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THE ECOTOXICOLOGICAL EFFECTS OF IVERMECTIN ON DUNG INSECT COMMUNITIES

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The ecotoxicological effects of ivermectin on dung insect communities

by

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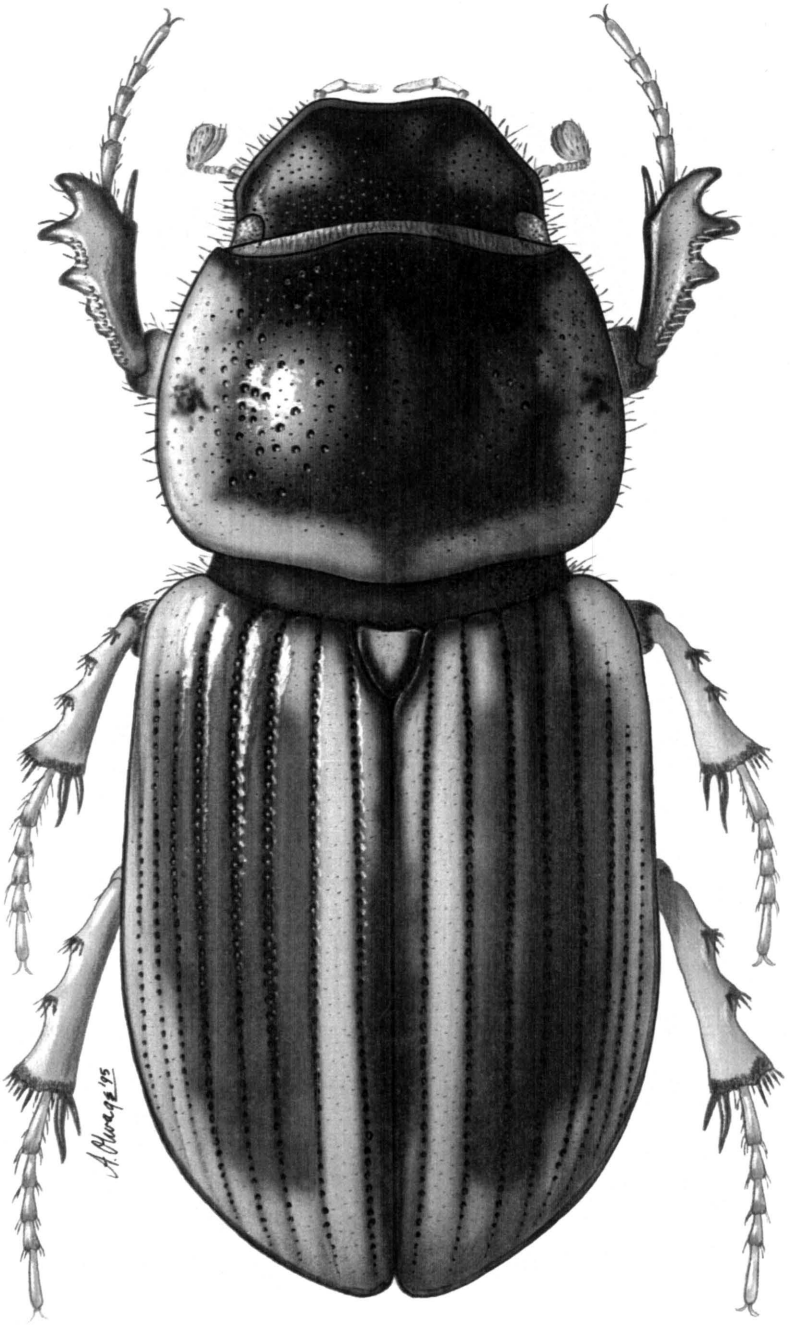
Dedicated to my parents
Horst and Heide Henneicke



Aphodius pseudolividus Balthasar

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Summary

Ivermectin is a broad-spectrum veterinary agent active against a range of nematodes and arthropods in livestock. Concern about the environmental safety of ivermectin has arisen because a considerable amount of the agent is excreted in the animals' dung where it remains active and has been shown to affect non-target organisms such as dung-breeding insects. The ecotoxicological effects of ivermectin on dung insects under South African conditions were assessed at three levels of complexity: (1) laboratory, (2) semi-field and (3) large-scale field studies.

For all studies cattle were treated with a single subcutaneous injection of 200μgkg^{-1} body mass according to the manufacturer's recommendations.

Lethal and sublethal effects of ivermectin and its residues in cattle dung were bioassayed in the laboratory using the two dung beetle species, *Euoniticellus intermedius* (Reiche) and *Onitis alexis* Klug, and the dung breeding fly, *Musca nevilli* Kleynhans. The parasiticide was found to reduce adult emergence and to prolong development. Studies on the effect of ivermectin on the fertility of *E. intermedius* and *M. nevilli* also showed a reduction. The duration and severity of the effects varied among species.

All field investigations took place in the summer rainfall region of South Africa. Firstly, field trials carried out in the Transvaal showed, in general, no differences in dung decomposition or colonization of pats from ivermectin-treated animals. However, dung decomposition rates varied among trials. Dung from treated animals was decomposed at the same rate, faster or more slowly than the control two, three and seven days after treatment, when the concentration of ivermectin in dung was high. Dung of both types of pats was broken down rapidly, usually within four days after placement. Treatment of cattle with ivermectin is, therefore, unlikely to affect the overall dung decomposition via repellence or attraction of dung insects to pats from treated animals.

Secondly, two large-scale field studies to determine the impact of ivermectin on dung insect communities under normal extensive farming conditions were conducted in the Free State Province. For the field studies entire herds were treated. Under drought conditions ivermectin appears to affect dung insect communities primarily through reduction in Shannon's species diversity and Pielou's evenness for up to three months after treatment. Under more favourable weather conditions with relatively high rainfall, little or no effect

was observed. The populations of *E. intermedius,* the most abundant scarabaeine species at the study site, appeared unaffected under both drought and average to high rainfall conditions.

The results of the field studies suggest that the seriousness of the impact depends on several factors, including climatic conditions, spatial scale of treatment (i.e. size of paddocks) and number of animals treated in a herd.

A qualitative frame-based model is proposed to assist farm management decisions with regard to the treatment of cattle with ivermectin.

Opsomming

Ivermectin is 'n breëspektrum veeartsenykundige middel wat op verskeie nematodes en geleedpotiges by lewende hawe inwerk. Daar is besorgdheid oor die uitwerking van ivermectin op die omgewing aangesien 'n aansienlike hoeveelheid van die middel in die diere se mis uitgeskei word waar dit aktief bly en klaarblyklik 'n uitwerking het op ander organismes soos insekte wat in die mis voortplant. Die eko-toksologiese werking van ivermectin op hierdie insekte onder Suid-Afrikaanse toestande is op drie vlakke ondersoek: (1) laboratorium- (2) semi-veld- en (3) grootskaalse veldstudies.

In elkeen van die studies is vee behandel met 'n enkele onderhuidse inspuiting van 200ugkg^{-1} volgens die vervaardiger se aanbevelings.

Die dodelike en minder dodelike uitwerking van ivermectin en die oorblyfsels daarvan in beesmis is in die laboratorium op twee miskewerspesies, *Euoniticellus intermedius* (Reiche) en *Onitis alexis* Klug, sowel as die misvlieg, *Musca nevilli* Kleynhans getoets. Daar is bevind dat die parasietdoder die verskyning van volwassenes inkort en ontwikkeling verleng. Studies oor die effek van ivermectin op die vrugbaarheid van *E. intermedius* en *M. nevilli* het ook 'n verlaging aangetoon. Die duur en graad van uitwerking het van spesie tot spesie verskil.

Alle veldnavorsing is in die somerreënvalstreke van Suid-Afrika gedoen. Eerstens het veldstudies in die Transvaal oor die algemeen geen verskille uitgewys in die ontbinding van mis of kolonisasie van misklonte van diere wat met ivermectin behandel is nie. Die grade van ontbinding van die mis het egter tussen die onderskeie studies verskil. Mis van behandelde diere het teen dieselfde tempo, of vinniger of stadiger ontbind as die kontrolemonster, oor twee, drie en sewe dae na behandeling toe die konsentrasie ivermectin in die mis hoog was. Die mis van beide soorte klonte het vinnig ontbind, gewoonlik binne vier dae na plasing. Dit is derhalwe onwaarskynlik dat die behandeling van beeste met ivermectin die ontbinding van mis oral sal beinvloed via die afweer of aantrekking van misinsekte na misklonte van behandelde diere.

Tweedens is twee grootskaalse veldstudies in die Vrystaat uitgevoer om te bepaal wat die invloed van ivermectin op kolonies misinsekt-gemeenskappe onder normale uitgebreide boerderytoestande is. Vir die veldstudies is hele kuddes behandel. Onder droogtetoestande skyn dit asof ivermectin 'n uitwerking op misinsekte het, hoofsaaklik deur vermindering van

Shannon se spesiediversiteit en Pielou se statistiese verspreiding, vir tot drie maande na behandeling. Onder meer gunstige weersomstandighede met relatief hoë reënval, is min of geen uitwerking waargeneem nie. Dit het voorgekom of die populasies van *E. intermedius*, the mees oorvloedige spesie in die studie-gebied, nie deur droogtetoestande of gemiddeld tot hoë reënval geraak is nie.

Volgens resultate van die veldstudies skyn dit asof die belangrikheid van die uitwerking van verskeie faktore afhang, insluitende klimaatstoestande, die ruimteskaal van behandeling (grootte van die kampe) en die aantal diere wat in 'n kudde behandel is.

'n Kwalitatiewe raamwerkmodel word voorgestel om boere behulpsaam te wees in die behandeling van beeste met ivermectin.

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1 General introduction

The term ecotoxicology was introduced by Truhaut in 1969 (Truhaut, 1977). It is derived from ecology, the scientific study of the interactions that determine the distribution and abundance of organisms (Krebs, 1985), and toxicology, which is traditionally defined as the scientific study of the effects of toxic substances on living organisms (Zakrewski, 1991). Ecotoxicology has, therefore, been defined by Forbes & Forbes (1994) as 'the field of study that integrates the ecological and toxicological effects of chemical pollutants on populations, communities and ecosystems with the fate (transport, transformation and breakdown) of such pollutants in the environment'.

1.1 The rationale for the study

The project on the ecotoxicological effects of ivermectin on the dung insect fauna was initiated after reports in the literature that ivermectin, a veterinary anti-parasitic agent, might constitute an environmental hazard (e.g. Schmidt, 1983; Coe, 1987). In particular, the landmark paper by Wall & Strong (1987) drew attention to the possible harmful effects of ivermectin on the dung-degrading insect fauna and consequently on the ecology of pasture ecosystems. Growing environmental awareness and the increasingly widespread use of ivermectin and other closely related compounds, such as abamectin, resulted in a debate in recent years concerning the environmental safety of these agents (e.g. Herd *et al.*, 1993a; Holter *et al.*, 1994; Wratten *et al.*, 1994).

Ivermectin belongs to a relatively new class of chemicals, the avermectins, which are highly potent broad-spectrum antiparasitic drugs (Campbell, 1989). They are very efficient at low doses against a wide range of nematodes and arthropods (insects, mites and ticks) and have veterinary, agricultural and medical applications (Campbell, 1989, 1991; Taylor *et al.*, 1990). Ivermectin was introduced to the marketplace by Merck, Sharp & Dohme in 1981 (Campbell, 1989) and had a major impact on the control of veterinary parasites

because of its combined action against both nematodes and arthropods (Campbell, 1985).

Most of the administered ivermectin, whether as a slow-release device, subcutaneous injection, pour-on or oral formulation, is excreted in the animals' dung where it remains active (Halley *et al.*, 1989c). This property has rendered avermectins potentially useful as larvicides in dung against economically important dung-breeding flies. However, avermectin residues in dung affect both pest species and non-target organisms, such as beneficial dung-breeding beetles (Strong & Brown, 1987; Strong, 1992). The presence of the active parasiticide in dung has led to concern that a depletion of local dung faunas due to avermectins may cause contamination of pastureland with undegraded cattle dung (Coe, 1987; Wall & Strong, 1987).

The present study focuses on the effects of ivermectin on the cattle dung insect fauna because of the existence of a large cattle industry in southern Africa, in which most beef cattle are farmed under extensive conditions, and consequently because of the ecological and economic importance of the insect fauna associated with cattle dung.

1.2 Dung composition and degradation

As a metabolic end product, dung consists of partially digested and undigested food particles, matter of endogenous origin and numerous microorganisms and their metabolic products (Marsh & Campling, 1970; Endrödy-Younga, 1982). Dung varies greatly in its moisture content, consistency, chemical composition, size, shape and mass (Endrödy-Younga, 1982; Edwards, 1991; Barth, 1993; Barth *et al.*, 1994a; Barth *et al.*, 1995).

The decomposition of dung depends on both abiotic and biotic factors. Abiotic factors include the geographical location, season, soil type and prevailing climatic conditions, such as temperature, rainfall and air movement (e.g. Castle & MacDaid, 1972; Hughes, 1975; Holter, 1979; Dickinson, *et al.*, 1981; Matthiesen & Hayles, 1983; Anderson *et al.*, 1984; Macqueen *et al.*, 1986; Ridsdill-Smith, 1986; Kirk & Wallace, 1990). A great variety of organisms exploit animal dung. These comprise protozoa, bacteria, fungi, nematodes, lumbricides, mites, insects and a number of other arthropods, such as millipedes and spiders (Mohr, 1943; Macqueen & Beirne, 1974; Macqueen, 1975; Holter, 1979; Stevenson &

Dindale, 1987; Skidmore, 1991).

The duration of the decomposition process varies considerably. For example, the time required for the degradation of cattle dung ranges from 42 up to 133 days in temperate European countries (Castle & MacDaid, 1972; Holter, 1979; Dickinson *et al.* 1981), 153 up to 1000 days in California (Anderson *et al.*, 1984) and about 305-450 days in Japan (Nakamura, 1975). The decomposition period in tropical and subtropical regions is considerably shorter and in the rainy season pats are usually decomposed within a few days after deposition (Waterhouse, 1974; Bornemissza, 1979; Chapter 3.1), sometimes even within hours (Bornemissza, 1976). Although these studies differed in their methodology and the definition of complete dung disintegration, they provide an idea about the time needed for dung decomposition in different geographical regions.

1.3 Insects associated with dung

Insects are the most successful group in exploiting animal dung (Macqueen & Beirne, 1974). Most dung frequenting insects belong to the orders Coleoptera and Diptera (Hanski & Cambefort, 1991c). Hymenoptera and Isoptera are represented to a lesser extent (Ferrar & Watson, 1970; Macqueen, 1975). Hymenoptera associated with dung are entomophagous (e.g. Braconidae, Ichneumonidae) and Isoptera, although coprophagous, frequent dried out older dung after the majority of other species have left (Ferrar & Watson, 1970; Macqueen, 1975; Hanski, 1991). Dipteran larvae are coprophagous (e.g. Muscidae, Scatophagidae, Sepsidae and Sphaeroceridae) except for a few entomophagous larvae which belong to the family Muscidae (Hanksi, 1991). Coleoptera are either coprophagous (e.g. Scarabaeinae, Aphodiinae, adult Hydrophilidae, Staphylinidae (Oxytelinae)) or entomophagous (e.g. Histeridae, larvae of Hydrophilidae; Staphylinidae (Aleocharinae, Staphylininae, Tachyporinae)) (Macqueen, 1975; Hanski & Koskela, 1977; Hanski, 1991).

An important component of the invertebrate fauna associated with dung is dung beetles. The term dung beetles applies to beetles which use dung as a food source for both larvae and adults. Dung beetles belong to the subfamilies Scarabaeinae, Geotrupinae and

Aphodiinae (Halffter & Edmonds, 1982)[1]. The Aphodiinae consist of approximately 2500 species in 100 genera, Geotrupinae comprise about 900 species in 60 genera and the Scarabaeinae include about 4500 species in 200 genera (Halffter & Edmonds, 1982). Species richness, as well as the ecological importance of dung beetles with regard to dung decomposition and nutrient cycling generally increases with decreasing latitude (Hanski & Cambefort, 1991c). Geotrupinae occur mainly in colder regions (Halffter & Edmonds, 1982). Aphodiinae are the dominant members of the dung beetle fauna in temperate and colder regions, whereas Scarabaeinae are dominant in tropical and subtropical regions (Halffter & Edmonds, 1982; Hanksi, 1991), probably because scarabaeine tunnellers (paracoprids) and rollers (telecoprids), which remove dung from the soil surface for breeding, have a competitive advantage over aphodiine dwellers (endocoprids), which breed directly in dung pats (Hanski & Cambefort, 1991c). Aphodiinae in warmer regions may also be less successful than Scarabaeinae because dung pats dry out faster than in colder regions (Hanski & Cambefort, 1991c). Scarabaeine distribution is more strongly limited by temperature and precipitation than that of Aphodiinae; they are usually absent from areas that receive less than 250 mm of precipitation and have an average annual daily temperature below 15°C (Halffter & Edmonds, 1982).

Africa's dung beetle fauna, with some 2000 species, is particularly diverse because of its large and diverse mammalian fauna and because of the favourable climatic conditions for breeding (Waterhouse, 1974; Endrödy-Younga, 1982). In southern Africa there are about 780 scarabaeine and 60 aphodiine species (Doube, 1991). The diversification of African dung beetles was possible as a result of efficient food source partitioning, e.g. with regard to age and kind of dung used, habitat, soil type, seasonal and daily activity patterns and differences in breeding biology (e.g. Halffter & Matthews, 1966; Endrödy-Younga, 1982; Halffter & Edmonds, 1982; Hanski & Cambefort, 1991a).

[1] treated as families by Hanski & Cambefort (1991a)

1.4 Chemistry, mode of action, pharmacokinetics and metabolism of ivermectin

Naturally-occurring avermectins were isolated from the fermentation broth of the soil-living actinomycete subsequently described as *Streptomyces avermitilis* by Burg *et al.* (1979) from Japan. They were discovered during the search for agents with anthelmintic activity at the Merck, Sharpe and Dohme research laboratories (Campbell, 1981). The discovery, development, pharmacokinetic properties and mode of action of avermectins have been summarised in Campbell (1989). Steel (1993) reviewed the pharmacokinetics of avermectins in ruminant livestock and horses with particular reference to the effect of dosage route and formulation on the residues and metabolites of avermectins in tissue and faeces.

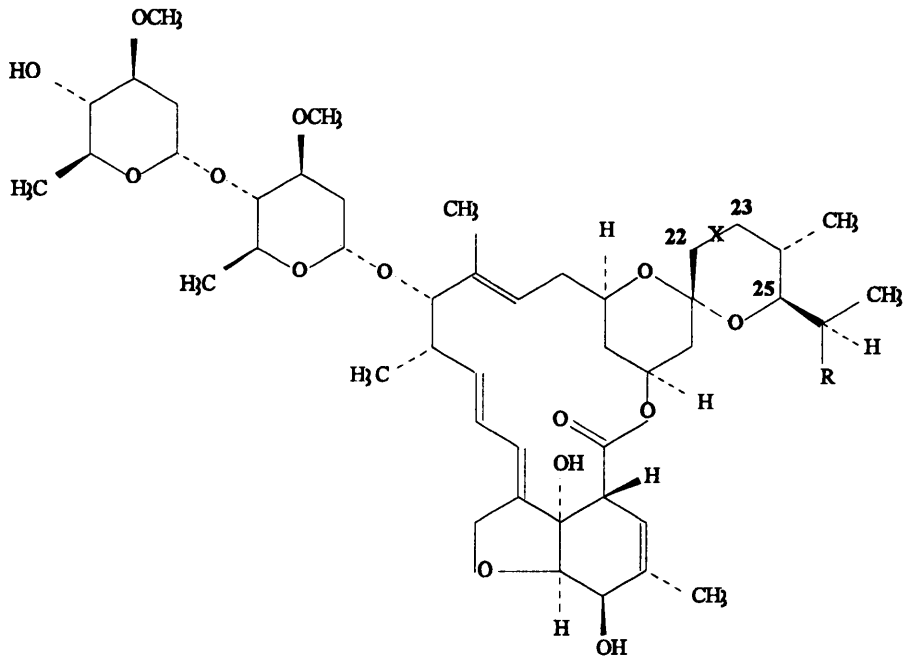

Fig. 1. The chemical structure of avermectin B_1 (abamectin) (X= -CH=CH-) and 22,23-dihydroavermectin B_1 (ivermectin) (X = $-CH_2-CH_2-$). R = CH2CH3 for "a" components; R = CH3 for "b" components (adapted from Campbell, 1989)

Structurally, avermectins are 16-membered macrocyclic lactone compounds with a disaccharide substituent at C-13 (Fig. 1). Abamectin (Avermectin B_1) is one of several, naturally-occurring fermentation products of *S. avermitilis*. It is a mixture of homologous avermectins containing at least 80% avermectin B_{1a} and not more than 20% avermectin B_{1b} (Campbell, 1989). Abamectin has been selected for industrial use because of its high potency as a parasiticide; it is also used in crop protection. Ivermectin is a semisynthetic derivative of abamectin. The two compounds differ in the bond between carbons 22 and 23. Ivermectin has a single bond and hydrogens on C-22 and C-23, whereas abamectin has a double bond (Fig. 1). Ivermectin contains a minimum of 80% 22,23-dihydro-avermectin B_{1a} and a minimum of 20% of the corresponding "b" homologue (Campbell, 1989).

Avermectins affect transmembrane chloride channel activity, causing increased permeability of the membrane to chloride ions. The resulting changes in membrane potential and concomitant inhibition of electrical activity initially lead to paralysis of the affected nerve and muscle cells and eventually to death of the affected organism (Turner & Schaeffer, 1989; Clark *et al.*, 1994).

The route of administration and formulation influences the bioavailability of ivermectin in the animal and the excretion pattern in the faeces (Fink & Porras, 1989; Steel, 1993). Lo *et al.* (1985) demonstrated that the non-aqueous solution of injectable ivermectin used commercially (60% (v/v) propylene glycol and 40% (v/v) glycerol formal) has a biological half-life of 8.3 days in cattle compared with a biological half-life of 2.0 day for an aqueous micellar solution. Between 62-83% of radioactively labelled ivermectin has been recovered in faeces and less than 2% in urine of cattle, sheep and rats seven days after subcutaneous injection, intraruminal and oral application (Chiu & Lu, 1989). Most of the given dose is eliminated as the parent drug and to a lesser extent in the form of its less toxic metabolites (Halley *et al.*, 1989a).

Data on ivermectin concentrations in freshly deposited cattle dung after a single subcutaneous injection ($200\mu gkg^{-1}$) and pour-on treatment ($500\mu gkg^{-1}$) are provided by Sommer *et al.* (1992), Sommer & Steffansen (1993) and after a single subcutaneous injection ($200\mu gkg^{-1}$) by Lumaret *et al.* (1993). Sommer & Steffansen (1993) observed that the highest proportion of ivermectin in dung after pour-on treatment occurs one day after administration, whereas the concentration of ivermectin after a single standard injection is

highest two days after treatment. The excretion half-lives for the pour-on treatment and standard injection were estimated as 2.5 days and 3.0 days respectively (Sommer & Steffansen, 1993).

1.5 Environmental safety of ivermectin

Aspects of the environmental safety of avermectins under veterinary and agricultural use have been reviewed by Halley *et al.* (1989a, b, c, 1993), Wislocki *et al.* (1989) and Bloom & Matheson (1993).

Ivermectin is registered for use in cattle as injection, pour-on, oral solution and paste, and, more recently, also as intraruminal slow-release device (DiNetta, 1989; A.B. Forbes, Merck, Sharp & Dohme, Inc., *pers. comm.*). The dose rate varies according to the mode of administration. The recommended dose of ivermectin registered for the use in cattle is $200\mu gkg^{-1}$ as injection and $500\mu gkg^{-1}$ as pour-on (Benz *et al.*, 1989). Ivermectin for cattle as a slow-release device bolus delivers 12 mg per day for 135 days.

Domestic livestock will be either treated when kept on a pasture, or in a small or commercial feedlot. Cattle usually receive one treatment, but for year-round parasite-control programmes may be treated up to three or four times a year (Halley *et al.*, 1989b). Ivermectin is released into the environment via dung of treated pastured animals and through cleanout dung from feedlots, which is used as fertilizer (Halley *et al.*, 1989b).

The fate of a compound in the environment is determined by its physical and chemical properties (e.g. photolytic stability, solubility in water, soil-binding ability) (Forbes & Forbes, 1994). Based on its high molecular weight, low water solubility, high octanol-water partition coefficient (K_{ow}) and organic-carbon binding constant (K_{oc}), ivermectin is expected to bind tightly to soil or sediments and is not likely to translocate or leach into surface or ground water (Halley *et al.*, 1989a).

Data on photodegradation, biotransformation and animal metabolism suggest that ivermectin is unlikely to bioaccumulate or to persist in the aquatic or terrestrial environment (Bloom & Matheson, 1993). For example, ivermectin has been shown to photodegrade with an estimated half-life of about three hours in summer sunlight as a thin dry film on glass in

New Jersey, USA (Halley *et al.*, 1989a, 1993). Simulations of photodegradation of ivermectin near the surface of flat bodies of water gave half-life values of 12 hours in summer and 39 hours in winter, clear skies provided (Bloom & Matheson, 1993). In New Jersey, U.S.A., the half-life of ivermectin in soil or a soil-faeces mixture has been reported to range from 91-271 days in winter and 7-14 days in summer (Halley *et al*, 1989a, 1993). However, photodegradation does not appear to affect ivermectin levels in dung pats. Sommer *et al.* (1992) and Sommer & Steffansen (1993) showed that ivermectin concentrations changed little over time in dung pats exposed for 45 days and 14 days in the field under northern temperate and subtropical conditions respectively.

Ivermectin has no antifungal, antibacterial or antiprotozoal activity and is not lethal to soil microorganisms (Halley *et al.*, 1989a).

Ivermectin has been shown to be highly toxic to freshwater organisms, such as the water flea *Daphnia magna* Straus and fish (e.g. *Salmo gairdneri* Richardson (rainbow trout)) (Halley *et al.*, 1989a). Nevertheless, it is expected that bioavailability of ivermectin under natural aquatic conditions would be less than under laboratory conditions due to its physical and chemical properties (low water solubility, its strong binding to soil and photodegradation) (Halley *et al.*, 1989c). Halley *et al.* (1989b) predicted that ivermectin concentrations in ground and runoff water can be expected to be below the no-effect level of 0.01 ppb for *D. magna*.

Studies on terrestrial organsims have shown that ivermectin and abamectin are unlikely to affect earthworms, but are highly toxic to target and non-target insects including Coleoptera, Diptera, Hymenoptera and Lepidoptera (Strong & Brown, 1987; Wislocki *et al.*, 1989). Avermectins exhibit wide safety margins in birds and mammals, although some adverse effects have been reported (Pulliam & Preston, 1989; Soll, 1989).

1.6 Impact of ivermectin on the dung insect fauna

Effects of avermectins on insects range from sublethal to lethal. Concentrations of avermectins that are not lethal to insects have been found to interfere, for example, with feeding, mating, development and reproduction. Duration of these effects and susceptibility

of organsims to the agents vary with species.

During the past decade, numerous single-species laboratory tests and field investigations have broadened our knowledge about the impact of avermectins, especially ivermectin and abamectin, on the dung fauna. Most of these studies were concerned with insects associated with cattle dung. A few studies have been conducted on the impact of ivermectin on dung-breeding flies and beetles in sheep dung (Cook, 1991, 1993; Mahon *et al.*, 1993; Mahon & Wardhaugh, 1991; Wardhaugh *et al.*, 1993) and on the decomposition of horse dung (Ewert *et al.*, 1991; Herd *et al.*, 1993c). Extensive reviews on the influence of avermectins on insects in general have been presented by Strong & Brown (1987) and on the dung insect fauna by Strong (1992, 1993). Roncalli (1989) summarized effects of ivermectin on the cattle dung fauna. An entire issue of *Veterinary Parasitology* was devoted to the impact of avermectin usage in domestic livestock on the environment (Herd *et al.*, 1993a). The ecological effects of avermectins on dung insects were recently reviewed by Wratten & Forbes (*in press*).

Despite the numerous publications on the adverse effects of avermectins on dung insects, there are gaps in the current state of our knowledge concerning their environmental impact. Herd *et al.* (1993b) pointed towards the need for the improvement of analytical techniques for the detection of avermectins in dung, the identification of bioindicators and the improvement of environmental stress indices. With respect to pastureland invertebrates, the authors highlighted the paucity of information on communities and functional groups (e.g. nematodes and dung beetles).

1.7 Aim and layout of the study

The purpose of this study is to improve our understanding of the influence of ivermectin on the dung insect fauna, in particular under Afrotropical conditions. With this objective in mind the impact of a single standard injection of ivermectin on the South African dung insect fauna was assessed at three levels of complexity: (1) single-species laboratory assays, (2) semi-field and (3) large scale field evaluations. A single standard injection was chosen because this is the treatment regime generally adopted in South Africa, instead of three

injections per year as is customary in Europe. Intraruminal slow-release devices are presently not commercially available in South Africa.

Following this introduction are four chapters. Chapter 2 evaluates lethal and sublethal effects (e.g. prolonged development time, reduced reproduction) of ivermectin residues in dung on three dung-breeding insect species in laboratory bioassays. One fly species (*Musca nevilli* Kleynhans, a vector of *Parafilaria bovicola* Tubangui) and two common dung beetle species (*Euoniticellus intermedius* (Reiche), *Onitis alexis* Klug) served as bioassay agents. Chapter 3 describes three field investigations. Firstly, the effect of ivermectin on dung decomposition and colonization of pats by dung insects was assessed in a semi-field study. Secondly, two field trials on a large scale examined short- and longterm effects of the compound on dung insect communities under extensive farming conditions. The fourth chapter assesses the potential use of a frame-based model to assist farm management decisions regarding the parasiticide's use. The last chapter, Chapter 5, summarizes the main findings and draws attention to areas in which further research is needed.

2 Laboratory studies

2.1 The effect of ivermectin on the development and reproduction of the dung- breeding fly *Musca nevilli* Kleynhans (Diptera, Muscidae)[1]

Introduction

Musca nevilli, together with *M. xanthomelas* Wiedemann and *M. lusoria* Wiedemann, is a vector of *Parafilaria bovicola* Tubangui in South Africa. The three species are called African face flies because of the resemblance of their feeding habits to that of the true face fly *M. autumnalis* (De Geer) which occurs in Europe and North America (Nevill & Sutherland, 1987). The flies breed in cattle dung and are lachrymophagous; they have also been reported to feed on wounds. Their life-cycles were described by Nevill & Sutherland (1987).

Parafilaria bovicola is a filarial parasite that lives in the subcutaneous tissue of cattle and causes bruise-like lesions on carcasses. Flies become infected with *P. bovicola* when they take a bloodmeal from wounds on cattle infested with the eggs of the parasite. The first, second and third larval stages of the nematode develop to the infective third stage larvae in the intermediate fly host. When an infected fly feeds on cattle, these infective larvae escape and develop further to the fourth and fifth stage on the definite bovine host (Nevill, 1979). The parasite is known to occur in the Far East, north, central and southern Africa, eastern Europe and Scandinavia (Swan *et al.*, 1983). Infestation of cattle with *P. bovicola* has been reported to cause considerable financial losses not only to the South African beef industry, but also to the

[1]The contents of Chapter 2.1 have already been published. The relevant reference is: Krüger, K. & Scholtz, C.H. (1995), The effect of ivermectin on the development and reproduction of the dung-breeding fly *Musca nevilli* Kleynhans (Diptera, Muscidae). *Agriculture, Ecosystems and Environment* **53**: 13-18. The contents of the article have been slightly modified for a more uniform presentation of chapters in the thesis.

Swedish and Zimbabwean beef industries (Van den Heever *et al.*, 1973; Carmichael & Koster, 1978; Chambers, 1983; Lundquist, 1983; Wallace *et al.*, 1983; Soll *et al.*, 1984).

The larvicidal effect of ivermectin on economically important dung-breeding Diptera, as well as non-target Coleoptera, has been well documented (Meyer *et al.*, 1980; Miller *et al.*, 1981; Ridsdill-Smith, 1988; Schmidt, 1983; Wardhaugh & Rodriguez-Menendez, 1988; Wardhaugh & Mahon, 1991; Fincher, 1992). Few studies, however, have been published on sublethal effects of ivermectin in dung, such as impairment of reproduction in dung-breeding insects. Cook (1991) reported sterility in adults of *Lucilia cuprina* Wiedemann (Diptera, Calliphoridae) which fed on dung from treated sheep. Diminished reproduction in other species of Diptera was found, for example, in *Glossina morsitans morsitans* Westwood (Glossinidae) and *Haematobia irritans* (L.) and *Stomoxys calcitrans* (L.) (Muscidae) fed on blood to which ivermectin had been added, as well as in *Lucilia sericata* (Meigen) (Muscidae) where ivermectin was topically applied to mature flies and *Calliphora vomitoria* (L.) (Calliphoridae) where third instar larvae were topically applied with the parasiticide (Langley & Roe, 1984; McGarry, 1986; Miller *et al.*, 1986; Strong, 1989).

The purpose of the present study was to evaluate the effect of a single subcutaneous injection of ivermectin (200μg kg^{-1}) in cattle on the development and reproduction of *Musca nevilli* exposed to dung of treated cattle.

Materials and methods

For each trial a group of between six and ten Friesian steers (200-450 kg body mass) held at the University of Pretoria's experimental farm in Pretoria was divided into two. The animals were not treated with any veterinary products for three months prior to commencement of trials. One group served as control and the other was treated with a single subcutaneous injection of ivermectin at the recommended dose of 200μg kg^{-1} body mass. The two groups of cattle were kept in separate enclosures and were maintained on hay and lucerne, water was freely available. Fresh dung from each group was collected one to four, and seven days after

treatment and subsequently at weekly intervals up to eight weeks after treatment. The dung obtained was mixed thoroughly for each group.

The flies from which the colony was established were provided by Dr. E.M. Nevill, Veterinary Research Institute, Onderstepoort, from his laboratory colony. Trials with *M. nevilli* were conducted in an insectary at 28-30°C, 12h photoperiod, and approximately 40% R.H.. Flies were kept in wire frame cages (410 mm x 270 mm x 90 mm) covered with mutton cloth. The cages were sprayed with water three times daily.

Five samples of 250 ml of dung from experimental and control cattle respectively were placed in plastic cups, the bottom of which had been removed. The cups were then placed on a large-mesh gauze resting on a container. Each cup was stocked with 25 newly-hatched first-instar larvae of *M. nevilli* from the laboratory colony. To pupate, third-instar larvae emerged from the bottom of the cup and fell into the container below. The dung was also checked for remaining larvae, and/or pupae. The number of third-instar larvae and, ultimately, pupae that developed were counted.

The pupae were transferred to the cages, in which the adults emerged. Adult flies were maintained on ox-liver and a 1:1 mixture of whole milk powder and sugar crystals provided in separate petri-dishes. Tap water was supplied in cotton-filled petri-dishes. The cages were examined daily for dead adults, which were subsequently counted and sexed.

When flies were ten days old and sexually mature (Nevill & Sutherland, 1987), each cage was provided with a 250 ml cup of fresh dung from untreated cattle. Flies were allowed to oviposit on the dung over a 24-hour period. This was repeated every second day for five times. The mean number of third-instar larvae obtained per female (five experimental and five control groups) was used as an indirect measure of fertility (i.e. the number of viable eggs laid by a female (Southwood, 1978)).

Each experiment was repeated once and the results were pooled. Data for treatment and control were compared by the non-parametric Wilcoxon two-sample test (Sokal & Rohlf, 1981) using a spreadsheet.

Results

SURVIVAL OF FIRST-INSTAR LARVAE

Table 1 shows the percentage of third-instar larvae, pupae, and adults which developed from first-instar larvae of *M. nevilli* in dung containing ivermectin residues and from control dung. No third-instar larvae were found in dung from treated cattle that was collected from 1 to 28 days after treatment. Significantly ($P<0.01$) fewer larvae, and consequently pupae and adults, developed five ($U_s=90$), six ($U_s=48$), and seven ($U_s=43$) weeks after treatment in dung from treated animals than in control dung (where U_s is Wilcoxon's two-sample statistic).

Five weeks after treatment only 4.8% first-instar larvae reached the third instar, 4.4% of the initial first-instar larvae pupated, and 3.6% emerged successfully from experimental dung. The number of third-instar larvae increased from 10.4% at six weeks after treatment to 50.2% at seven weeks after treatment. Adult emergence was 4.0% and 36.9% at six and seven weeks after treatment, respectively. No significant difference ($P>0.05$) between the percentage of larvae ($U_s=60$) and pupae ($U_s=35.5$) that developed in dung from animals treated eight weeks previously and the control dung could be observed. However, significantly ($U_s=86$, $P<0.001$) more adults emerged from dung from treated animals than from control dung, due to an unusual high pupal mortality during the second trial.

Larval mortality corrected by Abbott's formula (Abbott,1925) (Table 2) was found to be 100% up to four weeks after treatment. From week five, percentage corrected mortality decreased from 94.9% in week five and six, to 45.8% in week seven, and 0% in week eight.

