ISSN 0067-9208

NAVORSINGE VAN DIE NASIONALE MUSEUM

BLOEMFONTEIN

NATURAL SCIENCES

VOLUME 5, PART 12 NOVEMBER 1986

PERIODICITY IN AND ECOLOGICAL EQUIVALENCE BETWEEN THE GROUND-LIVING TENEBRIONIDAE (COLEOPTERA) IN THE SOUTHERN NAMIB AND KALAHARI ECOSYSTEMS WITH NOTES ON PHYLOGENETIC RELATIONSHIPS

by

SCHALK LOUW

National Museum, Bloemfontein

(With 6 figures)

ABSTRACT

Louw, Schalk. 1986. Periodicity in and ecological equivalence between the ground-living Tenebrionidae (Coleoptera) in the southern Namib and Kalahari ecosystems with notes on phylogenetic relationships. *Navors. nas. Mus., Bloemfontein* 5(12): 301-324. Relationships between the ground-living Tenebrionidae recorded in the southern Namib and Kalahari are investigated. Relationships within each of the ecosystems are presented from a seasonal and diel periodicity point of view, the latter in relation to habitat occupancy. Relationships between the two systems were studied primarily from an ecological equivalence point of view with brief mention of phylogenetic connection. Subsequent results, especially with regard to specialization, species commonness and ecological equivalence, give rise to brief discussions on the historic development of the two regions. **(Coleoptera: ground-living Tenebrionidae; Southern Namib and Kalahari; Ecology).**

ISBN 1 947014 22 5

CONTENTS

INTRODUCTION

In Buckley (1981), dune system parallels between the southern Kalahari and central Australia are described and the strong similarity in soil patterns, vegetation structure, plant life-forms and herbivorous fauna between the two ecosystems is pointed out. On a similar basis and as an initiation of comparative studies between specifically ground-living Coleoptera faunas in southern Africa, aspects of spatial and temporal distribution between the ground-living Tenebrionidae of the arid southern Namib and Kalahari were investigated by Louw (1983). That paper, in essence, only presented lists of where and when the different species occur in the two different biomes. Another paper concerning this topic (Louw 1984) very briefly noted some of the comparisons between the two faunas. With the present contribution, which is largely an elaboration of the 1984 paper, the main aim is to present some of the details concerning the ecological relationships between the faunas of the two areas and thereby point out some of the similarities and differences between the two dunefield ecosystems. Brief mention is also made of phylogenetic relationship.

To avoid unnecessary repetition, none of the microhabitat definitions and species lists presented in Louw (1983) are included in this paper. It must, therefore, be noted that the present paper is to be considered as a sequel to the 1983 publication and as such the two must be read in conjunction.

FAUNAL RELATIONSHIPS

Any ecosystem consists of physical and biotic components (*sensu* Clements and Shelford 1939) which are in constant interaction with one another in more or less definable patterns. These patterns of interaction were investigated as far as time-space niches of the ground-living Tenebrionidae of the two study sites (See Louw 1983, Figure 1) are concerned, and are subsequently compared between the sites.

INTERRELATIONSHIPS WITHIN SYSTEMS

The interrelationships of time and place of activity between members of a community are, together with other factors of co-existence, important for the survival of the individual members as well as for the maintenance of homeostasis of the system in general (see Andrewartha & Birch 1954; Clarke, Geier, Hughes & Morris 1967; Odum 1971; Krebs 1972).

To simplify the interpretation of the interrelationships in time and place between the ground-living Tenebrionidae within the same system, an ecosystem periodicity pattern is discussed below. During the period of one year four main seasons can be distinguished, namely summer, spring, winter and autumn (Odum, *op. cit.* proposed six seasons, but these seasons are only important where systems are strongly based on primary production, while in this case the climate regime is the most important variable). Superimposed on seasonal patterns are the diel temporal patterns of activity which may be crudely divided into diurnal and nocturnal periods. In most systems these time niches are further subdivided into specific periods of activity within the day or night hours and these very specific time niches are often directly controlled by changing temperature and moisture conditions. This was the case, for instance, during heavily overcast days when day temperatures were relatively low. During times like these shifts in activity cycles occurred and members of the nocturnal fauna were active during the daylight hours, *e.g. Eurychora, Stips dohrni* and *Stipsostoma sculpta* of the Namib fauna. Furthermore, the seasonal and diel periodicities form a pattern within the context of habitat niches which, in the case of an apterous, ground-living fauna, is primarily based on the type of substrate.

Namib

In the Namib ecosystem the family Tenebrionidae was by far the most numerous and diverse Coleopteran family recorded (see Louw 1983, Figure 6). The other families were recorded in very low numbers*, which suggest very low population densities. These families are therefore considered as insignificant elements in the niche pattern. It is realised, however, that they contribute to the overall diversity and homeostasis of the system.

(i) Seasonal periodicities. (see Louw 1983, Figures 11 & 12)

The majority of the species recorded from the Namib are not very strictly seasonal. Many of them do, however, have peak abundances during a specific season. In Louw 1983 these

* NOTE: It is realized that low numbers could also mean low susceptability to pitfall-trapping, *e.g.* species which seldom emerge from the sand will have a low incidence, but may in fact be quite common. To compensate for this, intensive manual collecting was also conducted. Numbers encountered in this manner did not differ significantly from those recorded by pitfall-trapping.

seasonal periodicities are dealt with under the subheading 'Distribution in time' on page 45. Here they are presented in Table 1. These species with clear-cut seasonal tendencies show well definable intrageneric seasonal displacement in *Onymacris, Zophosis* and *Lepidochora.*

Several species are fairly abundant the whole year round *viz. Zophosis (Gyrosis) moralesi, Zophosis (Protodactylus) giessi, Onymacris plana plana, Eurychora, Stips stali* and *Gonopus.* In a few species the data were insufficient for interpretation.

(ii) Diel periodicity (see Louw 1983, Figures 10, 11 & 12)
The majority (60,5%) of the ground-living Namib Tenebrionidae are nocturnal. The diel periodicity of the species of every microhabitat (see Louw 1983: 37) is considered separately in Table 2. Most of the species classified as nocturnal or diurnal in this table, have further specialised activity periods *e.g.* bimodal and unimodal, and these further serve to segregate time-niches within the same or overlapping habitat-niches. The exact diel activity of the most common and second most common (*re* Price 1975) nocturnal and diurnal species (see Table 3) is graphically presented in Figure 1 to illustrate these differences and how they may permutate through the seasons.

TABLE 1

SEASONAL PERIODICITY IN THE GROUND-LIVING TENEBRIONIDAE AT STUDY SITE IN NAMIB ECOSYSTEM

Season	Species
Winter	*Zophosis (Zophosis) omnigena*
	Onymacris boschimana subelongata
	Somaticus planatus drukeri
	Sulcipectus levis
	Uniungulum hoeschi
	Pterostichula aridipaludis
	Oxura rufotibiata planipennata
Spring	*Zophosis (Zophosis) hypallaga*
	Archinamibia peezi
	Lepidochora porti
Summer	*Asphaltesthes impressipennis*
	Vernayella pauliani
Autumn	*Zophosis (Zophosis) fortunata*
	Zophosis (Cerosis) hereroensis
	Onymacris rugatipennis albotessellata
	Stipsostoma sculpta
	Arthrochora arenicola
	Lepidochora discoidalis
	Pachynotelus comma nivea
	Drosochrus sp.

The nocturnal species *Eurychora* and *Gonopus* were present in all the microhabitats except the dune crest.

