excavated at Castricum lacked a protuberance of dung at the distal end, which means that no larva had entered the dung sausage, coming from the egg chamber. Hence, almost half of the eggs had probably not hatched, which emphasizes the importance of the drought in April.

We conclude that the pF values reached at 0.40-0.80 m below the surface at Castricum in April and/or August 1981 probably affected the survival rate of eggs and larvae, whereas at Wijster I pF values in August 1979 did not have such effects.

DISCUSSION

Soil bulk density

- (1) Since the beetles burrow by scraping away the sand in front of them, grain by grain, we had not expected the bulk density of the sand to have a negative effect on the depth of the burrows, provided the soil was not too dry. Moreover, Klemperer (1979) found that the termination of burrowing in *Geotrupes spiniger* (Marsham, 1802) (closely related to *T. typhoeus*) occurs in response to the length of the shaft already excavated, which is a stimulus independent of soil bulk density.
- (2) During observations of *T. typhoeus* in glass cages in the laboratory the careful and time-consuming preparation of the egg chamber (where the egg is deposited) and the brood chamber (where the dung sausage for the larva is made) was striking. The female, sometimes assisted by the male, tamped the wall below, beside and above her while slowly walking up and down the future brood chamber, alternated by scraping or plastering sand. Also, small amounts of sand were frequently removed from and pushed into the future egg chamber, alternated by 'measuring' movements.

This behaviour suggested that the sizes of the egg and brood chambers and the firmness of the walls were extensively inspected and improved before oviposition and dung provisioning. Carefully determining the diameter and the length of the brood chamber may be considered functional in ensuring that the future larva will be provided with sufficient dung. Making the walls firm may be functional in preventing them from collapsing when the female exerts pres-

sure while packing the brood chamber with dung.

These observations suggested that the lower the bulk density of the soil in which the beetles burrowed, the more time needed to be spent in preparing the egg and brood chambers. Taking into account that the length of the reproductive season is limited, we believe that this behaviour explains why fewer eggs and dung sausages were found in loosely packed soil than in densely packed soil.

Soil moisture

To ascertain the critical lengths of moist and dry periods and associated critical pF values at the depths where the eggs and larvae develop, the relations between soil moisture and survival rate of larvae should be studied further in experiments.

If our conclusions on the importance of drought as a factor affecting the survival of eggs and larvae can be confirmed by the results of laboratory experiments, we may infer that the higher risk of desiccation of eggs and larvae may well be an important cause of the absence of *T. typhoeus* from the whole dune area along the Dutch west coast and the Wadden islands, which was reported in an earlier paper (Brussaard 1983).

How cementing substances in the soil contribute to the effects of soil bulk density and soil moisture

The results presented earlier in the text show that bulk density and/or soil moisture have clear effects on the depth of the nesting burrows, the number of eggs laid/dung sausages made and/or the survival rate of

larvae. But, in addition, the degree of weathering of the parent material may have influenced these results under field conditions. The coastal dunes (on which Castricum is situated) are formed from Holocene calcareous sands that underwent relatively little soil formation. The soils in the Pleistocene regions of the Netherlands (on which Wijster and Maarheeze lie) are formed in decalcified or originally non-calcareous cover sands that have undergone strong podzolization (De Bakker 1979). In the lower horizons of these soils, accumulations of iron hydroxides, dispersed organic matter and/or amorphous silica or Al compounds may or do occur; these cause a stronger cementation of sand grains than in the soils formed in the coastal dunes. Hence, the beetles at Wijster probably experienced an even more compact soil than estimated from the bulk density alone. Since the substances mentioned also have a positive effect on the water-retaining capacity of the soil, they will have contributed to the course of the pF curve of Wijster I being somewhat lower overall than that of Castricum (fig. 3).

At Maarheeze, any cementing substances in the soil will have been far less effective in the drift-sands than in the undisturbed C horizons below them, because of the reworked nature of the drift-sands. We suggest that this phenomenon contributed to the results found in the comparative studies within the study area at Maarheeze (see paragraphs on "validation").

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G.Buurman drew the illustrations, Mrs. Th. van Hummel-Mom typed the manuscript and Mrs. J. Burrough-Boenisch edited and corrected the English.

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"A complete understanding of foraging behavior will require the integration of mechanistic approaches to behavior which emphasize proximal causation with evolutionary-ecological approaches which emphasize adaptive significance".

A.C. Kamil and T.D. Sargent, 1981.

In: A.C. Kamil and T.D. Sargent (eds.)

Foraging behavior: xiii-xvii.

A preliminary study of dung exploitation by the scarab
beetle *Typhaeus typhoeus* (Col., Geotrupidae) *)

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ABSTRACT

As a step towards being able to predict how much disturbance of stratified structures in sandy soils and mixing of soil constituents is caused by the scarab beetle *Typhaeus typhoeus*, the exploitation of dung (a prerequisite for the presence of the beetles) was studied. The working hypothesis was that the number of nests excavated by the beetles and, thereby, the beetles' influence on the soil, would be higher if relatively few dung pellets were available near the nest entrances at the places of settlement. This was confirmed by a field experiment.

The beetles made "dung sausages" as food sources for the larvae in horizontal "brood chambers" in the soil. In laboratory experiments the lengths of the dung sausages did not significantly differ within a wide range of frequencies of supply of various amounts of rabbit dung pellets, despite the longer time spent per dung sausage when less dung was supplied per unit of time. It is suggested that dung provisioning does not stop before the dung sausages have reached lengths (approximately 8.5-9.5 cm) pre-determined by the lengths of the brood chambers. There appeared to be a critical value between 1-2 and 4-5 dung pellets supplied per day, however, below which the finished dung sausages were significantly shorter (approximately 3.5 cm).

In laboratory and field experiments with various amounts of dung laid out in various patterns, the beetles effectively removed all the dung within a radius of 0.45 m around the nest entrance. Outside this area most beetles excavated a new nest near a cluster of dung pellets laid out 0.80-1.00 m away from the nest entrance. The zone between 0.45 and

0.80 m was transitional: some beetles collected dung there, others started excavating a new nest. Evidence is given that individual variation in foraging distance is connected with interactions between female and male beetle, which in turn appeared to be linked with the length of the brood chamber still to be provisioned with dung.

Not finishing dung provisioning before the dung sausage has reached a certain length is considered functional if thereby bigger off-spring result than if the dung sausage is finished earlier. Indeed, the sizes of the beetles were shown to correlate with the lengths of the dung sausages from which they had emerged.

In a field experiment the number of dung sausages made per nest could be inferred from the regular appearances of small amounts of sand on the surface, excavated from successive brood chambers. Between such appearances certain amounts of rabbit dung pellets were transported into the nest, from which the approximate lengths of the dung sausages could be inferred. The sex of the first beetle abandoning a nest could be derived from the amount of sand pushed up from a newly excavated burrow if the old nest was still inhabited by the partner.

In the field, dung collection behaviour on the surface was shown to correlate with precipitation.

Apart from its contribution to furthering our understanding of the beetles' influence on the soil, the study is discussed from the perspective of research on the ecological and evolutionary aspects of problems of food exploitation by dung beetles.

INTRODUCTION

The reproductive behaviour of the dung beetle *Typhaeus typhoeus* (Linnaeus, 1758) consists of burrowing a branching shaft, laying an egg in an egg chamber at the distal end of each branch, provisioning the branches with dung for the larvae and partly sealing the remaining burrow with sand (figure 1) (Brussaard 1983). Up to 450 kg of sand per hectare may be transported to the surface annually (Brussaard and Runia 1984). In addition to the back-filled parts of the burrows that seal in the "dung sausages", back-filled burrows come about when the newly emerged adults make their way to the surface (figure 1).