EFFECTS OF IVERMECTIN ON PUPATION AND ADULT EMERGENCE

The percentage of third-instar larvae which pupated successfully from dung containing ivermectin residues and control dung differed significantly ($U_s=31$, $P<0.05$), six weeks after treatment where 50.0% of the third-instar larvae pupated in experimental dung in contrast to 98.5% for control dung (Table 2). No significant differences ($P>0.05$) in numbers of pupae

Table 1. Percentage survival of *Musca nevilli* in dung from cattle injected with ivermectin (200μg kg^{-1}) and in control dung.

Time post-treatment (days)	Third-instar larvae (%)		Pupae (%)		Adults (%)	
	Ivermectin	Control	Ivermectin	Control	Ivermectin	Control
1	0.0	3.6 ± 9.7	0.0	63.6 ± 9.7	0.0	56.0 ± 11.9
2	0.0	74.0 ± 10.7	0.0	73.2 ± 10.7	0.0	66.8 ± 12.5
3	0.0	72.4 ± 11.5	0.0	72.4 ± 11.5	0.0	68.4 ± 13.2
4	0.0	82.7 ± 6.0	0.0	81.8 ± 4.9	0.0	81.8 ± 4.9
7	0.0	86.2 ± 13.1	0.0	85.8 ± 13.0	0.0	80.0 ± 17.0
14	0.0	69.8 ± 20.1	0.0	66.6 ± 20.2	0.0	66.4 ± 20.6
21	0.0	71.2 ± 15.5	0.0	70.4 ± 15.5	0.0	66.0 ± 14.4
28	0.0	62.8 ± 16.0	0.0	62.4 ± 16.1	0.0	60.4 ± 17.2
35	4.8 ± 4.9	76.9 ± 13.5^{a}**	4.4±4.0	74.7 ± 12.2^{a}**	3.6 ± 3.5	70.2 ± 11.9^{a}**
42	10.4 ± 5.4^{c}	85.1 ± 9.4^{b}**	6.4±6.1^{c}	84.0 ± 11.1^{b}**	4.0 ± 2.8^{c}	78.3 ± 10.3^{b}**
49	50.2 ± 11.2^{a}	72.0 ± 7.5^{c}**	47.6±9.3^{a}	70.4 ± 8.3^{c}**	36.9 ± 6.9^{a}	68.0 ± 6.3^{c}**
56	82.7 ± 8.9^{a}	76.0 ± 11.7	81.8±9.0^{a}	74.8 ± 12.7	79.6 ± 12.7^{a}	56.2 ± 10.2***

Each value is a mean of 10 samples each stocked with 25 first-instar larvae (±SD).
^{a,b,c} a: n=9, b: n=7, c: n=5.
**P<0.01, ***P<0.001; Wilcoxon's two-sample test.

Table 2. Percentage of *Musca nevilli* larvae pupated and adults emerged from dung of cattle treated with ivermectin (200μg kg^{-1}) and control dung together with percentage corrected mortality (Abbott, 1925).

Time post-treatment (days)	Percentage (± SD) of pupae		Percentage (±) of adults		Percentage correted mortality
	Ivermectin	Control	Ivermectin	Control	
1	0.0	100.0 ± 0.0	0.0	88.2 ± 13.3	100.0
2	0.0	98.9 ± 2.3	0.0	91.0 ± 7.4	100.0
3	0.0	100.0 ± 0.0	0.0	94.4 ± 8.7	100.0
4	0.0	99.0 ± 2.9	0.0	100.0 ± 0.0	100.0
7	0.0	99.5 ± 1.4	0.0	92.3 ± 9.2	100.0
14	0.0	95.6 ± 6.9	0.0	99.4 ± 1.9	100.0
21	0.0	98.9 ± 2.3	0.0	94.4 ± 9.4	100.0
28	0.0	99.3 ± 2.1	0.0	96.5 ± 5.4	100.0
35	96.4 ± 9.4	97.4 ± 3.4	81.0 ± 37.8	94.1 ± 6.6	94.9
42	50.0 ± 35.4	98.5 ± 4.0*	75.0 ± 28.9	93.4 ± 5.4	94.9
49	95.3 ± 6.1	97.7 ± 3.2	78.0 ± 7.3	96.9 ± 4.7***	45.8
56	98.9 ± 4.4	98.2 ± 4.0	97.2 ± 4.4	76.9 ± 17.6**	0.0

*P<0.5, **P<0.01, ***P<0.001; Wilcoxon's two-sample test.

formed from experimental and control larvae occurred five (U_s=37.5), seven (U_s=27.5), and eight (U_s=46) weeks after treatment.

Although fewer adults emerged from experimental than from control pupae, five (U_s=42.5) and six weeks (U_s=16) after treatment, no significant difference (P>0.05) was found, because of high variability in the number of adults emerged from dung containing ivermectin residues. The percentage of adults that emerged was 81.0% at five and 75.0% at six weeks after treatment from experimental pupae, and 94.1% and 93.4% respectively from control pupae (Table 2). Significantly (U_s=45, P<0.001) fewer adults emerged from experimental dung than from the control at seven weeks after treatment (78.0% and 96.9% respectively). At eight weeks after treatment significantly (U_s=79, P<0.01) fewer adults emerged from the control (76.9% compared with 97.2% from experimental pupae).

ADULT FERTILITY

Flies which developed in experimental dung were not sterile. Fertility was reduced by 60.0% at five weeks, 56.2% at six weeks, and 46.0% at seven weeks after treatment. A reduction in fertility of 5.84% at eight weeks after treatment was not significant compared with the control (U_s=12, P>0.05) (Table 3).

Table 3. Effect of a standard injection of ivermectin (200μg kg^{-1}) on the fertility of *Musca nevilli*. (The number of third-instar larvae obtained per female was taken as an indirect measure of fertility.)

Time post-treatment (days)	No. of larvae per female (± SD)		Percentage reduction in fertility
	Ivermectin	Control	
35	3.9 ± 1.0^a	9.7 ± 2.5^{b*}	60.0
42	4.0 ± 0.9^b	9.2 ± 2.0^{b*}	56.2
49	5.7 ± 1.3^b	10.6 ± 1.1^{b*}	46.0
56	9.5 ± 1.1^a	10.1 ± 2.7^a	5.8

^{a,b} a: n=4, b: n=5. *P<0.05; Wilcoxon's two-sample test.

Discussion

The results illustrate that a single subcutaneous injection of ivermectin (200μg kg^{-1}) is likely to prevent the development of *M. nevilli* in dung of treated cattle up to four weeks after treatment. Adult emergence was reduced up to seven weeks after ivermectin therapy. These findings are similar to results for the dung-breeding flies *M. vetustissima* Walker (Australian bush fly) and *Haematobia irritans* (L.) (horn fly) (Miller *et al.*, 1981; Schmidt, 1983; Fincher, 1992). Roncalli (1989) reported detrimental effects of ivermectin on larvae of *M. xanthomelas* (face fly), a vector of *P. bovicola,* but did not elaborate on the nature of these effects.

In some dipteran larvae (e.g. *C. vomitoria*), sublethal doses of ivermectin have been reported to reduce pupation and emergence of adults (Strong 1986, 1989). In this study no significant differences were observed between numbers of pupae that developed from larvae reared in dung containing ivermectin residues and control dung. An exception to this was found at six weeks after treatment, where a high number of larvae failed to pupate from dung from treated animals, which is likely to be an artifact arising from an unexplained high larval mortality. Fewer adults emerged from experimental dung five to six weeks after treatment compared with the control, but not significantly so. However, significantly fewer adults emerged at seven weeks after treatment from experimental dung, and eight weeks after treatment from control dung. The low percentage in the control is because of an unusually high pupal mortality during the second trial, which was caused by inadvertent exposure of the pupae to heat.

Ivermectin residues in dung have been reported to affect reproduction (Strong, 1993). This was confirmed in the present study, where ivermectin considerably diminished the fertility in adults of *M. nevilli* which developed in dung from treated cattle.

The effectiveness of treatment with ivermectin against parafilariasis results not only from suppression of *M. nevilli,* and possibly the other two known vector flies in South Africa, *M. xanthomelas* and *M. lusoria,* but also from chemotherapy of the nematode. Swan *et al.* (1983, 1991) have shown that ivermectin administered to cattle infested with *P. bovicola* 70 days before slaughtering reduced carcass lesions by 90%.

Although *P. bovicola* does not affect the condition of its host to any great extent, it does lead to financial losses because the trimming of lesions renders the carcasses less

attractive for sale (Soll *et al.*, 1991). Ivermectin treatment against parafilariasis is most successful 70 days before slaughtering when the animals have been transferred to feedlots. Because of the larvicidal effect of the parasiticide on economically important and beneficial dung-breeding insects, it would appear that the environmental impact of ivermectin usage is relatively limited in feedlots as undisturbed cleanout dung is colonized there, unlike in the field, by dung-breeding flies but very rarely by dung beetles. Indeed, it can be expected that ivermectin would be of additional benefit in reducing dipteran colonization around feedlots.

2.2 Lethal and sublethal effects of ivermectin on the dung-breeding beetles *Euoniticellus intermedius* (Reiche) and *Onitis alexis* Klug (Coleoptera, Scarabaeidae)

Introduction

Dung beetles are of considerable ecological and economical importance, especially in tropical and subtropical regions, because of their role in the decomposition of animal excrements, the recycling of nutrients and the resulting enhancement in the productivity of grassland ecosystems (Bornemissza, 1976, Heinrich & Bartholomew, 1979). Various dung beetle species were imported into several several countries (e.g. Australia, USA) that either possessed a depauperate dung beetle fauna or were suffering ecological disturbances following the introduction of cattle (Waterhouse, 1974; Bornemissza, 1976). The beetles were introduced in order to control dung-breeding flies and to remove cattle dung from the soil surface to avoid fouling of pastureland. Two species that have successfully been introduced from South Africa into Australia are *Euoniticellus intermedius* and *Onitis alexis* (Matthiesen *et al.*, 1986). *Euoniticellus intermedius* has also been introduced into the USA from Australia (Blume, 1984).

Euoniticellus intermedius and *O. alexis* are both euryoecious species that can adapt to a wide range of climatic and soil conditions (Endrödy-Younga, 1982; Rougon & Rougon, 1982). As a result, they are widely distributed throughout the Afrotropical region (Ferreira, 1968-69, 1978); *O. alexis* also extends into southern Europe and the Middle East (Durand, 1972; Nicolas, 1980 (both *in* Rougon & Rougon, 1982); Tyndale-Biscoe, 1988). *Euoniticellus intermedius* and *O. alexis* are particularly important because they are able to adapt to unfavourable environments. For example, both species persist during the dry season in the Sahel region of Niger (Rougon & Rougon, 1982, 1984). Dung beetles in areas such as these are of importance not only because of their role in dung decomposition but also because of their contribution to soil aeration and enhanced water percolation through their burrowing activity (Bornemissza, 1976; Coe, 1987). The biology of *E. intermedius* has been described by Halffter & Edmonds (1982), Rougon & Rougon (1982) and Blume (1984), and that of *O. alexis* by Halffter & Edmonds (1982), Rougon & Rougon (1982) and

Edwards & Aschenborn (1987). Both species are paracoprids, i.e., they construct their nests in the soil beneath a dung pat.

Ivermectin and abamectin residues in animal dung have been reported to affect the life cycle of dung-breeding insects through reduced larval survival, prolonged development periods and reduced reproductive potential (see reviews by Strong & Brown, 1987 and Strong 1992, 1993). For example, Sommer & Overgaard Nielsen (1992) reported that a standard injection of ivermectin (200μgkg^{-1}) inhibited the development of *Onthophagus gazella* (F.) from 2-7 days after injection and prevented normal head capsule development. Fincher (1992) studied the effect of a single standard injection of ivermectin on *E. intermedius* from Texas (USA). He observed that eclosion of adults was prevented one week after treatment. Dung from cattle that were treated with ivermectin (200μgkg^{-1}) was lethal to newly emerged adults of *Copris hispanus* L. and *Onitis belial* F. 2-3 days after treatment (Wardhaugh & Roderiguez-Menendez 1988). Dung from cattle that were injected with abamectin (200μgkg^{-1}) was lethal to newly emerged *Onthophagus binodis* (Thunberg) 3-5 days after treatment (Houlding *et al.*, 1991). No toxic effect has been reported on sexually mature dung beetles. The influence of ivermectin on the reproduction of scarab beetles has been studied to a lesser extent. Avermectins in dung from treated cattle have been shown to adversely affect the reproductive potential of *O. binodis* (Ridsdill-Smith, 1988; Houlding *et al.*, 1991) and *C. hispanus* (Wardhaugh & Roderiguez-Menendez, 1988).

Because of their ecological importance, *E. intermedius* and *O. alexis* were selected as test organisms in the present study to determine lethal and sublethal effects of ivermectin residues in dung from animals treated with a single standard injection of ivermectin at 200μgkg^{-1}.

Materials and methods

TREATMENT OF CATTLE AND DUNG COLLECTION

For each trial a group of at least six Friesian steers (200-450 kg body mass) held at the University of Pretoria's experimental farm in Pretoria was used. They were not treated with

any antiparasitic drug for at least three months before trials. Commercially obtained ivermectin was administered by subcutaneous injection at the prescribed dose of 200μgkg^{-1} to half the group of cattle. The other half served as control and remained untreated. The two groups of steers were kept in separate enclosures and were maintained on hay and lucerne; water was freely available.

Dung for the laboratory trials was collected one to four and seven days, and then at weekly intervals for up to four weeks, after treatment for *0. alexis* and for up to eight weeks after treatment for *E. intermedius*. The dung collected from the cattle was mixed thoroughly for each group and sampling day. Beetles were supplied with the dung on the same day that the dung was collected. Surplus dung needed to replenish the dung supply for the beetles was kept in the refrigerator at 3°C.

EXPERIMENTAL DESIGN

Laboratory colonies of *E. intermedius* and *O. alexis* were established from field-collected beetles (Farm Abel, Parys district, Free State Province, 26°54'S 27°35'E). In addition, specimens of *O. alexis* were collected from a farm at Boekenhoutskloof, approximately 40km north-east of Pretoria (25°33'S, 28°29'E). In both collecting areas veterinary products were not normally used to control parasites. Only the F1 generation of the two beetle species was used for the experiments with ivermectin. Each experiment was repeated once with new colonies of both beetle species and with new groups of treated and untreated cattle.

Euoniticellus intermedius. Rearing of beetles and trials were conducted in an insectary at 26-27°C, 12h photoperiod and approximately 60% RH. For each bioassay, 10 pairs of 10-day-old unmated beetles were each placed in a 1l gauze-topped plastic bucket (115 mm high and 125 mm in diameter), filled to three-quarters with compact, moist, sandy soil. Five pairs were supplied with manure from ivermectin-treated cattle and the remaining five pairs were given dung from untreated cattle for every dung collecting day. Each group was provided with 250 ml of dung twice a week. The contents of the buckets were sieved after seven days

and the brood balls (each containing one egg) removed. The brood balls were counted and placed in a 1l plastic bucket between layers of moist, sandy soil to prevent desiccation. The beetle pairs were then placed in new containers with fresh sand and the procedure repeated for another week. Beetles started emerging about three weeks after extraction of the brood balls.

The effect of ivermectin on the number of brood balls constructed, the time of development from egg to adult and numbers of adult beetles emerging was determined. As brood production during the first breeding week has been shown to be influenced by the dung used previously to maintain the colony (Tyndale-Biscoe *et al.*, 1981), only numbers of balls produced during the second breeding week were used to calculate the number of brood balls constructed. Because each brood ball formed by *E. intermedius* is supplied with an egg (Edwards, 1991), the ratio between the number of beetles emerged and number of brood balls formed, i.e. initial number of eggs laid, was taken as a measure of immature mortality.

To investigate the effect of ivermectin on fecundity and fertility 10 pairs of 10-day-old unmated beetles (five reared on experimental and five on control dung) were set up individually with dung from untreated cattle. In cases where less than five pairs per group were available, the maximum number of pairs available was used. The rearing procedure as described above was then repeated. The number of brood balls formed and hence the number of eggs laid was taken as a measure of fertility and number of beetles emerged (i.e. the number of viable eggs laid) as a measure of fecundity.

Onitis alexis. The colony was maintained and the tests were carried out under the same conditions as described for *E. intermedius*.

On each dung collecting day, 10 half-litre pats of dung (five experimental and five control) were set up in plastic containers (270x200x90 mm high) filled to three-quarters with moist compact sandy soil. Each was supplied with a pair of 10-day-old, unmated beetles and the box covered with a ventilated lid. The dung was replenished at one-week intervals and the brood collected after the third week as beetles usually start breeding after five days (Halffter & Edmonds, 1982).

Onitis alexis forms brood masses, often in the form of 'sausages' which contain several

eggs, in the soil beneath the dung. The number of eggs laid could thus not be estimated accurately. After collection, the brood was transferred to other fresh containers and placed between two layers of damp sand. Beetles began to emerge 10 weeks after the start of breeding. The numbers of adults emerged from each group were compared. Immature mortality could not be determined because the brood masses contain varying numbers of eggs.

The live mass of approximately 10-day-old unmated beetles was measured with a Sartorius electronic balance to determine the effect of ivermectin on the size of adult *O. alexis*.

DATA ANALYSIS

The results (number of brood balls formed, adult emergence, developmental time, fecundity and fertility for *E. intermedius*; adult emergence, developmental periods and adult live mass for *O. alexis*) were pooled for each dung collecting day. Differences between treatment and control were analysed by the non-parametric Mann-Whitney test (Sokal & Rohlf, 1981), using the STATGRAPHICS programme (version 5.0, Statgraphics Inc., 1985-1991).

Results

EUONITICELLUS INTERMEDIUS

1) Beetles reared in dung containing ivermectin residues and in control dung. The number of brood balls formed with dung from treated cattle and control dung, and hence the initial number of eggs laid, was similar from one to 56 days after treatment, except three days after treatment where it was lower in the treatment group ($Z=2.05$, $p<0.05$) (Table 4).

On average, fewer adults emerged from dung of treated cattle than from the control collected one day after treatment, but differences were not significant ($Z=0.74$, $p>0.05$). No

E. intermedius larvae survived in dung from treated animals collected 2-7 days after treatment. Highly significantly fewer adults emerged from dung collected 14 days after treatment from treated animals compared with the control (week 1: Z=3.36, p<0.001; week 2: Z=3.08, p<0.01) (Table 5). Percentage-corrected mortality by Abbott's formula (Abbott, 1925) was found to be 43.10% one day, 100% two, four and seven days and 97.38% three days after treatment. Percentage- corrected mortality decreased from 86.09% after 14 days to 30.37% after 21 days and 0% 28 days after treatment.

Table 4. Mean number of *Euoniticellus intermedius* brood balls formed with dung from cattle injected with ivermectin (200μgkg^{-1}), and with control dung, in their second breeding-week.

Time post-treatment (days)	Ivermectin		Control	
	n	Mean no. of brood balls per pair (±SD)	n	Mean no. of brood balls per pair (±SD)
1	7	7.57 ± 3.74	8	7.50 ± 5.24
2	9	3.89 ± 2.93	8	6.38 ± 4.60
3	8	6.00 ± 3.51	7	10.57 ± 2.30 *
4	8	5.63 ± 5.21	7	7.57 ± 3.55
7	8	4.88 ± 3.80	8	8.25 ± 2.43
14	10	4.90 ± 5.24	9	9.00 ± 2.83
21	8	7.63 ± 2.88	10	10.10 ± 4.38
28	9	9.11 ± 1.54	10	11.60 ± 3.13
35	8	10.75 ± 1.67	9	11.33 ± 2.74
42	9	9.44 ± 3.13	8	9.63 ± 3.58
49	9	10.33 ± 2.50	9	10.11 ± 5.11
56	10	11.60 ± 4.50	8	12.38 ± 3.96

* P<0.05; Mann-Whitney test.

Dung from cattle treated with ivermectin prolonged the development of *E. intermedius* significantly for one, and from 14-28 days after treatment compared with the controls (Day 1: Z=9.44, p<0.001; Day 14: Z=6.65, p<0.001; Day 21: Z=13.11, p<0.001; Day 28: Z=7.57, p<0.001) (Table 6); no beetles emerged from dung collected 2-7 days after dosing. The development time was on average about two and a half times longer for larvae reared in dung collected one, and from 14 to 21 days after treatment relative to the controls. The mean development time 28 days after treatment was 4.99 weeks for beetles that developed in dung from treated animals compared with 3.56 weeks for beetles from the control.

Table 5. Mean number of *Euoniticellus intermedius* emerged from dung of cattle treated with ivermectin (200μgkg^{-1}), and control dung.

Time post-treatment (days)	Week 1				Week 2				p ercentage corrected mortality
	Ivermectin		Control		Ivermectin		Control		
	n	x ± SD	n	x ± SD	n	x ± SD	n	x ± SD	
1	5	4.00 ± 2.74	7	6.44 ± 3.91	7	4.71 ± 3.73	6	7.00 ± 4.56	43.10
2	8	0.00 ± 0.00	6	8.50 ± 4.59***	9	0.00 ± 0.00	6	7.17 ± 2.14***	100.00
3	7	0.14 ± 0.38	8	8.38 ± 2.92***	8	0.00 ± 0.00	7	9.00 ± 2.58***	97.38
4	8	0.00 ± 0.00	6	7.67 ± 2.73***	5	0.00 ± 0.00	7	4.71 ± 3.50*	100.00
7	8	0.00 ± 0.00	8	7.00 ± 3.16***	7	0.00 ± 0.00	7	6.29 ± 2.43**	100.00
14	10	1.00 ± 1.33	9	7.56 ± 4.64***	6	1.17 ± 1.17	9	7.11 ± 2.52**	85.09
21	7	6.14 ± 1.95	9	8.00 ± 3.04	8	3.50 ± 1.85	10	9.20 ± 4.52**	30.37
28	8	5.63 ± 2.88	8	8.88 ± 2.95	9	6.89 ± 1.54	10	8.50 ± 4.06	0.00
35	5	5.80 ± 1.92	9	8.44 ± 3.28	8	9.00 ± 2.27	9	8.56 ± 2.13	0.28
42	7	8.86 ± 3.39	8	8.25 ± 4.59	9	8.33 ± 2.83	8	7.13 ± 3.72	0.00
49	7	7.14 ± 5.43	9	7.22 ± 3.80	9	8.44 ± 2.79	9	9.00 ± 5.07	0.00
56	9	8.11 ± 3.48	7	9.43 ± 3.21	10	10.60 ± 4.50	7	10.71 ± 2.81	0.00

* P<0.05, **P<0.01, ***P<0.001; Mann-Whitney test.

Table 6. Duration of development of *Euoniticellus intermedius* in dung of cattle treated with ivermectin (200μgkg^{-1}), and control dung.

Time post-treatment (days)	Ivermectin		Control	
	n	Mean development time in weeks (±SD)	n	Mean development time in weeks (±SD)
1	47	10.02 ± 3.52	89	3.85 ± 1.43***
14	15	10.40 ± 1.50	132	3.87 ± 0.93***
21	71	8.08 ± 1.98	164	3.29 ± 0.71***
28	107	4.99 ± 1.78	156	3.56 ± 0.84***
35	100	4.48 ± 1.57	153	3.99 ± 0.94
42	138	4.09 ± 0.80	123	3.96 ± 0.93
49	95	3.69 ± 0.73	146	3.61 ± 0.66
56	176	3.60 ± 0.95	141	3.58 ± 0.65

*** P<0.001; Mann-Whitney test.

Table 7. Fertility of *Euoniticellus intermedius* (F1 generation). Mean number of brood balls formed by beetles reared in dung of cattle treated with ivermectin (200μgkg^{-1}), and in control dung.

Time post-treatment (days)	Week 1				Week 2			
	Ivermectin		Control		Ivermectin		Control	
	n	x ± SD	n	x ± SD	n	x ± SD	n	x ± SD
1	8	5.75 ± 4.68	7	11.14 ± 3.18 *	8	10.75 ± 6.01	7	10.14 ± 3.24
14	6	11.17 ± 5.03	8	12.25 ± 4.74	6	12.67 ± 3.33	7	13.57 ± 3.64
21	8	8.13 ± 2.99	10	9.70 ± 5.01	8	9.00 ± 3.55	10	8.40 ± 3.31
28	8	6.75 ± 5.31	9	11.67 ± 4.85	9	8.22 ± 4.15	9	12.00 ± 5.36
35	10	9.80 ± 4.24	9	9.56 ± 5.17	10	8.10 ± 4.31	9	9.78 ± 3.83
42	9	9.78 ± 4.29	9	9.56 ± 4.53	8	9.25 ± 3.37	9	11.67 ± 3.43
49	9	5.78 ± 4.21	9	10.11 ± 3.72	7	6.86 ± 3.24	9	10.44 ± 3.78
56	10	9.90 ± 4.63	8	11.88 ± 3.09	10	9.00 ± 4.29	8	10.63 ± 3.70

* P<0.05; Mann-Whitney test.

2) Offspring of beetles reared in dung from treated cattle, and from control dung. The number of brood balls constructed with dung from untreated animals by beetles reared in dung from treated animals and untreated controls is given in Tables 7 and 8.

The fertility of *E. intermedius* was affected in the first week of breeding with dung collected one day after treatment, when significantly fewer brood balls compared with the control were formed ($Z=2.26$, $p<0.001$) (Table 7). For all other days after treatment no significant differences were found between treatment and control.

Significantly fewer adults emerged from the first breeding week where parent beetles were reared in dung collected one ($Z=2.21$, $p<0.05$) and 14 ($Z=2.21$, $p<0.05$) days after treatment (Table 8); no adults resulted from dung collected 2-7 days after ivermectin therapy. No significant differences ($p>0.05$) were found between treatment and control 21 to 56 days after treatment. Differences between the number of beetles emerged from parents reared in dung from treated cattle and the control in the second breeding week were not significant for any dung collection day ($p>0.05$)..

Table 8. Fecundity of *Euoniticellus intermedius* (F1 generation). Mean number of adult offspring from beetles reared in dung from cattle treated with ivermectin ($200\mu gkg^{-1}$), and control dung.

Time post-treatment (days)	Week 1				Week 2			
	Ivermectin		Control		Ivermectin		Control	
	n	x ± SD	n	x ± SD	n	x ± SD	n	x ± SD
1	8	5.25 ± 4.80	7	9.57 ± 2.51*	7	10.43 ± 5.16	7	8.71 ± 3.35
14	6	3.67 ± 2.73	8	10.13 ± 5.69*	6	6.20 ± 5.12	6	10.67 ± 4.50
21	7	5.57 ± 2.51	10	8.10 ± 4.07	8	7.50 ± 3.02	10	6.90 ± 3.73
28	5	6.80 ± 3.90	8	9.25 ± 5.60	7	7.71 ± 2.29	8	8.63 ± 3.42
35	10	8.90 ± 3.98	9	7.89 ± 4.96	10	6.40 ± 3.57	9	8.56 ± 4.45
42	8	7.50 ± 3.66	7	9.00 ± 3.83	6	6.33 ± 2.95	8	9.13 ± 3.68
49	4	5.52 ± 3.59	5	8.80 ± 1.30	4	4.75 ± 2.87	4	9.75 ± 2.22
56	9	8.67 ± 2.92	8	10.00 ± 2.78	9	7.89 ± 2.47	8	8.75 ± 3.37

* $P<0.05$; Mann-Whitney test.

Table 9. Mean number of *Onitis alexis* adults emerged from dung of cattle injected with ivermectin (200μg kg^{-1}), and control dung.

Time post-treatment (days)	Ivermectin		Control	
	n	No. of beetles emerged ± SD	n	No. of beetles emerged ± SD
1	8	11.13 ± 6.57	7	16.57 ± 9.18
2	10	1.40 ± 1.69	9	9.00 ± 4.94***
3	8	0.13 ± 0.33	8	19.75 ± 7.08***
4	8	0.44 ± 0.96	5	19.20 ± 9.37**
7	9	1.22 ± 2.57	6	4.00 ± 3.91*
14	6	11.00 ± 9.29	6	16.50 ±10.56
21	8	9.13 ± 6.23	6	12.88 ±14.36
28	7	5.57 ± 4.10	6	9.00 ± 5.13

* P<0.05, **P<0.01, ***P<0.001; Mann-Whitney test.

Table 10. Mean development time of *Onitis alexis* in dung from cattle injected with ivermectin (200μg kg^{-1}), and control dung.

Time post-treatment (days)	Ivermectin		Control	
	n	Mean development time in weeks (± SD)	n	Mean development time in weeks (± SD)
1	89	17.19 ± 6.19	116	12.54 ± 3.34***
2	13	15.38 ± 1.65	86	12.29 ± 3.25***
3	1	12	160	11.86 ± 1.78
4	4	15.25 ± 1.25	96	12.68 ± 1.99***
7	11	14.00 ± 2.32	32	12.28 ± 6.80***
14	66	14.48 ± 3.52	98	11.79 ± 2.44***
21	73	13.26 ± 5.54	99	10.93 ± 1.82***
28	39	15.77 ± 9.06	53	12.62 ± 4.11

***P<0.001; Mann-Whitney test.

Table 11. Mean live mass (g) of *Onitis alexis* males and females reared in dung of cattle injected with ivermectin (200μgkg^{-1}), and in control dung.

Time post-treatment (days)	Males				Females			
	n	Ivermectin	n	Control	n	Ivermectin	n	Control
1	17	0.354 ± 0.069	30	0.448 ± 0.116	18	0.351 ± 0.060	30	0.376 ± 0.091
2	3	0.279 ± 0.041	30	0.373 ± 0.086	7	0.350 ± 0.097	30	0.370 ± 0.056
3	-		27	0.343 ± 0.058	1	0.235 ± 0.000	28	0.351 ± 0.075
4	2	0.264 ± 0.049	29	0.368 ± 0.047	-		30	0.364 ± 0.077
7	-		10	0.343 ± 0.051	3	0.270 ± 0.055	20	0.319 ± 0.083
14	14	0.343 ± 0.069	26	0.313 ± 0.084	11	0.345 ± 0.091	16	0.328 ± 0.067
21	28	0.321 ± 0.041	30	0.409 ± 0.109	30	0.379 ± 0.095	30	0.422 ± 0.115
28	15	0.348 ± 0.059	28	0.389 ± 0.103	18	0.395 ± 0.103	12	0.402 ± 0.079

ONITIS ALEXIS

Significantly fewer adults emerged from dung of cattle injected with ivermectin two ($Z= 3.35$, $p<0.001$), three ($Z= 3.45$, $p<0.001$), four ($Z= 3.13$, $p<0.01$) and seven days ($Z= 2.49$, $p<0.05$) after treatment, but not longer than seven days (Table 9).

Table 10 shows the effect of ivermectin on development time. Ivermectin significantly prolonged the development in dung collected one day ($Z=9.44$, $p<0.001$), two days ($Z=4.63$, $p<0.001$), four days ($Z=3.36$, $p<0.001$), seven days ($Z=3.38$, $p<0.001$), 14 days ($Z=6.58$, $p<0.001$) and 21 days ($Z=5.69$, $p<0.001$) after treatment. No significant differences were found 28 days after treatment. Only one beetle emerged from dung from treated animals that was collected three days after treatment in comparison to 160 beetles of the control. No significant differences were found in live mass of beetles reared in dung form treated animals compared with the control (Table 11).

Discussion

Under laboratory conditions, ivermectin proved to be more toxic to *E. intermedius* than to *O. alexis* as expressed in direct mortality and prolonged development. For example, ivermectin significantly reduced adult emergence of *O. alexis* for up to seven days after treatment, but, unlike in *E. intermedius,* did not result in 100% mortality in any of the posttreatment periods tested. Even so, effects on populations of *O. alexis* in the field may well be serious as this species requires about twice as much time to complete its life cycle as does *E. intermedius*, resulting in a markedly longer recovery time for a population.

The number of eggs laid by *E. intermedius*, measured as the number of brood balls constructed, was similar for the treatment and control group, with the exception of three days after treatment when it was lower in dung from ivermectin-treated cattle. This is in accordance with Fincher (1992) who studied the effect of a standard injection of ivermectin ($200\mu gkg^{-1}$) on a population of *E. intermedius* introduced into the USA. He found that the number of brood balls formed by *E. intermedius* with dung from ivermectin-treated and control cattle collected was similar seven days after treatment.

Ivermectin prevented the development of *E. intermedius* from two to seven days after treatment. Again, a similar finding was reported by Fincher (1992), who observed that ivermectin prevented adult development of *E. intermedius* in dung collected one week after treatment. In the present study, significantly fewer adults emerged up to 14 days after treatment, in contrast to Fincher's findings who observed that the rate of adult eclosion from dung of treated cattle was similar to that of the control from two to 10 weeks after treatment.

The results of single species laboratory tests are dependent on a number of abiotic (e.g. temperature) and biotic (e.g. genetic heterogeneity) factors (Forbes & Forbes, 1994). The different findings between the present study and that of Fincher (1992) with regard to adult eclosion 14 days after treatment may be a result of either genetic variation or differences in laboratory conditions or a combination of both, although the age of individuals, temperature and relative humidity were similar in the two studies.

Lumaret *et al.* (1993) observed that ivermectin delayed the development of *Euoniticellus fulvus* (Goeze) in dung collected 10 days after cattle were treated with a standard injection of ivermectin, but they did not study subsequent effects. The present study demonstrates that ivermectin adversely affects the development period of *E. intermedius* in dung collected up to 28 days after treatment, and that of *O. alexis* in dung collected up to 21 days after treatment.

Another species that is widely distributed throughout the Afrotropical region is *Onthophagus gazella* Fabricius. This species has, like *E. intermedius,* been introduced into both Australia and the USA. *Onthophagus gazella* has been involved in several studies to assess lethal and sublethal effect of ivermectin (e.g. Fincher, 1992; Sommer *et al.*, 1993a). It appears that *O. alexis* is not only less susceptible to ivermectin compared with *E. intermedius* but also in comparison with *O. gazella,* because Fincher (1992) and Sommer *et al.* (1993a) observed that no adults of *O. gazella* emerged from dung collected seven and eight days after treatment respectively. This is similar to *E. intermedius,* where no adults resulted from dung of treated animals collected seven days after treatment.

Ivermectin residues in dung have been shown to affect reproduction of dung breeding flies and beetles (Strong, 1992, 1993; Hollbrook & Mullens, 1994; Krüger & Scholtz, 1995). Fincher (1992) found no differences in the numbers of offspring resulting from parents reared in dung of treated animals and controls. In the present study significantly

fewer adults resulted from the first breeding week from parents reared in dung collected one and 14 days after treatment (no adults were available to test the effect of ivermectin on fertility and fecundity 2-7 days after treatment). No differences were found thereafter for breeding weeks one and two for any dung collection day.

The respective live masses of adult *O. alexis* emerged from dung of ivermectin-treated cattle and the controls were measured on the assumption that prolonged development could result in smaller specimens; this in turn could lead to a competitive disadvantage over larger specimens. However, the masses of adults emerged from dung containing ivermectin residues and control dung were similar.

The results of this study on *E. intermedius* and *O. alexis* and of other studies on common species such as *O. gazella* (e.g. Fincher, 1992; Sommer *et al.*, 1993a) indicate that ivermectin could have adverse effects on populations of these species in the field. However, laboratory results depend on a number of factors, such as the developmental stage and age of the species under investigation and no further conclusions can be made without incorporating the results of field investigations. Two field studies conducted in the Free State Province (Chapter 3.2, 3.3) have shown that treatment of an entire herd with ivermectin appeared to have little effect on populations of *E. intermedius* under both drought and high rainfall conditions. However, treatment of cattle with ivermectin seemed to affect *O. gazella* one month after treatment under drought conditions. No conclusion could be drawn for *O. alexis* because of the sampling method used.

3 Field Trials

3.1 Effect of ivermectin on dung decomposition and colonization in a savanna ecosystem

Introduction

Several studies have been carried out on the effect of ivermectin and the related compound avermectin on the decomposition rate of cattle dung and, to a lesser extent, on horse dung. The results of these investigations were inconclusive and showed either a delay in dung degradation (Wall & Strong, 1987; Madsen *et al.*, 1990; Sommer *et al.*, 1992), no differences in the disintegration process (Schmidt, 1983; Jacobs *et al.*, 1988; Schaper & Liebisch, 1991; Barth *et al.*, 1993; Wratten *et al.*, 1993; Sommer *et al.*, 1993b; Barth *et al.*, 1994a,b) or an acceleration in dung decomposition (McKeand *et al.*, 1988; Wardhaugh & Mahon, 1991) of pats from animals treated with these agents. With the exception of the work done by Wardhaugh & Mahon (1991) in Australia and Sommer *et al.* (1993b) in Zimbabwe, these studies were conducted in the northern hemisphere, including Europe (Denmark, France, Germany, UK) and the USA.