TABLE 2

DIEL PERIODICITY IN THE GROUND-LIVING TENEBRIONIDAE AT STUDY SITE IN NAMIB ECOSYSTEM

Microhabitat	Species	
	Nocturnal	Diurnal
Dune crest	*Archinamibia peezi* *Lepidochora porti*	*Zophosis (Cerosis) hereroensis*
Slipface	*Lepidochora discoidalis* *Vernayella pauliani*	
Vegetated plinth	*Stips stali* *Arthrochora arenicola* *Uniungulum hoeschi* *Pterostichula aridipaludis* *Oxura rufotibiata planipennata* *Namibomodes maculicollis* *Caenocrypticus deserticus*	*Onymacris plana plana* *Onymacris rugatipennis albotessellata* *Pachynotelus comma nivea* *Fossilochile rufa*
Grassy plain	*Phanerotomea* sp. *Psammodes vialis* *Planostibes* sp.	*Onymacris boschimana subelongata* *Metriopus (Metriopus) depressus* *Cauricara (Cauricara) phalangium rufofemorata*
Open gravel plain	*Stipsostoma sculpta* *Sulcipectus levis* *Drosochrus* sp.	*Zophosis (Zophosis) hypallaga* *Zophosis (Zophosis) fortunata* *Zophosis (Zophosis) omnigena* *Eustolopus octoseriatus* *Cauricara (Cauricara) phalangium rufofemorata* *Somaticus planatus drukeri*

Kalahari

As in the Namib, the family Tenebrionidae of the Kalahari ecosystem was the most abundant and diverse group recorded during the survey (see Louw 1983, Figure 6). During certain times of the year, however, representatives of other Coleopteran families were also recorded in considerable densities. These other Coleopteran families, of which ground-living species were recorded during the survey, are Carabidae, Curculionidae and Alleculidae (see Table 4). The species of the former two families were recorded in combined densities that compared well with those of the Tenebrionidae. Alleculidae were only present in very low numbers.

TABLE 3

DOMINANT GROUND-LIVING COLEOPTERA AT STUDY SITE IN NAMIB ECOSYSTEM. NUMBERING SYSTEM OF MICROHABITATS AS GIVEN IN GENERALISED MICROHABITAT DIAGRAM (LOUW 1983, FIGURE 2); PERCENTAGES OF TOTAL POPULATIONS ENCOUNTERED IN EACH MICROHABITAT ARE GIVEN IN PARENTHESIS

I. Most common diurnal species

Time of year	**Species**	**Individuals and percentages per microhabitat**						
		A	**B**	**C**	**D**	**E**	**F**	**G**
Spring	*Zophosis hypallaga* (Tenebrionidae)						66(23)	227(77)
Summer	*Zophosis hypallaga* (Tenebrionidae)						39(35)	71(65)
Autumn	*Onymacris boschimana subelongata* (Tenebrionidae)	2(1)			8(4)	2(1)	97(49)	90(45)
Winter	*Onymacris boschimana subelongata* (Tenebrionidae)				49(6)	59(7)	636(77)	78(9)

II. Second most common diurnal species

Time of year	**Species**	**Individuals and percentages per microhabitat**						
		A	**B**	**C**	**D**	**E**	**F**	**G**
Spring	*Zophosis moralesi* (Tenebrionidae)				3 (2,5)	1(1,5)	66(56)	46(40)
Summer	*Zophosis moralesi)* (Tenebrionidae)						62(67)	30(33)
Autumn	*Zophosis hypallaga* (Tenebrionidae)				3(2)		47(34)	87(63)
Winter	*Zophosis hypallaga* (Tenebrionidae)					1(7)	9(64,5)	4(28,5)

III. Most common nocturnal species

Time of year	**Species**	**Individuals and percentages per microhabitat**						
		A	**B**	**C**	**D**	**E**	**F**	**G**
Spring	*Vernayella pauliani* (Tenebrionidae)	25(78)	7(22)					
Summer	*Vernayella pauliani* (Tenebrionidae)	22(14)	200(83)	7(3)				
Autumn	*Lepidochora discoidalis* (Tenebrionidae)	128(92)	10(7)	1(1)				
Winter	*Lepidochora discoidalis* (Tenebrionidae)	79(67)	39(33)					

Table 3 (continued)

IV. Second most common nocturnal species

Time of year	Species	Individuals and percentages per microhabitat A	B	C	D	E	F	G
Spring	*Lepidochora discoidalis* (Tenebrionidae)	17(28)	7(28)	1(4)				
Summer	*Stips stali* (Tenebrionidae)	9(37,5)		3(12,5)	11(46)		1(4)	
Autumn	*Vernayella pauliani* (Tenebrionidae)	14(30)	30(65)	2(4)				
Winter	*Uniungulum hoeschi* (Tenebrionidae)		1(2,5)	1(2,5)	2(5)	4(10)	18(45)	14(35)

(i) Seasonal periodicities (see Louw 1983, Figures 7 & 8)

Only a small number of apterous Tenebrionidae species, mostly of the winter fauna, proved to be strictly seasonal in their occurrence. The rest of the species were active during more than one of the seasons, but nevertheless still had distinct peaks of activity in one season only. In Louw 1983 seasonality was mentioned under the subheading 'Distribution in time' on page 43. Here they are presented in Table 5. These seasonal species show clearly definable intrageneric seasonal displacement occurring in *Zophosis, Stips, Tarsocnodes* and *Diestecopus*. In addition, by far the greatest number of species from the ecosystem are active in winter with a strict winter preference almost exclusively present in members of the Molurini (see Louw 1983, Table 2).

A few species are relatively abundant throughout the year (*viz. Zophosis (Heliophosis) kalaharica, Stenocara kalaharica, Herpiscius* and two unidentifiable species of *Gonopus).* In quite a number of species the data were inadequate for analysis.

(ii) Diel periodicity (see Louw 1983, Figures 7, 8 & 9)

As in the Namib, the majority (± 62%) of the species are nocturnal. Diel periodicity data are presented in Table 6 for each separate microhabitat (see Louw 1983: 37, 38) and it can be seen that alternating activities occur in practically all the microhabitats, except in the thorn bush dune top microhabitat. The hard, sandy 'Rhigozum' plain microhabitat covers the largest part of the survey area and had the greatest number of alternating species in the system.

Certain diurnal (*Somaticus aeneus* and *S. incostatus*) and nocturnal (*Pterostichula arenicola* and *Gonopus* (sp. 1)) species occur in approximately equal densities in all the plain microhabitats and time-niche displacement between them and the different species of each plain microhabitat consequently occurs. Nocturnal *Eurychora* and *Parastizopus armaticeps* are very euryoecious and therefore probably influence time-niches of the species of all the microhabitats where they occur.

In contrast to the situation in the Namib where the most common and second most common (*re* Price 1978) species (see Table 7) are always members of the Tenebrionidae, their counterparts in the Kalahari are in many cases members of the Carabidae and, in one case,