The activities of *T. typhoeus* and of related scarab beetles with similar behaviour contribute appreciably to the mixing of soil constituents and to the disturbance of stratified structures in sandy soils (Brussaard 1985; Brussaard and Runia 1984; Kalisz and Stone 1984). As a step towards being able to predict such influence on the soil, the effects of soil temperature on reproductive behaviour and larval development were reported in an earlier paper (Brussaard 1983) and the effects of soil bulk density and soil moisture on the habitat selection by *T. typhoeus* will be published elsewhere. As a next step we studied the exploitation of the main food source, rabbit droppings, by *T. typhoeus*, because dung is a prerequisite for the presence of the beetles. In the present paper, after giving some general information about the dung beetle, we report the results of this study.

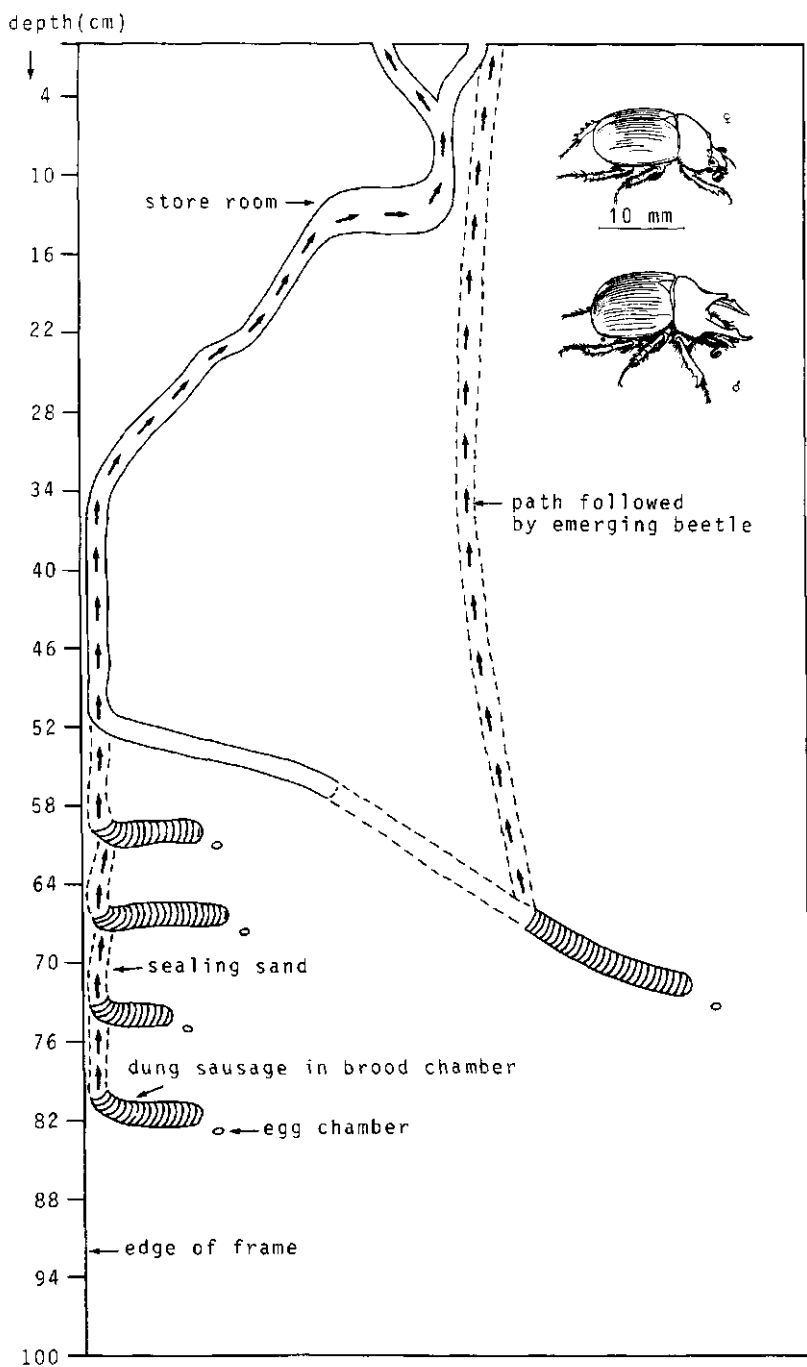


Fig. 1. Nest of *Typhaeus typhoeus*.

General biology of T. typhoeus

T. typhoeus is distributed from Morocco to southern Sweden, westwards to Ireland and eastwards to Poland and Yugoslavia. In The Netherlands the beetles are active from the second half of September onwards and throughout the winter whenever the temperature is above zero and there is no snow. Intense activity occurs in October and November, which is the main period of maturation feeding and from February to April, which is the main period of reproduction (Brussaard 1983). Their habitat is half-open heathland where they are mainly associated with rabbit dung (Brussaard 1983).

The beetles thrive in sandy soils whose bulk densities exceed $1.30 \times 10^3 \text{ kg/m}^3$ below 0.40 m under the surface (where the larvae develop), provided the water table is permanently below 0.80 m (unpublished results). In The Netherlands the generation time is two years if the overwintering larvae are exposed to temperatures approximating 5°C; if such a low temperature is not reached, the generation time is usually longer (Brussaard 1983).

Male and female co-operate during excavation of the nest and when provisioning the brood chambers with dung. The male gathers the dung pellets on the surface, the female stays below-ground to transform these into dung sausages (Brussaard 1983).

Working hypotheses

Our first hypothesis was: if there is always more than ample dung at a certain spot, a single nest will do for a female to lay all her eggs and make all associated dung sausages. If, however, dung is frequently in short supply, the beetles will from time to time settle elsewhere and, hence, excavate more nests, thereby having more influence on the soil.

Our second hypothesis was based on a study by Klemperer (1979) who found that in *Geotrupes spiniger* (Marsham, 1802) the female responds to the length of the horizontal brood chamber by stopping with dung provisioning when the brood chamber is filled up. We assumed that *T. typhoeus* (which is closely related to *G. spiniger* and shows a very similar behaviour) would react to that stimulus too.

Our third hypothesis was: continuing dung provisioning until the brood chamber is filled up is functional if thereby the beetles give rise to relatively large progeny, because large beetles are more successful breeders than small ones, at least in the competition for a nest or a partner (Palmer 1978).

Laboratory and field studies

Because in the field rabbit droppings can be found both clustered and scattered we studied the exploitation of dung and, in particular, the circumstances under which the beetles abandoned their nest to continue reproduction elsewhere, as influenced by various regimes of supply of rabbit dung pellets (1) in time and (2) in space. To further understand the exploitation of dung under natural field conditions we tried (3) to

develop methods by which invisible effects of below-ground behaviour could be inferred from effects of behaviour visible at the surface. We also studied (4) the possible correlation between foraging behaviour and humid weather conditions. Finally, we checked our working hypotheses (5) that more nests are excavated if the availability of dung at the places of settlement is relatively low and (6) that large dung sausages give rise to larger beetles than small dung sausages.

Later in the text these six experiments will be referred to by their number in brackets.

MATERIALS AND METHODS

General experimental conditions

In laboratory experiments dung beetles were kept in glass cages consisting of a wooden frame with two windows, fitted 15 mm apart and measuring 0.60 m wide and 1.00 m high. The beetles, one pair per cage, burrowed and reproduced in the sand between the windows. On top of the frame a walking surface was mounted, measuring $0.60 \times 0.50 \text{ m}^2$, (unless stated otherwise) on which dung could be put. An 8 mm wire mesh over the walking surface prevented the beetles from escaping. Black plastic sheets kept the below-ground parts of the cages dark.

For the field experiments we chose a heathland area with Orthic Podzols (FAO 1974) ("Haarpodzols" in the Netherlands classification) at Wijster in the Dutch province of Drenthe, where *Typhaeus typhoeus* naturally occurs. There we installed enclosures of various sizes, consisting of

0.50 m high stainless steel plates, inserted 0.20 m into the soil and spanned with 8 mm-mesh wire-netting to prevent beetles from flying in or out. We let one pair of beetles reproduce in each enclosure.