Avermectins act mainly as larvicides and a reduction in the number of larvae of dung-breeding beetles and flies has been reported in pats of treated animals compared with those of controls for varying periods after treatment (Wall & Strong, 1987; Strong & Wall, 1988; Sommer *et al.*, 1992; Barth *et al.*, 1993; Strong & Wall, 1994). According to Strong & Wall (1988), ivermectin mixed with cattle dung did not deter adult beetles and dung breeding flies from invading pats. However, Wall & Strong (1987) and Strong & Wall (1988) observed that pats from cattle treated with a sustained slow release device ($40\mu gkg^{-1}day^{-1}$) supported fewer beetles (Scarabaeidae (mainly *Aphodius* spp.), Geotrupidae, Staphylinidae, Carabidae, Hydrophilidae and Elateridae) than the controls. In contrast, Wardhaugh & Mahon (1991), in a study carried out in Australia, observed that cattle dung pats deposited three days after a single subcutaneous injection of avermectin ($200\mu gkg^{-1}$)

supported a higher number of dung beetles than did the controls, accounting for the faster decomposition rate of pats from avermectin-treated animals observed by these authors. Lumaret *et al.* (1993) also observed that dung from ivermectin-treated cattle (subcutaneous injection, 200μgkg^{-1}) was more attractive to dung beetles, but this effect lasted from five to 17 days after treatment. Studies by Holter *et al.* (1993) in Denmark (subcutaneous injection (200μgkg^{-1}) and ivermectin added to dung), Tanzania and Zimbabwe (subcutaneous injection (200μgkg^{-1})) yielded more inconsistent results: while ivermectin treatment of cattle was found to enhance the attractiveness of dung to scarabaeid and hydrophilid beetles in some trials, these beetles apparently preferred untreated control dung in other experiments.

The community structure of the cattle dung fauna of the northern temperate zone and the Afrotropical region differs in the relative abundance of the three major dung-frequenting insect groups, i.e., dung beetles, dung-breeding flies and predatory beetles. In the northern temperate region of Europe, predation by beetles of the families Staphylinidae and, to a lesser extent, Histeridae on dung-breeding flies dominates community interactions, whereas in the subtropics and tropics of the Afrotropical region community interactions are dominated by preemptive resource competition, notably by large dung beetles (Hanski & Cambefort, 1991c). In Australia, dung breeding flies were the most abundant group of the cattle dung fauna prior to the introduction of suitably adapted dung beetles (Hanksi & Cambefort, 1991c).

As was pointed out in Chapter 1, the composition of the dung beetle fauna changes from the northern temperate zone, where species breeding directly in a dung pat (i.e., *Aphodius* spp.) are predominant, to the subtropical and tropical regions, where scarabaeine beetles which bury dung in the soil are the major component.

Based on their breeding behaviour, dung beetles have been classified into four groups (e.g., Halffter & Matthews, 1966; Hammond, 1976; Klemperer, 1983). These include, firstly, telecoprids, which roll dung away from the pat and bury it in the soil or place it in grass tussocks, secondly, paracoprids, which construct their nests in the soil beneath a dung pat; thirdly, endocoprids, which make nests directly in a dung pat; and fourthly, kleptoparasites, which use dung that has already been buried by para- or telecoprids. The first three groups have also been termed rollers, tunnelers and dwellers respectively (Hanski

& Cambefort, 1991a).

In order to facilitate the analysis of various aspects of dung beetle ecology (e.g. competition among dung beetles, interaction with other dung insects) Doube (1990) further divided dung beetles into seven functional groups (FG I - FG VII), based on the way in which beetles exploit a dung pat and effect its degradation. This classification is based on the southern African dung fauna (Scarabaeinae and Aphodiinae (Doube, 1991)) and includes large (FG I) and small (FG II) telecoprids, fast-burying (FG III), larger, slow-burying (FG IV) and smaller, slow- burying paracoprids (FG V), kleptoparasites (FG VI) and endocoprids (FG VII).

With the exception of the studies by Holter *et al.* (1993) and Sommer *et al.* (1993b) nothing is known about the effect of ivermectin on dung decomposition and colonization in the subtropical zone. This is unfortunate since, for example, the rich South African dung fauna lends itself to assess whether any differences observed in dung decomposition rates are connected with certain functional groups of dung beetles. The objective of the present study was, therefore, to examine the effects of a single subcutaneous injection of ivermectin ($200\mu gkg^{-1}$) on dung decomposition and on colonization of pats by different functional groups of dung beetles and other insects.

Materials and methods

STUDY AREA

Field trials were carried out in the summer rainfall region on the farm Kiepersol in the Boekenhoutskloof area (25°33S 28°29E) approximately 40 km north-east of Pretoria, which is situated at about 1150m above sea level. The area falls in the savanna biome, the largest biome in southern Africa (Rutherford & Westfall, 1986) and was described by Acocks (1988) as sourish mixed bushveld. The Boekenhoutskloof area is characterized by deep sandy soils. The dung beetle fauna of this region is comparatively well known mainly

due to the past collecting efforts of the former CSIRO Dung Beetle Unit stationed at Pretoria. Cattle on the farm were usually not treated with antiparasitic products.

TREATMENT OF CATTLE AND DUNG COLLECTION

A group of 10 Friesian steers (200-400 kg body weight) held at the University experimental farm at Pretoria was used for each trial. The animals were not treated with any parasiticides for three months prior to trials. Ivermectin was administered in a single subcutaneous injection at the prescribed dose of $200\mu gkg^{-1}$ to five animals. The other half served as control and remained untreated. The two groups of steers were kept in separate enclosures and were maintained on hay and lucerne. Water was freely available.

Freshly deposited cattle dung was collected after one to four and seven days, and then at weekly intervals for up to four weeks after treatment. The dung obtained on each collection date was thoroughly mixed for each group.

The experiment was replicated three times during the peak beetle activity period in the austral summer. The trials were conducted during consecutive months from the end of October 1991 to the beginning of February 1992.

EXPERIMENTAL DESIGN

On each dung deposition day, 10 experimental and 10 control pats (1kg, 20±1 cm in diameter) were placed in a sandy soil pasture used for cattle grazing at approximately 0800h. The pats were evenly spaced at two-metre intervals in an alternating sequence in two rows (i.e., 2x10 block). Five samples, consisting of two experimental and two control pats each, to be collected 1-4 and seven days after dung deposition, were randomly chosen (i.e., one treatment and one control pat per row) and labelled with a plastic stake. Pats were not covered with wire mesh to prevent disturbance by birds and other animals because a suitably sized mesh would also have prevented larger dung beetles (e.g. *Pachylomerus femoralis* Kirby, a large dung ball roller) from reaching the pats. This would not only have affected the colonization of pats by dung beetles, but also the dung decomposition rate.

The pats were collected at the time intervals indicated above (i.e. 1-4, 7 days after dung deposition) after assessment of dung degradation. Again, the samples were retrieved in the morning (0800h)[1]. They were then transported to the laboratory in linen or plastic bags.

METEREOLOGICAL MEASUREMENTS

Temperature and relative humidity were measured with a thermohygrometer placed 1.5m above ground level. Measurements were taken on each sampling date. Rainfall data for Boekenhoutskloof were obtained from the recordings of the South African Weather Bureau, Pretoria.

DETERMINATION OF DUNG DECOMPOSITION

The dung pats placed out in the field were used for the assessment of both dung decomposition rate and pat colonization. Shredding of the pats by beetles resulted in considerable expansion of the surface area. For this reason it was not practicable to use the organic matter content of pats for the determination of dung decomposition as recommended by Herd *et al.* (1993b), or to assess surface area, which has been used by some workers (see Barth *et al.* 1994b). Instead, visual estimates of the decomposition process, documented by photographs, were made until the dung was completely degraded or dried out. The amount of dung removed was recorded as one of five categories following Hughes (1975). In order to describe local conditions more accurately, an additional category (No. 4, see below) was added.

[1]It was not possible to work with a larger sample size due to the number of cattle available and the resulting amount of dung.

Dung decomposition index :

5. Completely removed - only a thin crust or a few crumbs of dried dung or less remain above ground level on a mound/mounds of soil
4. Majority removed - only a small amount of dung (ca. 20%) left together with mound/s of soil
3. Partly removed - a large cavity in the dung pat has been replaced with soil, or most of the holes have been filled with sand; approximately 40% of the dung is left
2. Many holes - a considerable amount of dung is missing (ca. 40%) and some holes have been filled with sand
1. Few holes - holes have not been replaced by soil, approximately 20 % of the dung has been removed
0. Whole pats - little sign of dung decomposition, pats appear undisturbed.

In those cases where it proved impossible to assign the observed degradation of a pat to a particular categrory, the intermediate category was chosen. For example, if 50% of a pat were found to be removed, the assigned value for the index would be 2.5.

EXTRACTION AND IDENTIFICATION OF DUNG INSECTS

In the laboratory, the dung samples were transferred to Moczarsky-Winkler selectors (Endrödy-Younga, 1979), which operate on the principle of a Berlese extractor, to extract insects.

Species of dung beetles were identified by comparing specimens against identified insect collections at the Transvaal Museum (TM) and the National Collection of Insects (NCI) (both Pretoria), with the assistance of Dr S. Endrödy-Younga and Mr R.G. Oberprieler, respectively. Other dung-frequenting insects were identified to family.

The impact of ivermectin was determined, firstly, on Staphylinidae and Histeridae and the scarab subfamilies Scarabaeinae and Aphodiinae; secondly, on the functional groups of dung beetles and thirdly, on the five most abundant dung beetle species, together with *Euoniticellus intermedius* (Reiche) and *Liatongus militaris* (Castelnau), which have been

shown by Holter *et al.* (1993) to be particularly attracted to dung from treated cattle.

Members of the functional group FG VI (kleptoparasites) were included in functional groups FG IV and FG V (larger and smaller slow-burying paracoprids) in accordance with their size as the affinities of many species within the functional groups are unclear (Doube, 1990).

Voucher specimens were deposited in the Transvaal Museum, Pretoria, South Africa.

DATA ANALYSIS

Data on dung decomposition and insect counts were analysed separately for each dung deposition day (i.e. Days 1, 2, 3, 4, 7, 14, 21 and 28). Three-way analysis of variance was used to assess the effects of trial, treatment and pat age. The SAS® procedure ANOVA was used for balanced data (equal numbers of observations for each treatment combination) and GLM (General Linear Models) for unbalanced data (unequal numbers of observations for each treatment combination) (SAS Institute, 1989). Data were not available for all pats, because some of them had been destroyed by birds and/or baboons (Fig. 2d). Transformation of data (e.g. logarithmic transformation) did not result in the stabilization of variance and normal distribution required for an analysis of variance. The analyses were, therefore, performed in a non-parametric way by using the ranks of the variables for which normal scores were computed, so that the resulting variables appear to be normally distributed (SAS Institute, 1990). Van der Waerden's formula was used for the computation of the normal scores:

$$y_i = \Phi^{-1}(r_i)/(n+1),$$

where Φ^{-1} is the inverse cumulative normal (Probit) function, r_i is the rank of the ith observation, and n is the number of nonmissing observations for the ranking variable (SAS Institute, 1990).

Trial (Trial 1-3), treatment (ivermectin, untreated control) and pat age (1-4 and 7 days) were treated as fixed factors in the analyses. It was decided to treat trial as a fixed (as opposed to a random) factor because the timing of the trials was chosen on purpose to ensure that the three trials were conducted in consecutive months during peak beetle activity in summer.

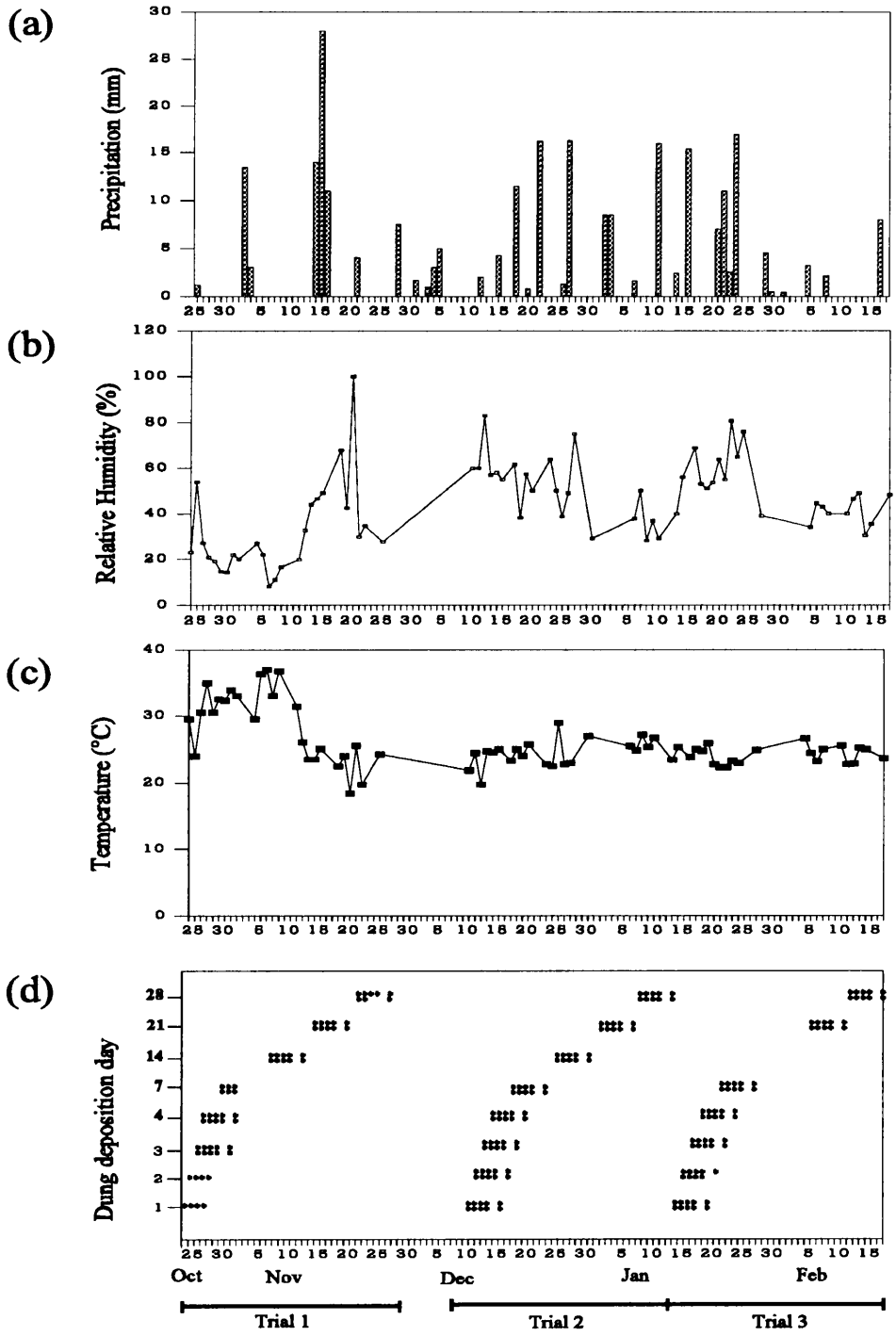

Fig. 2. Dung deposition days (20 pats per day) and periods of exposure together with air temperature, relative humidity and precipitation at the trial site during the trial period. Each point in (d) denotes two pats (one ivermectin treatment, one control) for each pat age (i.e. 1-4 and 7 days after treatment). Missing points denote pats that were destroyed by birds or baboons and which were excluded from all analyses.

Results

CLIMATIC CONDITIONS

The total amount of rainfall was similar during the first (74.7mm) (October-November, 1991) and third trial (74mm) (January-February, 1992). It was higher during the second trial (88.7mm) (December-January, 1991/1992). Temperature was higher and relative humidity lower during the first trial (October-November, 1991) compared with trials two and three (Fig. 2).

DUNG DECOMPOSITION

The results for the dung degradation index are presented in Figs. 3 and 4, and those of the statistical analysis in Appendix 1.

Dung decomposition in the trial area was very rapid, especially on the first day after pat deposition.The greater part of both types of pats was broken down within the first four days of exposure. After this period, dung remaining on the surface was usually dried out and only colonized by few individuals of a few insect species.

In general, there was considerable variation independent of treatment in the decomposition rates of pats among the three trials for each dung deposition day. These differences were significant for the pats placed out on Days 3, 4, 7, 14 and 28 (Days 4, 14: $p<0.01$; Days 3, 7, 28: $p< 0.001$).

As expected, the degree of dung decomposition depended on the time of exposure in the field (dung deposition Day 1: $p<0.05$; Day 2: $p<0.01$; Days 3, 4, 7, 14, 21, 28: $p<0.001$), except for pats placed out on Day 14. These pats were broken down within 24 hours during the second trial so that the decomposition rates were relatively similar for all pats (Fig. 4).

Overall, there were no significant differences in decomposition rate between treatments (ivermectin, control) for any dung deposition day ($p>0.05$). However, the treatment effect differed among trials on Days 2, 3 and 7 (Days 2, 7: $p<0.5$; Day 3: $p<0.001$).

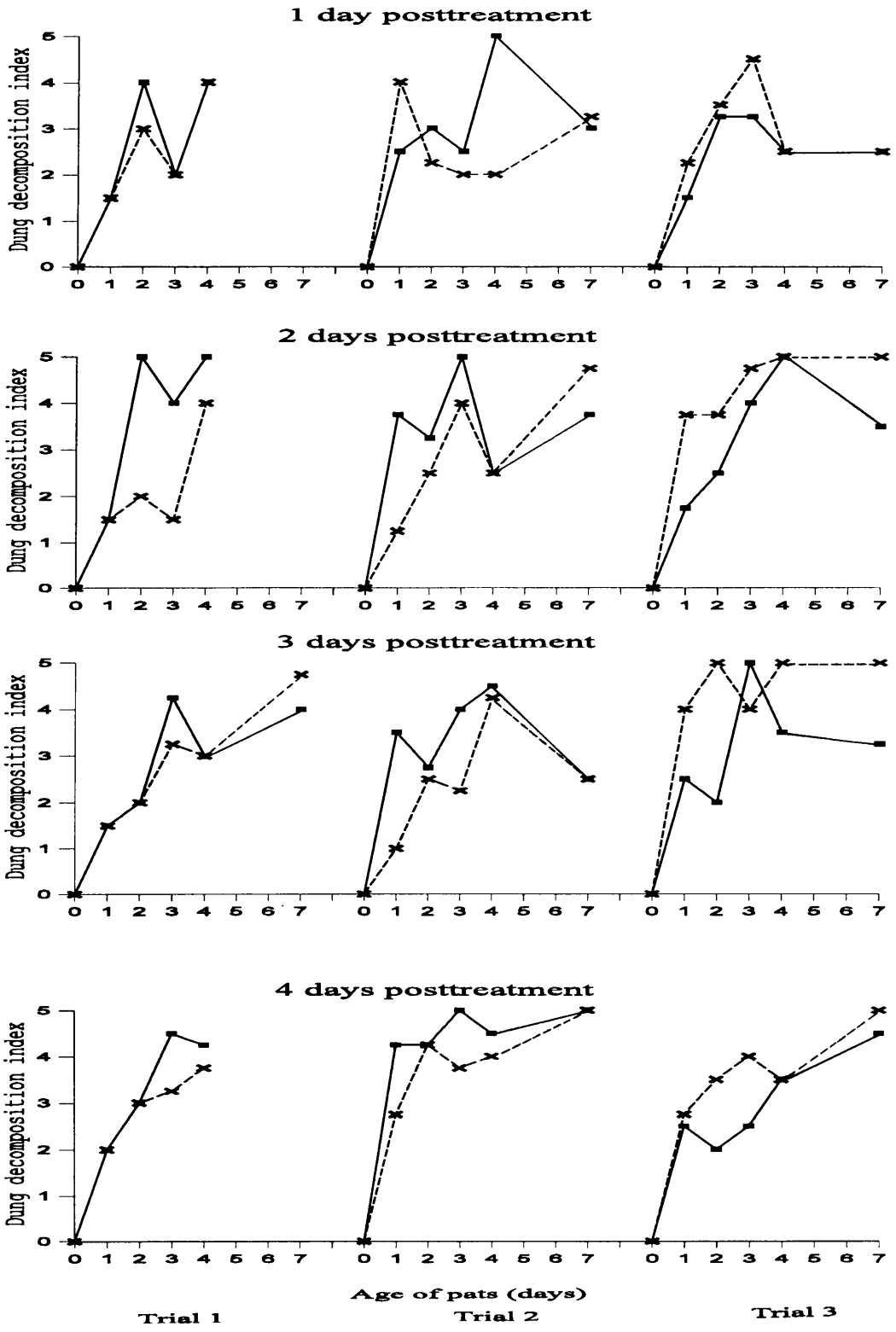

Fig. 3. Dung decomposition index (see text for explanation). Solid line: ivermectin treatment (200μgkg^{-1}), broken line: untreated control. The mean decomposition index calculated from two pats is given. In case only one pat was available the decomposition index for that pat is shown. Trial 1: October-November, Trial 2: December-January, Trial 3: January-February.

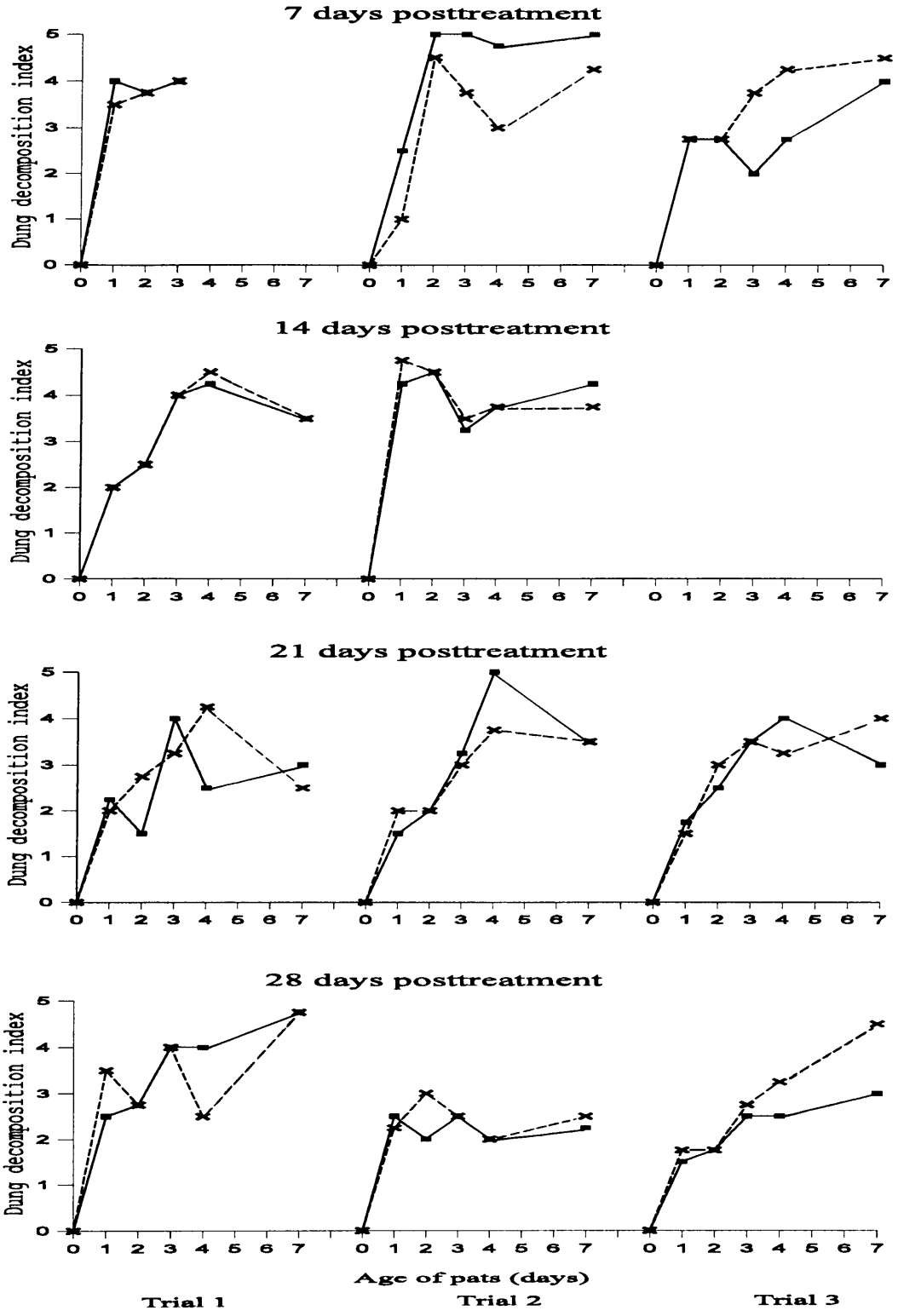

Fig. 4. Dung decomposition index (see text for explanation). Solid line: ivermectin treatment ($200\mu gkg^{-1}$), broken line: untreated control. The mean decomposition index calculated from two pats is given. In case only one pat was available the decomposition index for that pat is shown. Trial 1: October-November, Trial 2: December-January, Trial 3: January-February.

The disintegration of pats from ivermectin-treated cattle was faster than in the control during Trial 2 and slower during Trial 3 for all three dung deposition days (Figs. 3, 4). Furthermore, the decomposition rate of pats from ivermectin-treated animals was higher than that of their controls during Trial 1 for pats deposited on Day 2, and more or less similar for pats deposited on Days 3 and 7.

On Day 3 differences among the five pat ages were dependent on treatment (ivermectin, control) ($p<0.001$). Pats from ivermectin-treated cattle deposited on Day 3 exhibited a higher decomposition rate than their controls after three days of exposure in all three trials, whereas the decomposition rates between treatment and control were variable for all other days.

Although no attempt was made to quantify them, numerous holes made by dung-burying beetles were observed in the soil beneath dung pats of both groups (ivermectin and control).

DUNG COLONIZATION BY HISTERIDAE, STAPHYLINIDAE, SCARABAEINAE AND APHODIINAE

In the study area, the three most abundant beetle families recorded were the predacious Histeridae, the primarily predacious Staphylinidae (Aleocharinae, Staphylininae and Tachyporinae) and the coprophagous scarabaeid subfamilies Scarabaeinae and Aphodiinae.

The total numbers of Histeridae and Staphylindae were noticeably lower in pats from ivermectin-treated cattle (I) than in the untreated control pats (C) on Days 1 and 2, and higher in pats from treated animals on Day 28 (Table 12). However, with two exceptions the differences in the abundance of these two families between pats from treated and untreated cattle were not significant on any dung deposition day, nor for the 'trial by treatment' or 'treatment by pat age' interaction ($p>0.05$). The exceptions mentioned above refer to two instances in histerid abundance, when the effect of treatment varied across the three trials on Day 2 ($p<0.05$) and Day 28 ($p<0.01$) (Appendix 2a,b). For this family, the numbers of individuals extracted from pats of ivermectin-treated cattle deposited on Day 2 were lower for Trial 1 (C/I: 10/0) and Trial 2 (C/I: 61/8) and higher for Trial 3 (C/I: 8/49) compared with the controls. A similar pattern was observed for Day 28, when the abundance of histerids was lower in pats containing ivermectin residues than in the controls for Trial

1 (C/I: 36/21) and Trial 2 (C/I: 22/2) and higher in Trial 3 (C/I: 89/219).

In contrast to Histeridae and Staphylinidae, Scarabaeinae and Aphodiinae were more common in pats from treated animals than control pats on Day 2 (Table 12).

Table 12. Total number of specimens of the families Histeridae, Staphylinidae and the scarabaeid subfamilies Scarabaeinae and Aphodiinae collected in pats from ivermectin-treated ($200\mu gkg^{-1}$) and untreated control cattle. The number of specimens collected per group in the three trials was pooled for each dung deposition day.

Time after treatment (days)	Regime	Histeridae	Staphylinidae	Scarabaeidae		Totals
				Scarabaeinae	Aphodiinae	
1[d]	Ivermectin	83	15	864	193	1155
	Control	178	47	842	192	1259
2[d]	Ivermectin	57	11	926	235	1229
	Control	79	30	594	126	829
3[a]	Ivermectin	95	33	1012	242	1382
	Control	75	38	1091	350	1554
4[b]	Ivermectin	87	35	1575	264	1961
	Control	59	22	1367	279	1727
7[c]	Ivermectin	78	25	810	150	1063
	Control	61	25	865	136	1087
14[e]	Ivermectin	41	23	608	130	802
	Control	59	27	649	134	869
21[a]	Ivermectin	93	45	1119	332	1589
	Control	117	42	1438	318	1915
28[b]	Ivermectin	242	110	1042	263	1657
	Control	147	34	682	216	1079

[a,b,c,d,e] a: n= 60; b: n=56; c: n=52; d: n=48; e: n=40

In general, no significant treatment effect was observed for Scarabaeidae ($p>0.05$). However, the effect of treatment differed among trials on Day 2 ($p<0.01$) and Day 3 ($p<0.05$). The abundance of scarabaeine beetles was greater in pats from ivermectin-treated cattle than in

the controls in Trial 1 (C/I: 42/61), considerably lower in Trial 2 (C/I: 336/185) and about three times higher in Trial 3 (C/I: 216/680) on Day 2. On Day 3 scarabaeine beetle numbers were lower in pats containing ivermectin residues for Trial 1 (C/I/: 243/182) and Trial 2 (C/I: 376/158) and higher in Trial 3 (C/I: 472/672).

The effect of treatment was not the same for the different pat ages on Day 21 ($p<0.01$), because scarabaeine beetles were less abundant in pats of ivermectin-treated cattle than in the control that had been exposed for two days, and more abundant in pats exposed for three days in all three trials (C/I, pat age 2 days: T1: 62/109, T2:163/239, T3:93/133; pat age 3 days: T1:57/42, T2:127/58, T3:123/39) (Appendix 2c).

For Aphodiinae, differences between treatment and control and treatment interactions were not significant for any of the dung deposition days ($p>0.05$) (Appendix 2d).

EFFECT OF IVERMECTIN ON FUNCTIONAL GROUPS OF DUNG BEETLES

Table 13 gives the distribution of individuals among the functional groups of dung beetles. For both ivermectin treatment and control the majority of individuals belong to FG V, the smaller, slow-burying paracoprids (58.72-73.13%), followed by FG VII (endocoprids) (13.69-24.50%), FG II (small telecoprids) (6.58-13.16%) and finally FG IV (larger, slow-burying paracoprids) (2.50-8.06%). The ranking of the functional groups is the same for both ivermectin treatment and control. Doube (1990) observed that functional groups FG I (large telecoprids) and FG III (fast-burying paracoprids) dominate the dung beetle fauna on the sandy soil pastures at Boekenhoutskloof. During the present study only very few specimens of FG I (large telecoprids) and FG III (fast-burying paracoprids) were collected, presumably because dung pats which allow for beetle movements instead of pitfalls were used. FG III was undersampled because all species belonging to this group are crepuscular or nocturnal (Doube, 1990) or dig too deep to be retrieved by the method employed.

FG I and FG III were excluded from the statistical analysis because too few individuals were collected. For all other functional groups, no significant overall treatment effect was observed ($p>0.05$) (Appendix 3a-d). The treatment effect varied across the different trials on Day 2 for FG II and on Day 3 for FG V ($p<0.05$). For all other days after ivermectin

therapy the 'trial by treatment' interaction was not significant ($p>0.05$). On Day 2 the total number of individuals in FG II (small telecoprids) was lower in Trial 2 (C/I: 39/26) and higher in Trial 3 (C/I: 37/69) in pats from ivermectin-treated cattle compared with the controls. A total of only two individuals of FG II was collected in the first trial; these were found in pats from treated cattle. The effect of treatment differed among trials for FG V in that the number of individuals was lower in pats containing ivermectin residues than the controls (C/I: 225/175).

Table 13. Effect of ivermectin on the distribution of individuals among functional groups FG I to FG VII (Doube, 1991) of dung beetle communities (percentage calculated from the pooled total number of individuals collected per functional group in the three trials for each dung deposition day).

Time after treatment (days)	Regime	Percentage of individuals					
		FG I	FG II	FG III	FGIV + VI	FGV + VI	FG VII
1[d]	Ivermectin	0	9.56	0	6.43	65.37	18.64
	Control	0	6.58	0.10	5.32	69.15	18.86
2[d]	Ivermectin	0	8.35	0	2.50	68.91	20.24
	Control	0	10.56	0	8.06	62.22	19.22
3[a]	Ivermectin	0	12.36	0.08	4.31	63.72	19.54
	Control	0	10.69	0	4.37	60.51	24.43
4[b]	Ivermectin	0.05	13.10	0.05	3.81	68.57	14.41
	Control	0.06	10.39	0	4.86	67.74	16.95
7[c]	Ivermectin	0	8.96	0	3.33	71.46	16.25
	Control	0	8.29	0.10	4.80	73.13	13.69
14[e]	Ivermectin	0	7.86	0	3.93	70.33	17.89
	Control	0	12.39	0	3.19	67.18	17.24
21[a]	Ivermectin	0	13.16	0.07	5.03	58.72	23.02
	Control	0	10.88	0.06	4.90	65.55	18.62
28[b]	Ivermectin	0	7.59	0	5.44	66.67	20.31
	Control	0	8.91	0	5.46	61.14	24.50

[a,b,c,d,e] a: n= 60; b: n=56; c: n=52; d: n=48; e: n=40

The 'treatment by pat age' interaction was not significant, except for FG II (small telecoprids) observed 21 days after treatment ($p<0.01$). The effect of treatment in this instance was not the same for all pat ages: the number of individuals was higher in all pats containing ivermectin residues exposed for two days compared with the controls (Trial 1: C/I: 13/25; Trial 2: C/I: 35/60; Trial 3: C/I: 4/9), whereas it was variable for all other pat ages.

DUNG COLONIZATION BY THE FIVE MOST ABUNDANT SCARAB SPECIES AND *EUONITICELLUS INTERMEDIUS* AND *LIATONGUS MILITARIS*

The five most common species were (in decreasing order): (i) *Sisyphus* sp. 2 (FG II, small telecoprid), (ii) *Drepanocerus laticollis* Fåhreus (FG V, smaller slow-burying paracoprid), (iii) *Tiniocellus spinipes* Roth (FG V), (iv) *Aphodius pseudolividus* Balthasar (FG VII, endocoprid) and (v) *Colobopterus maculicollis* Reiche (FG VII) (Table 14a, b). Results of the three-way ANOVA of individuals collected per species are presented in Appendix 4a-e.

There was no significant treatment effect on the number of individuals of all five species and for all dung deposition days in pats from ivermectin-treated and control cattle ($p>0.05$). Interaction of treatment with trial and pat age was significant in some instances. These include Days 1, 2, 3, 21 and 28 and are: (i) 'trial by treatment' interaction: *Sisyphus* sp.2 and *D. laticollis* (Day 2, $P<0.05$), *T. spinipes* (Days 2 and 3, $p<0.05$) and *A. pseudolividus* (Day 28, $p<0.01$); (ii) 'treatment by pat age' interaction: *A. pseudolividus* (Day 1, $p<0.001$; Day 21: $p<0.01$), *Sisyphus* sp.2 (Day 21, $p<0.01$) and *T. spinipes* (Day 28, $p<0.05$). No significant interactions of treatment with trial or pat age were found for *C. maculicollis*. In order to clarify trends for the species and those days on which the treatment effect varied across trials, the control/ivermectin ratios for the number of individuals were calculated (Table 15). On Day 2 the ratios for *Sisyphus* sp.2, *D. laticollis* and *T. spinipes* were all greater than one for Trial 2 and smaller than one for Trial 3. This indicates that these species were more abundant in the controls in Trial 2 and more abundant in dung from ivermectin-treated animals in Trial 3. The same applies to *T. spinipes* on Day 3 and *A. pseudolividus* on Day 28.

Table 14a, b.Total number of specimens of the five most abundant species and *Euoniticellus intermedius* and *Liatongus militaris* collected from pats of ivermectin-treated (200μgkg^{-1}) and untreated control cattle 1-4 days after treatment (a) and 7-28 days after treatment (b). The number of individuals collected per species in the three trials was pooled for each dung deposition day. The species are listed in order of decreasing abundance.

14a. 1-4 days after treatment.

Species	Dung deposition day							
	1		2		3		4	
	Ivermectin[d]	Control[d]	Ivermectin[d]	Control[d]	Ivermectin[a]	Control[a]	Ivermectin[b]	Control[b]
Sisyphus sp.2	86	66	90	62	145	148	204	156
Drepanocerus laticollis	515	504	362	263	295	257	617	439
Tiniocellus spinipes	133	159	322	132	333	372	445	474
Aphodius pseudolividus	44	29	41	37	33	74	23	36
Colobopterus maculicollis	45	18	20	15	43	26	146	133
Euoniticellus intermedius	29	18	9	21	31	29	21	30
Liatongus militaris	36	34	9	27	12	23	32	22

14b. 7-28 days after treatment.

Species	Dung deposition day							
	7		14		21		28	
	Ivermectin[c]	Control[c]	Ivermectin[e]	Control[e]	Ivermectin[a]	Control[a]	Ivermectin[b]	Control[b]
Sisyphus sp.2	74	77	44	91	163	167	90	78
Drepanocerus laticollis	487	423	339	383	401	589	701	374
Tiniocellus spinipes	160	228	143	112	347	379	108	113
Aphodius pseudolividus	15	14	15	15	81	91	95	68
Colobopterus maculicollis	19	20	12	14	55	68	24	35
Euoniticellus intermedius	7	9	6	6	31	35	29	13
Liatongus militaris	24	35	22	18	32	29	24	19

[a,b,c,d] a: n=60, b: n=56, c: n=52, d: n=48, e: n=40.

Table 15. Control/ivermectin-ratios for species and dung deposition days where the abundance of the species was not the same for ivermectin treatment and control among the three trials (T1 to T3). The 'trial by treatment' interaction was not significant for all species on all days and only in cases of significant interactions are the ratios given in the table.