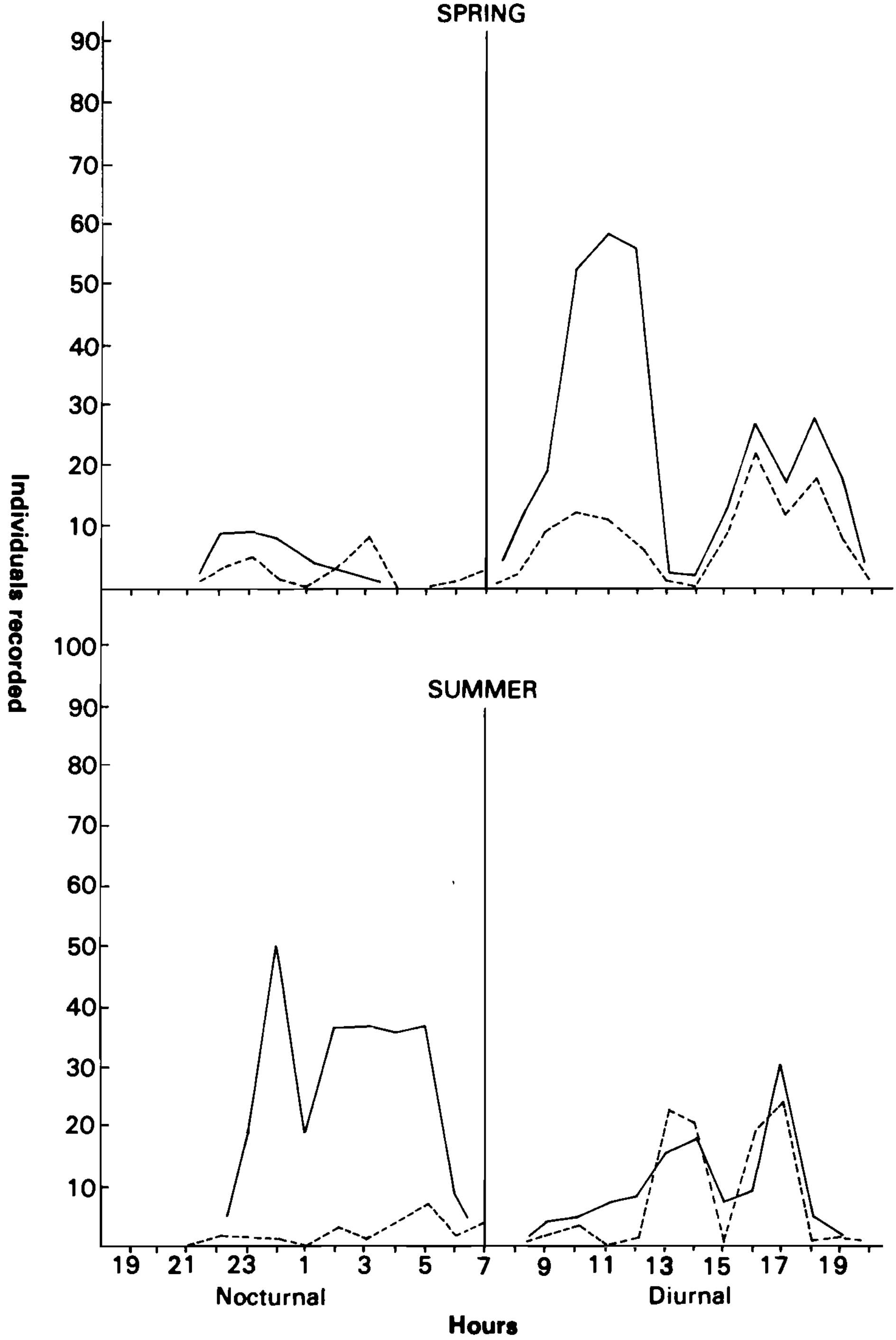

Figure 1: Diel activity of most common (———) and second most common (- - - -) nocturnal and diurnal apterous Tenebrionidae (see Table 1) from the study site in the Namib.

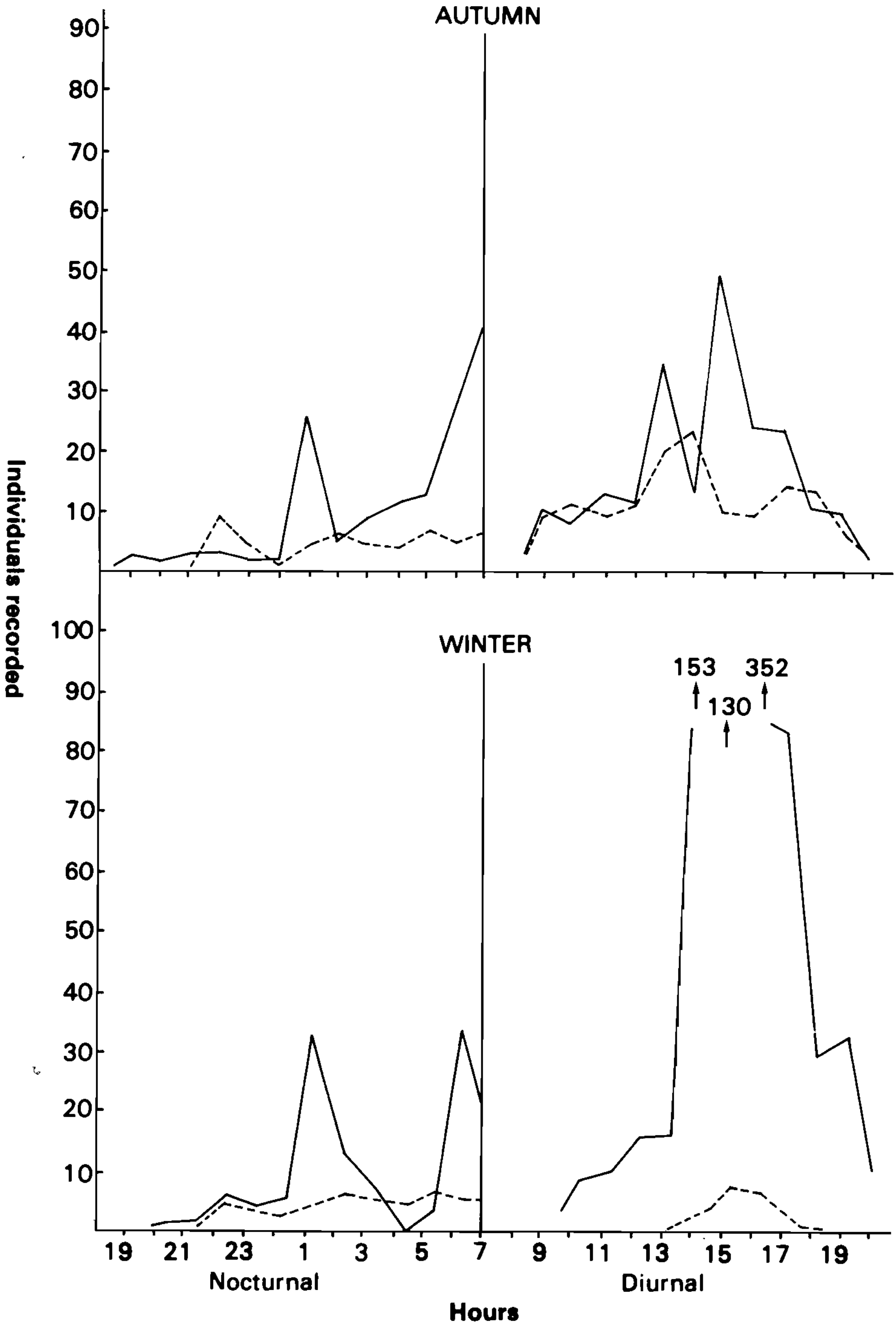

Figure 1 (continued)

TABLE 4

GROUND-LIVING COLEOPTERA, OTHER THAN TENEBRIONIDAE, RECORDED AT STUDY SITE IN KALAHARI

CARABIDAE	*Passalidium* sp.
	Platymetopus figuratus
	Cypholoba opulenta
	C. fritschi
	C. alstoni
	Baeoglossa melanaria
	Microlestia immerita
	Anthia thoracica
	Thermophilum homoplatum
	Thermophilum sp.
	Graphipterus marginatus
	G. bilineatus
	Crepidogastrinus kochi
	Crepidogaster kochi
CURCULIONIDAE	*Brachycerus* sp.
	Gyllenhalia crinita
	Spartecerus sp.
	Episus inermicollis
	Microcerus latipennis
	Microcerus costalis
	Siderodactylus sp.
	Hyomora kochi
	H. ditissima
	Ocladius sp.
	Cleonus sp.
	Neocleonus sp.
	Leptostethus sp.
	Philetaerobius nidicola
ALLECULIDAE	Gen. & sp. indet.

also of the Curculionidae. In Figure 2 the detailed diel activities of the most common and second most common species are plotted in terms of abundance related to time and the particular activity peaks within the diel period show up clearly.