All beetles had been captured just after emergence and prior to reproduction at the same site near Havelte in the Dutch province of Drenthe and had been kept separately with plenty of dung at 5°C until the start of the experiments.

For all experiments the pairs of beetles used were randomly selected unless stated otherwise.

Laboratory and field studies

(1) Different regimes of dung supply in time

- (a) From 23 February to 2 May 1979 twenty glass cages were kept in a greenhouse at 9°C (sometimes rising to approximately 15°C) under natural daylength conditions. The cages were divided into five groups of four cages each. The cages of groups I-V received 7, 29, 51, 73 or 95 rabbit dung pellets per cage per week, respectively. These numbers were derived from a pilot experiment with more than ample amounts of dung in which the number of rabbit dung pellets transformed into a dung sausage appeared to be approximately 40; the number of dung sausages made per female per week was 4-5 at 9°C. Hence, the dung supply in the present experiment was expected to range from too little

towards sufficient for at least some dung sausages every week.

In one of the cages of group I no reproductive activity was recorded. This cage was excluded from analysis of the results.

- (b) In addition, we successively monitored the reproductive behaviour of four pairs of dung beetles in glass cages, numbered A-D, supplied with 10 dung pellets per 5 days (compare 7 per week in group I of the above-mentioned experiment), 5 per day (compare 29 per week in group II), 10 per day (compare 73 per week in group IV) and more than ample amounts of dung (compare 95 per week in group V), respectively. Cages A-D were studied in the laboratory in January and February 1981 at 9°C and natural daylength. Observations by night were usually carried out under dim red light.

(2) Different regimes of dung supply in space

- (a) In a field experiment we let a pair of beetles start reproducing near a cluster of 40 dung pellets in a corner of each of six enclosures measuring $2 \times 2 \text{ m}^2$, by inserting a female beetle into a finger-wide and a few centimetres deep small hole, which was invariably accepted as the beginning of the nesting burrow; the male was inserted one day later to join the female.

Between 15 March and 15 May 1980 the enclosures were inspected daily and whenever the number of dung pellets had dropped to 10 or less, they were brought up to 40. On such occasions we laid

the dung pellets successively farther away from the nest entrance at the following distances: 0.25-0.35 m, 0.45-0.55 m, 0.65-0.75 m, etc. As soon as the beetles had abandoned their previous nest and had settled near the cluster of dung, we repeated the treatment, but now the dung was successively laid at distances 0.35-0.45 m, 0.55-0.65 m, etc.

(b) We designed a laboratory set-up consisting of three glass cages, on top of which a communal walking surface was mounted, measuring $2.40 \times 1.80 \text{ m}^2$. The cages were installed 0.30 m apart behind each other, along the long axis of the walking surface (figure 2). One pair of beetles was introduced into the middle cage in the way described above. Dung pellets from wild rabbits were put on the walking surface. The following treatments were applied in order to study the foraging behaviour of the male beetle:

- treatment 0: no dung on the surface. The dung pellets initially laid out near the nest entrance to impel the beetles to excavate a nest were removed by the researchers as soon as the beetles had started excavation. This was to obtain a provisional indication about the area that is searched by the male when he comes to the surface to collect dung for the first dung sausage.
- treatment 1: a cluster of 40 dung pellets in front of the nest entrance, which was replenished as soon as the number had dropped to 10 or less. This was to get the beetles reproducing.
- treatment 2: a cluster of 40 dung pellets, replenished as

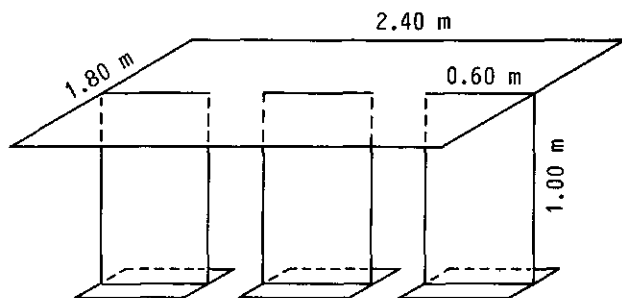


Figure 2. Diagram of set-up of laboratory equipment with three glass cages below a communal walking surface

above, which was progressively laid farther away from the nest entrance along a straight line in such a way that, eventually, the dung was laid above one of the outer glass cages, which served as an alternative place of settlement for the beetles.

- treatment 3: 192 dung pellets on eight concentric circles at 0.10 m spacing; i.e. one dung pellet per 100 cm^2 within a radius 0.80 m around the nest entrance. Besides, two clusters of 40 dung pellets each were laid out 1 m away from the nest entrance above each of the outer cages. The pattern of 192 dung pellets was derived from treatment 2, which suggested that in this way sufficient dung pellets for at least one dung sausage would be within easy reach of the male beetle.
- treatment 4: 96 dung pellets, laid out similarly as in 3; hence one dung pellet per 200 cm^2 , supposed to be more difficult to collect.

As soon as in treatments 2-4 the beetles had abandoned the nest in the middle cage and had settled in one of the outer cages, the middle cage was replaced by this outer cage and a new outer cage was installed, after which the next treatment was started.

During treatments 2-4 we partly attended more than half of the forays of dung collection by the beetle to record how much time was spent in finding a dung pellet and dragging it into the nest.

Throughout the experiment the same male beetle was used. The female had to be replaced during treatment 4, because of abnormal behaviour, presumably due to physiological ageing, and treatment 4 was thereupon restarted. This was considered to be acceptable because it was invariably the male who collected the dung pellets. The beetles used were of intermediate size.

The experiment was done in the laboratory at Wageningen between 18 December 1980 and 5 January 1981 and between 11 and 13 February 1981 at 5°C under natural daylength conditions. Observations by night were done under very dim light.

- (3) Inference of invisible effects of below-ground behaviour from effects of behaviour visible at the surface

Because the beetles usually transport some sand to the surface from every next brood chamber excavated, we could reconstruct how many dung sausages were made in every nest of experiment (2a). This reconstruction was checked by excavating the nests

after the experiment was terminated.

We also estimated how many dung pellets were used for every single dung sausage from the number collected between successive appearances of sand at the surface. To check our inference we measured the lengths of the dung sausages we excavated after the experiment.

Every day we closed each nest entrance that was open; this enabled us to monitor daily which burrow(s) was/were inhabited. We could also infer if a new burrow was inhabited by a male or by a female because we knew from earlier studies that a male on his own does not excavate a burrow deeper than approximately 0.15 m, whereas a female on her own, once fertilized, burrows deeper and, hence, pushes up more sand to the surface. If the entrance of the former nest was not opened up again after a new burrow had been made, we inferred that the latter was inhabited by both male and female.

(4) Dependence of foraging activity on precipitation

For each of the six enclosures of the field experiment (2a) plus a seventh, smaller one ($1 \times 1 \text{ m}^2$) the number of days with and without beetle activity on the surface was recorded between the first and last days of activity. The days with and without beetle activity on the surface were divided into days with and without precipitation and we tested whether dung collecting activity was correlated with precipitation.

(5) Number of nests per pair of beetles

We compared the number of nests made in field experiment (2a) with the number of nests made in a field experiment during March and April 1979 in the same area. In the latter experiment one pair of beetles was introduced into each of five enclosures, measuring $1 \times 1 \text{ m}^2$, and more than ample amounts of rabbit dung pellets were maintained in front of the entrance of the first nest. Two of these five pairs made a second nest, but apparently not because of a lack of dung in the neighbourhood, but rather because the ample amounts of dung resulted in the nest already being filled up before the female had laid all her eggs so that a second nest had to be made.