Species	Day 2			Day 3			Day 28		
	T 1	T 2	T 3	T 1	T 2	T 3	T 1	T 2	T 3
Sisyphus sp.2	0	1.08	0.54	-	-	-	-	-	-
Drepanocerus laticollis	1.10	1.93	0.31	-	-	-	-	-	-
Tiniocellus spinipes	0.11	1.64	0.25	2.81	2.29	0.88	-	-	-
Aphodius pseudolividus	-	-	-	-	-	-	1.1	4.5	0.09

The effect of treatment was dependent on the age of pats ('treatment by pat age' interaction) on Days 1 and 4 (*A. pseudolividus,* $p<0.001$ (Day 1), $p<0.05$ (Day 4)), Day 21 (*Sisyphus* sp.2, $p<0.01$; *A. pseudolividus,* $p<0.05$) and Day 28 (*T. spinipes*, $p<0.05$). The pat ages involved are one, two and three days of exposure, when insect numbers in pats were high. However, the effect of treatment with regard to exposure time of pats is not very conclusive. For example, *A. pseudolividus* was more abundant in pats of ivermectin-treated animals than in control pats exposed for 24 hours on Day 1 and less abundant on Day 4 (C/I-ratios Day 1: T1: 0.4, T2:0, T3: 0.5; Day 4: T1: 1.33, T2: 3/0, T3: 10.00). During both days the concentration of ivermectin in dung was high, though more so on Day 4 (Sommer *et al.*, 1992).

The abundances of both *E. intermedius* and *L. militaris* are given in Table 14a, b. The total number of beetles collected was very variable among trials and also between ivermectin treatment and control. For both *E. intermedius* and *L. militaris* no significant treatment effect, 'trial by treatment' interaction and 'treatment by pat age' interaction was observed.

Discussion

The dung degradation rate during the study period was very rapid, and usually pats were practically completely degraded within four days after deposition in the field. The speed with which pats were decomposed is characteristic for pastures on sandy soils, where paracoprids (tunnellers) and telecoprids (rollers) are abundant; members of both groups bury dung in the soil (Doube, 1990).

It was noticeable during the field investigations of the present study and from the number of insects collected that Diptera were uncommon during the trial. The experiment was conducted during a period when dung beetles were very active, which resulted in the aforementioned rapid disintegration of dung. Therefore, dung exposure time might have been too short for the development of fly larvae. A comparison of pats from treated and untreated animals with regard to colonization by fly larvae was, therefore, not possible. The same applies to scarabaeid larvae which develop in dung pats and would, therefore, have been collected had they been present.

Wardhaugh & Mahon (1991), commenting on the frequently contradictory findings with regard to the decomposition rates of dung from animals treated with avermectins, first noted that the impact of ivermectin residues on dung degradation is a complex phenomenon that appears to vary with dung insect community composition.

The results of the present study indicate that the effect of treatment may also be inconsistent within a single region, where the species composition was similar in all three trials. Similarly, Holter *et al.* (1993), comparing pats from ivermectin-treated ($200\mu gkg^{-1}$) and untreated control cattle in Denmark, found discrepancies among trials, where hydrophilid and *Aphodius* species showed a preference for control dung in one trial, but no such preference was observed in the other two trials.

In the present study, ivermectin had no impact on dung decomposition, colonization by adult dung insects, including the functional groups of dung beetles, if all three trials together are considered. However, as has just been pointed out, the effect of treatment was not the same in all trials. For example, differences in the dung decomposition rate among trials occurred on Days 2, 3 and 7, when ivermectin concentrations in dung were high (Sommer *et al.*, 1992; Lumaret *et al.*, 1993). For these dung deposition days disintegration of pats was faster in Trial 2 and slower in Trial 3 for pats containing ivermectin residues compared

with the controls, whereas it varied between the two groups in Trial 1.

In accordance with the differences in dung disintegration, fewer individuals of some insect groups were found in dung from ivermectin-treated cattle than in the controls on Days 2 and 3 in the second trial, when the decomposition rate was higher (i.e. less dung was left at the various ages of pats than in the controls) and more individuals in the third trial when the decomposition rate was lower (i.e. more dung was left than in the controls).

Differences among trials for pats from ivermectin-treated and control cattle occurred at 28 days after treatment. The differences were significant only in two instances. Firstly, members of the Histeridae were less common in the first and second trial in pats from ivermectin-treated cattle than the controls and more abundant in the third trial; secondly, *A. pseudolividus* was more common in the first two trials and less common in the third trial in pats from cattle injected with ivermectin. However, it is unlikely that these differences are attributable to ivermectin, because no differences in dung decomposition were observed between the two types of dung and no other insect groups or species showed significant 'trial by treatment' interactions 28 days after treatment. In addition, ivermectin concentrations in dung drop to very low levels about 14 days after treatment (Sommer *et al.*, 1992; Lumaret *et al.*, 1993).

Differences between treatments were also observed for different pat ages. These interactions, however, were probably an artifact due to small sample size (n=2) and no interpretations with regard to pat age are made here.

As was mentioned in the introduction to this chapter, dung from animals treated with avermectins has been reported to attract dung insects (Wardhaugh & Mahon, 1991; Holter *et al.* 1993; Lumaret *et al.*, 1993). Holter *et al.* (1993) observed that this attractiveness has been consistent with members of the scarabaeine tribe Oniticellini, but that findings for other groups are not conclusive. It has been suggested that the attraction of pats from animals treated with avermectins is not caused by the drugs themselves, but that some volatile metabolite of the agents, or changes in the gut flora caused by the avermectins, may be involved (Wardhaugh & Mahon, 1991; Holter *et al.*, 1993; Lumaret *et al.*, 1993). Another factor, the importance of the moisture content of dung and resulting differences in colonization by the dung fauna and in dung decomposition was highlighted by Barth *et al.* (1995). They observed that a difference in moisture content of dung as slight as 1-2% can have major effects on colonization by dung insects.

The results of the present study are not sufficient to draw far-reaching conclusions on the attractiveness of dung from ivermectin-treated cattle for groups of insects or individual species. Dung decomposition during the trials was so rapid that any differences in numbers of individuals of groups/species are more a reflection of the degree of dung disintegration than of attraction or repellance. The moisture content of the different dung types was not assessed in the present study nor in other studies where ivermectin affected dung decomposition. It is, therefore, not possible to make a connection between the attractiveness of dung from cattle treated with avermectins and the dung moisture content.

In conclusion, the effect of treating cattle with ivermectin on the dung decomposition process and colonization of pats may be variable even within a single region and when the composition of the dung fauna is similar. Pats from treated animals may be decomposed and colonized more slowly, faster or at the same rate as those of untreated cattle. The mechanisms which cause the differences are presently unresolved. However, there is little evidence that dung insects avoid pats from ivermectin-treated cattle for breeding, so that treatment of entire herds with the agent may have consequences for local populations of these species, in particular if they have only one or two generations per year. Accumulation of undegraded cattle dung on pastures in the Afrotropical region, caused by repellance to dung beetles of pats from ivermectin-treated cattle seems unlikely, because dung degradation is very rapid and a repellance would only delay degradation for a very short period of time. However, effects of ivermectin on populations of dung beetles could be reduced by treatment of cattle before or after the peak activity of dung beetles.

3.2 Changes in the structure of dung insect communities after ivermectin usage under drought conditions in a grassland ecosystem

Introduction

Several field studies have been conducted to assess the effect of ivermectin on attraction of dung beetles to dung from treated animals, pat colonization and dung decomposition, and to determine the concentration of ivermectin in dung after treatment of cattle (e.g. Wall & Strong, 1987; Madsen *et al.*, 1990; Sommer *et al.*, 1992, 1993a, b; Sommer & Overgaard Nielsen, 1992; Sommer & Steffansen, 1993; Holter *et al.*, 1993; Lumaret *et al.*, 1993; Wratten *et al.*, 1993; Strong & Wall, 1994; Chapter 3.1). These studies have shown that geographical location and climate can influence results; for example ambient temperature and rainfall can affect the composition of the dung fauna in general (and dung insects in particular) and the rate of dung pat decomposition.

However, these field studies have provided only limited insight into the extent to which ivermectin treatment affects natural populations and communities. Consequently, the need for studies to examine the ecological effects of avermectins on communities of pastureland invertebrates has been stressed by Herd *et al.* (1993b). Moreover, most of the longer-term field investigations done to date were conducted in the temperate zone of the northern hemisphere, where earthworms play a major role in the degradation of dung, in contrast to mediterranean and subtropical climates, where dung beetles are of greater importance (Holter, 1979; Hanski & Cambefort, 1991a; Lumaret *et al.*, 1992).

Natural or anthropogenic disturbances can strongly influence the structure of ecological communities (Pickett & White, 1985; Petraitis *et al.*, 1989; Samways, 1994). The response of communities to disturbances has been extensively discussed in relation to various stability concepts, such as resilience (the ability of a system to return to the initial equilibrium following disturbance) (Pimm, 1984). Recovery of a community is measured in terms of convergence to pre-disturbance levels or, more frequently, an undisturbed control (Peterson & Stevenson, 1992; Rodríguez, 1994). Grover & Lawton (1994) defined community convergence as the attainment in one or more communities of 'the same "state" in terms of

identities and absolute and relative abundance of constituent species'. However, for natural communities the concept of convergence is best perceived as relative rather than absolute (Jørgenson, 1990), because natural communities are subject to fluctuations in environmental factors unrelated to disturbances. It is thus very unlikely that the original state or a state identical to an undisturbed control can be reached. Dung insect communities, which inhabit an ephemeral and patchily distributed resource, are especially subject to frequent changes. In order to account for natural variability, the convergence of the disturbed system to a contemporaneous control, rather than to pre-disturbance levels, is considered to be a suitable criterion for recovery (Fairweather, 1993; Rodríguez, 1994).

In the present study the ecotoxicological effects of ivermectin on dung insect communities were assessed in a large-scale field investigation. The objectives of the study were: (i) to determine if ivermectin usage has an impact on dung insect communities under normal extensive farming conditions in South Africa; (ii) to examine potential depressive long-term effects of ivermectin on the communities, should such an impact occur; and (iii) to determine whether the system is able to recover within a reasonable time scale, should there be a disturbance.

Materials and methods

STUDY SITE

The study was carried out in the summer rainfall region of South Africa on two virtually adjacent commercial farms under the same management (Farms Abel and Middelpunt, 26°54'S 27°35'E). The farms are situated about 14km east of Parys (Free State Province), about 1350m above sea level. The study site belongs to the grassland biome (Rutherford & Westfall, 1986) and was classified by Acocks (1988) as Bankenveld, a false grassland type. The soil type is variable but is predominated by clay-loam.

METEOROLOGICAL MEASUREMENTS

Temperature and precipitation were recorded at the nearest meteorological stations of the South African Weather Bureau at Potchefstroom and Parys, respectively.

ALLOCATION AND TREATMENT OF CATTLE

The trial was conducted during the austral summer, coinciding with the peak beetle activity period, and extended over three months from December 1992 to March 1993.

A breeding herd of commercial cattle consisting of 80 cows, some with calves, was divided randomly into four equal-sized groups and confined to two pairs of adjacent paddocks of about 80 ha each. The two pairs of paddocks were about 200 m apart; their position is shown in Fig. 5. The pairs of adjacent paddocks were randomly allocated to treatment or control. The paddocks designated P1 and P2 served as control paddocks (C), and the remaining paddocks, P3 and P4, as treatment paddocks (I). The reason for allocating adjoining paddocks to each group was that cattle confined to a relatively large area were treated to reduce the effect of immigration of insects from surrounding paddocks. Although the trial paddocks were surrounded by paddocks which were also stocked with cattle, these rarely stayed in close vicinity to the trial area.

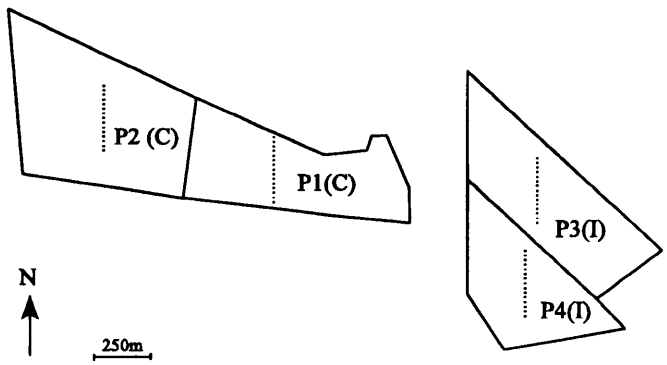

Fig. 5. Position of the treatment (I) and control paddocks (C). Surrounding areas were also occupied by cattle. Treatment of entire herds with a single subcutaneous injection of ivermectin ($200\mu gkg^{-1}$) in paddocks P3 and P4. Herds in paddocks P1 and P2 were untreated (controls). Solid lines denote fences and dotted lines the line transects of artificial standardized pats placed out before, and one, two and three months after treatment of cattle.

Cattle were maintained according to the normal farm policy with respect to grazing and pasture management.

It was not possible for logistical reasons to replicate the experiment in the same year and so replication was planned for the subsequent year. However, the experiment could not be adequately repeated as intended because the higher rainfall experienced during the rainy season of 1993/94 affected the abundance of dung insects, so that a comparison of the two years is rather complex. The results of this second study will therefore be reported separately in Chapter 3.3.

SAMPLING PROCEDURES

Insects were collected in dung pats as opposed to dung-baited pitfall traps because pats reflect a more natural situation and allow for species interactions (Holter, 1982). The colonization of pats by dung beetles and other dung insects is influenced by such dung characteristics as pat size, moisture content and nutritional properties (Peck & Howden, 1984; Cambefort, 1991; Barth, 1993; Barth *et al.*, 1995). Therefore, two types of pats were used in the trials. Artificial standardized 1kg pats, made from thoroughly mixed dung from an untreated herd held at the University of Pretoria's experimental farm, served to provide quantitative data. Dung was collected approximately one week before field sampling days and kept frozen up to one day before use, when it was defrosted. Secondly, fresh naturally-voided pats from treated and untreated animals were marked and sampled in the trial paddocks to confirm that the artificial pats provided a representative sample of the resident dung insect community and to evaluate any direct effects of ivermectin on the dung fauna.

One day before treatment of cattle 10 artificial standardized pats were placed out and labelled at 50 pace intervals in a line transect across each paddock shortly after dawn. After 24 hours, the pats and 50 mm of underlying soil were dug up and placed individually in Berlese-type extractors.

The cattle in the treatment paddocks were then treated with a single standard injection of ivermectin ($200\mu gkg^{-1}$) according to the manufacturer's recommendations. Those in the

other paddocks served as controls and remained untreated. Sampling of pats was carried out at monthly intervals for three months. For this, 10 artificial control pats of the type described above were placed out in a transect. In addition, 10 fresh, naturally-voided pats were selected randomly and labelled in each paddock. All pats were collected after 24 hours and placed in extractors in a greenhouse. Insects were extracted, identified to species level, where possible, and enumerated. Carabidae, Hydrophilidae and Scarabaeoidea were identified with the assistance of Dr S. Endrödy-Younga (Transvaal Museum, Pretoria) and Staphylinidae with help from Dr M. Uhlig (Zoologisches Museum der Humboldt-Universität, Berlin). Samples remained in the extractors long enough to allow for larval and pupal development. The term 'Diptera species' refers to the number of extracted pupae. Voucher specimens were deposited in the Transvaal Museum, Pretoria, South Africa.

DATA ANALYSIS

A combination of several community measures (univariate, graphical and multivariate) were used to assess the impact of ivermectin on dung insect communities.

Overall diversity was compared using species richness (S) and the Shannon index (H'; based on the natural logarithm) (Magurran, 1988). Although the interpretation of diversity indices has many limitations, they are still of importance for environmental impact studies (Forbes & Forbes, 1994). The Shannon index was selected because it is widely used and significant differences between two samples can be assessed by calculating a *t*-value using the method developed especially for this index by Hutcheson (1970) (Magurran, 1988). The evenness of species abundance, which measures the degree to which the species are equally represented in a community, was determined using Pielou's J' evenness (J'= H'/ln S; Pielou, 1975).

Graphical presentations of species frequency distributions to elucidate dominance patterns within communities were plotted in the form of k-dominance curves. These curves are cumulative ranked abundances plots, where the cumulative ranked abundance of each species is plotted against the species rank or logarithmic species rank, in order from most abundant to least abundant species (Lambshead *et al.*, 1983; Magurran, 1988). The

advantage of presenting distributional properties of a community in form of a rank abundance plot is that information on patterns of relative species abundances can be extracted without reducing that information into a single summary statistic, such as a diversity index.

Multivariate methods are more sensitive to subtle changes in species composition and/or abundance than univariate measures, among other reasons because the latter can have very similar results although communities may differ in their taxonomic composition (Warwick & Clarke, 1991; Warwick, 1993).

Large sets of species abundance data frequently include a high number of zero counts (45-86% in the present study) and have highly-skewed abundance matrices. Therefore, they rarely meet assumptions underlying standard multivariate methods such as principal components analysis (PCA) (Beals, 1973; Clarke, 1993). Another widely used method for the analysis of species abundance data is detrended correspondence analysis (DCA; Hill & Gauch, 1980), a form of correspondence analysis (CA). This method has recently been employed by McCracken & Foster (1993) to assess the impact of ivermectin on colonization of pats by dung insects. However, methods like PCA and CA are relatively inflexible, particularly with regard to the abovementioned large number of zero counts often present in species abundance matrices (e.g. Field *et al.*, 1982). The greatest flexibility concerning the assumptions made about data is offered by non-metric multidimensional scaling (MDS; Kruskal & Wish, 1978), since it uses the rank order of dissimilarities or similarities between samples (Clarke, 1993). This ordination technique attempts to construct a configuration, in a specified number of dimensions, so that the rank order of the distances between samples in the configuration agrees exactly with the rank order of the matching (dis)similarities. A measure of how well the two sets of ranks agree is Kruskal's stress formula 1 (Kruskal & Wish, 1978). For example, a stress value smaller than 0.05 for a two-dimensional ordination corresponds to an excellent configuration with no prospect of a misleading interpretation. A stress value smaller than 0.1 implies a good ordination with no real prospect of misinterpretation, whereas two-dimensional ordinations with a stress value greater than 0.2 should be interpreted with caution (Clarke, 1993).

Ordination techniques are generally based on a measure of dissimilarity of species composition calculated between every pair of samples. An advantage of MDS is that,

unlike, for example, DCA and PCA, it permits a choice in the definition of (dis)similarities between samples so that the most appropriate (dis)similarity measure for the respective data can be used. In other words, the dissimilarity measure is not dictated by the mechanics of the ordination method but by relevant ecological assumptions (Clarke, 1993).

MDS has recently been recommended for the multivariate analysis of ecological data (e.g. Kenkel & Orloci, 1986; Clarke, 1993). Examples where non-parametric MDS has been employed in ecological studies include Samways (1990), Gray *et al.* (1990), Warwick *et al.* (1991) and Clarke (1993 and references therein).

The MDS analysis was carried out on the mean abundances of species in the treatment and control communities using the Bray-Curtis coefficient (Bray & Curtis, 1957; Faith *et al.*, 1987),

$$\delta_{jk}=100 \sum_{i=1}^{p} |y_{ij}-y_{ik}| / \sum_{i=1}^{p} (y_{ij}+y_{ik})$$

where y_i is the abundance of species i in the jth or kth sample and p is the number of species. The index ranges from zero, where two samples are totally similar, to 100, where two samples are totally dissimilar, i.e. have no species in common.

The Bray-Curtis index has been claimed to be the most suitable index for comparison of community structure based on species abundance data (e.g. Clarke, 1993). The index enables the choice of transformation (e.g., $y^{0.5}$, $y^{0.25}$, log(1+y)) of the abundance data, which determines the relative weight given to rare and common species in defining sample similarity. Another property of the index is that it is invariant to the number of species that are jointly absent from both samples (Clarke, 1993), unlike for example the Euclidean distance.Thus, samples are not more similar because species are absent from both.

Having considered the results of the previous analyses, it is now necessary to identify the species responsible for any observed patterns. Species causing differences or dissimilarities between communities in the treatment and control paddocks were identified using the 'similarity percentages' procedure (SIMPER) as described by Clarke (1993). This procedure partitions the mean Bray-Curtis dissimilarity between all possible cross-regime pat pair combinations for each sampling day into contributions of each species and ranks them in

order of their importance. The contribution of each species ($\delta_{jk}(i)$) to the dissimilarity between sample j and k is determined as follows:

$$\delta_{jk}=\sum_{i=1}^{p}\delta_{jk}(i)$$

where

$$\delta_{jk}(i)=100|y_{ij}-y_{ik}|/\sum_{i=1}^{p}(y_{ij}+y_{ik}).$$

$\delta_{jk}(i)$ averaged over all pat pair combinations gives the mean contribution $\overline{\delta}_i$ from the ith species. A measure of how consistently a species contributes to the mean dissimilarity is the mean-to-standard deviation ratio. A large mean-to-standard deviation ratio (i.e.$\overline{\delta}_i/SD\delta_i \geq 1.4$[1]) indicates that a species contributes consistently to the mean dissimilarity between two communities and thus is a good 'discriminating species'.

In a similar way species that are typical or characteristic of a community can be determined using the Bray-Curtis similarity S ($S_{jk}=100-\delta_{jk}$) (Clarke, 1993). The mean contribution of a species ($\overline{S}_i$) to the similarity within a community is defined as the mean over all pairs of pats (j,k) of the ith term $S_{jk}(i)$:

$$S_{jk}=\sum_{i=1}^{p}S_{jk}(i)$$

where

$$S_{jk}(i)=200\min(y_{ij},y_{ik})/\sum_{i=1}^{p}(y_{ij}+y_{ik}).$$

[1]The value 1.4 is a subjective distinction. It has been chosen based on the fact that a mean-to-standard deviation greater than about the square root of 2 is indicative of a real effect, under normal distribution assumptions. However, the data are neither normal nor independent.

The respective data for the two treatment and control paddocks were pooled for the analyses with the exception of the k-dominance plots. The dominance pattern for each paddock was plotted separately to determine if the treatments and control paddocks showed the same patterns.

For the multivariate analyses the original species abundance data were fourth-root transformed ($Y^{0.25}$) to achieve a balance of contributions from rare and common species (Clarke, 1993). The species abundance data from natural pats, which varied in size, were standardized to relative abundance before fourth-root transformation.

The programmes to compute the Bray-Curtis coefficient and to perform the 'similarity percentage' analyses were written in SAS®[2] (SAS Institute Inc.). Non-parametric multidimensional scaling (MDS) was performed by the SAS procedure MDS (SAS Institute Inc., 1992). Tests for significant differences between two samples for the Shannon diversity index were carried out on a spreadsheet. For the remaining analyses the PRIMER (Plymouth Routines In Multivariate Ecological Research) (Clarke, 1993) programmes DIVERSE and DOMPLOT were used.

Results

42 422 specimens representing 88 species were processed. These include 48 Scarabaeinae and 14 Aphodiinae (Scarabaeidae), 11 Staphylinidae, 5 Histeridae, 2 Hydrophilidae, 1 Carabidae and 7 Diptera (Cyclorrhapha) species.

[2] The programmes are available on request from the Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

CLIMATE

The rainfall before and during the rainy season in 1992/93 was low except for November and December 1992 (Fig. 6).

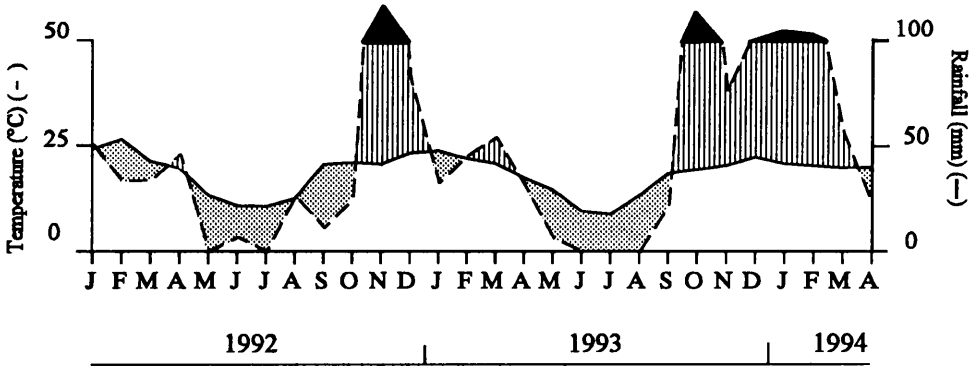

Fig. 6. Climate diagram (after Walter & Lieth, 1964) depicting the mean monthly temperature (Potchefstroom) and precipitation (Parys) for the period of January 1992 to March 1994. The dotted areas denote the arid periods (precipitation < evaporation) and the vertical lines denote the humid periods (precipitation > evaporation). Solid black areas denote the months receiving in excess of 100mm on a reduced scale (1:10).

OVERALL DIVERSITY

The values for the overall diversity are shown in Table 16.

The rainfall the in the year preceding the trial was below average in the rainy season (October 1991 to March 1992; Appendix 5). In the summer rainfall region of South Africa, dung beetle activity usually reaches its peak in December and January when rainfall is high (Davis, 1990). As a result of the low rainfall, species richness was lower than expected for the pre-treatment communities (December 1992). A comparison of the designated treatment with the designated control paddocks shows that species richness and H' were lower in the former. The difference between the two types of paddocks with respect to H' were significant (H': $t_{\infty}=2.16$, $P<0.05$). However, J' showed few differences between both types of camps.

Table 16. Overall insect diversity in artificial and naturally-voided pats in treatment (I) (P3 & P4) and control (C) (P1 & P2) paddocks (n=20). Season 1992/1993.

Time after treatment (months)	Regime	Number of individuals (N)	Species richness (S)	Shannon's diversity (H')	Evenness (J')
Artificial pats					
0	I	743	32	2.52	0.73
	C	1008	39	2.64	0.72
1	I	1546	42	2.24	0.60
	C	1997	51	3.05	0.78
2	I	2239	54	2.81	0.70
	C	3763	61	2.56	0.62
3	I	1782	47	2.41	0.63
	C	4644	65	2.75	0.66
Naturally-voided pats					
1	I	4274	45	1.46	0.38
	C	3522	60	2.17	0.53
2	I	4490	58	2.41	0.59
	C	3803	59	2.86	0.70
3	I	4885	55	2.43	0.61
	C	3726	69	2.94	0.69

Rainfall was comparatively high during November and December, and the number of species increased in both treatment and control paddocks one month after treatment (January). Again, species richness was lower in the treatment paddocks than in the controls. The differences in species diversity observed before treatment increased; H' was highly significantly lower ($P<0.001$) in treatment paddocks compared with the controls in both naturally-voided ($t_{\infty}=18.27$) and artificial pats ($t_{\infty}=18.58$). This difference could be a characteristic of the paddocks themselves and not due to the ivermectin treatment of cattle. However, whereas H' in the control communities increased, it decreased in the treatment communities in the artificial standardized pats. Comparably, species evenness, which was similar in both types of communities before treatment, increased in the control paddocks but dropped in the treatment paddocks relative to both the contemporary control and the pre-treatment communities.

No clear pattern was evident two months after treatment because natural and artificial pats showed different trends for H', J' and species richness.

Three months after treatment, H' was highly significantly lower ($P<0.001$) in treatment paddocks relative to the controls in both naturally-voided ($t_{\infty}=17.51$) and artificial pats ($t_{\infty}=8.77$); species richness and J' were also reduced. Shannon's diversity and J' in artificial pats were also lower within the treatment paddocks compared with two months after treatment.

RANK ABUNDANCE PLOTS

Figures 7 and 8 represent the k-dominance plots for artificial and natural pats. The most elevated curve corresponds to the least diverse community if the curves do not overlap. If the curves do cross they are strictly speaking not comparable, because different diversity indices give opposing results (Lambshead *et al.* 1983).

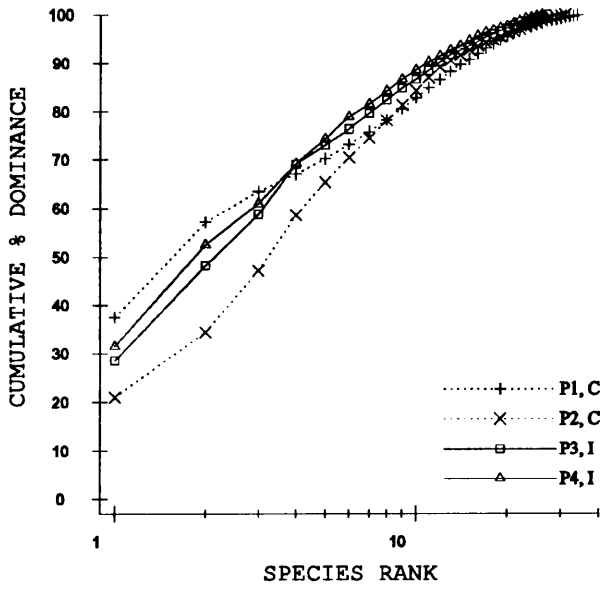

Fig. 7. k-dominance curve for dung insect abundance in artificial standardized pats in the treatment (I) paddocks P3 and P4 and control (C) paddocks P1 and P2 before injecting cattle with ivermectin ($200\mu gkg^{-1}$).

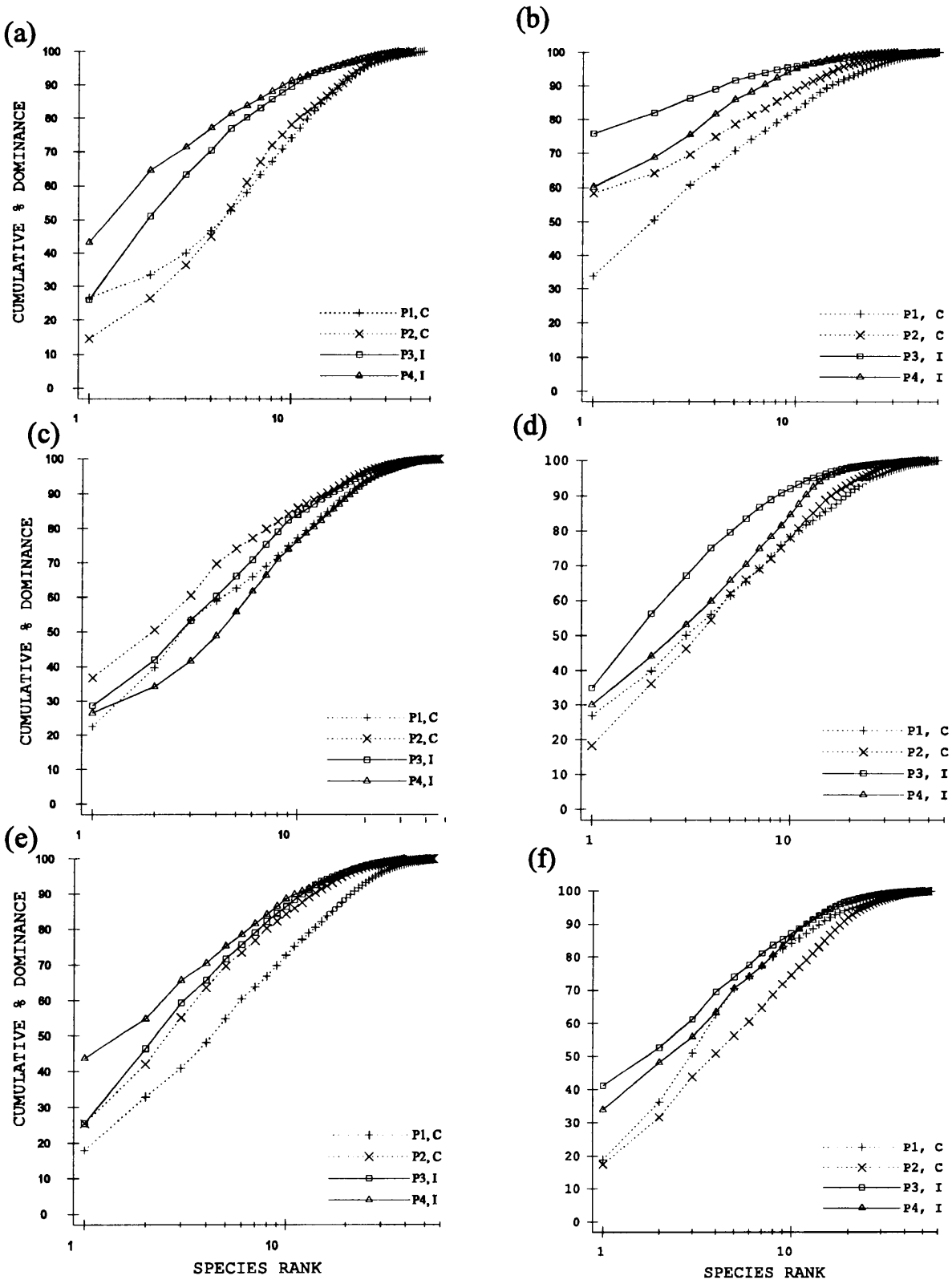

Fig. 8. k-dominance curves for dung insect abundance in artificial and naturally-voided pats in treatment (I, solid lines) and control (C, broken lines) paddocks. a,c,e: artificial pats; b,d,f: naturally-voided pats. a,b: one month after treatment, c,d: two months after treatment, e,f: three months after treatment.

The interpretation of the pre-treatment curves (Fig. 7) is hampered by the crossing-over of curves. The curves for P3 and P4 (I) cross over that of P1 (C) and are therefore not comparable. Paddock 2 (C), whose curve does not overlap with those of the other paddocks, has the relatively least elevated curve and represents the most diverse community.

One and three months after treatment the curves for the treatment paddocks lie clearly above the controls of both artificial and naturally-voided pats. This indicates higher dominance and therefore a lower diversity in the treatment paddocks (Fig. 8a, b, e, f). Two months after treatment the curves for natural pats show that the treatment paddocks were less diverse than the controls, whereas those for artificial pats indicate that the two types of camps had similar diversity (Fig. 8c,d).

MULTIDIMENSIONAL SCALING ORDINATIONS

The non-metric MDS configuration for mean species abundance data of a community for all sampling dates in artificial pats is presented in Fig. 9. The overall MDS configuration for naturally-voided pats is shown in Fig. 10. The pre-treatment samples for artificial pats (standardized to relative abundances) have been included in the MDS analysis for natural pats to facilitate comparison of communities before and after treatment, because no pre-treatment sampling was carried out for natural pats.

Of importance in the plots is the relative position of the points. Each point represents a community at a given time. If two communities are very similar the points will be close together; conversely, if the communities have, for example, only a few species in common, the points will be widely separated.

Artificial pats. Both the treatment and control communities changed gradually with time. The treatment communities were rather different from the controls before treatment. The dissimilarity between the two types of communities increased slightly one month after treatment. Two months after ivermectin therapy the treatment communities were more similar to the controls than before treatment and one and three months after treatment. The treatment and control communities were most dissimilar three months after treatment.

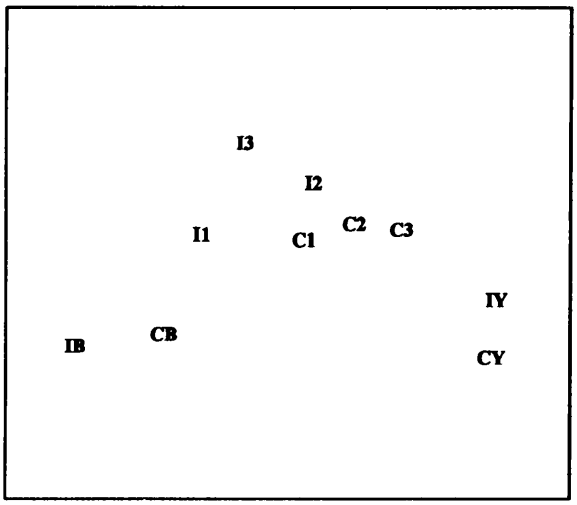

Fig. 9. Two-dimensional non-metric scaling ordination of fourth-root transformed mean species abundance data in artificial standardized pats. Each point presents the communities in the treatment (I) and control paddocks (C) at a given time. B: before treatment; 1, 2, 3: one, two and three months after treatment; Y: one year after treatment (stress = 0.04)[3,4].

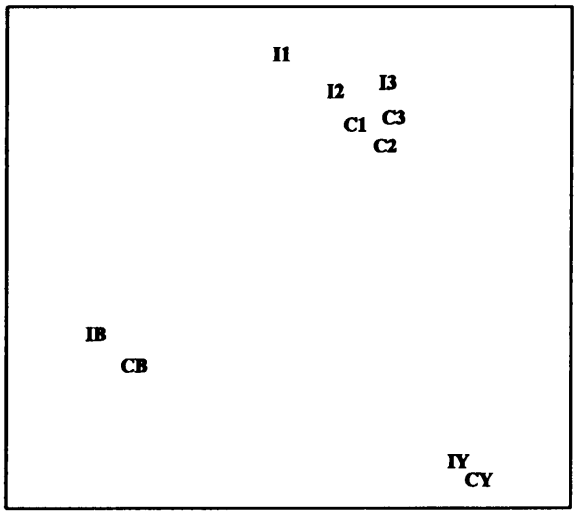

Fig. 10. Two-dimensional non-metric multidimensional scaling ordination of fourth-root transformed mean relative species abundance data in naturally-voided pats. Each point presents the communities in the treatment (I) and control (C) at a given time. B: before treatment; 1, 2, 3: one, two and three months after treatment; Y: one year after treatment (stress = 0.03)[3].

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[3]Samples collected one year after treatment have been included in the analysis because the sample size for a two-dimensional MDS should be greater than eight, as the interpretation of the stress value depends on the number of samples (Kruskal & Wish, 1978). The results for these samples are discussed in Chapter 3.3.