INTERRELATIONSHIPS BETWEEN NAMIB AND KALAHARI

Although the Namib and Kalahari ecosystems are widely separated, absolute isolation between the two does not occur. The area between the two systems, namely the southern central transitional region (Penrith, 1977) has several isolated dune areas which could be surveyed for trends in the apterous faunas. Two other possibilities offer themselves for assessing historical and present links between the two ecosystems. The first is to establish ecological equivalents in the two systems and to determine the degree of relationship of these, and the second is to compare the taxonomic composition and degree of relationship of the two faunas as such.

TABLE 5

SEASONAL PERIODICITY IN THE GROUND-LIVING TENEBRIONIDAE AT STUDY SITE IN KALAHARI ECOSYSTEM

Season	Species
Winter	*Zophosis (Zophosis) permiscens*
	Onymacris multistriata
	Physosterna torulosa
	Renatiella scrobipennis
	Stenocara brevicollis brevicollis
	Stips dohrni
	Cimicichora hessei
	Platyphanus similis
	Cryptochile consita
	Somaticus aeneus
	Somaticus planatus planatus
	Somaticus regalis
	Somaticus strangulatus
	Somaticus fitzsimonsi
	Somaticus incostatus
	Pterostichula arenicola
	Pterostichula dubia
	Oxura rufotibiata rufotibiata
	Tarsocnodes tarsalis
	Nicandra sp.
	Diestecopus sp. 2
Spring	*Epiphysa flavicollis*
	Stenocara kalaharica
Summer	*Zophosis (Zophosis) amita*
	Parastizopus armaticeps
Autumn	*Zophosis (Zophosis) jacoti*
	Metriopus (Metriopus) hoffmannsseggi
	Eurychora sp.
	Stips gebieni
	Iugidorsum cumstriis cumstriis
	Decoriplus hieroglyphicus
	Tarsocnodes madida
	Phanerotomea sp.
	Psammodes vialis
	Amiantus sp.
	Diestecopus sp. 1

TABLE 6

DIEL PERIODICITY IN GROUND-LIVING TENEBRIONIDAE AT STUDY SITE IN KALAHARI ECOSYSTEM

Microhabitat	Species Nocturnal	 Diurnal
Grass-shrub dune top	*Tarsocnodes tarsalis* *Herpiscius* sp.	*Zophosis (Heliphosis) kalaharica* *Onymacris multistriata*
Thorn bush dune top	*Miripronotum prominoculatum* *Eremostibes opacus*	
Vegetated plinth	*Pterostichula dubia* *Oxura rufotibiata rufotibiata* *Gonopus* sp. 1 *Diestecopus* sp. 1	*Zophosis (Zophosis) jacoti* *Stenocara kalaharica* *Somaticus regalis*
Dune base		*Somaticus fitzsimonsi*
Grassy plain	*Platyphanus similis* *Tarsocnodes madida*	*Decoriplus hieroglyphicus*
Rhigozum plain	*Stips dohrni* *Iugidorsum cumstriis* *Planostibes cf. cribricollis* *Amathobius mesoleius* *Stenolamus kalaharicus* *Cheirodes* sp. *Drosochrus* sp. *Nicandra* sp. 1 *Nicandra* sp. 2 *Diestecopus* sp. 2	*Zophosis (Zophosis) permiscens* *Renatiella scrobipennis* *Metriopus (Metriopus) hoffmannseggi* *Somaticus planatus planatus* *Somaticus strangulatus*
Calcrete-gravel plain	*Amiantus* sp.	*Zophosis (Zophosis) amita* *Physosterna torulosa* *Stenocara brevicollis brevicollis* *Stenocara gracilipes* *Cryptochile consita*

Ecological equivalence

Although the species composition of the Kalahari and Namib ecosystems differ extensively, the physical habitat of the two systems is very similar, *i.e.* low rainfall and high temperatures (decisive limiting factors), similar substrates (decisive for habitat-niches) and a topography consisting of dunes and interdune plains. This implies that similar niches are available in the two systems and that ecological equivalents may be expected. For the purpose of this study, only the apterous, ground-living detritivorous - phytophagous Tenebrionidae were investigated and a relatively large number of equivalents were recorded (see Table 8). In two cases a Kalahari species was found to have two Namib counterparts.

TABLE 7

DOMINANT GROUND-LIVING COLEOPTERA AT STUDY SITE IN KALAHARI ECOSYSTEM. NUMBERING SYSTEM FOR MICROHABITATS AS GIVEN IN GENERALISED MICROHABITAT DIAGRAM (LOUW 1983, FIGURE 3); PERCENTAGES OF TOTAL POPULATION ENCOUNTERED IN EACH MICROHABITAT ARE GIVEN IN PARENTHESIS.

I. **Most common diurnal species**

Time of year	Species	Individuals and percentages per microhabitat						
		A	B	C	D	E	F	G
Spring	*Graphipterus marginatus* (Carabidae)			23(9,5)	3(1)	3(1)	184(77)	25(10,5)
Summer	*Zophosis amita* (Tenebrionidae)		2(2)	57(54)	11(10)	7(6)	25(23)	6(5)
Autumn	*Metriopus hoffmannseggi* (Tenebrionidae)		4(1)	51(15)	23(7)	8(2)	155(45)	102(30)
Winter	*Somaticus aeneus* (Tenebrionidae)	3(2)	3(2)	29(19)	10(7)	11(7)	77(51)	17(11)

II. **Second most common diurnal species**

Time of year	Species	Individuals and percentages per microhabitat						
		A	B	C	D	E	F	G
Spring	*Philetaerobius nidicola* (Curculionidae)		3(2)	17(11)	12(8)	55(37)	61(41)	2(1)
Summer	*Zophosis permiscens* (Tenebrionidae)			2(7,5)			21(81)	3(11,5)
Autumn	*Somaticus aeneus* (Tenebrionidae)	3(1)	15(5)	33(12)	11(4)	21(7,5)	136(49)	55(20,5)
Winter	*Onymacris multistriata* (Tenebrionidae)	80(81)	7(7)	12(12)				

III. **Most common nocturnal species**

Time of year	Species	Individuals and percentages per microhabitat						
		A	B	C	D	E	F	G
Spring	*Microlestia immerita* (Carabidae)	5(4,5)	16(14)	17(15)	6(5,5)	21(20)	37(33)	9(8)
Summer	*Microlestia immerita* (Carabidae)	3(3)	21(20)	15(14)	9(8,5)	21(20)	27(26)	8(7,5)
Autumn	*Iugidorsum cumstriis* (Tenebrionidae)	1(1)		4(4,5)	3(3,5)	4(4,5)	47(55)	26(30,5)
Winter	*Pterostichula arenicola* (Tenebrionidae)			9(19,5)	4(8,5)		32(70)	1(2)

Table 7 (continued)

IV. Second most common nocturnal species

Time of year	Species	Individuals and percentages per microhabitat						
		A	B	C	D	E	F	G
Spring	*Cypholoba alstoni* (Carabidae)	21(42)	3(6)	17(34)	1(2)	5(10)	3(6)	
Summer	*Cypholoba alstoni* (Carabidae)	18(30)	21(35)	10(16,5)	3(5)		8(13,5)	
Autumn	*Microlestia immerita* (Carabidae)		14(24,5)	21(36,5)	7(12)	3(5)	6(10,5)	6(10,5)
Winter	*Tarsocnodes tarsalis* (Tenebrionidae)	37(95)	1(2,5)	1(2,5)				

Phylogenetic relationships

Because several of the common apterous Tenebrionidae of the Namib and the Kalahari have been rather intensively studied from a taxonomic point of view, phylogenetic bonds between the faunas of these two areas could be investigated and are briefly commented on.