In the first nests of these two pairs the numbers of dung sausages were as high as 10 and 11. We excavated several tens of nests under natural field conditions and never found nests with more than 6 dung sausages. Hence, making a second nest because the first nest is filled up, must be exceptional under natural conditions. So we feel justified in counting the beetles in the two just-mentioned enclosures as having stayed near the dung in only "one" nest, to allow a proper comparison with the beetles in the enclosures of experiment (2a).

(6) Relationship between dung sausage length and beetle size

The beetles that emerged from the dung sausages made in experiment (1a) were reared as part of a more extensive

experiment, reported in an earlier paper (Brussaard 1983), to which the reader is referred for details on methods.

RESULTS AND CONCLUSIONS

- (1) Different regimes of dung supply in time
 - (a) Table 1a shows the mean lengths of the dung sausages in the glass cages of groups I-V. Table 1b shows that the dung sausages in the glass cages of group I were significantly shorter than those in each of the other groups, whereas no significant differences existed between groups II-V.
 - (b) In glass cage A of the monitoring experiment with a ration of 10 dung pellets per 5 days, a single small dung sausage was made. This was sealed with sand after 5 days, just before a new amount of 10 dung pellets was supplied. From these a second dung sausage was made which was already sealed after one day. The sealing was followed by behaviour that suggested that the beetles intended to leave. Results of behaviour in glass cages B-D are given in table 2.

The results presented in (a) and (b) are consistent with the hypothesis that the female usually fills up the brood chamber over a pre-determined length. Only if the dung supply is below a certain threshold is the dung sausage sealed before this length is reached. This threshold coincided with 7 to 29 dung

group	I	II	III	IV	V
number of dung pellets/week	7	29	51	73	95
mean lengths \pm S.D. (cm)	\bar{n} 7 2.9 ± 0.8	\bar{n} 1 7.5	\bar{n} 3 6.7 ± 2.1	\bar{n} 8 9.4 ± 2.1	\bar{n} 5 9.8 ± 2.5
of dung sausages in four replicates	1 5.0	3 9.2 ± 1.2	3 11.7 ± 3.0	5 11.7 ± 3.5	8 8.6 ± 2.7
(group I three replicates)	4 2.9 ± 1.0	1 6.0	2 8.5 ± 1.5	9 7.5 ± 1.5	4 9.4 ± 1.7
		7 9.9 ± 2.0	6 6.7 ± 3.4	4 8.8 ± 2.3	7 9.0 ± 1.6
	\bar{N}	\bar{N}	\bar{N}	\bar{N}	\bar{N}
grand mean \pm S.D. (cm)	12 3.1 ± 1.0	12 9.2 ± 2.0	14 8.0 ± 3.5	26 9.1 ± 2.7	24 9.1 ± 2.3

Table 1a. Mean lengths of dung sausages in laboratory experiment (1a) with beetles in glass cages, provided with different rations of rabbit dung pellets per week.

I vs. II : U = 0***	II vs. III : U = 66.5 ns	III vs. IV : z = 0.61 ns	IV vs. V : z = 0.42 ns
I vs. III : U = 22.5***	II vs. IV : z = 0.30 ns	III vs. V : z = 0.90 ns	
I vs. IV : z = 4.88**	II vs. V : z = 0.11 ns		
I vs. V : z = 4.78***			

Table 1b. Results of significance tests of differences between lengths of dung sausages in glass cages of groups I-V. Numbers of observations in groups I-V can be read from the columns headed by N in table 1a.

Mann-Whitney U-test, two-sided, *** = $P < 0.001$, ns = not significant at 0.05 level.

cage no.	supply of dung pellets	length of dung sausages (cm)	no. of dung pellets		time spent by	
			n	used per dung sausage	beetles per dung sausage (days)	
A	10 per 5 days	2	*)	*)	*)	
B	5 per day	3	6-8	41-45		9-12
C	10 per day	3	7.5-8.5	40		4-5
D	excessive	6	7-8.5	40-50		1.4-1.6

Table 2. Results of a laboratory experiment in glass cages in which the supply of dung was different in time.

n = number of dung sausages made during monitoring period

*) regime of dung supply below critical value for continuous reproductive behaviour (see text).

pellets supplied per week in (a) and with 10 dung pellets per 5 days to 5 pellets per day in (b). On average, these results amount to similar thresholds: between 1 and 4 or 2 and 5 dung pellets per day, respectively, under the experimental conditions of these studies.

(2) Different regimes of dung supply in space

(a) Table 3 shows that in four of the six enclosures in the field three nests were made, in one enclosure two nests were made and in another one the beetles stayed at the place where they started reproduction. In all enclosures dung pellets within a distance of 0.45 m from the nest entrance were effectively removed by the beetles. In enclosures 2, 3 and 5 the beetles even appeared to be able to collect dung pellets from approximately 0.85 m from the nest entrance, but they only dragged in a few and then settled near the cluster at that distance. For these beetles the critical distance was apparently between 0.65 and 0.85 m. In enclosure 6 as many as 29 of the 40 dung pellets were taken away from a distance of 0.85-0.95 m. Because in the latter case the beetles stopped reproduction thereafter, this distance is the best possible estimate of the male's abilities.

(b) In the experimental series with three glass cages below a communal walking surface, the male, having come to the surface to collect dung for the first time, thoroughly searched the area within a radius of 0.40-0.50 m around the nest, now and

enclosure no.	nest no.	greatest distance from where dung pellets were collected (m)	distance of settlement from previous nest
1	1	0.25-0.35	
	2	0.35-0.45	0.55
	3	0.35-0.45	0.55
2	1	0.45-0.55	
	2	0.80-0.90*	0.80
	3	0.55-0.65	0.80
3	1	0.45-0.55	
	2	0.80-0.90*	0.80
	3	0.55-0.65	0.83
4	1	0.25-0.35	
	2	0.35-0.45	0.35
5	1	0.45-0.55	
	2	0.75-0.85*	0.80
	3	0.55-0.65	0.87
6	1	0.85-0.95	

then returning and putting his head into the nest entrance for a few seconds (treatment 0). We thereupon laid 40 dung pellets near the nest entrance to start treatment 1.

Three aspects of the male's behaviour were striking during treatments 1-4. Firstly, the male alternated forays to collect dung pellets with periods of staying below-ground. The longest bout of dung pellet collection observed lasted slightly more than two hours, but to judge from the distances from where dung pellets were sometimes collected, some may have lasted longer. No more than 1-2 such dung collection periods were registered per 24-hour day. Hence, the male beetle stayed below-ground for several hours between successive bouts of dung collection. Secondly, the male usually searched for the next dung pellet in the neighbourhood of the previous one, walking in a straight line from the nest entrance to the dung. Thirdly, he almost invariably dragged the dung pellet in a straight line into the nest, if he had found it within a distance approximately 0.40 m away from the nest entrance; but if he found it between approximately 0.40 and 0.80 m he left

Table 3. Results of a field experiment in six enclosures, each having one pair of beetles. Clusters of dung pellets were laid successively further away from the nest entrance.

* fewer than 10 dung pellets dragged into first nest, prior to settling near the cluster of dung at this distance

the dung pellet half-way, put his head into the nest entrance, went back to the dung pellet and continued dragging it in. If the distance to be covered exceeded approximately 0.80 m, the "inspection" behaviour was repeated twice or more.

During treatment 2 the male settled in the outer glass cage when the dung cluster was at a distance 0.85-0.95 m away from the nest entrance in the middle cage. Before doing so, however, he had already transported five dung pellets from this distance to the nest. After having finished the second dung sausage, the female came to the surface, found the cluster of dung above the outer glass cage, joined the male and started burrowing a new nest. We then started treatment 3, after having replaced the middle cage by the newly occupied outer cage.