[4]No values for the axes of the MDS plot are given, because such plots can be arbitrarily scaled, located, rotated or inverted as they show the relative position of samples to each other (Clarke, 1993).

These observations are in accordance with the results of overall diversity and k-dominance plots.

Naturally-voided pats. The overall MDS configuration for communities in naturally-voided pats shows that the treatment communities were relatively different from their controls one month after treatment. This difference was more pronounced in naturally-voided pats than artificial ones. In contrast to artificial pats, the two types of communities became gradually more similar two and three months after treatment.

SPECIES ANALYSIS

The artificial standardized pats are superior to naturally-voided ones for quantitative observations. Although naturally-voided pats may reflect pat colonization more realistically, this type of pat varied considerably in size (ca. 0.8-5kg), and these differences exerted a strong influence on the colonization of pats. The following analysis concentrated, therefore, on artificial pats.

Unless stated otherwise, species typical of a community and good discriminating species were found to belong to the Scarabaeidae (Coleoptera).

The previous analyses have shown that some differences existed between the two types of paddocks before treatment. To assess whether the differences observed one and three months after treatment were due to ivermectin treatment or a reflection of differences between the paddocks themselves, the typical species for the respective communities were identified, as well as those that were responsible for these differences. The term typical (characteristic) or discriminant species refers to those species that contribute to 70% of the within-group similarity and 50% of the between-group dissimilarity respectively.

Before treatment. Four species (12.5%) in the treatment (I) and six species (15.38%) in the control paddocks (C) were characteristic for the respective communities (i.e. treatment, control). Of these, two species (*Euoniticellus intermedius* (Reiche), $\overline{Y}_I = 4.95$, $\overline{Y}_C=15.00$; *Sisyphus* sp.1, $\overline{Y}_I=3.45$, $\overline{Y}_C=1.45$) were characteristic in both types of paddocks.

Species that were mainly responsible for differences between paddocks before treatment were predominant either in the treatment or the control paddocks. Only one species contributed relatively consistently to this dissimilarity (*Aphodius pseudolividus* Balthasar) (Table 17a).

One month after treatment (artificial pats). The communities changed with time and 10 species were characteristic of the control community compared with six in the previous month. In contrast, only half the number of species (i.e. five) was characteristic of the treatment paddocks, compared with four of the pre-treatment community. The number of typical species in the control communities increased to 19.61%, but decreased to 11.90% in the treatment communities. These results are indicative of a higher species dominance pattern between the two types of communities, as also observed in the k-dominance plot (Fig. 8c, d).

Six discriminant species, which contributed relatively consistently to the differences between the two types of communities were identified: *Colobopterus maculicollis* Reiche (Aphodiinae), *Onthophagus gazella* Fabricius, *Onthophagus* sp.12, *Sphaeridium* sp.1 (Hydrophilidae) with a lower abundance and Diptera spp. 3 and 6 with a higher abundance in the treatment paddocks compared with the controls (Table 17b). This is in contrast to the pre-treatment communities, for which only one species was consistently discriminant.

One month after treatment (naturally-voided pats). A comparison of treatment versus control paddocks for naturally-voided pats showed that only *O. gazella*, which was less abundant in the treatment paddock ($\overline{Y}_I$= 1.00, $\overline{Y}_C$=6.30), contributed relatively consistently to the intra-group differences. One beetle species that contributed to the dissimilarity between communities (*C. maculicollis*), was absent in the treatment paddocks in naturally-voided pats. Two fly species (Diptera spp.3 and 6) that had a high abundance in artificial (untreated) pats appear to have dominated the communities in the treatment paddocks (Table 17). However, these had low abundance in naturally-voided (treated) pats in the same paddock (Diptera sp.3: $\overline{Y}_I$=0.65, $\overline{Y}_C$=0.01; Diptera sp.6: $\overline{Y}_I$=0.05, $\overline{Y}_C$=0.40).

Two months after treatment (artificial and naturally-voided pats). In accordance with the lack of differences between communities two months after treatment, nine (16.67%) and ten (16.39%) species were characteristic in artificial pats in treatment and control paddocks respectively, indicating a similar dominance profile. With regard to artificial pats, four species contributed relatively consistently to the between-group differences. All four species were less (*Onthophagus* spp.2, 10 and 12, *Caccobius* sp.2) abundant in the treatment paddocks (Table 18a). However, if naturally-voided pats are considered, no species contributed very consistently to differences between the treatment and control communities.

Three months after treatment (artificial pats). In accordance with the previous analyses differences between the treatment and control community were also obvious in the species analysis.

Eleven species (16.92%) were characteristic of the control community, compared with six species (12.79%) in the treatment community in artificial pats. This suggests an increase in dominance compared with the contemporary control community and also in comparison with the treatment community of the previous month.

Six species made a consistent contribution to the intra-group dissimilarity and had a lower abundance in treatment paddocks compared with the controls (*Onthophagus* spp.2, 10 and 12, *Caccobius* sp.1, *Aphodius amoenus* Boheman, *Sisyphus* sp.1) (Table 18b).

With regard to naturally-voided pats, only one species, *A. moestus* Fabricius, which was more abundant in treatment paddocks than in the controls ($\overline{Y}_I$ = 92.05, $\overline{Y}_C$ =9.10), contributed consistently to between-group dissimilarity.

The most abundant scarabaeine species during the trial was *E. intermedius* with a total of 4198 specimens collected. This species was typical in all communities (treatment, control) at all sampling dates, its rank being between the first and fifth position for both artificial and naturally-voided pats. This species did not contribute towards the differences between the treatment and control communities with regard to artificial pats, nor did it make a consistent contribution with regard to naturally-voided pats.

Table 17. Mean abundance ($\bar{Y}$) of dung insects in treatment paddocks (I) and control paddocks (C) in artificial pats in 1992/93. Species are listed in decreasing order of importance in their contributions ($\bar{\delta}_i$) to the mean dissimilarity ($\bar{\delta}$) between treatment and control paddocks, with a cut-off of the cumulative per cent contribution ($\Sigma\bar{\delta}_i\%$) at 50%.

a. Mean dissimilarity between treatment and control for artificial pats before treatment, $\bar{\delta}$=56.86

Species	$\bar{Y}_I$	$\bar{Y}_C$	$\bar{\delta}_i$	$\bar{\delta}_i/SD(\delta_i)$	$\Sigma\bar{\delta}_i\%$
Aphodius pseudolividus	0.70	4.40	3.67	1.51	6.46
Scarabaeoid larvae	5.05	5.60	3.49	1.07	12.60
Aphodius moestus	8.25	3.80	3.10	1.15	18.05
Euoniticellus africanus	0.30	1.50	2.85	1.39	23.07
Onthophagus sp.12	4.90	2.30	2.78	1.18	27.95
Aphodius dorsalis	0.25	3.40	2.77	1.10	32.83
Liatongus militaris	1.50	0.70	2.62	1.32	37.43
Aphodius amoenus	1.50	1.20	2.39	1.11	41.52
Onthophagus sp.10	0.35	1.65	2.31	1.05	45.58
Chironitis scabrosus	1.10	1.80	2.15	1.03	49.36

b. Mean dissimilarity between treatment and control for artificial pats one month after treatement, $\bar{\delta}$=58.88

Species	$\bar{Y}_I$	$\bar{Y}_C$	$\bar{\delta}_i$	$\bar{\delta}_i/SD(\delta_i)$	$\Sigma\bar{\delta}_i\%$
Diptera sp.6	26.45	2.75	3.93	1.56	6.67
Diptera sp.3	18.00	4.55	3.34	1.60	12.35
Colobopterus maculicollis	0.05	4.25	2.64	1.56	16.84
Onthophagus sp.12	1.40	8.60	2.56	1.46	21.19
Onthophagus gazella	0.80	3.55	2.47	1.69	25.39
Aphodius moestus	7.45	7.55	2.41	1.26	29.49
Sphaeridium sp.1	0.60	3.95	2.25	1.41	33.30
Onthophagus sp.10	0.30	3.15	2.21	1.37	37.06
Sisyphus sp.1	3.70	3.45	2.09	1.26	40.61
Aphodius pseudolividus	2.10	7.60	2.08	1.25	44.13
Euoniticellus africanus	0.40	2.50	1.99	1.28	47.51

Table 18. Mean abundance ($\bar{Y}$) of dung insects in treatment paddocks (I) and control paddocks (C) in artificial pats in 1992/93. Species are listed in decreasing order of importance in their contributions ($\bar{\delta}_i$) to the mean dissimilarity ($\bar{\delta}$) between treatment and control paddocks, with a cut-off of the cumulative per cent contribution ($\Sigma\bar{\delta}_i$%) at 50%.

a. Mean dissimilarity between treatment and control for artificial pats two months after treatment, $\bar{\delta}$=52.94

Species	$\bar{Y}_I$	$\bar{Y}_C$	$\bar{\delta}i$	$\bar{\delta}i/SD(\delta i)$	$\Sigma\bar{\delta}i$%
Onthophagus sp.2	1.00	28.05	2.63	1.59	4.98
Onthophagus sp.12	6.65	60.50	2.56	1.67	9.8
Onthophagus sp.10	1.30	16.95	1.96	1.58	13.51
Aphodius moestus	10.15	1.55	1.93	1.36	17.16
Caccobius sp.2	0.30	2.95	1.73	1.56	20.43
Sphaeridium sp.1	5.90	2.75	1.69	1.23	23.63
Onthophagus sp.13	0.10	3.70	1.62	1.32	26.68
Aphodius pseudolividus	7.90	3.25	1.61	1.15	29.72
Aphodius russatus	6.55	6.90	1.53	1.08	32.61
Sisyphus sp.1	3.95	4.20	1.52	1.20	35.48
Diptera sp.3	7.05	0.10	1.50	0.88	38.31
Caccobius sp.1	1.40	6.10	1.49	1.26	41.12
Colobopterus maculicollis	1.45	2.70	1.39	1.10	43.75
Onthophagus gazella	3.25	1.80	1.37	1.21	46.34
Aphodius sp.1	1.65	1.50	1.35	1.21	48.88

b. Mean dissimilarity between treatment and control for artificial pats three months after treatment, $\bar{\delta}$=56.19

SPECIES	$\bar{Y}_I$	$\bar{Y}_C$	$\bar{\delta}i$	$\bar{\delta}i/SD(\delta i)$	$\Sigma\bar{\delta}i$%
Aphodius moestus	30.65	7.40	2.67	1.28	4.75
Onthophagus sp.12	4.36	53.80	2.61	1.51	9.40
Onthophagus sp.10	1.45	25.40	2.51	1.51	13.86
Onthophagus sp.2	0.25	4.00	2.11	1.77	17.62
Caccobius sp.1	1.90	16.90	2.07	1.43	21.30
Aphodius amoenus	0.25	2.30	1.91	1.50	24.71
Sisyphus sp.1	0.20	4.40	1.81	1.45	27.93
Aphodius sp.1	0.35	11.25	1.81	1.13	31.15
Aphodius impurus	2.50	4.90	1.59	1.21	33.99
Aphodius pseudolividus	10.60	39.30	1.56	1.26	36.76
Philonthus sp.	0.55	2.10	1.54	1.25	39.50
Aphodius russatus	1.35	3.55	1.51	1.24	42.18
Caccobius viridicollis	0.15	2.30	1.49	1.25	44.84
Sphaeridium sp.1	3.95	4.55	1.44	1.16	47.40
Colobopterus maculicollis	4.05	10.30	1.39	1.18	49.87

Discussion

When interpreting the above results, it is important to bear in mind that disparities between different types of camps after treatment may be due to pre-treatment differences and thus simply reflect characteristics of the respective paddocks. Furthermore, even if the communities of the various paddocks had been similar prior to treatment, it would not be possible to attribute any differences subsequently observed to ivermectin without separating the intrinsic characteristics of the paddocks from the effect of the agent's residues. To this end, the results of the various analyses are compared below.

Before ivermectin therapy, the areas to serve as treatment paddocks supported a smaller number of species and Shannon's diversity was lower than in the controls. Intuitively, one would expect that with improved weather conditions species diversity and evenness should increase, as observed in the control communities, even if to a lesser extent after treatment. Contrary to this expectation, species diversity, evenness and the number of typical species (as defined above) dropped and species dominance increased in the treatment communities in both artificial and natural pats. This suggests that the changes one month after treatment within the treatment community and the differences to the control community are most likely due to the treatment of cattle with ivermectin.

Few differences between communities in treatment and control paddocks were obvious two months after treatment as artificial and naturally-voided pats showed contradicting results. As was mentioned by Scholtz & Krüger (1995), several factors could be responsible for the apparent recovery. One possibility is that recovery was caused by immigration of insects from areas surrounding the treatment paddocks. This assumption is weakened, however, by a renewed drop in diversity and evenness and an increase in dominance of some species in the treatment paddocks relative to the controls three months after ivermectin therapy. Hence, the recovery after two months is more likely due to emergence of beetles from the pre-treatment period and to recovery from sublethal effects. For example, Houlding *et al.* (1991) found that although a single subcutaneous injection of abamectin initially reduced egg production and oviposition rate in *Onthophagus binodis* Thunberg females, this effect was not permanent. The above theory would also explain the differences between treatment and control paddocks three months after ivermectin

treatment: the depressive effect in the treatment paddocks could be a reflection of the conditions one month after treatment, diminished by the emergence of insects from the pre-treatment period and possibly also from immigration of insects from neighbouring paddocks.

Three months after treatment, differences between the two types of communities were again observed in both artificial standardized and naturally-voided pats. These differences are of a similar nature to those found one month after treatment but were less pronounced. Species richness, Shannon's diversity and evenness were lower in the treatment communities than in the controls, as was the percentage of typical species.

The present study offered an opportunity to compare the results from single-species laboratory tests with those of a field investigation. Three common beetle species which occur in the trial area (*Euoniticellus intermedius*, *Onitis alexis* and *Onthophagus gazella*) have been involved in laboratory tests (e.g. Roncalli, 1989; Fincher, 1992; Holter *et al.*, 1993; Sommer *et al.*, 1993a; Chapter 2.2). In this study, *O. alexis*, a crepuscular species which buries dung at considerable depths beneath pats (ca. 37 cm), was probably undersampled due to our sampling technique. Therefore, no trends for populations of this species could be observed.

Single-species studies on the effect of ivermectin on *O. gazella* have shown that injectable ivermectin inhibited larval development for up to 21 days after treatment (Roncalli, 1989). Sommer *et al.* (1993a) recorded significant reductions in mandibular and clypeal widths of surviving third-instar larvae of this species that had developed in dung excreted 16 days after treatment. *O. gazella* did not contribute to differences between the pre-treatment communities. However, it was less common in treatment paddocks than in the control areas and made a high and consistent contribution to differences between the treatment and control communities one month after treatment.

Laboratory studies have shown that ivermectin is lethal to *E. intermedius* larvae for at least 14 days after treatment, reduces adult emergence for at least 21 days and prolongs larval development for 28 days after treatment (Fincher, 1992; Chapter 2.2). Holter *et al.* (1993) observed in a trial in Zimbabwe that *E. intermedius* preferred dung from cattle injected with ivermectin over control dung two and eight days after treatment when ivermectin concentrations in dung were high. However, during the present field study, *E.*

intermedius, which was the most abundant scarabaeine species, contributed little to the dissimilarity between treatment and control paddocks, suggesting that the influence of ivermectin on their populations in the field was not marked. Since no attempt was made to monitor the immigration of insects from surrounding paddocks, it is not possible to clarify whether ivermectin had little effect on the population of this species or whether immigration of *E. intermedius* specimens from adjoining areas was responsible.

Fincher (1992) studied the effect of injectable ivermectin on the progeny of two species of *Philonthus* (Staphylinidae) in the laboratory. He showed that these predators were significantly affected only one week after ivermectin treatment of cattle with a standard injection ($200\mu gkg^{-1}$). In agreement with Fincher's findings staphylinid predators, although abundant as adults and larvae during the trial, contributed very little to overall dissimilarities between treatment and control paddocks.

Finally, from the results of the present study it seems most likely that ivermectin affected the dung insect community by decreasing species diversity and evenness.

The normal commercial use of ivermectin is in the control and treatment of parasitism in livestock. The focus for (anthelminthic) prophylaxis is the young animal, which for epidemiological reason is the class of stock most likely to benefit from such treatment. In the present study, the treatment regimen was a departure from that most commonly adopted in South Africa in that ivermectin was administered to the adult cattle, rather than to weaners or selected animals (Forbes, 1993). The purpose of this was to expose the entire insect fauna within the treatment paddocks synchronously to faecal residues. It is likely that when used more typically in young animals, any effects resulting from ivermectin therapy would be less pronounced.

As it is believed that an organism already stressed by its environment is more likely to be affected by exposure to a pollutant (Moriarty, 1983) it seems plausible that the ecotoxicological effects of ivermectin during periods of drought are likely to be more severe than under more favourable weather conditions. Southern Africa is regularly affected by drought (see Tyson, 1990, 1993) and the effects reported above therefore do not represent a special case.

3.3 Changes in the structure of dung insect communities after ivermectin usage under favourable weather conditions in a grassland ecosystem

Introduction

The previous chapter (Chapter 3.2) was concerned with the impact of ivermectin on dung insect communities under drought conditions. The present chapter reports on the effect of ivermectin during a season with relatively high rainfall.

Materials and methods

The trial was carried out in the Free State Province on the same farms used in the previous study (see Chapter 3.2).

Temperature and rainfall data for the nearest weather stations (Potchefstroom and Parys) were obtained from the South African Weather Bureau (Fig. 6, Chapter 3.2).

As in 1992/93, field work was conducted during the austral summer, coinciding with peak beetle activity period, and extended over three months (December to March) in 1993/94.

At the beginning of the season (i.e. 12 months after the first treatment; Chapter 3.2), 10 artificial standardized pats (1 kg) of the type described previously were collected in each paddock (i) to assess any remaining effects of the ivermectin treatment of the previous year and (ii) to serve as pre-treatment samples. Artificial pats were placed in a transect across each paddock as in the preceding year and dung pats were collected before treatment and seven days and one, two and three months after treatment. In addition to the 10 artificial pats, 10 naturally-voided pats were randomly marked in each paddock after treatment as in the previous study. Colonization of naturally-voided pats varied considerably during the first study (Chapter 3.2), primarily because of the great differences in size (ca. 0.8-5kg). In the present study care was taken to collect pats in a more restricted size range (ca. 1-3kg) to enable a more meaningful interpretation of the data for the naturally-voided pats.

It was further decided to change the experimental design for the present study slightly

as it became obvious that replication would not be possible due to the different rainfall pattern. The present trial differed in that one paddock again served as control (P2) and another hosted the treatment animals (P4), while the regime was switched in the remaining two paddocks (P1: treatment, P3: control) (Fig. 11). Consequently, each treatment paddock adjoined a control paddock.

Weather conditions were very unfavourable for beetle activity two months after treatment. Continuous rainfall negatively affected colonization as most pats were permanently waterlogged. Results for this period will therefore not be discussed.

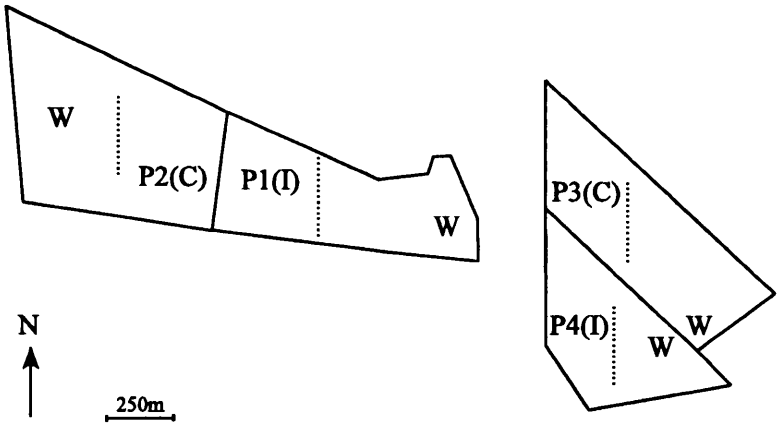

Fig. 11. Position of the treatment (I) and control (C) paddocks. Surrounding areas were also occupied by cattle. Treatment of entire herds was with a single subcutaneous injection of ivermectin ($200\mu gkg^{-1}$) in paddocks P1 and P4. Herds in paddocks P2 and P3 were untreated (controls). The solid lines denote the fences and the dotted lines depict the transects with the artificial standardized pats in the respective camps. 'W' denotes the watering points.

Insects were extracted from pats and identified as described in Chapter 3.2. Only endocoprid scarabaeoid larvae (i.e., those that develop within dung pats) were collected; these belonged mainly to the genus *Aphodius* Illiger. The term 'Diptera species' refers to the number of pupae extracted from pats.

Voucher specimens were deposited in the Transvaal Museum, Pretoria, South Africa.

DATA ANALYSIS

A combination of various community measures (univariate, graphical and multivariate) was

used. The univariate measures included species richness (S), Shannon's diversity index (H') and Pielou's evenness (J') (Pielou, 1975, Magurran, 1988). k-dominance plots were used for the graphical presentation of species dominance patterns (Lambshead *et al.*, 1983; Magurran, 1988). The multivariate analyses were done using non-metric multidimensional scaling (MDS; Kruskal & Wish, 1978) and similarity percentage analysis (SIMPER) as detailed by Clarke (1993). The methods are described in Chapter 3.2. The MDS was carried out on the mean abundances of species in the respective paddocks at each sampling date. The SIMPER analysis to determine the discriminant species (see Chapter 3.2) was done by comparing the species abundances for all possible cross-regime pat-pair combinations for each time after treatment. In other words, the species abundances in each pat in the treatment community were compared with the species abundances in each other pat in the control community. To identify the typical species of a community all possible pat-pair combinations within a paddock were compared for a given time.

For the multivariate analyses, species counts were fourth-root transformed ($y^{0.25}$) to achieve a balance in the contribution from rare and common species (Clarke, 1993). Species abundance data for naturally-voided pats were standardized to relative abundances before transformation to account for differences in the sizes of pats. Thus the artificial standardized pats give a reflection of absolute species abundances, whereas the naturally-voided pats are indicative of changes in the relative species composition.

Results

47 611 specimens representing 98 species were processed. These include 56 Scarabaeinae, 14 Aphodiinae and 1 Dynastinae (Scarabaeidae), 12 Staphylinidae, 5 Histeridae, 2 Hydrophilidae, 1 Carabidae and 7 Diptera (Cyclorrhapha) species.

Although it is not obvious from the total number of specimens collected, more specimens were sampled in 1993/94 (artificial pats: 23 633, n=160 (excluding two months after treatment)) than in 1992/93 (artificial pats: 17 722, n=160) (Chapter 3.2) as a result of the higher rainfall in 1993/94. That the total number of specimens collected is not considerably greater than in the previous year is a reflection of the restriction in size range

of naturally-voided pats (see above).

OVERALL DIVERSITY

Artificial pats. Prior to treatment, the values for species richness, H' and J' were fairly similar in P1, P2 (control in 1992/93) and P3 (treatment in 1992/93) (Table 19). Paddock 4 (treatment in 1992/93) had lower values for species richness, H' and J' compared with the remaining three paddocks. The comparison between P2 and P3 showed no significant differences (t_{∞}=1.41, p>0.05) for H', whereas H' for all other camp combinations was highly significantly different (P1,P2: t_{∞}=5.02; P1,P4: t_{∞}=10.77; P2,P4:t_{∞}=17.46; P3,P4:t_{∞}=13.69; p<0.001) with one exception (P1,P3: t_{∞}=3.01, p<0.01).

There is no evidence for an effect that could be attributed to the ivermectin treatment of cattle for the P1/P2 paddock combination in artificial pats. During the posttreatment period, P1 (I) was overall more diverse than P2 (C) (7 days after treatment: t_{∞}.=6.93, 1 month after treatment: t_{∞}.=7.60, p<0.001; 3 months after treatment: t_{∞}.=2.87, p<0.01). A comparison of changes within P1 (I) shows that although species richness dropped steadily from seven days to three months after ivermectin therapy, H' (2.96 to 3.22) and J' (0.77 to 0.79) remained relatively high throughout. The pattern in the control (P2) was similar with regard to species richness; H' and J' varied.

A comparison of P4 (I) with P3 (C) shows that species richness, H' and J' remained lower in P4 (I) compared with P3 (C), except for one month after treatment when H' and J' were higher. A within-camp comparison of species richness, H' and J' for P4 (I) and P3 (C), respectively, reveals no obvious pattern that could be linked to ivermectin treatment.

Naturally-voided pats. In contrast to artificial pats, H' was lower in P1 (I) than in P2 (C) in naturally-voided pats seven days and one and three months after treatment. The most obvious difference was found three months after treatment, when H' and J' dropped considerably in P1 (I) relative to all other camps (P2, P3 (C) and P4 (I); t_{∞}=10.72 to 15.12; p<0.001). No clear pattern emerges from changes within camps P1(I) and P2 (C).

Paddocks P3 (C) and P4 (I) were very similar with regard to H' (t_{∞} =1.96, p=0.05) seven days after treatment. Once more a within-camp comparison of P3 (I) and P4 (C) reveals no indication of a treatment effect.

Table 19. Overall insect diversity in artificial and naturally-voided pats in experimental (I) and control paddocks (C) (n=10).

Time after treatment	Paddock and Regime	Number of individuals (N)	Species richness (S)	Shannon's diversity (H')	Evenness (J')
Artificial pats					
0	P1, I	1951	49	2.37	0.61
	P2, C	3507	48	2.55	0.66
	P3, C	1790	49	2.50	0.64
	P4, I	1923	42	1.89	0.51
7 days	P1, I	2073	64	3.22	0.78
	P2, C	3211	60	3.01	0.74
	P3, C	2535	56	2.85	0.71
	P4, I	2644	59	2.70	0.66
1 month	P1, I	1014	47	2.96	0.77
	P2, C	2092	54	2.62	0.66
	P3, C	1490	58	2.88	0.71
	P4, I	689	46	3.13	0.82
2 months	P1, I	238	33	2.69	0.77
	P2, C	602	35	2.74	0.77
	P3, C	145	25	2.68	0.83
	P4, I	62	20	2.56	0.86
3 months	P1, I	826	41	2.92	0.79
	P2, C	811	42	2.75	0.74
	P3, C	423	40	2.59	0.70
	P4, I	452	36	2.27	0.63
Naturally-voided pats					
7 days	P1, I	908	45	2.59	0.68
	P2, C	1603	55	3.17	0.79
	P3, C	3338	54	2.33	0.58
	P4, I	1487	46	2.41	0.63
1 month	P1, I	1007	49	3.03	0.78
	P2, C	1694	58	3.16	0.78
	P3, C	3149	48	2.70	0.70
	P4, I	1440	54	2.81	0.71
2 months	P1, I	1055	29	1.40	0.42
	P2, C	412	33	2.60	0.74
	P3, C	132	23	2.46	0.79
	P4, I	242	23	2.37	0.76
3 months	P1, I	1263	39	1.45	0.40
	P2, C	570	38	2.31	0.64
	P3, C	479	29	2.51	0.75
	P4, I	354	37	2.69	0.75

P1 = Paddock 1, P2 = Paddock 2, P3 = Paddock 3, P4 = Paddock 4.

RANK ABUNDANCE PLOTS

The most elevated curve corresponds to the least diverse community if the curves do not overlap. If the curves do intersect they are strictly speaking not comparable (Lambshead *et al.*, 1983).

In the pre-treatment plot, the curve for P4 (treatment in 1992/93) is the most elevated, indicating a lower diversity compared with the other three paddocks. The curves for P1, P2 and P3 overlap for artificial pats before treatment and could therefore not be interpreted.

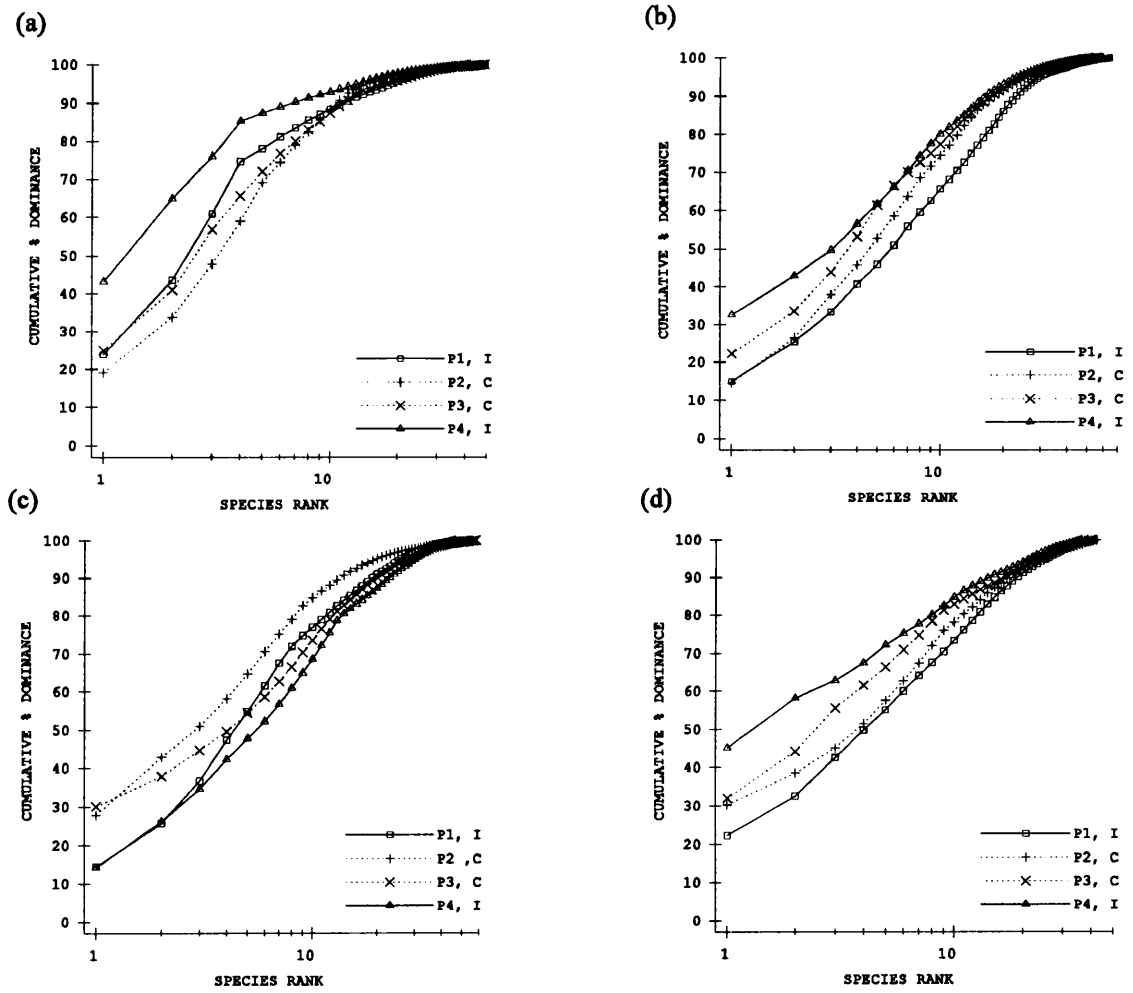

Fig. 12. k-dominance curves for dung insect abundance in artificial standardized pats in treatment (I) paddocks P1 and P4 and control (C) paddocks P2 and P3; (a) before treatment, (b) 7 days, (c) 1 month and (d) 3 months after treatment.

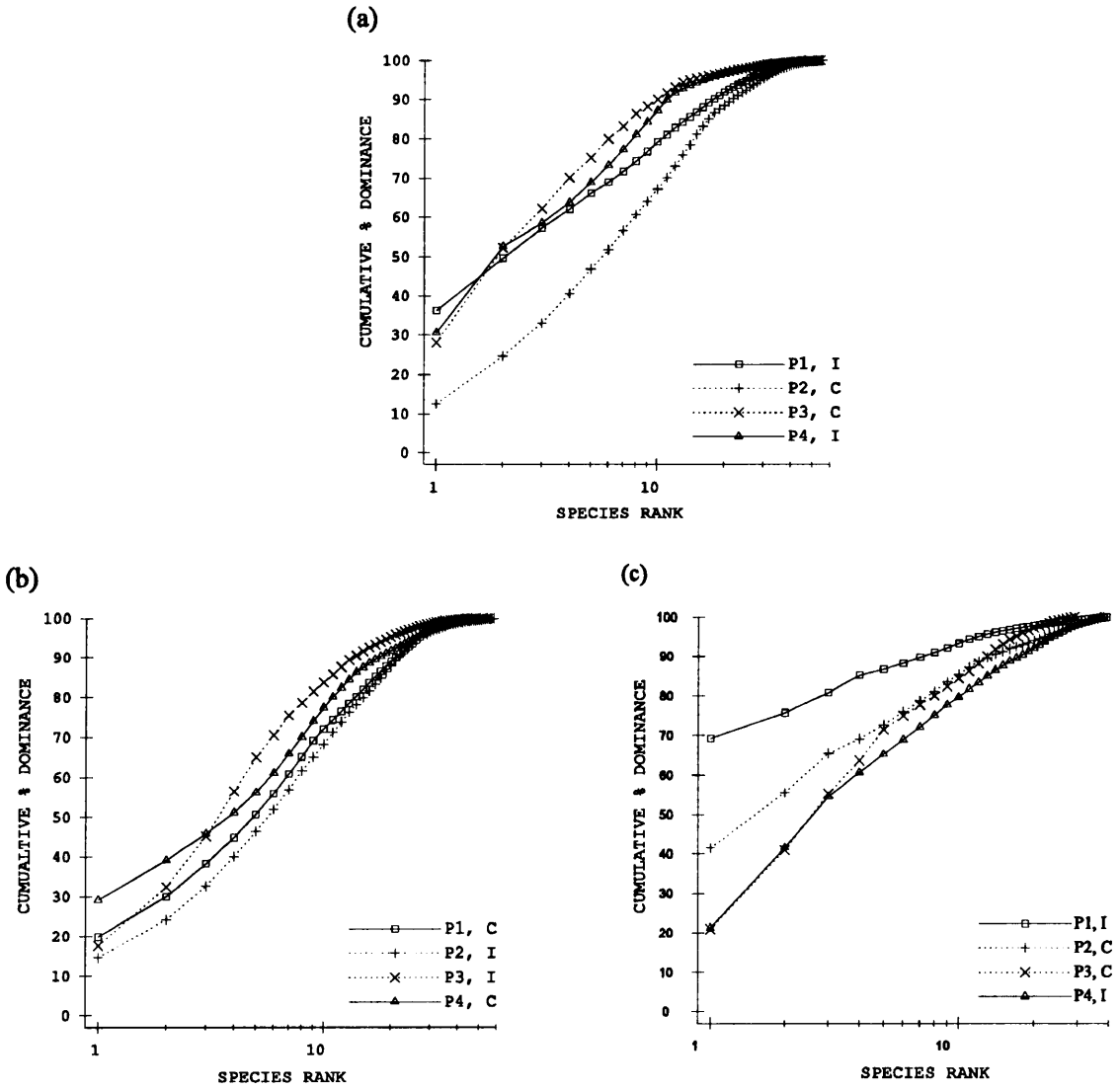

Fig. 13. k-dominance curves for dung insect abundance in naturally-voided pats in treatment (I) paddocks P1 and P4 and control (C) paddocks P2 and P3; (a) 7 days, (b) 1 month and (c) 3 months after treatment.

No patterns were evident for artificial pats in posttreatment periods (Fig. 12). However, some trends were apparent in naturally-voided pats. Paddock P2 (C) had the least elevated curve seven days after treatment, while the curves for the other three paddocks overlap. This indicates that P2 (C) supported the most diverse community compared with P1 (I), P3 (C) and P4 (I) (Fig. 13a). One month after treatment the curves for P1 (I), P2 (C) and P4

(I) were very similar, suggesting a similar dominance profile. The curve for P3 (C) crosses over those of P1 (I) and P4 (I); it is slightly more elevated than that of P2 (C) (Fig. 13b). Three months after treatment, the curve for the first treatment paddock (P1) lies clearly above those of the remaining three paddocks suggesting a low species diversity and high species dominance. This is in keeping with the drop in H' and J'. The shape of the curve of P2 (C) is similar to that of P1 (I). Both exhibit a similar change in dominance pattern, although this change is less pronounced in the control community. The remaining three curves intersect and no further conclusions could therefore be drawn (Fig. 13c).

MULTIDIMENSIONAL SCALING ORDINATIONS

The non-metric MDS configuration for mean species abundance data for all sampling dates in artificial pats is presented in Fig. 14. The overall MDS configuration for naturally-voided pats is shown in Fig. 15. The pre-treatment samples for artificial pats (standardized to relative abundances) have been included in the MDS analysis for natural pats to facilitate comparison of communities before and after treatment, because no pre-treatment sampling was carried out for natural pats. As pointed out in the Materials and Methods section, the artificial standardized pats provide an absolute measure of species abundances, whereas naturally-voided pats are a reflection of relative species abundances.

Artificial pats. The pre-treatment communities were fairly similar, especially in P1 (control in 1992/93) and P3 (treatment in 1992/93). This supports the finding of previous analyses that there were no remaining effects from the treatment of the preceding year. The communities of P1, P4 (I) and P3 (C) were plotted closely together seven days and one month after treatment, respectively, whereas those of P2 (C) for these periods were relatively distant. This difference was particularly evident one month after treatment, when H' and J' were lower in P2 (C) than in the other three camps at the same time. The communities two months after treatment differed from all others due to the high rainfall during this period. No differences are obvious between controls and treatment camps three months after treatment. The results are in accordance with the overall species diversity and the k-dominance plots in that no effect attributable to ivermectin was observed.