A relatively high number of genera recorded from the Namib and Kalahari are common to both areas (see Table 9). Although many of these genera are widely distributed in southern Africa, some are endemic to the arid western part, which mostly consists of the Namib and Kalahari. Also presented in Table 9 are species that are common to both areas (it is believed that there are more than is presented here but they are not listed due to uncertainty regarding their taxonomic status). In one case (*viz. Stips dohrni namibensis*) the two areas also have a subspecies in common, whilst the other common species are all subspecifically different. Although the Namib and Kalahari each have several endemic species (see Table 9) which clearly separate them from one another, the occurrence of several common taxa, even down to the subspecific level, clearly indicates that there is also a definite faunistic relationship between the two areas. In Table 10,species exhibiting actual phylogenetic relationships are listed together with the authors in whose work this is discussed. These relationships are not always clear and phylogenetic polarity cannot be determined. It can be mentioned, however, that in some cases the Namib species is more apomorphic (*viz. Zophosis hypallaga* and *Z. permiscens*), whilst in other cases the Kalahari species is more apomorphic (*viz. Onymacris multistriata* and *O. boschimana subelongata*).

DISCUSSION

Each of the ecosystems here treated has a specific pattern based on distribution in time and place. In the Kalahari the ground-living Tenebrionidae revealed a relatively high degree of specialisation as far as the time-niche is concerned. Seasonal occurrences (especially in Molurini), diel preferences and modality are more orderly than is the case in the Namib (see Louw 1983 Tables 1 & 2 and Figures 7 & 8, 11 & 12). As far as the place niche is concerned, the Namib reveals a higher degree of specialisation than the Kalahari (see Tables 3 & 7 and Figures 3 - 6).

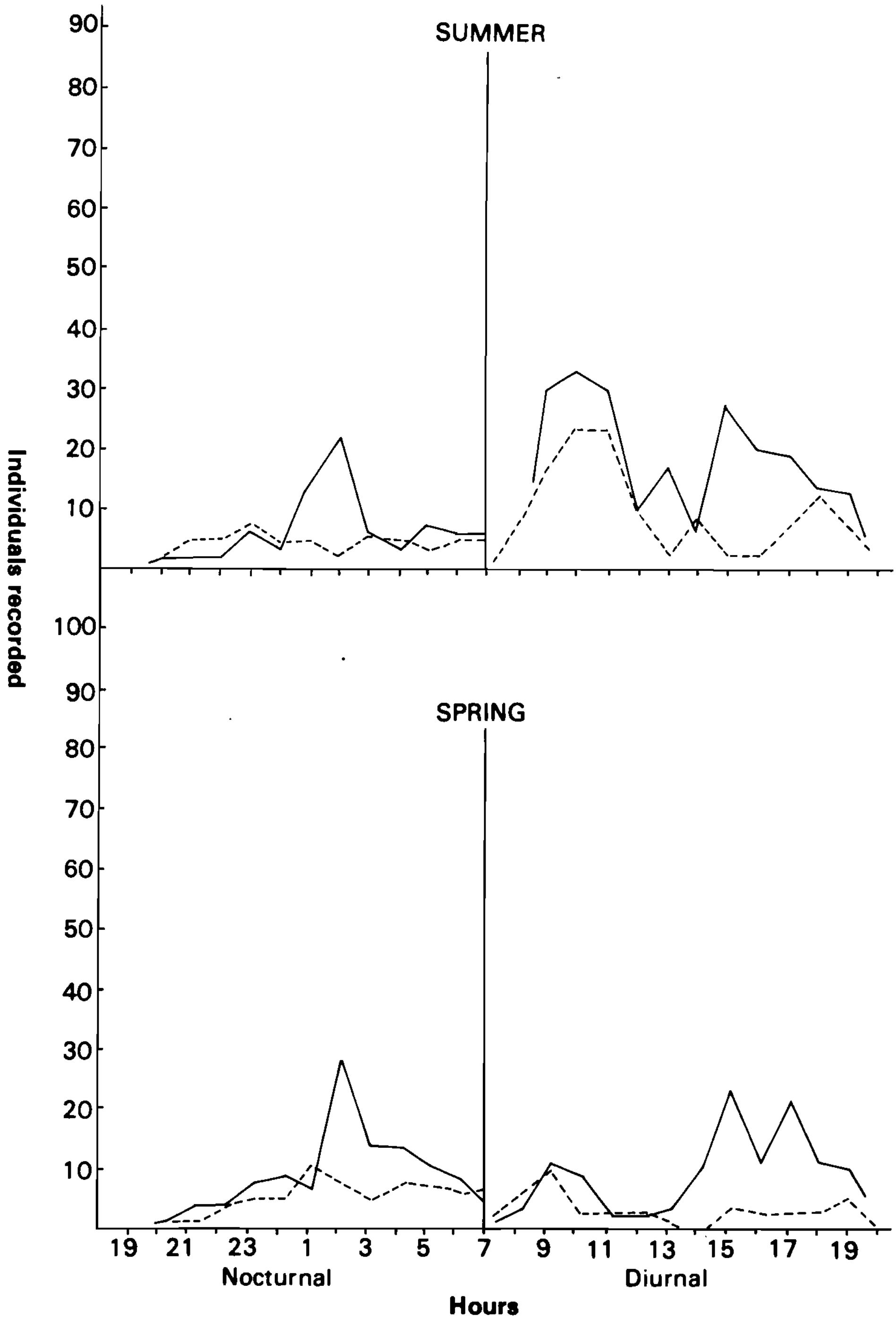

Figure 2: Diel activity of most common (———) and second most common (- - - -) nocturnal and diurnal apterous Coleoptera (see Table 3) from the study site in the Kalahari.