During treatment 3 the male predominantly searched the same area during the same bout of dung pellet collection, but the direction from where dung pellets were gathered differed between successive forays. While collecting dung pellets for the third dung sausage in this new cage (i.e. the fifth dung sausage of this pair of beetles) the male reached one of the clusters of dung that we had again laid out above the outer glass cages, 1.00 m away from the nest entrance of the present middle cage. He gathered 11 dung pellets there during three of six bouts of collecting, before eventually settling in the outer glass cage. Having finished the third dung sausage in the middle cage, the female again joined the male in the outer cage.

The behaviour during treatment 4 was similar to that during treatment 3.

Figure 3a shows that during treatments 2-4 of experiment (2b) it took the beetle more time on average to find a dung pellet at increasing distances from the nest entrance. The same holds for the time spent in dragging a dung pellet into the nest (figure 3b). As could be expected, collecting a dung pellet from a certain distance took the beetle more time on average if the dung was sparse (upper lines in figures 3a and 3b) than if it was clustered (lower lines in figures 3a and 3b). Since our measurements indicated that the variable "time" was not normally distributed, we could not test if these differences were significant. To judge from figure 3 distance seems to influence the collecting efficiency more than the pattern of dung pellets around the nest.

Table 4 shows that the beetles did not abandon the nest if the dung pellets could be collected within a distance averaging 0.45 m from the nest entrance. Above this distance the picture is less clear. We shall return to this point in the discussion.

From the results presented in (a) and (b) we conclude that under the conditions studied:

- dung is initially searched for within a distance of 0.45 m from the nest entrance
- all dung pellets within a radius of 0.45 m around the nest

mean time spent in finding
a dung pellet (sec)

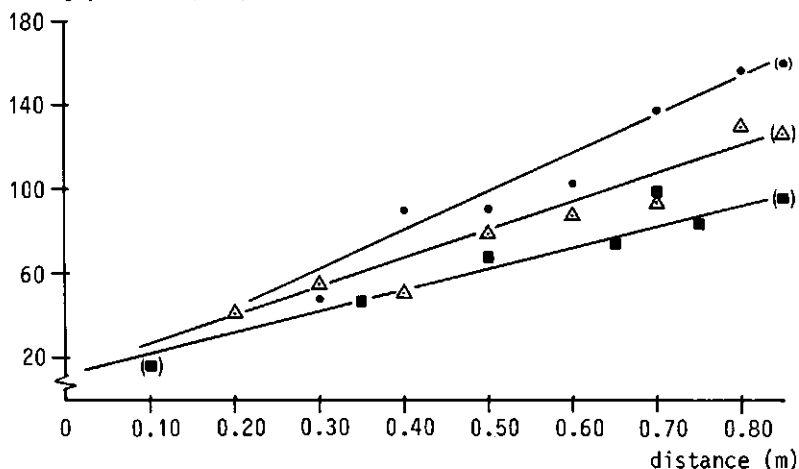


Figure 3a. Distance covered and mean time spent by male beetle in finding a dung pellet

squares: clusters of 40 dung pellets;

treatment 2 of experiment (2b);

Spearman's $\rho = 0.90$, $\rho / \sigma = 1.80$

($0.025 < P < 0.05$, one-sided)

triangles: 1 dung pellet per 100 cm^2 within a

radius 0.80 m around the nest entrance;

treatment 3 of experiment (2b);

Spearman's $\rho = 0.96$, $\rho / \sigma = 2.35$

($0.005 < P < 0.01$, one-sided)

dots: 1 dung pellet per 200 cm^2 within a

radius 0.80 m around the nest entrance;

treatment 4 of experiment (2b);

Spearman's $\rho = 1.00$, $\rho / \sigma = 2.24$

($0.025 < P < 0.01$, one-sided)

mean time spent in dragging
a dung pellet into the nest
(sec)

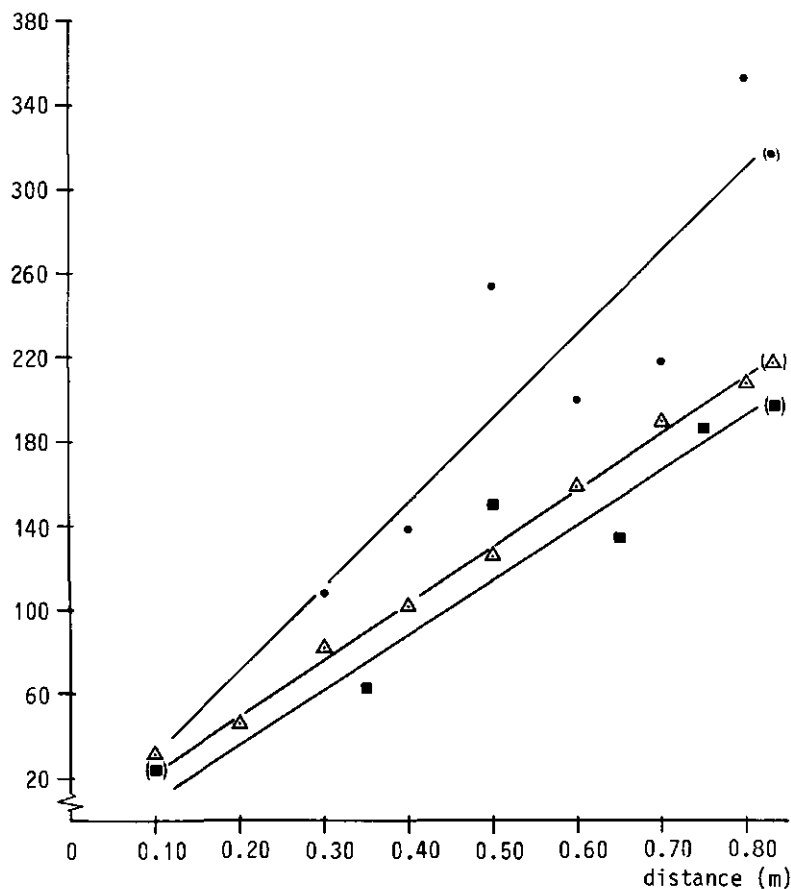


Figure 3b. Distance covered and mean time spent by male beetle in dragging a dung pellet into the nest. Symbols and treatments as explained below figure 3a.

squares: Spearman's $\rho = 0.80$, $\rho / \sigma = 1.39$
($0.05 < P < 0.10$, one-sided)

triangles: Spearman's $\rho = 1.00$, $\rho / \sigma = 2.65$
($0.0005 < P < 0.005$, one-sided)

dots: Spearman's $\rho = 0.83$, $\rho / \sigma = 1.85$
($0.025 < P < 0.05$, one-sided)

treatment	dung sausage no.	number of dung pellets collected during successive forays	mean distance		beetles stay/leave
			from where dung pellets were collected (m)		
(1) cluster of dung in front of nest entrance	1	47 (total)	-		stay
(2) cluster of dung put at increasing distance from nest entrance	2	8 2 14 2 3 3 1	0.10 0.35 0.50 0.65 0.70 0.75 0.80		leave

(3) 192 dung pellets	3	15	0.31	
spread uniformly		26	0.42	
within a radius		10	0.43	stay
of 0.80 m around	4	31	0.58	
nest entrance		24	0.54	stay
	5	4	0.65	
		4	0.74	
		8	0.89	
		9	0.88	
		2	0.65	
		6	0.53	leave
(4) 96 dung pellets	6	22	0.36	
spread uniformly		20	0.58	stay
within a radius	7	22	0.66	
of 0.80 m around		17	0.70	
nest entrance		4	0.73	leave

Table 4. Results of a laboratory experiment in which the supply of dung was varied in space.

entrance are effectively removed by the male beetle
-having exhausted the dung within 0.45 m from the nest
entrance, most beetles excavate a new nest near a cluster of
dung at a distance 0.80-1.00 m away from the nest entrance
-the zone between 0.45 and 0.80 m is transitional in that
some beetles stay in the nest and forage from that zone,
others start excavating a new nest

- (3) Inference of invisible effects of below-ground behaviour from
effects of behaviour visible at the surface

For 14 of 16 nests we excavated after termination of the field
experiment (2a), we appeared to have correctly inferred the
number of dung sausages per nest; in two cases our estimate
was one less than found. We conclude that our method of
estimating the number of dung sausages is satisfactory.