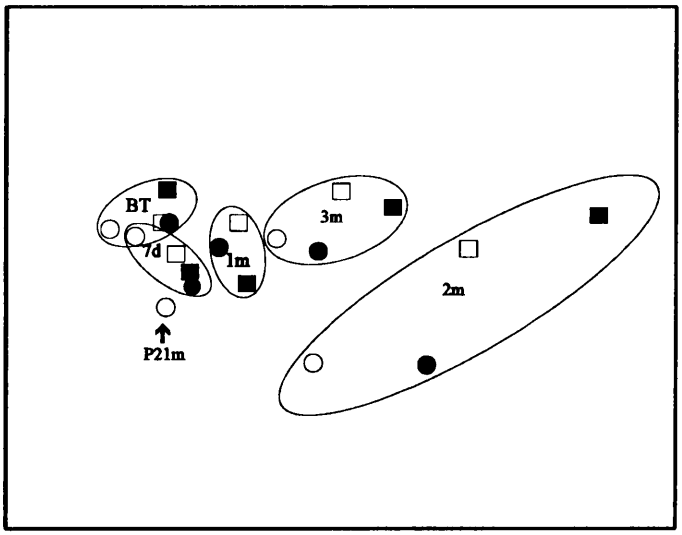

Fig. 14. Two-dimensional non-metric scaling ordination of fourth-root transformed mean species abundance data in artificial standardized pats. Each point presents a community at a given time. Paddocks P1 (filled circle) and P4 (filled square): ivermectin treatment, paddocks P2 (open circle) and P3 (open square): control. BT: before treatment, 7d: seven days after treatment, 1m, 2m and 3m: one, two and three months after treatment (stress: 0.10).

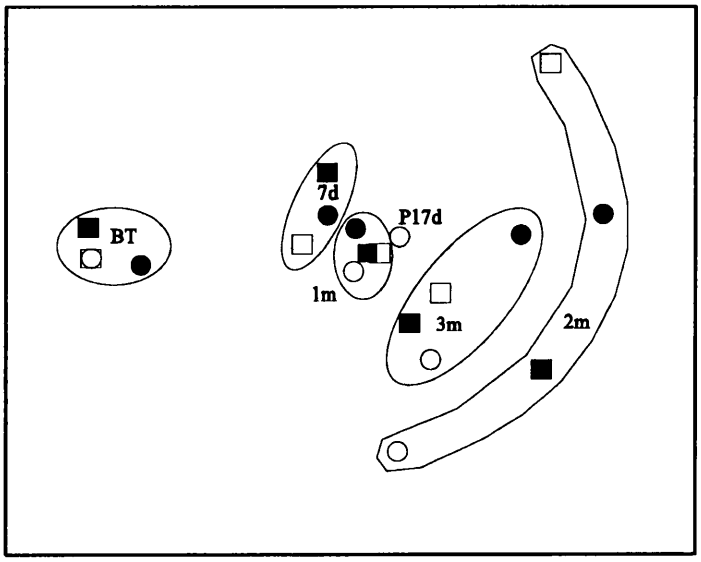

Fig. 15. Two-dimensional non-metric scaling ordination of fourth-root transformed mean species abundance data (standardized to relative abundances) in naturally-voided pats. Each point represents a community at a given time. Paddocks P1 (filled circle) and P4 (filled square): ivermectin treatment; paddocks P2 (open circle) and P3 (open square): control. BT: before treatment; 7d: seven days after treatment; 1m, 2m and 3m: one, two and three months after treatment (stress: 0.11).

Naturally-voided pats. Clear differences are evident between P1 (I) and P2 (C) seven days after treatment. The communities in these paddocks had become more similar one month after treatment. Three months after treatment the community of P1 (I) was distinct from that of P2 (C), which confirms the results of previous analyses.

The MDS configuration for species abundances in all naturally-voided pats collected seven days after treatment is shown in Fig. 16. Pat samples for treatment paddock P4 are tightly clustered with those of control paddock P3. Furthermore, samples from both treatment paddock P1 and control paddock P2 differ clearly from paddocks P3 (C) and P4 (I), as well as from each other. These findings are in accordance with the results of the preceding analyses and are indicative of small differences in species abundances between P3 and P4.

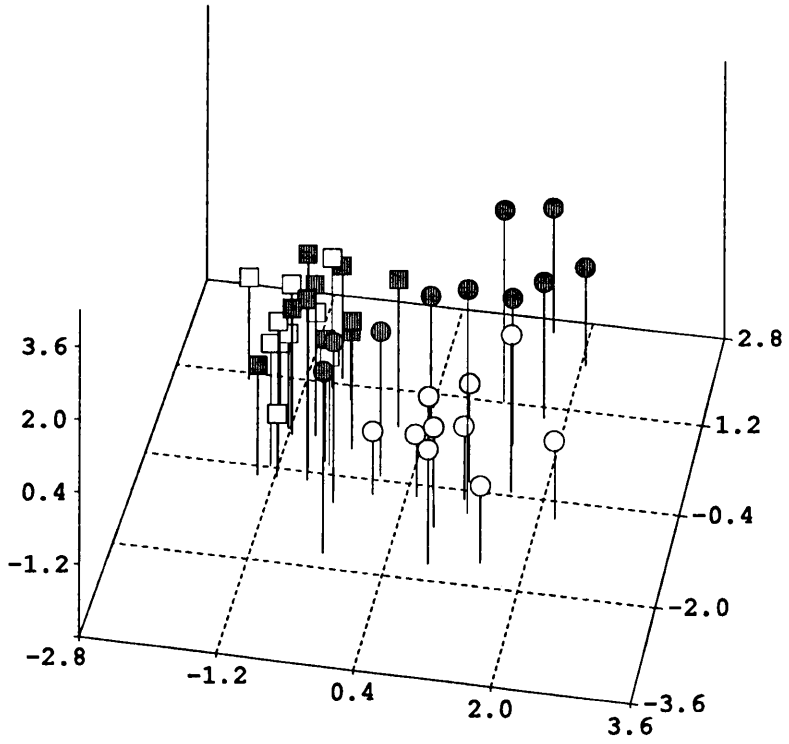

Fig. 16. Three-dimensional non-metric scaling ordination of fourth-root transformed species abundance data (standardized to relative abundances) in naturally-voided pats seven days after treatment. Each point is derived from the species counts in a single pat. Paddock P1 (shaded circle) and P4 (shaded square): ivermectin; paddock P2 (open circle) and P3 (open square): control (stress = 0.14).

SPECIES ANALYSIS

Unless stated otherwise, species contributing to dissimilarity between communities (i.e. discriminant species) and species typical for communities belonged to the Scarabaeidae (Coleoptera). The term typical (characteristic) species refers to those species that contribute to 70% of the within-group Bray-Curtis similarity. Discriminant species are those species that contribute to 50% of the dissimilarity between treatment and control communities. Species are good discriminant species if they make a high and consistent contribution (i.e. high mean-to-standard deviation ratio ($\bar{\delta}_i/SD\delta_i \geq 1.4$)) (see Chapter 3.2).

A pairwise comparison of paddocks indicated that the P3 (C) and P4 (I) ($\bar{\delta}$=42.48) were more similar to each other with regard to naturally-voided pats than all other paddock-pair combinations ($\bar{\delta}$=54.83 to 58.48) seven days after treatment. The Bray-Curtis coefficient, Shannon's diversity, k-dominance plots and the MDS configuration indicate that little difference existed between P4 (I) and P3 (C) at the time. Any non-lethal effect ivermectin might have had in P4 (I) would have been obliterated by insects from the adjacent control paddock (P3). The other treatment paddock (P1) can therefore be compared meaningfully for the posttreatment period only with control paddock P2. Because the two communities were rather similar with regard to artificial pats, the results for the species analysis concentrate on naturally-voided pats for the posttreatment period. Both P1 and P2 served as control paddocks in 1992/93.

Typical and discriminant species in artificial pats before treatment. Before treatment, one year after the first trial, five (P4, treatment in 1992/93), six (P1, control in 1992/93), seven (P3, treatment in 1992/93) and nine (P2, control 1992/93) species were characteristic of the communities in the four paddocks.

The four most typical species (*Colobopterus maculicollis* Reiche, *Euoniticellus intermedius* (Reiche), *Liatongus militaris* (Castelnau) and *Sisyphus* sp.1) were the same in all four paddocks, although their ranking was not necessarily identical. This, together with the previous analysis, suggests that no treatment effect remained from 1992/93.

Table 20. Mean abundance ($\overline{Y}$) of dung insects in experimental paddock P1 (I) and control paddock P2 (C) before and after treatment of cattle with ivermectin in 1993/94. Relative species abundances in naturally-voided pats are given in brackets. Species are listed in decreasing order of importance in their contributions ($\overline{\delta}_i$) to the mean dissimilarity ($\overline{\delta}$) between treatment paddock P1 and control paddock P2, with a cut-off of the cumulative per cent contribution ($\sum\overline{\delta}_i\%$) at 50%.

a. Mean dissimilarity for artificial pats before treatment, $\overline{\delta}$=41.28

Species	$\overline{Y}_I$	$\overline{Y}_C$	$\overline{\delta}_i$	$\overline{\delta}_i/SD(\delta_i)$	$\Sigma\overline{\delta}_i\%$
Drepanocerus patrizii	2.1	35.4	2.45	1.63	5.93
Caccobius sp.1	0.9	12.1	1.87	1.66	10.45
Onthophagus sp.12	6.5	16.3	1.70	1.26	14.55
Onthophagus sp.13	0.0	2.3	1.57	1.91	18.37
Caccobius viridicollis	1.9	10.3	1.46	1.45	21.91
Onthophagus sp.10	4.0	18.8	1.38	1.48	25.24
Euoniticellus africanus	0.8	3.6	1.33	1.40	28.45
Drepanocerus fastiditus	0.7	7.9	1.33	1.29	31.66
Philonthus sp.5	0.6	2.0	1.24	1.35	34.66
Proagoderus lanister	3.0	0.5	1.22	1.20	37.62
Aphodius pseudolividus	2.1	1.1	1.18	1.25	40.49
Onthophagus sp.7	1.1	1.5	1.09	1.20	43.14
Sisyphus sp.1	26.8	49.4	1.02	0.81	45.62
Phalops wittei	2.6	2.5	1.02	1.02	48.08

b. Mean dissimilarity for naturally-voided pats seven days after treatment, $\overline{\delta}$=55.64

Species	$\overline{Y}_I$ (Relative abundances (%))	$\overline{Y}_C$ (Relative abundances (%))	$\overline{\delta}_i$	$\overline{\delta}_i/SD(\delta_i)$	$\Sigma\overline{\delta}_i\%$
Diptera sp.2	0.0 (0.00)	10.2 (6.36)	2.26	2.17	4.07
Scarabaeoid pupae	0.5 (0.55)	13.5 (8.42)	2.06	1.46	7.78
Diptera sp.1	0.0 (0.00)	20.1 (12.54)	2.05	1.14	11.47
Hydrophilidae larvae	0.1 (0.11)	4.2 (2.62)	1.99	3.07	15.05
Aphodius pseudolividus	32.9 (36.23)	6.5 (4.05)	6.90	1.53	18.58
Scarabaeoid larvae	12.2 (13.44)	12.0 (7.49)	1.88	1.57	21.95
Diptera sp.5	0.0 (0.00)	5.0 (3.12)	1.64	1.30	24.90
Euoniticellus intermedius	3.7 (4.07)	1.4 (0.87)	1.57	1.33	27.73
Onitis alexis	2.2 (2.42)	0.8 (0.50)	1.44	1.15	30.30
Aphodius sp.5	1.1 (1.21)	4.2 (2.62)	1.37	1.27	32.78
Onitis tortuosus	0.8 (0.88)	0.4 (0.25)	1.34	1.29	35.18
Colobopterus maculicollis	1.3 (1.43)	2.9 (1.81)	1.33	1.27	37.57
Aphodius impurus	2.6 (2.86)	4.8 (2.99)	1.30	1.27	39.90
Aphodius sp.1	6.9 (7.60)	19.4 (12.10)	1.24	1.04	42.13
Sisyphus sp.1	1.6 (1.76)	1.4 (0.87)	1.22	1.24	44.32
Aphodius dorsalis	0.5 (0.55)	2.6 (1.62)	1.21	1.19	46.50
Histeridae sp.3	05. (0.55)	0.6 (0.65)	1.21	1.24	48.67

Table 21. Mean abundance ($\overline{Y}$) of dung insects in treatment paddock P1 (I) and control paddock P2 (C) before and after treatment of cattle with ivermectin in 1993/94. Species are listed in decreasing order of importance in their contributions ($\overline{\delta}_i$) to the mean dissimilarity ($\overline{\delta}$) between treatment paddock P1 and control paddock P2, with a cut-off of the cumulative per cent contribution ($\sum\overline{\delta}_i\%$) at 50%.

a. Mean dissimilarity for naturally-voided pats one month after treatment, $\overline{\delta}$=48.54

Species	$\overline{Y}_I$ (Relative abundances (%))	$\overline{Y}_C$ (Relative abundances (%))	$\overline{\delta}_i$	$\overline{\delta}_i$/SD(δ_i)	$\Sigma\overline{\delta}_i\%$
Diptera sp.1	4.3 (4.27)	24.8 (14.64)	1.93	1.13	3.97
Diptera sp.5	1.4 (1.39)	12.5 (7.38)	1.67	1.47	7.42
Aphodius sp.1	0.2 (0.20)	5.9 (3.48)	1.63	1.55	10.77
Philonthus spp.	5.3 (5.26)	2.8 (1.65)	1.61	1.42	14.09
Scarabaeoid larvae	20.0 (19.86)	14.4 (8.50)	1.55	1.33	17.29
Onthophagus gazella	10.2 (10.13)	4.3 (2.54)	1.54	1.23	20.47
Sphaeridium sp.1	5.9 (5.86)	2.4 (1.42)	1.50	1.30	23.55
Onthophagus sp.2	0.5 (0.50)	4.9 (2.89)	1.48	1.46	26.59
Pseudoclavinia sp.1	2.1 (2.09)	0.5 (0.30)	1.38	1.34	29.43
Aphodius moestus	4.9 (4.87)	7.9 (4.66)	1.29	1.32	32.10
Aphodius impurus	2.9 (2.88)	16.1 (9.50)	1.29	1.20	34.75
Philonthus sp.5	1.8 (1.79)	0.1 (0.66)	1.28	1.19	37.39
Aphodius sp.5	0.7 (0.70)	3.0 (1.77)	1.26	1.53	39.99
Histeridae sp.3	1.7 (1.69)	0.5 (0.30)	1.16	1.22	42.38
Aphodius pseudolividus	0.8 (0.79)	4.5 (2.66)	1.14	1.03	44.74
Sisyphus sp.1	0.9 (4.07)	5.4 (1.77)	1.14	1.44	47.08
Aphodius russatus	0.9 (0.89)	5.4 (13.19)	1.14	1.16	49.42

a. Mean dissimilarity for naturally-voided pats three months after treatment, $\overline{\delta}$=63.79

Species	$\overline{Y}_I$ (Relative abundances (%))	$\overline{Y}_C$ (Relative abundances (%))	$\overline{\delta}_i$	$\overline{\delta}_i$/SD(δ_i)	$\Sigma\overline{\delta}_i\%$
Colobopterus maculicollis	1.9 (1.50)	8.1 (14.21)	4.07	1.69	6.37
Onthophagus sp.12	0.2 (0.16)	2.1 (3.68)	3.21	1.35	11.38
Diptera sp.1	87.4 (69.20)	23.6 (41.40)	2.82	0.91	15.79
Philonthus spp.	1.6 (1.27)	1.9 (3.33)	2.72	1.26	20.05
Aphodius sp.1	5.6 (4.43)	5.6 (9.82)	2.70	1.19	24.27
Philonthus sp.5	0.3 (0.24)	1.4 (2.46)	2.52	1.26	28.20
Sphaeridium sp.1	0.8 (0.63)	2.0 (3.51)	2.34	1.06	31.85
Onthophagus sp.1	0.3 (0.24)	0.55 (1.75)	2.28	1.16	35.42
Diptera sp.5	0.9 (0.71)	1.5 (2.63)	2.28	0.98	38.99
Carabidae larvae	1.9 (1.50)	0.3 (0.53)	2.09	1.03	42.27
Diptera sp.3	1.5 (1.19)	0.3 (0.53)	2.09	1.01	45.53
Aphodius impurus	1.5 (1.19)	0.4 (0.70)	2.02	1.16	48.69

Six species contributed relatively consistently to the differences between the communities in the designated treatment paddock P1 and the designated control paddock P2 (*Drepanocerus patrizii* Boucomont, *Caccobius* sp.1, *Onthophagus* sp.13, *Caccobius viridicollis* Fåhreus, *Onthophagus* sp.10, *Philonthus* sp.5 (Staphylinidae)). All six species were less abundant in the paddock designated for treatment than the control paddock (Table 20a).

Typical species in naturally-voided pats after treatment. The composition of typical species was similar for both treatment and control communities. With the exception of three months after treatment, dung beetles were the most characteristic species of the dung insect communities. Species that were not typical in both treatment and control were usually to a large extent responsible for the differences between the two types of communities. Typical species are, therefore, not discussed further.

Discriminant species in naturally-voided pats after treatment. Differences observed seven days after treatment were mainly due to a reduction in the number of insect larvae and pupae (Table 20b). Pupae of four fly species (one not listed in Table 20b) were extracted from pats collected in the control paddock (P2). In contrast, none were found in pats sampled in the treatment paddock (P1). Scarabaeoid pupae and hydrophilid larvae had a lower abundance in P1 (I) than in P2 (C). The mean abundance of scarabaeoid larvae was similar in both types of paddocks. The low number of pupae in the treatment paddocks suggests that the majority of larvae were unable to reach the pupal stage. All four discriminant scarabaeine species were more abundant in the treatment than the control paddock. Conversely, five out of six aphodiine species which contributed to the dissimilarity between the treatment and control community were less abundant in the former.

One month after treatment, six taxa contributed consistently to the dissimilarities between P1 (I) and P2 (C). Four taxa (Diptera sp.5, *Aphodius* sp.1, *Philonthus* spp. (Staphylinidae), *Onthophagus* sp.2 and *Aphodius* sp.5) had a lower abundance in the treatment paddock than in the control. *Sisyphus* sp.1, which had a higher abundance in P1 (I) seven days after treatment, was again more common in the treatment paddock. The only indication of a treatment effect was the lower abundance of Diptera spp. 1 and 5 in the

treatment communities (Table 21a).

Three months after treatment one species in particular *(C. maculicollis)* contributed to the dissimilarity between P1 (I) and P2 (C). This species contributed little to the differences between the two types of communities before and one month after treatment. It was a typical species of both treatment and control communities in artificial pats ($\overline{Y}_I$=46.5, $\overline{Y}_C$=51.3) and naturally-voided pats ($\overline{Y}_I$=8.3, $\overline{Y}_C$=10.8) one month after treatment. In contrast, *C. maculicollis* was considerably less abundant in P1 (I) than in P2 (C) in both artificial pats ($\overline{Y}_I$=4.4, $\overline{Y}_C$=24.5) and naturally-voided pats ($\overline{Y}_I$=1.9, $\overline{Y}_C$=8.1) three months after ivermectin therapy.

Two fly species, Diptera spp. 1 and 5, made a relatively high contribution to the dissimilarity between P1 (I) and P2 (C) three months after treatment. Both species were absent in the treatment communities seven days after ivermectin injection and their abundance was reduced one month after treatment compared with the control. Three months after ivermectin therapy, the abundance of Diptera sp.5 remained lower in P1 (I) than P2 (C). Conversely, Diptera sp.1, the most abundant species in both the treatment and control community, was considerably more common in P1 (I) than P2 (C) (Table 21b).

Discussion

Rainfall throughout the rainy season, including the trial period, was relatively high, which was reflected in species richness, species diversity and species evenness.

Overall, no effects that could be attributed to the treatment of cattle with ivermectin were observed in artificial pats. With regard to naturally-voided pats, negative effects were recorded seven days after treatment, when fewer hydrophilid larvae and scarab and dipteran pupae were extracted from pats containing ivermectin residues than from the controls. This effect was likely due to direct ivermectin toxicity as the concentration of the agent in faeces is high at this time (Sommer *et al.*, 1992). Ivermectin during this period is lethal to larvae of a number of dung breeding flies and beetles (Strong & Wall, 1987; Strong 1992). The reduction in the number of dipteran pupae and scarabaeoid larvae seven days after treatment compares with the findings of field studies by McCracken & Foster (1993), Barth *et al.*

(1994) and Strong & Wall (1994).

One month after treatment, there were little observable effects in the present study as opposed to 1992/93 (Chapter 3.2), although the reduced number of Diptera spp. 1 and 5 (Cyclorrhapha) in the treatment community may have some significance in this respect. Ivermectin has been shown to reduce emergence of some fly species up to 4 weeks after treatment in the laboratory (e.g. Chapter 2.1; Wall & Strong, 1987; Strong, 1992). Madsen *et al.* (1990) reported that ivermectin therapy (200μgkg^{-1}, single injection) clearly affected cyclorrhaphan larvae and pupae in cattle dung pats in the field up to 30 days after treatment in Denmark. The observed reductions of the Diptera spp. 1 and 5 one month after treatment could thus be due to a prolonged effect of ivermectin. In general, it seems probable that effects in the previous season (Chapter 3.2) were more pronounced due to higher stress levels to which dung insect populations were subjected.

No results are available for the period of two months after treatment due to waterlogging of pats caused by high rainfall.

Three months after treating cattle with ivermectin Shannon's diversity dropped and species dominance increased considerably in naturally-voided pats in the treatment paddock (P1) compared with its control (P2). The MDS analysis also revealed that the two types of communities were rather different. This phenomenon may or may not have been due to indirect effects of ivermectin (e.g. prolonged development period), similar to those observed in 1992/93 (Chapter 3.2).

The results of the species analysis showed that Diptera sp. 1 was very common in the treatment community three months after treatment. This to some extent explains the high species dominance and low Shannon's diversity. The high abundance of Diptera sp. 1 may also be indicative of disturbance because dung beetles are usually the dominant members of the dung insect fauna in the trial area. Diptera sp.1, however, was also common in the control community.

The findings of the species analysis with regard to other dung frequenting insects highlighted *C. maculicollis* (Aphodiinae) as a good discriminant species between the treatment and control communities three months after treatment. This species was a dominant member of both communities one month after treatment. Its abundance dropped considerably in the treatment paddock compared with the contemporaneous control three

months after ivermectin therapy. Similarly, *C. maculicollis* discriminated between treatment and control communities in the 1992/93 season one, two and three months after ivermectin injection (Chapter 3.2). It was absent from naturally-voided pats one month after treatment and occurred in reduced numbers in artificial pats at all times after ivermectin injection in the treatment community (Tables 17a, 18a,b; Chapter 3.2). The lower abundance of *C. maculicollis* in the present study could therefore be indicative of an impact of ivermectin. However, results of the species analysis for other dung beetle species are inconclusive. It is, therefore, not possible to establish whether the observed effects three months after treatment were caused by ivermectin or are due to another factor not apparent during the trial.

Unlike during 1992/93 (Chapter, 3.2), when depressive, possibly ivermectin-related effects were observed *throughout* the trial, no such continuous effects were noted in the present study. It is concluded that these effects were likely to be caused by drought-related stress on populations together with a larger spatial scale of treatment (160 ha, in adjacent paddocks 1992/93 vs. 80 ha, in separate paddocks 1993/94).

The importance of spatial scale in the analysis of species abundance has been demonstrated in several studies (e.g. Sotherton *et al.*, 1987; Jepson & Thacker, 1990; Duffield & Aebischer, 1994). These have shown that the impact of pesticides on invertebrate populations and its interpretation depends on the size of the treatment area. The effect of the spatial scale of treatment in the present study was not only evident when comparing the two seasons, but presumably also from reactions of communities during the second season, when the two control and the two treatment paddocks responded differently. Discrepancies in the effect of ivermectin in the two classes of paddocks with regard to naturally-voided pats can possibly be explained by the respective position of the watering points as cattle tend to concentrate around these. In the two adjacent paddocks P3 (control) and P4 (treatment), both watering points are situated in close proximity at their common border (Fig. 11). Dung insects therefore disperse between pats from treated and untreated cattle, so that any non-lethal effect ivermectin may have had under these conditions would have been moderated by immigrating insects from the control paddock and *vice versa*. In the other adjacent paddocks, P1 (treatment) and P2 (control), the watering points are widely separated. The dispersal rate of beetles is likely to be lower if

fresh dung is available in abundance as dung beetle movement between droppings has been shown to be density-dependent (Hanski, 1991); hence, sub-populations from one paddock may not readily mix with those of another.

The results of the present study together with those of Chapter 3.2 suggest that the environmental impact of ivermectin is likely to be determined by several factors. Firstly, the spatial scale of treatment may influence the duration and thus the severity of the effect. For example, the impact of ivermectin is likely to be less pronounced if untreated cattle are kept close to treated animals. Secondly, the effect of ivermectin also depends on climatic conditions, which probably determine the susceptibility of dung insect communities to the drug residues. Severe climatic conditions (e.g. drought) may act synergistically with ivermectin treatment and so affect communities more strongly than would be the case under favourable weather conditions.

4 Model

4.1 A qualitative frame-based model to assist farm management decisions

Introduction

Complex system models have been built by applied ecologists with a view to predicting the effects of different management actions on animals and plants in an ecosystem since the early 1970's (Scheffer & Beets, 1994). These models are based on numerical equations (e.g. difference of differential equations), and the output is a quantitative description of a system's behaviour. However, the construction of conventional system models is often hampered by many factors (e.g. Rykiel, 1989, Scheffer & Beets, 1994). One problem is that ecological systems are usually very complex and a great number of variables have to be considered, which makes the construction of such a model difficult and time consuming. Another obstacle, and one that is faced by many ecologists, is the problem of obtaining sufficient quantitative data to construct and support the model. A reason for this lies in the difficulty of performing controlled, replicated large field experiments. The development of a system model for the dynamics of dung insect communities is no exception, because dung insects, which inhabit a patchily distributed and temporal resource, are subject to frequent changes in a suite of environmental conditions (see Chapter 1).

Although the quantitative knowledge about abiotic and biotic interactions in a system may be limited, its dynamics are often understood in a qualitative sense. Based on this qualitative knowledge, and in order to cope with the lack of quantitative data, the concept of rule-based modelling was first used by Starfield & Bleloch (1986) for the construction of qualitative dynamic models. In qualitative models numerical equations are substituted by logical expressions in the form of IF ⟨premise⟩ THEN ⟨conclusion⟩ statements or rules. For example, dung beetle activity is primarily connected with rainfall in the Afrotropical region. Although it may not be possible to quantify the relationship between rainfall and dung beetle activity exactly, it is known that IF rainfall throughout the rainy season is low,

THEN the abundance of dung beetles will also be low.

This qualitative approach has recently been shown to be very useful in exploring interactions between abiotic and biotic components in a system. Starfield *et al.* (1989) have described how a rule-based model can be used in the management of an estuarine lake, where changes in the salinity affect biotic components of the system. A further example, on the effects of fire on the vegetation in a national park in northern Australia, is provided by Davis *et al.* (1989).

In order to simplify the development of parsimonious system models Starfield *et al.* (1993) proposed the concept of frame-based modelling as an additional modelling tool. In accordance with the knowledge of a system, a frame-based model can be either quantitative or qualitative.

In a frame-based model each frame presents a distinct state of a system, for example different successional stages of a community or different states such as a disturbed and undisturbed community. Such models are characterized by the construction of a separate model or set of simple models for each frame. In contrast to a conventional system model, models from different frames do not interact. Rules determine whether the assumptions underlying the model(s) in a frame are fulfilled or if conditions in a frame have changed, and a transition from one frame to another, hence from one model to another, should take place.

An advantage of the frame-based system model is that the intellectual control over the model is more easily maintained than in a complex system model. In addition, a frame-based model can be modified more easily than a traditional model and changes are less time consuming.

Both the rule- and frame-based modelling paradigms are based on concepts of artificial intelligence (AI), especially expert system technology (Starfield *et al.*, 1993). Expert systems (ES) are computer programmes which imitate the reasoning process that an expert would follow in solving a specific problem. Many commercially available ES are rule-based systems where both the knowledge and the problem solving procedures are stored primarily in the form of rules. In AI and ES applications, frames can be described as data structures that include all the pertinent knowledge about a particular object (Turban, 1992). The use of AI techniques in ecological modelling has been judged by Rykiel (1989) as promising in the investigation of ecological processes and problems.

Based on results of the field studies at Parys (Chapter 3.2, 3.3), the potential of a qualitative frame-based model is assessed, with the objective to assist farm management decisions with regard to treatment of cattle.

Model description

The field trials conducted at Parys (Chapter 3.2, 3.3) indicated that under subtropical conditions the effect of ivermectin on the dung insect fauna is determined by several factors. Some of these factors, such as length of the dry season and the amount of rainfall received during the wet season, influence dung insect communities in general. Others include the spatial scale of treatment, the proportion of animals treated in a herd and, if surrounding cattle are treated or untreated.

In the African grassland biome, dung insect dynamics are greatly influenced by climatic conditions. Rainfall in particular has a major influence on the distribution and abundance of dung beetles (Cambefort, 1991). The grassland biome is concentrated mainly on the high central plateau, notably of the Free State Province, in inland areas of the seabord of Natal and in some mountain areas of the south-eastern Cape Province (Rutherford & Westfall, 1986). The biome lies within the summer rainfall area, where the rainy season coincides with the summer, and the dry season with the winter months. The winter dry season, hereafter referred to as dry season, in a 'normal' year begins in mid-April and ends in mid-October. Accordingly, the wet season begins in October and extends to April. Rainfall is highest from December to January, when temperatures are also high. The length of the dry season in a year is variable, as is the amount of rainfall.

Because dung beetles constitute the most important part of the dung fauna in the Afrotropical region (see Chapter 1) the emphasis in the model is on their dynamics. Most dung beetle species emerge after the onset of rainfall in the wet season and are active throughout this season until late autumn (Doube, 1991). Peak beetle activity coincides with the period of highest rainfall and temperature, rainfall being the more important factor (Davis, 1990). Only a few beetle species are active during the winter months. The breeding success of dung beetles and the survival of immature stages has been shown to be reduced

during times of drought (e.g. *Onthophagus granulatus* Boheman (Tyndale-Biscoe *et al.*, 1981)). Therefore, a long dry season in winter is expected to result in higher larval and pupal mortality than would occur in a dry season of normal or short duration.

The state of a system can be arrayed on a single continuum (Westoby *et al.*, 1989) from a disturbed community condition, with low species diversity (i.e. species richness) and high species dominance, to an undisturbed community condition, where species diversity and evenness are high (Fig. 17). The term condition is a technical expression for the community position on the continuum (Westoby *et al.*, 1989). As dung insect activity is dependent on rainfall, the condition of a community improves with abundant rains. Low rainfall or drought, as well as the treatment of cattle, has a negative influence on the community condition (Doube, 1987, Chapter 3.2).

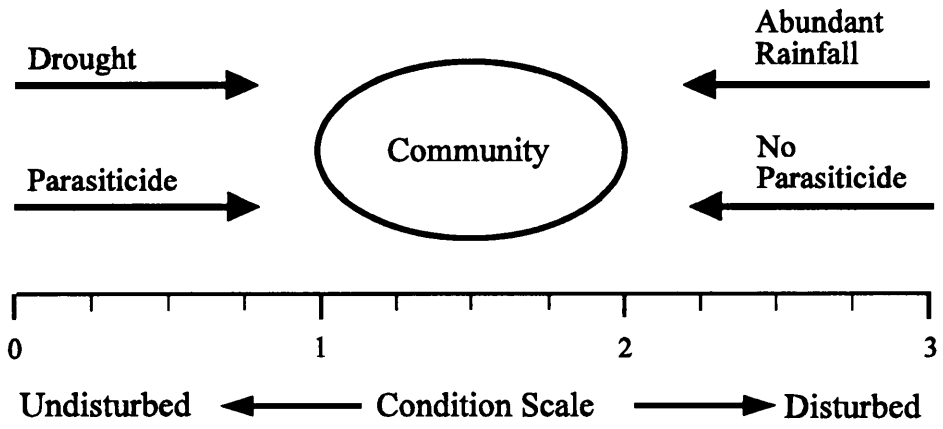

Fig. 17. Community continuum and diagram of the major abiotic effects on dung insect communities (modified after Westoby *et al.*, 1989).

The driving variables in this model are defined qualitatively by different states. For example, the rainfall pattern can be divided into the three different states: 1. low, 2. normal and 3. high. These states are fairly general and relate to below average, average and above average rainfall in the wet season.

The time step chosen for this model is one year, starting with the beginning of the dry season (April) and ending with end of the rainy season (March).

DRIVING VARIABLES

The driving variables of the model are:

Climate: Two variables:

(i) Duration of dry season with two states, 1 = short/normal, 2 = long (corresponding to less than, or equal to, six months and more than 6 months)

(ii) Amount of rainfall in the wet season with three levels, 1 = below average (low), 2 = average (normal), 3 = above average (high) (corresponding to less than, or equal to, 500 mm, more than 500 and less than 600 mm, more than, or equal to, 600 mm).

Drug: Standard injection of ivermectin ($200\mu gkg^{-1}$). Qualitative variable with four states, 0 = no treatment, 1 = single injection, 2 = two injections, 3 = three injections.

Cattle: Two variables:

(i) Proportion of cattle treated with two states, 1= only weaners or a few selected animals, 2 = entire herd or majority of herd (a few selected animals refers to those animals which show signs of parasite attack; majority of herd: weaners are exempted from treatment or a few animals remain untreated).

(ii) Cattle in areas adjacent to treatment paddocks with two states, 1 = untreated cattle in close proximity to treated animals, 2 = no cattle or no untreated cattle near treated animals.

Short term changes in temperature during the wet or dry season and short dry periods during the wet season cause temporary changes in dung insect populations (Doube, 1991). However, these changes are of a transient nature and their inclusion in the model would not change the overall model output. Temperature in general has not been built into the model, because beetle activity in the summer rainfall region is linked to both rainfall and

temperature (Davis, 1990).

Another variable that influences dung insects is pasture quality, because it determines the quality of dung and the breeding activity of beetles (Edwards, 1991). However, pasture quality, like temperature, is only of limited importance. It is unnecessary to include the condition of natural pastures, where no fertilizers are used, as it is correlated with rainfall (Edwards, 1991), one of the driving variables in the model.

In South Africa, cattle paddocks of natural pastures are often relatively large (e.g. 80 ha in the Parys trials (Chapter 3.2, 3.3)) due to a generally low carrying capacity of pastureland. Therefore, untreated and treated cattle in neighbouring paddocks need not be in close proximity, unless they come into contact, i.e. stay in the vicinity of the common border. Untreated cattle are considered to be in close proximity to treated cattle if animals from both herds meet regularly. An example is provided by the Parys trial of the 1993/94 season (Chapter 3.3), where the watering points of an untreated and a treated herd were situated close to each other at the common border of the two paddocks (P3 and P4, Fig. 11). Conversely, an example where treated cattle were not in close proximity to untreated animals is provided in Chapter 3.2; here, the treatment paddocks were separated from the controls by a grassland corridor approximately 200 m wide. The placement of watering points in paddocks P1 and P2 (Chapter 3.3; Fig. 11) constitutes an intermediate case. Immigration of dung insects on a larger spatial scale was not included as it is expected to be strongly correlated with rainfall.

FRAMES

In accordance with the objective of the model and the knowledge of the system, three frames were chosen: undisturbed, partially disturbed and disturbed dung insect community (Fig. 18).

The condition of the community may be determined from empirical quantitative or qualitative results. Obviously, the quantitative characterization of a community is more accurate, but requires monitoring over a period of many years which is often not feasible for lack of resources. On the other hand, the qualitative characterization of a community

is problematic in that it is subjective and dependent on the experience of the investigator.

In the present study the community condition was determined using the results of the Parys trials which were based on different community measures (Chapters 3.2 & 3.3).

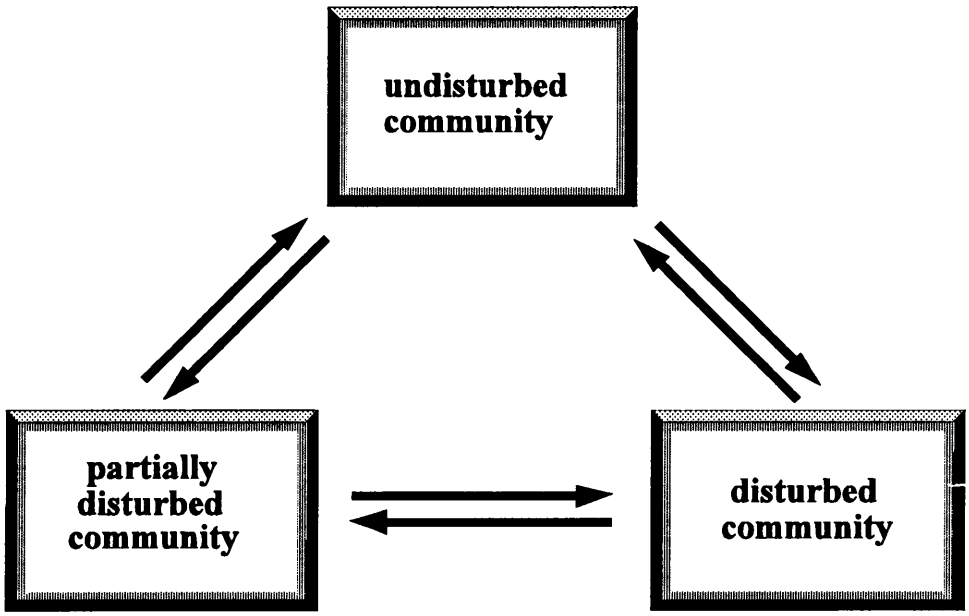

Fig. 18. Frames and pathways between frames for dung insect communities in the frame-based model.