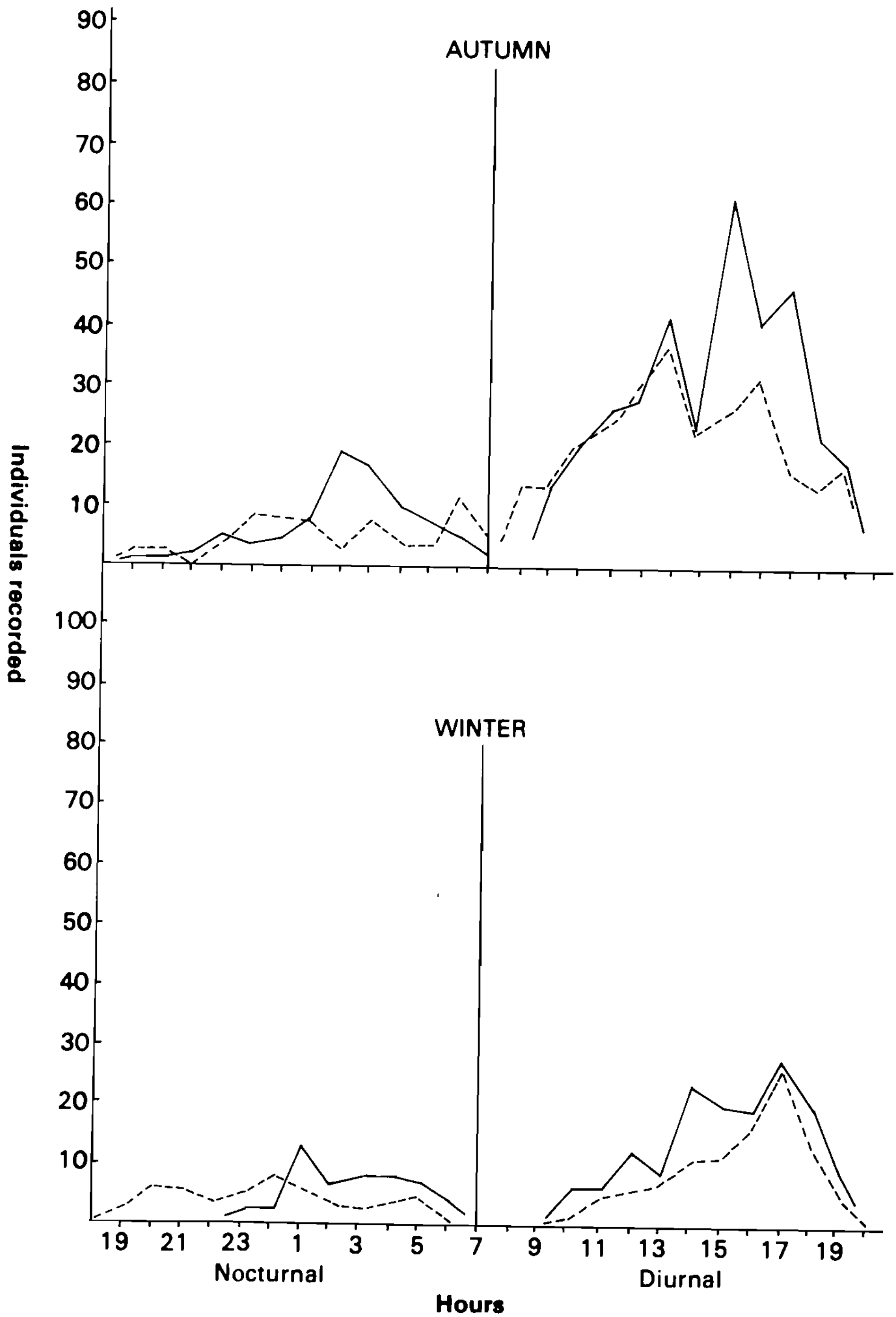

Figure 2 (continued)

TABLE 8

ECOLOGICAL EQUIVALENCE BETWEEN DETRITIVORIUS TENEBRIONIDS IN THE STUDY SITES OF THE NAMIB AND KALAHARI ECOSYSTEMS (PARTIALLY AFTER LOUW 1984)

Niche	Kalahari	Namib
Nocturnal; at base of plants on dune.	*Cimicichora hessei** (Eurychorini)	*Arthrochora arenicola** (Eurychorini)
Diurnal; sparsely vegetated dune crest.	*Zophosis (Zophosis) deyrollei jacoti*** (Zophosini)	*Zophosis (Cerosis) hereroensis** (Zophosini)
Nocturnal; dune crest.	*Tarsocnodes tarsalis*** (Molurini)	*Lepidochora discoidalis**; *Vernayella pauliani** (Eurychorini; Caenocryptocini)
Nocturnal; vegetated plinth.	*Miripronotum prominoculatum** (Molurini)	*Uniungulum hoeschi** (Molurini)
Diurnal; vegetated plinth.	*Somaticus regalis* (Adesmiini)	*Onymacris rugatipennis albotessellata*** (Adesmiini)
Diurnal; sparsely vegetated plinth.	*Onymacris multistriata*** (Adesmiini)	*Onymacris plana plana*** (Adesmiini)
Diurnal; sparsely vegetated plinth.	*Zophosis (Heliophosis) kalaharica*** (Zophosini)	*Zophosis (Gyrosis) orbicularis***; *Zophosis (Gyrosis) moralesi*** (Zophosini)
Winter; diurnal; vegetated plain.	*Metriopus (Metriopus) hoffmanseggi*** (Adesmiini)	*Onymacris boschimana subelongata*** (Adesmiini)
Summer; diurnal; vegetated plain.	*Renatiella scrobipennis*** (Adesmiini)	*Cauricara (Cauricara) phalangium rufofemorata*** (Adesmiini)
Autumn; nocturnal; vegetated plain.	*Iugidorsum cumstriis cumstriis** (Molurini)	*Sulcipectus levis** (Molurini)

* — Endemic genera

** — Endemic species/subspecies

TABLE 9

COMMON AND ENDEMIC GROUND-LIVING TENEBRIONIDAE OF STUDY SITES IN NAMIB AND KALAHARI ECOSYSTEMS

Common genera	Endemic Namib genera	Endemic Kalahari genera	Common species
*Zophosis**	*Archinamibia*	*Cimicichora*	*Stips dohrni*
Onymacris	*Eustolopus*	*Platyphanus*	*Somaticus planatus*
Physosterna	*Cauricara*	*Tarsocnodes*	*Oxura rufotibiata*
*Metriopus**	*Arthrochora*	*Miripronotum*	*Psammodes vialis*
*Eurychora**	*Lepidochora*		
Stips	*Fossilochile*		
Pterostichula	*Sulcipectus*		
Oxura	*Uniungulum*		
*Phanerotomea**	*Argenticrinis*		
*Psammodes**	*Namibomodes*		
*Gonopus**	*Caenocrypticus*		
*Planostibes**	*Vernayella*		
*Drosochrus**			

* — Genera widely distributed in southern Africa.

TABLE 10

HOMOLOGOUS SPECIALISTS IN THE GROUND-LIVING TENEBRIONIDAE OF THE STUDY SITES IN THE NAMIB AND KALAHARI ECOSYSTEMS, ACCORDING TO VARIOUS AUTHORS

Namib	Kalahari	Author
Zophosis hypallaga	*Zophosis permiscens*	Penrith, 1977
Zophosis fortunata *Zophosis omnigena*	*Zophosis amita*	Penrith, 1977
Somaticus planatus drukeri	*Somaticus planatus planatus*	Koch, 1955
Pterostichula fontanalis	*Pterostichula arenicola*	Louw, 1979
Pterostichula aridipaludis	*Pterostichula dubia*	Louw, 1979
Oxura rufotibiata planipennata	*Oxura rufotibiata rufotibiata*	Louw, 1979
Onymacris boschimana subelongata	*Onymacris multistriata*	Penrith, 1984