There appeared to be a correlation between the numbers of dung
pellets estimated as having been used for successive dung
sausages made, and the measured lengths of excavated dung
sausages: Spearman's rank correlation test, $n = 26$, $\rho =$
 0.408 , $\rho / \sigma = 2.04$ ($0.01 < P < 0.025$, one-sided). We conclude
that this result is encouraging but that our method should be
improved to be able to infer more precisely the amounts of
dung available for the larvae and, hence, to predict the sizes
of the beetles that emerge (see further paragraph (6)).

From experiment (2a) we learned that in only one case the
female first abandoned the old nest and settled at a new site,

in four cases the male went first and in four more cases both male and female had settled at a new site within the 24-hour interval before we inspected the enclosures. Acknowledging that the male invariably collects the dung pellets for the female as long as the couple is not split up and that, hence, the male is the first to be confronted with a shortage of dung (meanwhile the female is still provisioning dung) we conclude that the results on first settlements support the hypothesis that as a rule the male leaves the old nest first.

(4) Dependence of foraging activity on precipitation.

In the seven enclosures used to investigate if dung gathering activity is correlated with precipitation, 242 "beetle-days" were recorded, averaging approximately 35 per pair of beetles between the start and the last time of activity on the surface. On 144 of those 242 days at least some precipitation was recorded; on 98 days there was none. On 134 days dung collection was recorded, on 108 days there was none. The null hypothesis that collecting dung on the surface by the male beetle is independent of precipitation had to be rejected (table 5, $\chi^2 = 4.74$; $0.02 < P < 0.05$).

(5) Number of nests per pair of beetles.

From the comparison of experiment (2a) in which the dung was supplied at increasing distances from the nest entrance, with the 1979 field experiment in which dung was always present in

	+ rain	- rain	Σ
+ activity	88	46	134
- activity	56	52	108
	Σ 144	98	242

Table 5. Two-by-two table showing that in experiment

(4) dung collection activity is not independent of precipitation
 ($\chi^2 = 4.74$, $0.02 < P < 0.05$).

front of the nest entrance, it appeared that the null hypothesis that the number of nests excavated by the beetles is independent of the distance of the dung from the nest entrance had to be rejected (table 6, $\chi^2 = 7.64$; $0.001 < P < 0.01$).

(6) Relationship between dung sausage length and beetle size.

For 9 of the juvenile dung beetles that emerged from the glass cages of experiment (1a) we knew exactly from which of the dung sausages they had emerged. There appeared to be a significant correlation between the length of the dung sausage (i.e. a measure of the amount of food available for the larva) and the weight of the emerging beetle (i.e. a measure of beetle size): Spearman's rank correlation test, $n = 9$, $\rho = 0.90$, $\rho / \sigma = 2.53$ ($0.005 < P < 0.01$, one-sided); figure 4.

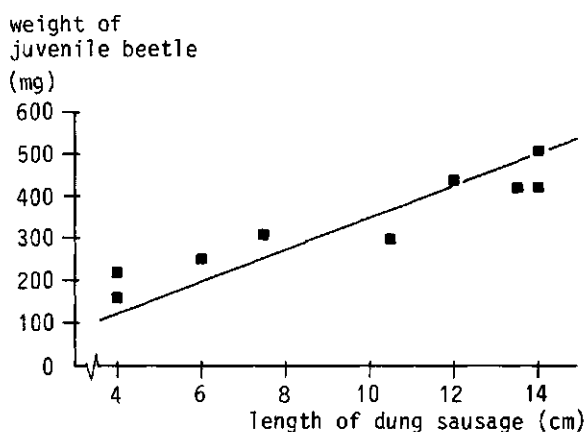


Figure 4. Length of dung sausage and weight of juvenile beetle.

Spearman's $\rho = 0.90$, $\rho / \sigma = 2.53$

($0.005 < P < 0.01$, one-sided)

	single nest	more than one nest	Σ
dung in front of nest entrance	5	0	5
dung at increasing distances	1	5	6
	Σ 6	5	11

Table 6. Two-by-two table showing that in experiment (5)

the number of nests excavated is not
independent of the distance of the dung
from the nest entrance

($\chi^2 = 7.64$, $0.001 < P < 0.01$).

DISCUSSION

The foraging behaviour of the dung beetles is in many respects reminiscent of that of parasitoids searching for hosts, predators searching for prey, and flower-visiting insects, which are all confronted with the problem: when and how long is a certain foraging situation profitable and how long is a certain foraging behaviour efficient? (See e.g. Kamil and Sargent 1981).

For the dung beetle *Typhaeus typhoeus* four stimuli are apparently important in determining whether it will stay or abandon a nest and its associated dung situation:

- 1) The distance from where the dung pellets have to be collected
- 2) The number of dung pellets per unit of surface, which is of some importance but apparently less than 1
- 3) The frequency with which dung pellets can be obtained
- 4) Stimulation of the male by the female

The latter point needs some explanation. Table 4 shows that the dung pellets gathered for dung sausages 2, 5 and 7 had to be collected from relatively great distances. For dung sausages 2 and 5 only a few pellets were collected per foray. During the periods in which the latter dung sausages were made, we observed that the female, repeatedly confronted with a shortage of dung pellets below-ground, scratched the male's elytra and thorax more frequently and more vigorously than otherwise, apparently to stimulate him to go for more dung. Probably, the stimulus for the male to persist in trying to collect dung pellets thereby remained high, despite the low availability of dung, and the threshold to abandon the nest only became sufficiently low after a fair number of

dung pellets had been dragged into the nest and the female's stimulatory behaviour had diminished. If supported by additional evidence, this may help explain why in some cases when no dung remained within 0.45 m, dung was collected from the zone between 0.45 and 0.80 m away from the nest entrance and even from a distance of 1 m, before the beetles eventually abandoned the nest.

Dung sausages of pre-determined lengths may be functional in many respects as compared with shorter dung sausages:

- the larva may have a better chance to complete its development because more food is available and moisture conditions are better
- development of the larva may proceed more rapidly
- larger progeny from the larger dung sausages (figure 4) may produce more eggs or may produce eggs for a longer period of time and may proceed more rapidly in dung provisioning (in the case of females), may collect dung from greater distances (in the case of males) and may excavate nests more rapidly (both males and females), thereby having a better chance to have progeny in their turn
- larger beetles may be better able to burrow through cemented soil layers
- larger beetles may be more able to maintain higher than ambient temperatures (Heinrich and Bartholomew 1979)
- larger beetles may have better chances of avoiding predation
- larger beetles may be more successful competitors for a nest or a partner (Palmer 1978)

There may be more factors than the stimuli mentioned earlier that influence whether beetles stay or leave a nest, such as the probably

greater chance of predation if the dung pellets are to be collected from increasing distances. In general, there may be a selected range of spreading the risk between staying or leaving which has led to "giving-up times" that are efficient in terms of continuation of reproduction within a certain time and with a certain rate. There are some noteworthy advantages in using *Typhaeus typhoeus* rather than another species for the study of such problems under natural conditions. Firstly, *T. typhoeus* is active between late September and early May, when only few other dung beetles live on the same food source. Secondly, in many places where *T. typhoeus* occurs in The Netherlands, the only food available for the beetles is rabbit droppings. Thirdly, the food source is immobile, apart from occasional transport by wind.