This characterization of communities according to the Parys trials is based on the following:

1. The effects of treatment under drought conditions were deduced from the first season (1992/93) (Chapter 3.2). At the beginning of this season the dung insect community was partially disturbed due to the below average rainfall between October 1991 and the beginning of the trial (C.H. Scholtz, *pers. comm.*). The treatment conditions in 1992/93 were as follows: treatment of the entire herd, one standard injection with ivermectin and no untreated cattle present in close proximity. The results indicate that the effect lasted for three months after treatment late in summer. The community under these conditions is

considered to be disturbed, i.e. a switch occurred from partially disturbed to disturbed. The only component affecting the control community was the low rainfall during the wet season and this community is therefore considered to have remained partially disturbed (Chapter 3.2).

2. Rainfall before and during the 1993/94 trial was high (709 mm in the wet season). Because the treatment and control communities of the preceding season were similar in structure one year after treatment, both were considered as undisturbed before the beginning of the trials in December. Two different treatment scenarios then took place: i) treatment of entire herd, one standard injection with ivermectin and no untreated cattle in close proximity, and ii) treatment of entire herd with one standard injection of ivermectin and untreated cattle present in close proximity. In the first case, the treatment community showed some negative effects seven days after treatment; however, results from later collection dates are inconclusive, although there were differences between the communities, particularly in natural pats three months after treatment. In the second case, no effects were observed one month or later after treatment as the treatment community was very similar to the control, and the community remained undisturbed in comparison to the control.

If no data are available, the condition of a community may be determined from field observations as follows:

In the Undisturbed Frame the speed of dung decomposition may be used as a measure of the dung insect activity and community condition. In an undisturbed community dung pats are rapidly colonized by numerous species. Pats are quickly decomposed in the wet season, normally within a few days after deposition. However, when judging the community condition by speed of decomposition several facts should be kept in mind. Firstly, the speed with which dung pats are broken down depends on the soil type and pats on sandy soils are usually broken down faster than on clay-loam soils. Deep sandy soil is preferred over clay or loam soils by paracoprids and large telecoprids (Doube, 1991). The decomposition process is also influenced by rainfall, daily temperature and the position of the pats with regard to sun and shade.

The Partially Disturbed Frame is characteristic for communities after a normal or long

dry season and low rainfall in the preceding wet seasons for about two or three consecutive years. In this frame, dung insects are less abundant and less active than in the undisturbed community, and species diversity and/or evenness appear to be lower than in the Undisturbed Frame for a short time period (i.e., a few weeks) in the wet season.

The Disturbed Frame represents a stressed community, a state that occurs, for example, after a long drought. Under extreme conditions, only few specimens representing fewer species may be observed in dung pats (e.g. low species diversity), which in turn may not be decomposed quickly, i.e. within a few days, and may accumulate on the soil surface.

Disturbance of a community may also be expressed in terms of changes in species dominance (see Chapters 3.2 & 3.3). These changes obviously need not be accompanied by noticeable effects on dung decomposition.

A disturbance (perturbation) in the model is defined following Underwood (1989) as 'any natural, accidental or deliberately induced change in the environment'. To retain the simplicity of the model communities may switch to the Partially Disturbed or Disturbed Frame as a result of changes in both climatic conditions, which are an intrinsic part of the system, and treatment circumstances, although the reason for a transition to these frames may be different. A community may be affected in a different way by drought than by a combination of drought and treatment. Many dung beetle species are able to adapt to drier conditions. For examples, *Onitis alexis* Klug is well adapted to a semiarid climate; it rapidly removes dung from the soil surface and forms sausages that are arranged in close proximity to one another about 37 cm deep in the soil; this technique maintains the optimum humidity for larval development (Rougon & Rougon, 1982). *Euoniticellus intermedius* (Reiche) changes the architecture of its nest according to climatic circumstances (Rougon & Rougon, 1982): during the rainy season the nest is in the form of a main burrow from which extend several branched galleries containing ovoid brood masses. During the dry season the nest resembles that of *O. alexis*. However, the reproductive success of several dung-breeding beetles and flies has been shown to vary with climate; for example, low rainfall results in a decline of pasture quality, which in turn entails a lower breeding success (Doube, 1987).

KEY VARIABLES AND PROCESSES WITHIN EACH FRAME:

In order to monitor the state of a community, a community condition variable has been introduced (Fig. 17). It is a real number and ranges from zero to three.

1. The Undisturbed Frame (Frame 1):
Key variables: all driving variables (Dry Season, Rainfall, Drug, Proportion of Treated Cattle and Surrounding Cattle). The community variable cannot be smaller than zero to enable communities to react quickly to changes in abiotic conditions.

2. The Partially Disturbed Frame (Frame 2):
Key variables: all driving variables (see above). The community variable cannot be smaller than zero and greater than three.

3. The Disturbed Frame (Frame 3):
Key variables: all driving variables (see above). For the same reason as in the undisturbed frame, the community variable cannot be greater than three.

Although the key variables are common to all frames, they have different effects in different frames (see Tables below).

SWITCHING RULES

The switch from one frame to another is determined by the magnitude of the community variable. A transition from one frame to another can be caused by natural events (e.g. drought) or by management actions (e.g. treatment). A community can switch gradually from the Undisturbed over the Partially Disturbed to the Disturbed Frame and vice versa. Transitions can also take place more rapidly, because dung insects react very quickly to changes in abiotic factors. Therefore, a community can switch directly from undisturbed to disturbed and vice versa. From this it follows that a transition can occur between all frame

combinations and in all directions (Fig. 18).

1. Rule for switching from Undisturbed or Partially Disturbed to Disturbed: the switch occurs when the community variable is equal to or greater than two.

2. Rule for switching from Undisturbed to Partially Disturbed: the switch occurs when the community variable is equal to or greater than one.

3. Rule for switching from Partially Disturbed or Disturbed to Undisturbed: the switch occurs when the community variable is smaller than one.

4. Rule for switching from Disturbed to Partially Disturbed: the switch occurs when the community variable is smaller than two and equal or greater than one.

ASSUMPTIONS

1. A long dry season in winter as well as low rainfall in the wet season will affect already stressed communities more severely than unstressed ones.

2. Favourable weather conditions (short/normal dry season, normal or high rainfall) will have an increasingly positive effect on communities; these effects will be most dramatic in already disturbed communities.

3. Severe climatic conditions (e.g. long dry period, low rainfall) will act synergistically with treatment.

4. The Parys trials were restricted to one treatment per year. Two and three treatments per year have been included in the model under the assumption that the effect of the parasiticide on the community will increase with the number of treatments.

5. The treatment of a few animals only will have little overall effect on communities.

TABLES

Tables 22-26 provide the basis of the model. They show how much is added or subtracted from the community variable according to frame, climatic and treatment circumstances. If a factor has a positive influence on communities a value is subtracted, if it has a negative influence a value is added. The actual values in the tables were determined in accordance with the results of the Parys trials and the range of the community variable. To quote Starfield & Bleloch (1986), 'while the actual numbers used [in the tables] might be inaccurate, there is a logic behind their relative values'. For example, a community switches from undisturbed to partially disturbed if the entire herd or the majority of a herd is treated without having an untreated herd in close proximity, even if the weather conditions are favourable for dung insects (e.g. normal length of dry season, average rainfall). Accordingly, the combined value of the treatment factors should be greater than one.

The magnitude of the values in the tables generally increases from the undisturbed to the disturbed frame in accordance with the assumptions that the different climate and treatment factors have an increasing influence on communities from undisturbed to disturbed.

Effect of climate:

The dynamics of dung insects are more influenced by rainfall than the length of the dry season. This is reflected in Tables 22 and 23, where the values for dry season are lower than those for rainfall and thus have less influence on the magnitude of the community variable.

High soil moisture over a longer time period is unfavourable for dung insects, causing high larval mortality, especially in rollers and tunnellers (Lumaret & Kirk, 1991). Therefore, high rainfall has a less positive effect on communities than average rainfall.

With increasing insect numbers in dung pats, intra- and interspecific competition becomes more intense. It has been reported that strong competition can decrease diversity (Doube,

1987). Consequently, the effect of favourable climate is less positive on undisturbed communities than disturbed communities, where insects are expected to be less diverse than in undisturbed ones.

Table 22. Values to add to the community variable according to community condition and length of dry season.

		Frame		
		1 (undisturbed)	2 (partially disturbed)	3 (disturbed)
Dry Season	1 (normal)	-0.05	-0.08	-0.12
	2 (long)	0.08	0.12	0.20

Table 23. Values to add to the community variable according to community condition and rainfall.

		Frame		
		1 (undisturbed)	2 (partially disturbed)	3 (disturbed)
Rain	1 (low)	0.35	0.38	0.44
	2 (average)	-0.45	-0.65	-0.85
	3 (high)	-0.40	-0.60	-0.80

Effect of treatment:

The model is applicable only if no other veterinary drugs apart from ivermectin are used and if animals are treated with a single standard injection at, or shortly after, the beginning of the rainfall in the wet season. Further treatments take place during the remainder of the wet season until the beginning of the dry season.

Table 24. Values to add to the community variable according to community condition and ivermectin usage.

		Frame		
		1 (undisturbed)	2 (partially disturbed)	3 (disturbed)
Ivermectin usage	0 (none)	0.00	0.00	0.00
	1 (1x)	0.45	0.47	0.50
	2 (2x)	0.60	0.65	0.70
	3 (3x)	0.80	0.90	1.00

No treatment of cattle has neither a positive nor a negative effect on the community. The community under 'no treatment' conditions is driven by climate only.

Table 25. Values to add to the community variable according to community condition and proportion of animals treated in a herd.

		Frame		
		1 (undisturbed)	2 (partially disturbed)	3 (disturbed)
Proportion of herd treated	1 (e.g. weaners)	-0.41	-0.42	-0.43
	2 (e.g. entire herd)	0.55	0.58	0.65

A high value is subtracted from the community variable when the proportion of animals treated in a herd is low, assuming that the treatment of only a few individuals has little overall effect on communities.

Table 26. Values to add to the community variable according to community condition and condition of surrounding cattle.

		Frame		
		1 (undisturbed)	2 (partially disturbed)	3 (disturbed)
Surrounding cattle	1 (none or treated)	0.00	0.00	0.00
	2 (untreated)	-0.45	-0.65	-0.80

The values in the tables for treatment of cattle have been chosen in such a way that if the entire herd is treated once a year without untreated animals in close proximity, a switch occurs from undisturbed to partially disturbed if the rainfall is normal, and from partially disturbed to disturbed if the rainfall is low.

The model has been implemented on a micro-computer in Turbo Pascal (Appendix 6).

Results

Cycles of dry and wet years occur in South Africa. The most well- known cycle in most of the summer rainfall region is an 18-year oscillation, with nine predominantly dry and nine predominatly wet years (Tyson, 1990, 1993). This type of climate cycle has been prevalent in the study area over the past 25 years (Appendix 5). The output of the model simulating the effect of a 18-year cycle (strictly with nine dry years with low and nine years with average rainfall) on dung insect communities is given in Figure 19. The figure shows that the community condition slowly decreases with an increasing number of dry years and recovers relatively fast with improving weather conditions.

Figure 20 shows the output of the model after a yearly treatment of the herd has been added to the 18-year climate cycle. The cattle adjoining the treated herd were treated in alternate years. If only weaners or a few selected animals are treated then the line closely traces that of climate without treatment, indicating that the effect of treating only a few animals would be minimal. If an entire herd is treated the output of the model shows a

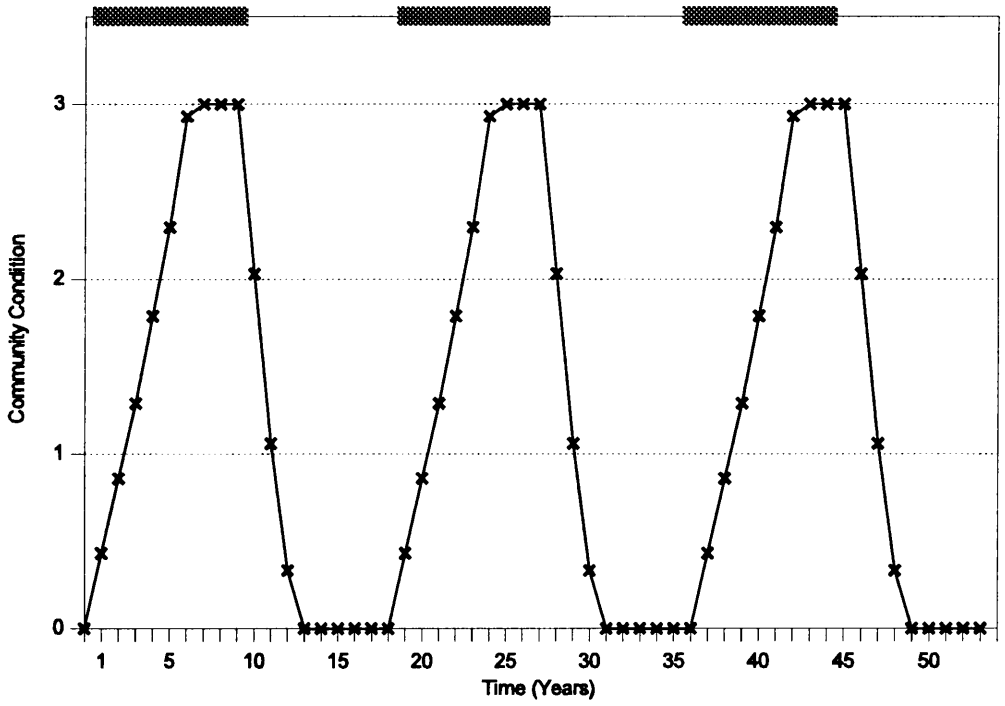

Fig. 19. Model output for the effect of an 18-year climate oscillation on a dung insect community. The grey bars denote the nine-year periods of drought.

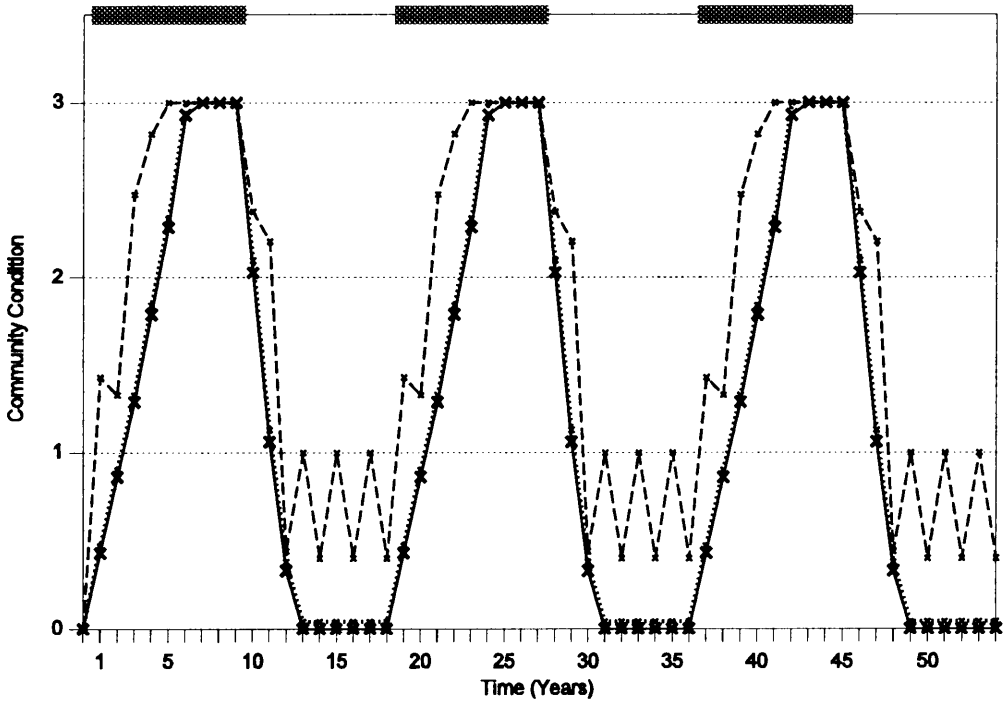

Fig. 20. Model output for an 18-year climate oscillation (solid line) with treatment added to the cycle. Treated animals were present in close proximity in alternate years. Dotted line: treatment of weaners or selected animals; broken line: treatment of the entire herd/majority of herd. The grey bars denote the nine-year periods of drought.

rapid decrease in community condition with worsening climatic conditions if no untreated animals are in close proximity. If an untreated herd is in close proximity the community recovers slightly in the Partially Disturbed Frame. This effect is likely due to the immigration of beetles from the untreated area, leading to an approximation of both dung communities. In the disturbed frame the condition of a community does not improve under the same circumstances, but decreases to a lesser extent than in communities not surrounded by treated animals. With improving weather conditions the communities in treated camps can improve rapidly if one or several untreated herds are in the vicinity.

Fig. 21 presents the results of simulations of other climate cycles. Apart from the 18-year oscillation, climate cycles of 3-6 years, which have been connected with the variable fluctuations of the El Niño/Southern Oscillation phenomenon (ENSO), occur throughout southern Africa (Tyson, 1993). Another climate cycle, which affects most of the summer rainfall region is a 2-3 year Quasi-Biennial Oscillation (QBO) caused by the periodic reversal of equatorial stratospheric winds (Tyson, 1993).

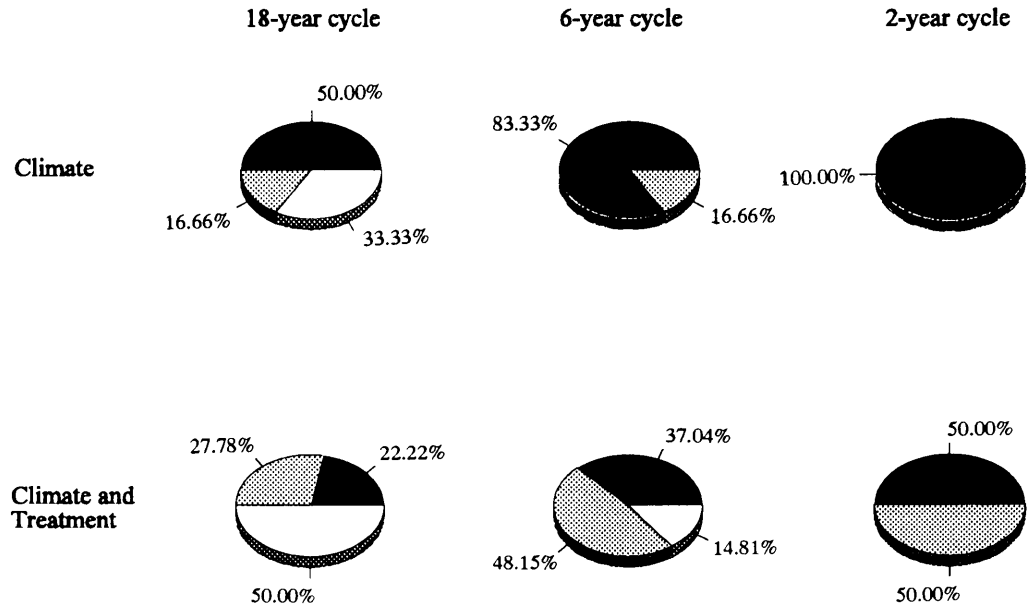

Fig. 21. Effects of different climate cycles on the percentage of time spent in the Undisturbed (black area), Partially Disturbed (dotted area) and Disturbed Frame (white area) after model runs of 54 years. The first row gives the effect of climate without treatment. The second row shows the effect of climate with treatment of the entire herd or majority of herd with treated animals in the vicinity every alternate year.

In the absence of treatment, the amount of time spent in the Undisturbed Frame increases rapidly with a shortening of the climate cycles from an 18-year over a 6-year to a 2-year oscillation (from 50.00% and 83.33% to 100% from the disturbed to undisturbed condition). Only with a period of nine dry and nine wet years does the community reach the disturbed state (residence time in frame: 33.33%). If treatment of a herd is added to the 18-year climate cycle, and assuming the presence of treated animals in the vicinity every alternate year, then the time spent reaches 50.00% in the Disturbed, 27.28% in the Partially Disturbed and 22.22% in the Undisturbed Frame. During a 6-year cycle more than 60% of the time is spent in the Partially Disturbed (48.15%) and Disturbed Frame (14.81%). During a period of a 2-year oscillation 50% of the time is spent in the Partially Disturbed Frame and the remainder of the time in the Undisturbed Frame.

Discussion

The model presented above was constructed to investigate the interactions among dung insect communities, climate and the broad-spectrum veterinary drug ivermectin, using the available knowledge on the dynamics of dung insects/beetles and expressing these dynamics as parameters based on logical yet subjective arguments.

Based on the limited experience gained in the trials conducted at Parys and the interpretation of results given in Chapters 3.2 and 3.3, the model can only reflect the current level of understanding. This notwithstanding, it may be easily adjusted when more complete data become available, or the interpretation of available data changes.

It is common practice to verify (establishment of truth) and validate (establishment of legitimacy) models (Oreskes *et al.*, 1994). However, because of the dynamics particular to natural systems and the frequently unpredictable and unanticipated way in which natural systems change, models of natural systems are not susceptible to proof and their primary value is thus heuristic (Oreskes *et al.*, 1994). Confirmation of observations only support the probability of the model, i.e. confirmations are a matter of degree. Unfortunately, no independent data set is presently available to test the fit of the model presented in this chapter.

Presently, it is not customary in South Africa to treat entire herds with ivermectin due to the high cost of treatment, but only some individuals in a herd (Chapter 3.2). However, with new drugs with a mode of action similar to that of ivermectin reaching the market, the price of these 'new-generation' parasiticides may drop in future and the usage of ivermectin or related products may be extended, e.g. to entire herds. Should this scenario of increased drug usage become a reality, a model of the type presented above could provide assistance in farm management. As was pointed out by Walters (1993), environmental managers are required to make decisions that necessarily involve at least a crude prediction about the consequences of each management choice.

The objective of the model is to aid in the decision-making process pertaining to the treatment of cattle in such a way that treatment effects are minimized. As mentioned above, rainfall is the major driving force in the dynamics of dung insect communities. Both drought and extensive treatment will have a negative influence on the dung insect fauna. Therefore, management should respond to drought conditions by minimizing treatment where possible. This can be achieved by treating only selected animals or, should it be necessary to treat an entire herd, by ensuring that neighbouring herds are left untreated.

An advantage of the biological abstraction of the type of model presented in this chapter is that because of its simplicity it may help farm managers to understand the interaction among dung insect dynamics and treatment of cattle more easily than in a complicated system model. A further strength of this modelling approach is that it facilitates the communication between managers and scientists and that experiences of farm managers can easily be incorporated (Davis *et al.*, 1989; Starfield *et al.*, 1993).

5 Conclusion

5.1 Introduction

The present study makes an important contribution to our knowledge about the effects of ivermectin in that it evaluates these effects at the laboratory, semi-field and and large-scale field levels. It comprises the first attempt to assess the effect of ivermectin under commercial use on dung insect communities in a longer-term study.

The findings of the various studies in this thesis have been discussed in the relevant chapters and only the main results will be collated in this section.

Lumaret *et al.* (1993) suggested that the effect of ivermectin on the dung beetle fauna varies with the composition of the latter; this view is supported by the findings of the present study. Ivermectin appeared to have little or no effect on dung decomposition in a savanna ecosystem, where telecoprid and paracoprid scarabaeid beetles dominate the dung fauna. In contrast, a delay in dung decomposition has been reported in some cases in Europe (e.g. Wall & Strong, 1987; Madsen *et al.*, 1990), where the dung beetle fauna is dominated by aphodiine endocoprids. The impact of ivermectin, if applied regularly over several years, on dung decomposition remains to be examined in long term studies (see below).

One important finding of the present study is that the effect of ivermectin on dung insect communities appears to depend not only on geographic (e.g. northern vs. southern hemisphere) but also on local climatic conditions. Little or no effect on dung insect communities in a grassland ecosystem was observed in a season with a relatively high rainfall, whereas communities which were already stressed by drought conditions showed a decrease in Shannon's diversity and an increase in species dominance.

Large scale field investigations have the advantage over laboratory studies that they reflect environmental processes more realistically. Biological systems are influenced by a variety of fluctuations in biotic and abiotic parameters, which also influence the impact of a disturbance. As Fairweather (1993) noted, it is not so much the localized loss of a species or a habitat that is of concern, because this readily occurs at the local level for a variety of

reasons, but the unnatural loss of the ability of species to recover, evolve or respond to various disturbances (perturbations). However, no obvious such losses seem to have occurred during the present study, and the results of the long term field study under drought conditions showed that the dung insect communities in the treatment paddocks had recovered from any observable direct and indirect effects ivermectin within one year after treatment. The impact of ivermectin therefore appears to be of a temporary nature.

As the output of the model presented in Chapter 4 emphasised, the effect of ivermectin can probably be controlled to a large extent by farm management practices. If only weaners in a herd are treated, which is currently standard practice in South Africa, any impact of ivermectin residues is negligible. If entire herds are treated, however, especially under conditions of drought, it is desirable to ensure that untreated herds are present in close proximity to allow for dung beetle immigration.

5.3 Future Research

The scientific understanding of the impact of avermectins is not yet complete. A number of points which need to be adressed have been listed by Herd *et al.* (1993b) (see Chapter 1). An essential factor mentioned by these authors is the assessment of the long-term impact of avermectins by monitoring populations and communities over a prolonged period of time to enable a comparison to be made between areas where avermectins are frequently used and areas where no parasiticides are used.

Very little is known about the effect of broad-spectrum parasiticides other than avermectins on the dung fauna. Future research should, therefore, not only concentrate on avermectins but should also be directed towards other such drugs, and not only to assess the effect of a single parasiticide but also to investigate alternative management strategies. An example is provided by Strong & Wall (1994), who compared the effect of the milbemycin moxidectin, which is structurally related to avermectins (Steel, 1993), with ivermectin in a field study.

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Appendix 1.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) on dung decomposition. For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment															
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	0.194 n.s.	2	2.258 n.s.	2	6.920 ***	2	5.186 **	2	5.346 ***	1	4.984 **	2	0.287 n.s.	2	10.938 ***
Treatment	1	0.047 n.s.	1	1.337 n.s.	1	0.115 n.s.	1	0.896 n.s.	1	0.237 n.s.	1	0.016 n.s.	1	0.061 n.s.	1	0.770 n.s.
Patage	3	6.627 *	3	7.923 **	4	14.448 ***	3	13.875 ***	2	5.245 ***	4	2.944 n.s.	4	28.290 ***	4	12.826***
Trial x Treatment	2	1.793 n.s.	2	4.395 *	2	6.811 ***	2	1.716 n.s.	2	2.695 *	1	0.001 n.s.	2	0.445 n.s.	2	0.324 n.s.
Trial x Patage	6	10.349 **	6	5.747 n.s.	8	7.028 **	6	4.020 n.s.	4	8.888 ***	4	12.000 **	8	4.659 n.s.	8	11.453 ***
Treatment x Patage	3	4.402 n.s	3	0.118 n.s.	4	5.864 ***	3	2.056 n.s.	2	0.579 n.s.	4	0.213 n.s.	4	1.177 n.s.	4	0.472 n.s.
Model	17	21.559 *	17	21.542 **	21	41.186 ***	17	27.749 ***	13	22.991***	15	20.157 *	21	34.919 ***	21	37.696 ***
Error	22	11.038	22	9.251	38	9.385	30	11.603	22	5.846	24	11.634	38	16.907	34	9.072
Corrected Total	39	32.597	39	30.793	59	50.571	47	39.352	35	28.837	39	31.792	59	51.826	55	46.769
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 2a.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for Histeridae. For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment													
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	3.862 **	2	1.172 n.s.	2	0.683 n.s.	2	5.409 **	2	10.817 ***	1	3.564 **	2	4.864***	2	5.244 **
Treatment	1	0.217 n.s.	1	1.469 n.s.	1	0.109 n.s.	1	0.040 n.s.	1	0.087 n.s.	1	0.292 n.s.	1	0.194 n.s.	1	0.043 n.s.
Patage	3	6.855 ***	3	5.080 *	4	11.078 ***	3	5.253 **	2	1.882 n.s.	4	11.190 ***	4	17.748 ***	4	9.992 ***
Trial x Treatment	2	0.105 n.s.	2	2.676 *	2	0.470 n.s.	2	0.984 n.s.	2	1.911 n.s.	1	0.137 n.s.	2	0.384 n.s.	2	3.942 **
Trial x Patage	6	8.990 ***	6	3.994 n.s.	8	11.916 **	6	5.802 *	4	3.581 *	4	3.902 **	8	10.612 ***	8	4.992 n.s.
Treatment x Patage	3	0.893 n.s	3	1.786 n.s.	4	0.555 n.s.	3	2.977 n.s.	2	0.622 n.s.	4	0.834 n.s.	4	1.759 n.s.	4	1.435 n.s.
Model	17	23.794 ***	17	18.423 **	21	24.812 **	17	20.464 **	13	18.900 ***	15	19.919 ***	21	35.562 ***	21	26.077 ***
Error	22	5.481	22	7.929	38	15.287	30	11.467	22	6.665	24	6.339	38	7.916	34	11.612
Corrected Total	39	29.275	39	26.351	59	40.099	47	31.931	35	25.565	39	26.259	59	43.478	55	37.689
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 2b.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for Staphylinidae. For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment															
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	2.501 n.s.	2	0.381 n.s.	2	2.230 *	2	3.146 *	2	3.296 n.s.	1	7.419 ***	2	2.747 *	2	6.081 **
Treatment	1	0.382 n.s.	1	0.098 n.s.	1	0.000 n.s.	1	0.702 n.s.	1	0.021 n.s.	1	0.088 n.s.	1	0.011 n.s.	1	0.137 n.s.
Patage	3	2.510 n.s.	3	6.692 **	4	21.776 ***	3	6.802 **	2	1.709 n.s.	4	5.984 ***	4	15.770 ***	4	7.395 *
Trial x Treatment	2	0.233 n.s.	2	2.124 n.s.	2	0.171 n.s.	2	1.385 n.s.	2	0.721 n.s.	1	0.088 n.s.	2	1.175 n.s.	2	0.980 n.s.
Trial x Patage	6	5.721 n.s.	6	1.944 n.s.	8	4.051 n.s.	6	4.751 n.s.	4	0.368 n.s.	4	5.984 ***	8	2.609 n.s.	8	4.110 n.s.
Treatment x Patage	3	0.873 n.s.	3	2.324 n.s.	4	1.170 n.s.	3	1.223 n.s.	2	0.449 n.s.	4	0.189 n.s.	4	1.703 n.s.	4	1.648 n.s.
Model	17	13.955 *	17	14.474 *	21	29.398 ***	17	18.008 **	13	6.564 n.s.	15	19.751 ***	21	24.016 **	21	20.085 n.s.
Error	22	8.377	22	8.669	38	11.202	30	10.744	22	13.446	24	1.546	38	15.960	34	19.448
Corrected Total	39	22.333	39	23.143	59	40.599	47	28.752	35	20.010	39	21.296	59	39.976	55	39.533
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 2c.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for Scarabaeinae. For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment															
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	2.678 n.s.	2	0.652 n.s.	2	1.853 *	2	18.057 ***	2	12.275 ***	1	3.143 **	2	0.470 n.s.	2	0.034 n.s.
Treatment	1	0.187 n.s.	1	0.233 n.s.	1	0.000 n.s.	1	0.000 n.s.	1	0.426 n.s.	1	0.059 n.s.	1	0.597 n.s.	1	1.492 n.s.
Patage	3	3.422 n.s.	3	8.732 ***	4	22.162 ***	3	11.160 ***	2	3.265 *	4	10.994 ***	4	35.870 ***	4	21.329 ***
Trial x Treatment	2	0.373 n.s.	2	3.776 **	2	2.710 *	2	0.367 n.s.	2	0.977 n.s.	1	0.002 n.s.	2	0.115 n.s.	2	1.329 n.s.
Trial x Patage	6	13.393 **	6	5.041 n.s.	8	10.554 ***	6	3.944 *	4	3.068 n.s.	4	5.978 *	8	4.108 *	8	6.380 n.s.
Treatment x Patage	3	1.056 n.s.	3	2.769 n.s.	4	1.257 n.s.	3	0.338 n.s.	2	0.346 n.s.	4	1.278 n.s.	4	2.000 *	4	2.526 n.s.
Model	17	23.934 **	17	23.348 **	21	38.537 ***	17	33.857 ***	13	20.357 **	15	21.455 **	21	43.159 ***	21	33.606 ***
Error	22	9.818	22	7.712	38	10.761	30	6.348	22	9.066	24	9.207	38	6.839	34	14.391
Corrected Total	39	33.752	39	31.060	59	49.297	47	40.205	35	29.423	39	30.661	59	49.999	55	47.997
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 2d .