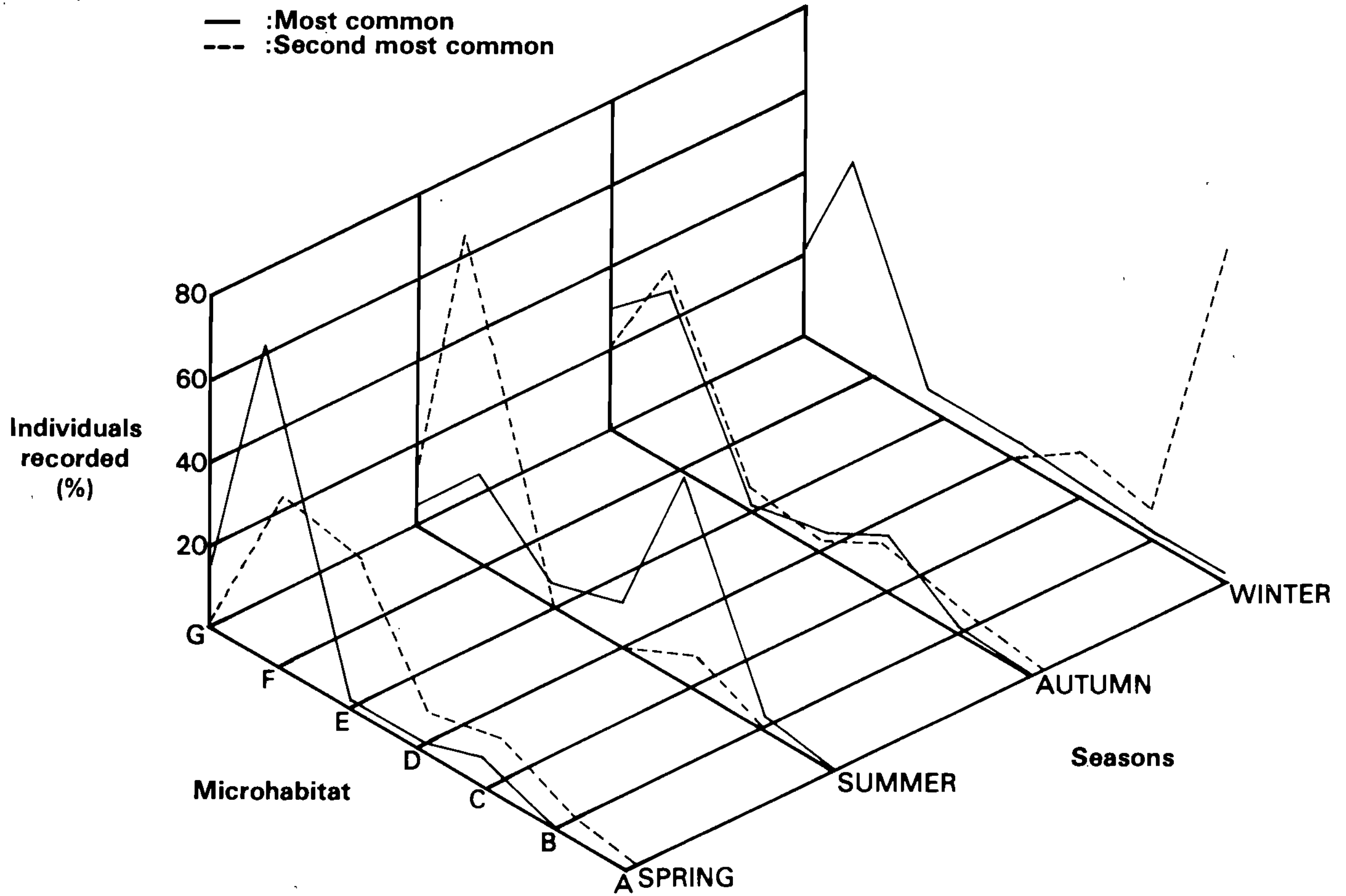

Figure 3: Seasonal distribution in microhabitats of the most common and second most common diurnal apterous beetle species in the Kalahari (see Table 1). Lettering of microhabitats corresponds to generalised microhabitat diagram (see Louw 1983, Figure 3).

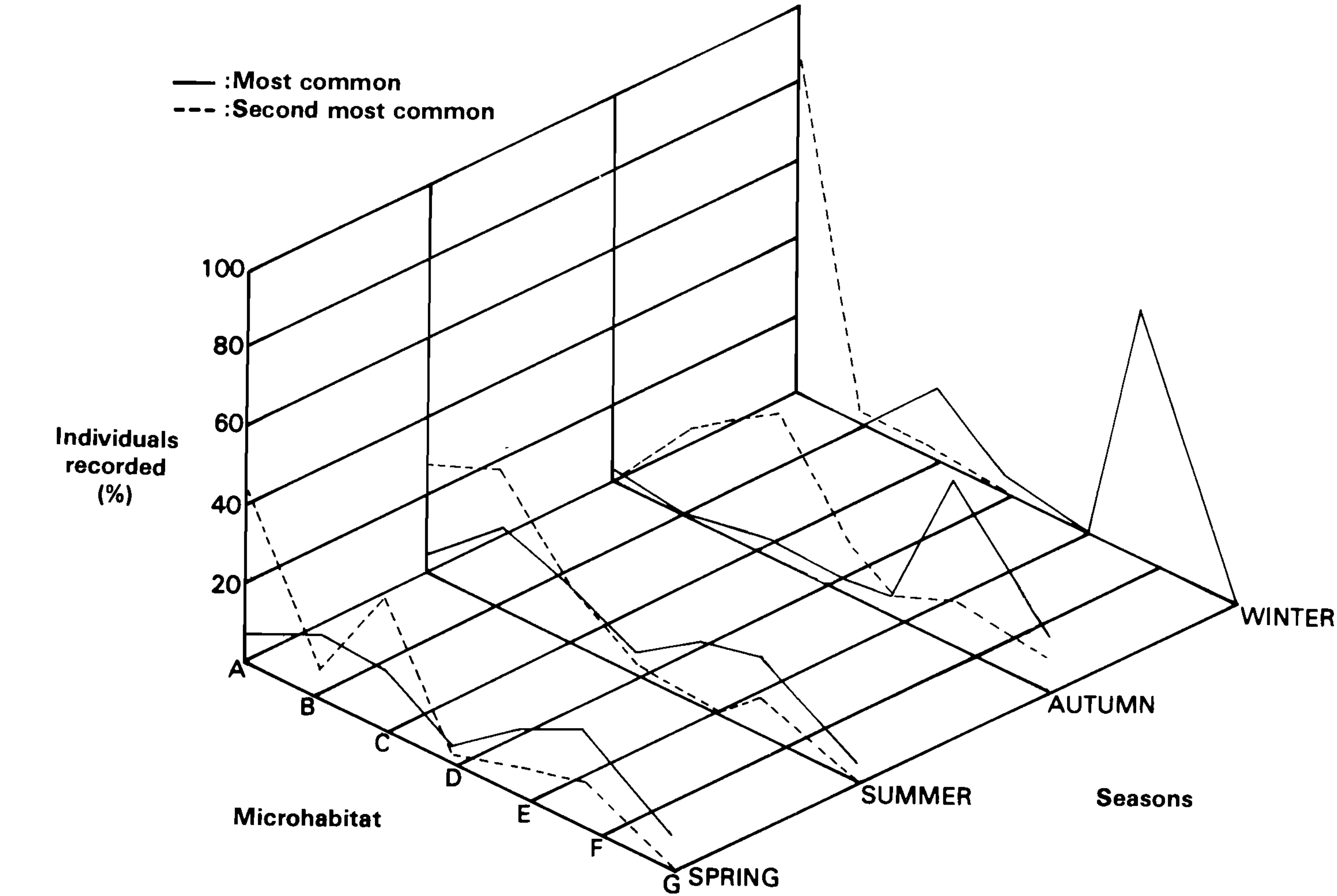

Figure 4: Seasonal distribution in microhabitats of the most common and second most common nocturnal apterous beetle species in the Kalahari (see Table 1). Lettering of microhabitats corresponds to generalised microhabitat diagram (see Louw 1983, Figure 3).