Hence, provided adequate data can be collected on the amounts of rabbit droppings produced in time and space, *T. typhoeus* appears to be an excellent object of study to further investigate the ecological and evolutionary aspects of problems of food exploitation by both adults and larvae. This enhances the promising pedological prospects of such a further study, referred to in the introduction to the present paper.

ACKNOWLEDGMENTS

Prof. Dr. L.J. Pons and Ir. K.J. Hoeksema suggested that dung beetles are important agents in reworking the soil and thereby provided the stimulus for the present study. Ir. J.G.A. Outhuis collected the data in table 2. Ir. A.F.M. Olsthoorn and Mr. E. Hoogendoorn were indispensable in the field work and Mr. P. Looijen skillfully constructed the

laboratory equipment.

Prof. Dr. L.J. Pons, Dr. S. Slager, Dr. P.J. den Boer and Dr. T.S. van Dijk critically read the manuscript. Mr. G. Buurman made the drawings, Mrs. N. van Boven typed the manuscript and Mrs. J. Burrough-Boenisch corrected the English. We are sincerely indebted to them all.

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SUMMARY

This thesis deals with cylindrical structures with meniscate infillings found in sandy soils and measuring approximately 14 mm in diameter and up to 15 cm in length; it also deals with the organisms that are considered responsible for the formation of these structures, viz. scarab beetles.

The structures, called traces or trace fossils in the ichnological literature, have been observed at numerous places in The Netherlands and the surrounding countries, in particular at depths up to 2 m below the surface in Pleistocene cover sands and river terrace sands, where they disturb the horizontal stratification of the sediment or the horizontal lamination of the soil profile. Because of their small range in size and their meniscate infillings the traces were assumed to have a biogenic origin. Dung beetles or other scarab beetles that burrow into the soil as adults and/or larvae were, as a working hypothesis, postulated to be possible trace-makers. Therefore, the dung beetle *Typhaeus typhoeus*, which burrows up to 1 m or even deeper into sandy soils, was chosen to be studied as a model species. Its behaviour of back-filling excavated burrows with sand and the conditions under which it did this were described (chapter 2). The back-filling traces made by this beetle and by another scarab beetle, *Lethrus apterus*, appeared to be very similar in size and infilling to the observed structures mentioned above (chapters 3 and 4).

Apparently ancient traces were dated in two ways (chapter 3). Firstly, from literature data on fossil body remains of beetles it

was ascertained during which Pleistocene and Holocene periods scarab beetles the size of *T. typhoeus* had been present. These periods appeared to be the Pleistocene interstadials, the early Preboreal and the period since the Atlantic. Secondly, the ages of the ancient traces were calibrated by clay illuviation phenomena inside the back-filling traces and in the matrix where the back-filling traces disturb bands of clay illuviation in river terrace sands. In most cases the back-filling and the clay illuviation appeared to have occurred concurrently. Combined with knowledge of the circumstances that favour clay illuviation it was inferred from the results on fossil beetles and clay illuviation that the early Preboreal conditions of ameliorating climate favoured both dung beetle activities and clay illuviation, and therefore most of the ancient traces must have come about during that period.

In order to compare the microstructure inside the back-filled burrows with that in the undisturbed matrix, soil samples from six localities in The Netherlands where traces, ancient or recent, had been observed, were thin-sectioned and subjected to micromorphometric analysis (chapter 5). As compared with the undisturbed matrix, the volume (measured in per cent) of pores larger than 0.030 mm was up to 38 % greater in the burrows. Because 0.195 mm approximates the critical pore diameter below which roots of plants cannot penetrate densely packed sandy soils, pores larger than that size were likewise compared, with the same result. The inference that rooting would thus be more intensive in the back-filled burrows than in the undisturbed matrix was confirmed by observations.

To develop a method for predicting the influence of the beetles on the soil, the habitat selection of *T. typhoeus* as influenced by soil temperature, soil bulk density and soil moisture was studied (chapters 2 and 6). The soil temperature threshold for the nesting behaviour of the beetles appeared to be between 1° and 5°C. The threshold for the hatching of eggs was found to be between 5° and 9°C. Development of larvae was slow at 9°C and apparently normal at 13° and 17°C. A cold spell of approximately 5°C during about six weeks of the development of the third instar was shown to be very favourable for the subsequent metamorphosis of the larvae into adults. If the third instar larvae were not subjected to such a cold spell, the generation time was extended beyond the normal period of two years. This was shown to occur under field conditions.

Soil bulk density appeared not to influence the depths of the nesting burrows of *T. typhoeus*, but the number of eggs laid per beetle and the number of dung sausages made as food provisions for the larvae diminished with decreasing bulk densities of the soil. This was attributed to a behavioural response of the beetles during the phases of preparation of the egg chambers and the brood chambers for the larvae. Under field conditions the density of the beetle population was shown to be higher in relatively densely packed soil.

Both high and low soil moisture contents adversely affected the reproductive behaviour and development of the beetles. The beetles did not excavate nesting burrows beyond the upper level of the saturation zone. The survival rate of eggs and larvae was adversely affected by conditions of high soil moisture (> 20 % by volume).

Evidence is also given for a low survival rate of eggs and larvae in conditions of low soil moisture ($pF > 2.7$).

Having described the soil conditions that are favourable for the reproductive behaviour and development of *T. typhoeus*, the exploitation of dung (a prerequisite for the occurrence of the beetles) was studied as the next step towards understanding the beetles' quantitative influence on the soil (chapter 7). The beetles effectively removed all rabbit dung pellets within a radius of 0.45 m around the nest entrance. They went on dung provisioning for the larvae as long as they could obtain 4-5 rabbit dung pellets per day. If the dung was 0.80 m or more away from the nest entrance, abandoning the nest and settlement near a cluster of dung pellets elsewhere frequently occurred. The zone between 0.45 and 0.80 m from the nest entrance was transitional in that some beetles collected dung there, others started a new nest in that zone. Evidence is given that individual variation in foraging distance was connected with below-ground interactions between male and female beetle, which in turn appeared to be linked with the amount of dung that still had to be provisioned as food for the larva. Dung collection was shown to occur mostly on days with precipitation.

Apart from its contribution to furthering our understanding of the influence of scarab beetles on the soil, the study is discussed from the perspective of research on the ecological and evolutionary aspects of the behaviour of dung beetles.

SAMENVATTING

EEN BODEMBIOLOGISCH ONDERZOEK OVER DE MESTKEVER

TYPHAEUS TYPHOEUS (COLEOPTERA, GEOTRUPIDAE)

Dit proefschrift gaat over cilindervormige structuren met een schotelvormige opvulling, die voorkomen in zandgronden. Deze structuren hebben een diameter van ongeveer 14 mm en ze zijn tot 15 cm lang. Het proefschrift gaat ook over de organismen die verantwoordelijk worden geacht voor de vorming van deze structuren, namelijk mestkevers en andere bladsprietkevers, behorende tot de superfamilie Scarabaeoidea.

De structuren, die in de ichnologische literatuur "sporen" of "spoor-fossielen" worden genoemd, zijn op talrijke plaatsen in Nederland en de omliggende landen waargenomen, in het bijzonder tot 2 m beneden de oppervlakte in Pleistocene dekzanden en rivierterraszanden, waar ze de horizontale gelaagdheid van het sediment of het bodemprofiel verstoren. Vanwege hun geringe variatie in afmetingen en hun schotelvormige opvulling werd aangenomen dat de sporen een biogene oorsprong hebben. Mestkevers of andere bladsprietkevers die in de bodem graven als volwassen kevers en/of als larven werden, bij wijze van werkhypothese, beschouwd als mogelijke spoor-vormers. Daarom werd de driehoornmestkever *Typhaeus typhoeus*, die tot 1 m of zelfs dieper in zandbodems graaft, gekozen om als model-soort te worden bestudeerd. Kevers die tot deze soort behoren vullen de gangen die ze uitgraven weer op met zand en de omstandigheden waaronder dit gedrag wordt vertoond, werden beschreven (hoofdstuk 2). De sporen van het

weer opvullen van gangen die gemaakt worden door deze en een verwante kever, *Lethrus apterus*, bleken veel gelijkenis te vertonen in afmetingen en in opvulling met de bovenvermelde structuren (hoofdstuk 3 en 4).