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for Aphodiinae. For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment															
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	1.011 n.s.	2	1.056 n.s.	2	4.407 **	2	8.608 ***	2	4.114 *	1	5.915 ***	2	0.223 n.s.	2	1.237 n.s.
Treatment	1	0.153 n.s.	1	0.009 n.s.	1	0.113 n.s.	1	0.162 n.s.	1	0.099 n.s.	1	0.055 n.s.	1	0.121 n.s.	1	0.477 n.s.
Patage	3	16.592 ***	3	13.710 ***	4	25.890 ***	3	14.047 ***	2	9.570 ***	4	10.282 ***	4	38.986 ***	4	29.601 ***
Trial x Treatment	2	0.116 n.s.	2	0.830 n.s.	2	0.598 n.s.	2	0.387 n.s.	2	1.547 n.s.	1	0.044 n.s.	2	0.027 n.s.	2	1.004 n.s.
Trial x Patage	6	6.598 **	6	1.394 n.s.	8	2.670 n.s.	6	2.265 n.s.	4	1.614 n.s.	4	3.555 *	8	1.281 n.s.	8	2.398 n.s.
Treatment x Patage	3	0.883 n.s.	3	1.689 n.s.	4	0.921 n.s.	3	0.319 n.s.	2	0.918 n.s.	4	0.107 n.s.	4	0.246 n.s.	4	0.608 n.s.
Model	17	25.590 ***	17	20.140 **	21	34.599 ***	17	25.787 ***	13	17.862 *	15	19.959 ***	21	40.885 ***	21	36.179 ***
Error	22	5.347	22	8.083	38	12.100	30	10.351	22	10.253	24	5.720	38	8.004	34	9.703
Corrected Total	39	30.937	39	28.223	59	46.700	47	36.139	35	28.115	39	25.678	59	48.890	55	45.883
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 3a.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for individuals of FG II (small telecoprids). For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment															
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	3.199 *	2	3.031 *	2	4.737 ***	2	7.122 ***	2	8.408 ***	1	5.409 ***	2	6.445 ***	2	0.731 n.s.
Treatment	1	0.000 n.s.	1	0.318 n.s.	1	0.008 n.s.	1	0.162 n.s.	1	0.014n.s.	1	0.119 n.s.	1	0.250 n.s.	1	0.084 n.s.
Patage	3	7.162 **	3	6.661 **	4	15.015 ***	3	12.674 ***	2	5.393 ***	4	10.172 ***	4	24.039 ***	4	11.464 ***
Trial x Treatment	2	0.384 n.s.	2	2.524 *	2	1.127 n.s.	2	0.045 n.s.	2	0.130 n.s.	1	0.015 n.s.	2	0.738 n.s.	2	1.169 n.s.
Trial x Patage	6	5.721 *	6	2.395 n.s.	8	6.741 ***	6	4.617 *	4	4.167 *	4	4.804 **	8	8.369 ***	8	12.845 ***
Treatment x Patage	3	1.679 n.s.	3	1.564 n.s.	4	1.122 n.s.	3	0.236 n.s.	2	0.538 n.s.	4	1.452 n.s.	4	2.258 **	4	1.494 n.s.
Model	17	22.664 **	17	19.073 **	21	28.750 ***	17	24.857 ***	13	18.650 ***	15	21.972 ***	21	42.100 ***	21	27.683 ***
Error	22	7.080	22	7.935	38	7.224	30	7.849	22	5.849	24	5.051	38	5.523	34	11.899
Corrected Total	39	29.744	39	27.008	59	35.974	47	32.706	35	24.500	39	27.023	59	47.623	55	39.583
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 3b.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for individuals of FGIV and FG VI (larger slow-burying paracoprids and kleptoparasites). For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment															
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	4.290 *	2	3.166 *	2	0.251 n.s.	2	6.674 ***	2	6.836 **	1	4.747 ***	2	0.071 n.s.	2	0.620 n.s.
Treatment	1	0.129 n.s.	1	0.579 n.s.	1	0.404 n.s.	1	0.207 n.s.	1	0.435 n.s.	1	0.000 n.s.	1	0.717 n.s.	1	0.076 n.s.
Patage	3	0.551 n.s.	3	3.686 *	4	19.525 ***	3	11.800 ***	2	1.355 n.s.	4	6.400 **	4	23.036 ***	4	11.750 ***
Trial x Treatment	2	0.483 n.s.	2	2.028 n.s	2	1.502 n.s.	2	0.588 n.s.	2	0.805 n.s.	1	0.147 n.s.	2	2.763 n.s.	2	2.674 n.s.
Trial x Patage	6	10.768 *	6	6.003 *	8	4.810 n.s.	6	2.555 n.s.	4	5.020 n.s.	4	3.780 n.s.	8	2.992 ***	8	5.853 n.s.
Treatment x Patage	3	0.988 n.s.	3	0.316 n.s.	4	1.397 n.s.	3	1.251 n.s.	2	0.252 n.s.	4	1.260 n.s.	4	0.920 n.s.	4	0.956 n.s.
Model	17	18.201 n.s.	17	17.730 *	21	27.890 ***	17	23.076 ***	13	14.702 *	15	16.334 **	21	30.499 ***	21	21.727 *
Error	22	12.588	22	8.614	38	10.612	30	10.744	22	11.135	24	7.738	38	16.004	34	18.413
Corrected Total	39	30.788	39	26.344	59	38.502	47	33.820	35	25.838	39	24.072	59	46.503	55	40.140
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 3c.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for individuals of FG V and FG VI (smaller slow-burying paracoprids and kleptoparasites). For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment															
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	1.894 n.s.	2	0.587 n.s.	2	3.108 *	2	19.811 ***	2	13.214 ***	1	3.143 *	2	0.827 n.s.	2	0.074 n.s.
Treatment	1	0.168 n.s.	1	0.351 n.s.	1	0.006 n.s.	1	0.002 n.s.	1	0.457 n.s.	1	0.051 n.s.	1	0.623 n.s.	1	1.416 n.s.
Patage	3	3.272 n.s.	3	8.837 ***	4	21.515 ***	3	9.481 ***	2	2.730 n.s.	4	10.579 **	4	35.064 ***	4	20.081 ***
Trial x Treatment	2	0.643 n.s.	2	3.532 n.s.	2	2.319 *	2	0.223 n.s.	2	1.225 n.s.	1	0.003 n.s.	2	0.197 n.s.	2	1.239 n.s.
Trial x Patage	6	13.106 *	6	4.957 n.s.	8	9.812 **	6	4.606 **	4	2.810 n.s.	4	5.632 *	8	4.253 *	8	5.908 n.s.
Treatment x Patage	3	0.709 n.s.	3	2.947 n.s.	4	1.207 n.s.	3	0.330 n.s.	2	0.346 n.s.	4	1.576 n.s.	4	1.831 n.s.	4	3.062 n.s.
Model	17	22.041 *	17	23.156 **	21	37.968 ***	17	34.391 ***	13	20.780 ***	15	20.985 **	21	42.795 ***	21	32.274 ***
Error	22	11.582	22	7.935	38	11.329	30	5.809	22	8.667	24	9.668	38	7.196	34	15.736
Corrected Total	39	33.623	39	31.061	59	49.297	47	40.200	35	29.448	39	30.653	59	49.991	55	48.012
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 3d.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for individuals of FG VII (endocoprids). For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment															
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	1.465 n.s.	2	1.202 n.s.	2	4.171 **	2	8.586 ***	2	4.604 *	1	5.739 ***	2	0.127 n.s.	2	1.032 n.s.
Treatment	1	0.108 n.s.	1	0.003 n.s.	1	0.093 n.s.	1	0.154 n.s.	1	0.045n.s.	1	0.066 n.s.	1	0.105 n.s.	1	0.327 n.s.
Patage	3	15.999 ***	3	13.026 ***	4	26.267 ***	3	14.047 ***	2	9.798 ***	4	10.429 ***	4	39.947 ***	4	30.186 ***
Trial x Treatment	2	0.206 n.s.	2	1.221 n.s.	2	0.591 n.s.	2	0.395 n.s.	2	1.247 n.s.	1	0.038 n.s.	2	0.001 n.s.	2	1.405 n.s.
Trial x Patage	6	7.233 **	6	1.670 n.s.	8	2.623 n.s.	6	2.270 n.s.	4	1.619 n.s.	4	3.453 *	8	1.140 n.s.	8	2.573 n.s.
Treatment x Patage	3	0.732 n.s.	3	1.774 n.s.	4	0.900 n.s.	3	0.325 n.s.	2	0.720 n.s.	4	0.103 n.s.	4	0.244 n.s.	4	0.391 n.s.
Model	17	25.570 **	17	20.332 **	21	34.645 ***	17	25.779 ***	13	18.032 *	15	19.827 ***	21	41.563 ***	21	36.724 ***
Error	22	5.739	22	7.901	38	12.080	30	10.357	22	10.392	24	5.855	38	7.687	34	9.497
Corrected Total	39	31.309	39	28.234	59	46.724	47	36.137	35	28.424	39	25.682	59	49.251	55	46.221
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 4a.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for individuals of *Sisyphus* sp. 2. For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment															
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	4.874 **	2	3.276 *	2	4.767 ***	2	8.892 ***	2	10.482 ***	1	5.289 ***	2	7.315 ***	2	1.453 n.s.
Treatment	1	0.015 n.s.	1	0.403 n.s.	1	0.006 n.s.	1	0.016 n.s.	1	0.000 n.s.	1	0.194 n.s.	1	0.176 n.s.	1	0.014 n.s.
Patage	3	12.452 ***	3	6.533 **	4	14.999 ***	3	9.854 ***	2	4.990 ***	4	10.051 ***	4	21.552 ***	4	8.307 **
Trial x Treatment	2	0.205 n.s.	2	2.622 *	2	1.146 n.s.	2	0.151 n.s.	2	0.218 n.s.	1	0.036 n.s.	2	0.398 n.s.	2	0.506 n.s.
Trial x Patage	6	4.172 *	6	2.515 n.s.	8	6.770 ***	6	4.194 *	4	4.614 **	4	4.965 **	8	8.081 ***	8	14.486 ***
Treatment x Patage	3	1.052 n.s	3	1.759 n.s.	4	1.165 n.s.	3	0.231 n.s.	2	0.621 n.s.	4	1.503 n.s.	4	2.947 **	4	1.098 n.s.
Model	17	22.769 ***	17	19.775 **	21	28.852 ***	17	23.339 ***	13	20.925***	15	22.038 ***	21	40.469 ***	21	25.418 ***
Error	22	5.673	22	7.390	38	7.124	30	7.888	22	3.998	24	4.987	38	6.720	34	12.196
Corrected Total	39	28.442	39	27.165	59	35.976	47	31.226	35	24.922	39	27.025	59	47.189	55	37.614
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 4b.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for individuals of *Drepanocerus abyssinies*. For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment							
	1	2	3	4	7	14	21	28
	DF SS	DF SS	DF SS	DF SS	DF SS	DF SS	DF SS	DF SS
Trial	2 2.394 n.s.	2 0.133 n.s.	2 4.496 **	2 16.234 ***	2 14.169 ***	1 3.570 **	2 3.406*	2 0.224 n.s.
Treatment	1 0.440 n.s.	1 0.215 n.s.	1 0.263 n.s.	1 0.067 n.s.	1 0.261 n.s.	1 0.155 n.s.	1 0.570 n.s.	1 1.557 n.s.
Patage	3 2.486 n.s.	3 7.922 **	4 6.069 **	3 1.514 n.s.	2 0.280 n.s.	4 9.376 **	4 25.701 ***	4 18.820 ***
Trial x Treatment	2 0.222 n.s.	2 2.741 *	2 2.895 n.s.	2 0.316 n.s.	2 2.184 n.s.	1 0.012 n.s.	2 0.927 n.s.	2 0.527 n.s.
Trial x Patage	6 9.869 *	6 6.255 *	8 16.611 ***	6 6.527 *	4 1.376 n.s.	4 6.339 *	8 3.923 n.s.	8 5.820 n.s.
Treatment x Patage	3 0.560 n.s	3 2.427 n.s.	4 0.926 n.s.	3 1.030 n.s.	2 0.337 n.s.	4 1.662 n.s.	4 1.423 n.s.	4 1.942 n.s.
Model	17 17.548 n.s.	17 21.316 **	21 31.260 ***	17 25.687 ***	13 18.608**	15 21.114 **	21 35.951 ***	21 30.029 ***
Error	22 13.313	22 8.165	38 17.248	30 10.030	22 8.991	24 9.119	38 13.694	34 16.565
Corrected Total	39 30.861	39 29.480	59 48.508	47 35.716	35 27.599	39 30.233	59 49.645	55 46.594
Type of Analysis	GLM	GLM	ANOVA	ANOVA	ANOVA	ANOVA	ANOVA	GLM

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 4c.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for individuals of *Tiniocellus spinipes*. For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment							
	1	2	3	4	7	14	21	28
	DF SS	DF SS	DF SS	DF SS	DF SS	DF SS	DF SS	DF SS
Trial	2 0.767 n.s.	2 2.364 *	2 1.750*	2 12.962***	2 6.485***	1 5.208 ***	2 0.287 n.s.	2 1.156 n.s.
Treatment	1 0.008 n.s.	1 0.186 n.s.	1 0.026 n.s.	1 0.001 n.s.	1 0.551 n.s.	1 0.040 n.s.	1 0.061 n.s.	1 05981 n.s.
Patage	3 10.892 ***	3 8.599 ***	4 26.593 ***	3 12.779 ***	2 6.247 ***	4 12.031 ***	4 28.290 ***	4 20.314 ***
Trial x Treatment	2 1.248 n.s.	2 2.189 *	2 1.971*	2 0.542 n.s.	2 0.462 n.s.	1 0.083 n.s.	2 0.445 n.s.	2 0.633 n.s.
Trial x Patage	6 8.191 **	6 3.635 n.s.	8 3.476 n.s.	6 2.115 n.s.	4 6.128 **	4 4.111 **	8 4.659 n.s.	8 6.664 *
Treatment x Patage	3 0.055 n.s	3 2.158 n.s.	4 0.786 n.s.	3 0.051 n.s.	2 0.263 n.s.	4 1.076 n.s.	4 1.177 n.s.	4 3.637 *
Model	17 23.342 ***	17 21.107 **	21 34.602 ***	17 28.451 ***	13 20.137***	15 22.551 ***	21 34.919 ***	21 33.487 ***
Error	22 5.707	22 6.589	38 7.663	30 7.376	22 6.443	24 4.477	38 16.907	34 9.510
Corrected Total	39 29.049	39 27.695	59 42.265	47 35.828	35 26.58	39 27.028	59 51.826	55 42.997
Type of Analysis	GLM	GLM	ANOVA	ANOVA	ANOVA	ANOVA	ANOVA	GLM

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 4d.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for individuals of *Aphodius pseudolividus*. For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment															
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	2.332 ***	2	0.156 n.s.	2	0.386 n.s.	2	2.417 *	2	0.233 n.s.	1	3.469 **	2	0.160 n.s.	2	5.117 ***
Treatment	1	0.066 n.s.	1	0.177 n.s.	1	0.149 n.s.	1	0.118 n.s.	1	0.364 n.s.	1	0.025 n.s.	1	0.159 n.s.	1	0.823 n.s.
Patage	3	12.253 ***	3	9.781 ***	4	15.090 ***	3	11.651 ***	2	6.616 **	4	4.483 *	4	23.732 ***	4	14.880 ***
Trial x Treatment	2	0.402 n.s.	2	0.799 n.s.	2	0.012 n.s.	2	0.467 n.s.	2	0.893 n.s.	1	0.066 n.s.	2	0.098 n.s.	2	2.492 **
Trial x Patage	6	2.890 **	6	2.004 n.s.	8	5.171 *	6	2.415 n.s.	4	1.253 n.s.	4	2.196 n.s.	8	1.401 n.s.	8	4.0.35*
Treatment x Patage	3	2.872 ***	3	1.288 n.s.	4	1.212 n.s.	3	3.388 *	2	1.102 n.s.	4	1.453 n.s.	4	4.056 *	4	0.926 n.s.
Model	17	21.524 ***	17	17.680 **	21	22.020 ***	17	20.456 ***	13	10.461 n.s.	15	11.693 *	21	29.607 ***	21	30.035 ***
Error	22	2.659	22	7.631	38	10.906	30	8.412	22	11.458	24	7.352	38	11.918	34	7.612
Corrected Total	39	24.184	39	25.310	59	32.925	47	28.868	35	21.919	39	19.046	59	41.524	55	37.648
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 4e.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for individuals of *Colobopterus maculicollis*. For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment															
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	1.388 n.s.	2	2.229 **	2	0.087 n.s.	2	1.607 ***	2	1.643 n.s.	1	1.451 *	2	2.618 *	2	0.344 n.s.
Treatment	1	0.808 n.s.	1	0.160 n.s.	1	0.001 n.s.	1	0.000 n.s.	1	0.001 n.s.	1	0.141 n.s.	1	0.006 n.s.	1	0.290 n.s.
Patage	3	5.969 *	3	8.448 ***	4	18.860 ***	3	14.431 ***	2	9.298 ***	4	4.317 **	4	22.788 ***	4	10.596 **
Trial x Treatment	2	1.152 n.s.	2	0.856 n.s.	2	0.229 n.s.	2	0.204 n.s.	2	0.024 n.s.	1	0.226 n.s.	2	0.869 n.s.	2	0.131 n.s.
Trial x Patage	6	2.202 n.s.	6	2.472 n.s.	8	1.022 n.s.	6	4.146 ***	4	0.958 n.s.	4	4.414 **	8	2.143 n.s.	8	2.280 n.s.
Treatment x Patage	3	0.493 n.s	3	2.524 **	4	0.524 n.s.	3	0.246 n.s.	2	0.002 n.s.	4	1.464 n.s.	4	1.370 n.s.	4	2.423 n.s.
Model	17	14.774 *	17	17.403 ***	21	20.724 ***	17	20.635 ***	13	11.927 *	15	12.013 *	21	29.794 ***	21	15.945 n.s.
Error	22	9.419	22	3.699	38	8.731	30	2.973	22	9.174	24	5.737	38	12.394	34	16.623
Corrected Total	39	24.193	39	21.103	59	29.456	47	23.607	35	21.101	39	17.750	59	42.188	55	32.567
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 4f.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for individuals of *Euoniticellus intermedius*. For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment													
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	1.293 n.s.	2	1.274 n.s.	2	1.175 *	2	2.382 **	2	1.234 n.s.	1	0.312 n.s.	2	1.366 n.s.	2	0.115***
Treatment	1	0.136 n.s.	1	0.187 n.s.	1	0.050 n.s.	1	0.001 n.s.	1	0.380 n.s.	1	0.018 n.s.	1	0.015 n.s.	1	0.206 n.s.
Patage	3	5.453*	3	7.207 **	4	15.383 ***	3	8.698 ***	2	3.137 *	4	6.816 **	4	14.959 ***	4	2.479 ***
Trial x Treatment	2	1.352 n.s.	2	0.683 n.s.	2	0.356 n.s.	2	0.224 n.s.	2	0.576 n.s.	1	0.085 n.s.	2	0.268 n.s.	2	0.674 n.s.
Trial x Patage	6	2.399 n.s.	6	2.565 n.s.	8	3.579 *	6	4.006 **	4	1.702 n.s.	4	0.915 n.s.	8	5.741 n.s.	8	2.912***
Treatment x Patage	3	1.408 n.s	3	0.365 n.s.	4	0.977 n.s.	3	0.500 n.s.	2	0.965 n.s.	4	0.027 n.s.	4	0.787 n.s.	4	0.846 n.s.
Model	17	14.918 *	17	14.334 *	21	21.520 ***	17	15.812 ***	13	7.994 n.s.	15	8.173 n.s.	21	23.135 **	21	7.475 n.s.
Error	22	8.410	22	7.534	38	6.647	30	4.981	22	9.657	24	8.285	38	13.631	34	15.446
Corrected Total	39	23.329	39	21.867	59	28.167	47	20.794	35	17.651	39	16.458	59	36.767	55	22.920
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 4g.

Three-way analysis of variance for the effects of trial (Trial 1-3), treatment (ivermectin, control) and pat age (1-4, 7 days) for individuals of *Liatongus militaris*. For balanced data the SAS® procedure ANOVA was used and for unbalanced data the SAS® procedure GLM (SAS, 1989). Type III SS is given for the results of the GLM.

Source of variation	Days after treatment													
	1		2		3		4		7		14		21		28	
	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS	DF	SS
Trial	2	3.095*	2	4.464 *	2	0.157 n.s.	2	10.149 ***	2	5.577*	1	2.382 **	2	1.449 n.s.	2	1.425 n.s.
Treatment	1	0.000 n.s.	1	0.324 n.s.	1	0.764 n.s.	1	1.071 n.s.	1	0.206 n.s.	1	0.077 n.s.	1	0.002 n.s.	1	0.000 n.s.
Patage	3	6.463 **	3	1.153 n.s.	4	13.688 ***	3	2.613 n.s	2	0.291 n.s.	4	3.025 *	4	7.141 *	4	8.570 ***
Trial x Treatment	2	0.816 n.s.	2	1.321 n.s.	2	0.445 n.s.	2	0.149 n.s.	2	2.245 n.s.	1	0.211 n.s.	2	1.859 n.s.	2	0.763 n.s.
Trial x Patage	6	8.774 **	6	5.467 n.s.	8	4.553 n.s.	6	1.282 n.s.	4	6.145 *	4	4.472 **	8	2.452 n.s.	8	6.942 *
Treatment x Patage	3	0.454 n.s	3	0.367 n.s.	4	1.034 n.s.	3	1.303 n.s.	2	0.146 n.s.	4	2.753 n.s.	4	1.208 n.s.	4	1.627 n.s.
Model	17	19.815 **	17	13.406 n.s.	21	20.641 **	17	16.567 n.s.	13	14.609 n.s.	15	12.920 **	21	14.111 n.s.	21	20.084 **
Error	22	8.189	22	8.728	38	12.088	30	15.167	22	11.681	24	6.221	38	25.845	34	11.431
Corrected Total	39	28.004	39	22.134	59	32.728	47	31.734	35	26.29	39	19.141	59	39.956	55	31.515
Type of Analysis	GLM		GLM		ANOVA		ANOVA		ANOVA		ANOVA		ANOVA		GLM	

*P<0.05, **p<0.01, ***p<0.001, n.s.: not significant

Appendix 5.

Monthly rainfall (mm) at Parys (26°54'S 27°28'N) for 01/01/1970 to 31/05/1995 supplied by the South African Weather Bureau.

* : unreliable due to missing data or accumulation
= : total for year is unreliable due to missing data
YTOT : total for the year; the value may be incorrect if only part of a years' data are extracted.

YEAR	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NO V	DEC	YTOT
1970	87.9	58.7	39.4	18.2	21.8	10.5	17.0	0.0	13.0	39.1	170.6	167.3	643.5
1971	122.7	45.8	0.0	119.5	11.7	8.2	1.9	0.0	34.0	67.3	118.8	109.0	638.9
1972	109.9	34.7	95.2	12.3	0.0*	10.4	0.0	1.1	16.6	42.0	67.3*	94.8	491.5=
1973	79.4	113.0*	68.6	105.0*	0.0	0.0	0.0	30.2	23.9	49.4	97.5	121.5*	688.5=
1974	152.7	94.8	47.2*	96.5	4.5	6.0	0.0	0.0	2.9	71.8	81.7	81.8	639.9=
1975	123.6	104.6	75.5	80.9	17.3	9.5	0.0	3.1*	8.9	29.2	107.6	140.8	701.0=
1976	199.8	122.7	157.1	42.0	48.5	1.5	0.0	0.0	35.6	117.4	72.7	158.4	955.7
1977	116.2*	58.4	92.2	33.8	1.5	0.0	0.0	0.0	68.2	48.2	66.4	104.3	589.2=
1978	242.5*	78.3*	175.7	46.5	1.2	0.3	0.3	15.0	18.0	104.7	37.5	60.8	780.8=
1979	93.3	44.4	58.6	16.6	21.0	5.9	17.2	95.1	16.7	127.4	79.1	115.8	691.1
1980	179.8	58.7*	33.3	40.4	1.4	0.0	0.0	3.2	33.0	31.5	116.1	60.0	557.4=
1981	223.1	121.1	76.6	9.8	7.5	3.1	0.0	41.6	14.8	59.3	92.1	85.9	734.9
1982	130.0	52.5	44.1	70.0	0.0	0.0	27.8	0.0	7.5	95.2	41.0	88.4*	556.5=
1983	76.8	53.5	10.0	25.0	35.6	35.5	22.0	0.0	7.0	117.0	93.0	55.5	530.9
1984	78.5	11.5	74.0*	21.2	6.0	31.0	7.8	25.0	8.5	77.5	59.0	102.6	502.6=
1985	81.7	68.0	88.0	0.0*	22.0	0.0	0.0	0.0	24.0	90.0	29.5	115.0	518.2=
1986	92.0	18.0	67.0	39.5	0.0	31.0	3.0	48.0	7.5	122.0	88.0	93.0*	609.0=
1987	76.0	30.0	28.0*	29.0	0.0	0.0	0.0	11.0	160.0	67.0	104.5	103.5	609.0=
1988	74.0	96.5	121.5	50.0*	11.0	20.0	1.0	1.5	55.0	137.0	74.5	101.5	743.5=
1989	108.0	125.5	53.5	75.0	15.0	14.5	0.0	12.0	0.0	52.5	133.0	65.0	654.0
1990	112.0	121.5	94.0	88.5	25.0	0.0	3.0	8.0	10.0	11.0	22.5	77.7	573.2
1991	184.0	69.0	69.5	0.0	0.0	13.0	0.0	0.0	8.0	135.0	35.0	91.5	605.0=
1992	50.5	33.0	33.5	46.0	0.0	6.5	0.0	26.0	11.0	24.5	244.5	81.5	557.0
1993	32.0	45.5	54.0	31.0	6.0	0.0	0.0	0.0	21.5	208.2	76.0	106.5	580.7
1994	138.0	124.0	56.5	22.0	0.0	0.0	0.0	0.0	9.0	15.5	58.5	57.0	481.2=
1995	96.5	28.0	83.0	19.0	10.0								236.5=

Average (AVE) monthly rainfall for Parys (26°54'S 27°28'N) from 1904 to 1994. Data for calculation are not used if (1) accumulation occurred in the month (MON) and (2) if data for certain days in the month are unavailable.

MON	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NO V	DEC	YR
AVE	96.6	75.2	72.8	45.2	18.2	8.1	6.9	8.5	19.7	64.5	79.8	86.4	581.9

Appendix 6a.

```
program IVOMEC;
{
This programme simulates the interactions among dung insect communities,
climate and the broad-spectrum veterinary agent ivermectin. The
programme was written in Turbo Pascal (version 7.0, Borland International
Inc.)
}

var
  InData,                {data input file}
  OutData : Text;        {output file}
  Weather,               {defines if user input or random generation}
  IDry,                  {user dry season}
  LDry,                  {long dry season}
  IRain,                 {user rainfall}
  LRain,                 {low rainfall}
  HRain,                 {high rainfall}
  SCattle,               {cattle in surrounding areas}
  PCattle,               {proportion of animals treated in a herd}
  Drug,                  {frequency of drug usage}
  CntY,                  {counts years}
  CntDry,                {counts dry years}
  CntWet,                {counts wet years}
  Cycle,                 {type of climate cycle}
  SFrame,                {starting frame}
  Frame,
  I : integer;
  Count : array[1..3] of integer;
  Dry, PCa, SCa : array[1..2,1..3] of real;
  Rai : array[1..3,1..3] of real;
  Drg : array[0..3,1..3] of real;
  RNum, RDry, RRain, Chg, S1, S2, S3, S4, S5, SClim, Clim, Treat, DCom : real;
  YearCh, Key : char;
const
  YearSentinel = '/';


Procedure Startup;
{
Pre : The pointer for InData is at the start of the first data line.
Post: The pointer for InData is at <EOLN>, i.e., at the begining of the
      next line which contains the data for Year 1. The value for the
      starting Frame is written to file OutData.
}
begin {startup}
  Readln (InData, SFrame, Weather, SClim);
  Writeln (OutData, 'starting frame: ', SFrame :1, ',  starting climate value: ',
           SClim :4:2);
  Writeln (OutData)
end; {startup}

Procedure Tables;
```

```
begin {Tables}
  Dry[1,1] := -0.05;  Dry[1,2] := -0.08;  Dry[1,3] := -0.12;
  Dry[2,1] :=  0.08;  Dry[2,2] :=  0.12;  Dry[2,3] :=  0.20;
  Rai[1,1] :=  0.35;  Rai[1,2] :=  0.38;  Rai[1,3] :=  0.44;
  Rai[2,1] := -0.45;  Rai[2,2] := -0.65;  Rai[2,3] := -0.85;
  Rai[3,1] := -0.40;  Rai[3,2] := -0.60;  Rai[3,3] := -0.80;
  Drg[0,1] :=  0.00;  Drg[0,2] :=  0.00;  Drg[0,3] :=  0.00;
  Drg[1,1] :=  0.45;  Drg[1,2] :=  0.47;  Drg[1,3] :=  0.50;
  Drg[2,1] :=  0.60;  Drg[2,2] :=  0.65;  Drg[2,3] :=  0.75;
  Drg[3,1] :=  0.80;  Drg[3,2] :=  0.90;  Drg[3,3] :=  1.00;
  PCa[1,1] := -0.41;  PCa[1,2] := -0.42;  PCa[1,3] := -0.43;
  PCa[2,1] :=  0.55;  PCa[2,2] :=  0.58;  PCa[2,3] :=  0.65;
  SCa[1,1] :=  0.00;  SCa[1,2] :=  0.00;  SCa[1,3] :=  0.00;
  SCa[2,1] := -0.45;  SCa[2,2] := -0.65;  SCa[2,3] := -0.80;
end; {Tables}

Procedure YNumber;
{
Writes current year to the output file.
Pre : The pointer for InData is at the start of the data line.
Post: The pointer for InData is just past the sentinel character. Each
      data character is written to file OutData except for the sentinel.
}
begin {YNumber}
  Read(InData, YearCh);
  while (YearCh <> YearSentinel) and (not EOLN(InData)) do
    begin {while}
      Write(OutData, YearCh);
      Read(InData, YearCh);
    end; {while}
end; {YNumber}

Procedure DryCycle;
begin {DryCycle};
  Cycle := 1;
  CntDry := CntDry + 1;
  {Writeln ('Number of dry years: ', CntDry :4);} {for testing}
  RDry := Random;
  if (Rdry >  0.2) then IDry := 2;
  if (Rdry <= 0.2) then IDry := 1;
  RRain := Random;
  if (RRain >= 0.3)                    then IRain := 1;
  if (RRain <  0.3) and (RRain >= 0.2) then Irain := 2;
  if (rrain <  0.2)                    then Irain := 3
end; {DryCycle}

Procedure WetCycle;
begin {Wetcycle};
  Cycle := 2;
  CntWet := CntWet + 1;
  {Writeln ('Number of wet years: ', CntWet :4);} {for testing}
  RDry := Random;
  if (Rdry >  0.2) then IDry := 1;
  if (Rdry <= 0.2) then IDry := 2;
  RRain := Random;
  if (RRain <= 0.2)                    then IRain := 1;
```

```
  if (RRain >  0.2) and (RRain <= 0.7) then Irain := 2;
  if (rrain >  0.7)                    then Irain := 3
end; {WetCycle}

Procedure ClimCycle;
begin {ClimCycle}
  if (Cycle = 1) then
    if (CntDry = 10) then Wetcycle
                     else DryCycle;
  if (Cycle = 1) and (CntDry = 10) then Cycle := 2;
  if (Cycle = 2) then
    if (CntWet = 10) then DryCycle
                     else WetCycle;
  if (Cycle = 2) and (CntWet = 10) then Cycle := 1;
end; {Climcycle}

Procedure RClimate;
{
Generates a random climate cycle for an 18-year oscillation; i.e. nine
predominantly dry years and nine predominantly wet years.
}
begin {Random Climate}
  Randomize; {initialize random number generator}
  if CntY = 1 then
    begin
      RNum := Random;
      if (RNum >   0.5) then DryCycle;
      if (RNum <=  0.5) then WetCycle;
    end;
  if (CntY > 1) then ClimCycle
end; {Random Climate}

Procedure RData;
{
Reads values for input data;
Pre : The pointer in InData is just past the sentinel character.
Post: The pointer in InData is at <EOLN>.
}
begin {Read Data}
  if (Weather = 1) then
    begin {read variables to EOLN}
      Read (InData, IDry, IRain, Drug, PCattle, SCattle);
    end;
  if (Weather = 2) then
    begin
      RClimate;
      Read (InData, Drug, PCattle, SCattle)
    end;
end; {Read Data}

Procedure SwtoUn;
begin {switch to Disturbed Frame}
  Frame := 1;
  Chg := 1;
  S1 := 0.0;  S2 := 0.0;  S3 := 0.0;  S4 := 0.0;  S5 := 0.0
end; {switch to Disturbed}
```

```
Procedure SwtoPD;
begin {switch to Partially Disturbed Frame}
  Frame := 2;
  Chg := 1;
  S1 := 0.0;  S2 := 0.0;  S3 := 0.0;  S4 := 0.0;  S5 := 0.0
end; {switch to Partially Disturbed}

Procedure SwtoDist;
begin {switch to Undisturbed Frame}
  Frame := 3;
  Chg := 1;
  S1 := 0.0;  S2 := 0.0;  S3 := 0.0; S4 := 0.0;  S5 := 0.0
end; {switch to Undisturbed}

Procedure UnDisturbed;
begin {UnDisturbed}
  if (Drug = 0) then
    begin {climate only}
      S1 := S1 + Dry[IDry,1];
      S2 := S2 + Rai[IRain,1];
      Clim := Clim + S1 + S2;
      if (Clim < 0) then Clim := 0.0;
      DCom := Clim
    end; {climate only}
  if (Drug > 0) then
    begin {climate & drug}
      S1 := S1 + Dry[IDry,1];
      S2 := S2 + Rai[IRain,1];
      S3 := S3 + Drg[Drug,1];
      S4 := S4 + PCa[PCattle,1];
      if (PCattle = 1) then S5 := S5 + SCa[1,1]
                       else S5 := S5 + SCa[SCattle,1];
      Clim := Clim + S1 + S2;
      if (Clim < 0) then Clim := 0.0;
      {Writeln ('climate: ', Clim :4:2);} {for testing}
      Treat := S3 + S4 + S5;
      DCom := Clim + Treat
    end; {climate & drug}
  if  (DCom >= 2)                  then SwtoDist;
  if ((DCom >= 1) and (DCom < 2)) then SwtoPD
end; {UnDisturbed}

Procedure PartDisturbed;
begin {PartDisturbed}
  if (Drug = 0) then
    begin {climate only}
      S1 := S1 + Dry[IDry,2];
      S2 := S2 + Rai[IRain,2];
      Clim := Clim + S1 + S2;
      if (Clim < 0) then Clim := 0.0;
      DCom := Clim
    end; {climate only}
  if (Drug > 0) then
    begin {climate & drug}
      S1 := S1 + Dry[IDry,2];
```

```
      S2 := S2 + Rai[IRain,2];
      S3 := S3 + Drg[Drug,2];
      S4 := S4 + PCa[PCattle,2];
      if (PCattle = 1) then S5 := S5 + SCa[1,2]
                       else S5 := S5 + SCa[SCattle,2];
      Clim := Clim + S1 + S2;
      {Writeln ('climate: ', Clim :4:2);} {for testing}
      if (Clim < 0) then Clim := 0.0;
      if (Clim > 3) then Clim := 3.0;
      Treat := S3 + S4 + S5;
      DCom := Clim + Treat
    end; {climate & drug}
  if (DCom >= 2) then SwtoDist;
  if (DCom <  1) then SwtoUn
end; {PartDisturbed}

Procedure Disturbed;
begin {Disturbed}
  if (Drug = 0) then
    begin {climate only}
      S1 := S1 + Dry[IDry,3];
      S2 := S2 + Rai[IRain,3];
      Clim := Clim + S1 + S2;
      if (Clim > 3) then Clim := 3.0;
      Dcom := Clim
    end {climate only};
  if (Drug > 0) then
    begin {climate & drug}
      S1 := S1 + Dry[IDry,3];
      S2 := S2 + Rai[IRain,3];
      S3 := S3 + Drg[Drug,3];
      S4 := S4 + PCa[PCattle,3];
      if (PCattle = 1) then SCattle := 1;
      if (IRain = 1) and (SCattle = 2) then S5 := S5 + SCa[SCattle,3]/2
                                       else S5 := S5 + SCa[SCattle,3];
      Clim := Clim + S1 + S2;
      if (Clim > 3) then Clim := 3.0;
      {Writeln ('climate: ', Clim :4:2);} {for testing}
      Treat := S3 + S4 + S5;
      DCom := Clim + Treat
    end {climate & drug};
  if (DCom <  1) then SwtoUn;
  if (DCom >= 1) then
  if (DCom <  2) then SwtoPD
end; {disturbed}

Procedure ProcessYear;
begin {Process Year}
  RData;
  Writeln (OutData, '                                    ', IDry :1, '      ',
          IRain :1, '    ', Drug :1, '    ', PCattle :1, '       ',   SCattle:1);
  S1 := 0.0;
  S2 := 0.0;
  S3 := 0.0;
  S4 := 0.0;
  S5 := 0.0;
```

```
    Chg := 0;
    Treat := 0.0;
    DCom := 0.0;
    if (Chg = 0) and (Frame = 1) then UnDisturbed;
    if (Chg = 0) and (Frame = 2) then PartDisturbed;
    if (Chg = 0) and (Frame = 3) then Disturbed;
    if (DCom >  3.0) then DCom := 3.0;
    if (DCom <  0.0) then DCom := 0.0;
    if (CntDry = 10) then CntDry := 0;
    if (CntWet = 10) then CntWet := 0
  end; {Process Year}

  Procedure DoOneYear;
  {processes data line for one year;
   pre :  CntY is the number of the year being processed. The file-position
          pointer for InData is at the start of a data line.
   post:  A report for one year is written to the output file. The file-
          position pointer has been advanced to start of next line.
  }
  begin {DoOneYear}
    YNumber;
    IRain := 0;
    IDry := 0;
    Drug := 0;
    PCattle := 0;
    SCattle := 0;
    While not (EOLN(InData)) do
    ProcessYear;
    Writeln ('community value in year ', CntY :1, ': ', DCom :4:2); {for testing}
    Write (OutData, '        ', Frame :1, '     ', DCom :4:2);
    Writeln (OutData, '   ', Clim :4:2, '    ', Treat :4:2);
  end; {DoOneYear}

  begin {main}
    Assign (InData,  'B:random.TXT');
    Assign (OutData, 'B:\OUTDATA.TXT');
    Reset (InData);
    Rewrite (OutData);
    Writeln (OutData, 'frame: 1,2,3 = undisturbed, partially disturbed, disturbed');
    Writeln (OutData, 'dry season: 1,2 = normal,long');
    Writeln (OutData, 'rainfall: 1,2,3 = low, normal, high');
    Writeln (OutData, 'treatment: 0,1,2,3 = none, once, twice, three times a year');
    Writeln (OutData, 'proportion of cattle: 1,2 = selected animals, herd');
    Writeln (OutData, 'surrounding cattle: 1,2 = treated, untreated');
    Writeln (Outdata);
    Writeln (Outdata);
    Startup;
    Frame := SFrame;
    Clim := SClim;
    Tables;
    Cycle := 0;
    CntDry := 0;
    CntWet := 0;
    CntY := 0;
    Writeln (OutData, '        Frame CValue Climate Treatment DrySea Rain Drug PCattle
SCattle');
```

```
  for I := 1 to 3 do Count[I] := 0;
  while not EOF(InData) do  {process all years}
    begin {while}
      CntY := CntY + 1;
      DoOneYear;
      Count[Frame] := Count[Frame] + 1;
      Writeln (' Year ', CntY :2, ' processed');
    end {while};
  Writeln (OutData);
  Writeln (OutData);
  Writeln (OutData, '    UD    PD     D');
  for I := 1 to 3 do write (OutData, Count[I] :6);
  Writeln;
  Close (InData);
  Close (OutData)
end. {main}
```

Appendix 6b.

An example of an input file: the values in the first row determine, from left to right, the starting frame, the type of climate (i.e. user input (1) vs. random (2)) and the starting climate value. The following rows present, from left to right, the input for the length of dry season, amount of rainfall, drug usage, proportion of cattle treated in a herd and condition of surrounding cattle. In case of random climate generation only the last three parameters are given. For definition of input variables see Chapter 4.

```
1 1 0.00
Year 1/   2 1 1 2 1
Year 2/   2 1 1 2 2
Year 3/   2 1 1 2 1
Year 4/   1 2 1 2 2
Year 5/   1 2 1 2 1
Year 6/   1 2 1 2 2
Year 7/   2 1 1 2 1
Year 8/   2 1 1 2 2
Year 9/   2 1 1 2 1
Year 10/  1 2 1 2 2
Year 11/  1 2 1 2 1
Year 12/  1 2 1 2 2
```