Van sporen die klaarblijkelijk oud waren, werd de ouderdom als volgt bepaald (hoofdstuk 3). In de eerste plaats werd aan de hand van literatuurgegevens over fossiele keverresten vastgesteld, gedurende welke Pleistocene en Holocene perioden bladsprietkevers zo groot als *T. typhoeus*, aanwezig waren geweest. Deze perioden bleken te zijn: de Pleistocene interstadialen, het vroeg Preboreaal en de periode sinds het Atlanticum. In de tweede plaats werd de ouderdom van de oude sporen geijkt aan klei-inspoelingsverschijnselen in de weer opgevulde gangen en in de matrix op plaatsen waar de sporen klei-inspoelingsbanden in rivierterraszanden verstoren. In de meeste gevallen vond het weer opvullen van gangen gelijktijdig plaats met de klei-inspoeling. Gecombineerd met kennis over de condities die bevorderlijk zijn voor klei-inspoeling werd geconcludeerd dat de vroeg-Preboreale omstandigheden van een verbeterend klimaat gunstig zijn geweest voor zowel mestkevers als klei-inspoeling, zodat de meeste oude sporen gedurende die periode tot stand moeten zijn gekomen.

Om de microstructuur in de opgevulde gangen met die in de ongestoorde matrix te kunnen vergelijken, werden op zes plaatsen in Nederland waar sporen (hetzij oud, hetzij recent) waren vastgesteld, bodemonsters genomen. Daarvan werden slijpplaten gemaakt, die micromorfometrisch werden geanalyseerd (hoofdstuk 5). Vergeleken met de

onverstoorde matrix was het volume aan poriën groter dan 0.030 mm in de gangen 38 % hoger. Omdat 0.195 mm bij benadering de kritische poriëndiameter is, waarbeneden wortels van planten niet kunnen doordringen in dicht gepakte zandgronden, werden poriën groter dan die afmeting op dezelfde wijze vergeleken, met hetzelfde resultaat. De gevolgtrekking dat de beworteling in de opgevulde gangen intensiever zou zijn dan in de onverstoorde matrix werd door waarnemingen bevestigd.

Om een methode te ontwikkelen om de invloed van de kevers op de bodem te voorspellen, werd de habitatselectie van *T. typhoeus* bestudeerd, onder invloed van bodemtemperatuur, bodemdichtheid en bodemvochtigheid (hoofdstuk 2 en 6). De drempel in de bodemtemperatuur voor het voortplantingsgedrag van de kevers bleek te liggen tussen 1° en 5°C. De drempel voor het uitkomen van de eieren bleek te liggen tussen 5° en 9°C. De ontwikkeling van de larven was langzaam bij 9°C en ogenschijnlijk normaal bij 13° en 17°C. Een koude-periode van circa 5°C gedurende ongeveer zes weken tijdens de ontwikkeling van het derde larve-stadium bleek zeer bevorderlijk te zijn voor de daaropvolgende metamorfose van de larven tot volwassen kevers. Als de derde-stadium larven niet aan zo'n koude-periode werden blootgesteld, dan werd de generatieduur verlengd tot langer dan de normale periode van twee jaar. Dit bleek onder veldomstandigheden voor te komen.

De bodemdichtheid bleek de diepte van de broedgangen van *T. typhoeus* niet te beïnvloeden, maar het aantal eieren dat per kever werd gelegd en het aantal mestpropfen dat als voedselvoorraad voor de larven werd aangelegd nam af met afnemende dichtheid van de bodem. Dit werd

toegeschreven aan een gedragsrespons van de kevers gedurende de fasen van het in gereedheid brengen van de eikamer en de broedkamer. Onder veldomstandigheden bleek de dichtheid van de keverpopulatie groter te zijn in relatief dicht gepakte bodems.

Zowel hoge als lage bodemvochtigheid tastte het voortplantingsgedrag en de ontwikkeling van de kevers aan. De kevers groeven geen broedgangen uit beneden het niveau van de verzadigde zone. Het aantal in de loop der tijd overlevende eieren en larven werd nadelig beïnvloed door omstandigheden van hoge vochtigheid (> 20 vol. %). Ook bij lage bodemvochtigheid ($pF > 2.7$) was het aantal in de loop der tijd overlevende eieren en larven laag. Nadat de bodemomstandigheden die gunstig zijn voor het voortplantingsgedrag en de ontwikkeling van *T. typhoeus* waren beschreven, werd de exploitatie van mest (een voorwaarde voor het voorkomen van de kevers) bestudeerd als de volgende stap ter verklaring van de kwantitatieve invloed van de kevers op de bodem (hoofdstuk 7). De kevers verwijderden effectief alle konijnekeutels binnen een straal van 0.45 m rond de ingang van het nest. Ze gingen door met het aanleggen van voedselvoorraden voor de larven zolang ze 4-5 konijnekeutels per dag konden bemachtigen. Als de mest 0.80 m of meer van de ingang van het nest verwijderd lag, werd het nest veelal verlaten en vestigden de kevers zich elders bij een verzameling keutels. De zone tussen 0.45 en 0.80 m van de ingang van het nest bleek een overgangszone te zijn, waarbinnen sommige kevers mest verzamelden, andere een nieuw nest begonnen. Er bleek evidentie te zijn dat de individuele variatie in de afstand vanwaar mest werd verzameld, verband hield met interacties ondergronds tussen de mannetjeskever en het vrouwtje, die op hun beurt verband leken te

houden met de hoeveelheid mest die nog moest worden aangebracht als voedsel voor de larve. Het verzamelen van mest bleek grotendeels plaats te vinden gedurende etmalen met neerslag.

Het onderzoek heeft geleid tot een beter begrip van de invloed van bladsprietkevers op de bodem. Daarnaast wordt in het proefschrift ingegaan op de perspectieven van verder onderzoek naar de oecologische en evolutionaire aspecten van het gedrag van mestkevers.

CURRICULUM VITAE

Lijbert Brussaard werd geboren op 26 september 1951 te Oud-Beijerland. Vanaf 1963 bezocht hij het Johannes Calvin Lyceum te Rotterdam, waar in 1969 het examen gymnasium β werd afgelegd. Vanaf 1969 studeerde hij biologie aan de Vrije Universiteit te Amsterdam. Na het kandidaatsexamen in 1972 werden doctoraalbijvakken bewerkt in de milieukunde (deels aan de Universiteit van Amsterdam) en de diersystematiek. Het doctoraalhoofdvak dieroecologie werd bewerkt aan het Biologisch Station van de Landbouwhogeschool te Wijster. Het doctoraal examen werd afgelegd in 1977 (cum laude), waarbij tevens de eerstegraads lesbevoegdheid in de biologie werd verkregen.

Van 1978 tot 1982 was hij als wetenschappelijk assistent verbonden aan de vakgroep Bodemkunde en Geologie van de Landbouwhogeschool te Wageningen, waar, in samenwerking met de vakgroep Dieroecologie, het onderzoek werd verricht, waarvan dit proefschrift het resultaat is. Van 1982 tot 1984 was hij eveneens aan de Landbouwhogeschool verbonden als wetenschappelijk ambtenaar met een taak op het gebied van de stimulering van het bodembologisch onderzoek en onderwijs. Vanaf 1984 is hij als wetenschappelijk ambtenaar in vaste dienst bij de afdeling Bodembioogie van het Instituut voor Bodemvruchtbaarheid te Haren.