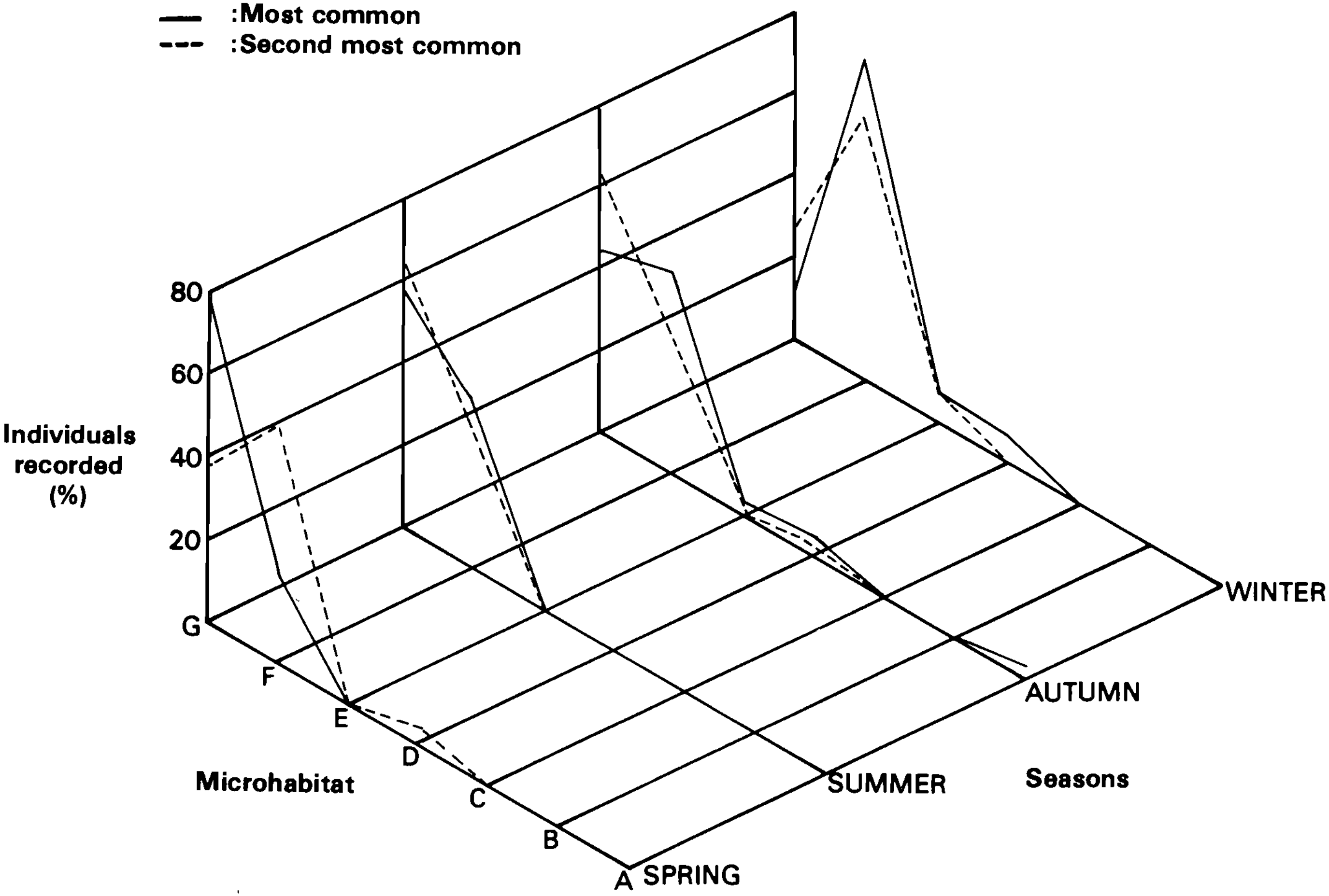

Figure 5: Seasonal distribution in microhabitats of the most common and second most common diurnal apterous beetle species in the Namib (see Table 3). Lettering of microhabitats corresponds to generalised microhabitat diagram (see Louw 1983, Figure 2).

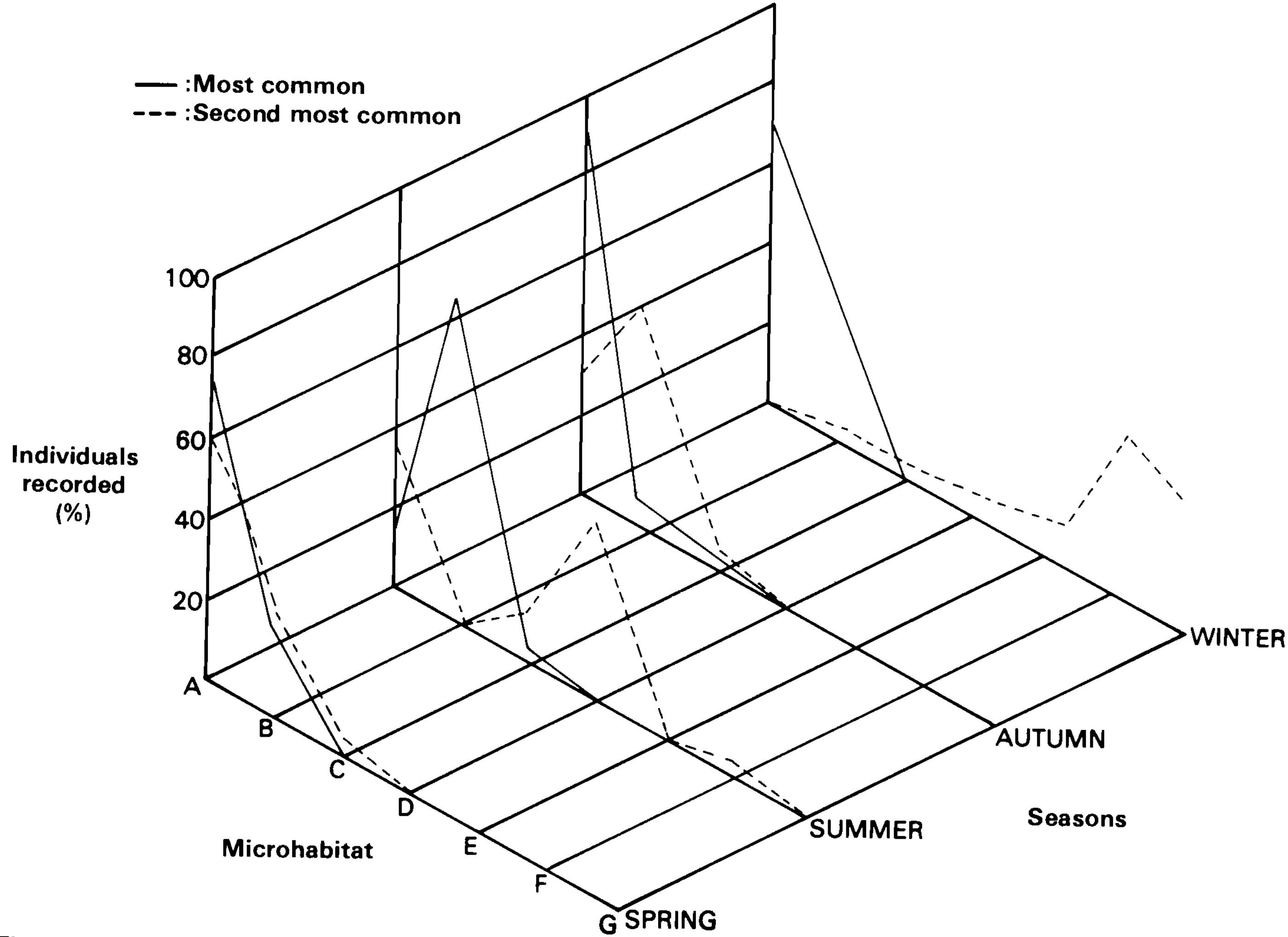

Figure 6: Seasonal distribution in microhabitats of the most common and second most common nocturnal apterous beetle species in the Namib (see Table 3). Lettering of microhabitats corresponds to generalised microhabitat diagram (see Louw 1983, Figure 2).

The high degree of ecological equivalence (Table 8) combined with homologous specializations of the apterous Tenebrionidae (Table 10), are important indications of a strong phylogenetic and ecological bond existing between the Namib and Kalahari ecosystems. Indicative of the closeness of this bond is the fact that taxonomic similarity of the ecological equivalents of these two systems is predominantly above genus and below tribe level.

The relatively strong overall resemblance between the two faunas as well as studies concerning relationships in the Tenebrionidae (in particular Penrith 1977, 1979, 1984) present considerable evidence that these faunas have a common origin. In this regard and by comparing the ecological equivalents of the two regions, it is believed that the faunas developed divergently from a common ancestral fauna rather than the Namib fauna being directly derived from that of the Kalahari.

According to Odum (1971) evaluation of community classification is primarily based on trophic and other functional levels. Ross (1982) and Price (1975) are more specific and stipulate that the level (or consumer layer) that can be attained in the ecological succession of a community is indicative of how stable such a community is. In the Kalahari ecosystem the most common species of the Coleoptera community fill three trophic levels, *viz.* saprofites (Tenebrionidae), phytophages (Curculionidae) and predators (Carabidae) (see Table 7), whilst in the Namib ecosystem the most common species are all only saprophites (Tenebrionidae) (see Table 3). The assumption is therefore that the Kalahari is the more stable ecosystem. The implication of this is not necessarily greater age, but rather that conditions are less harsh in the Kalahari than in the Namib (see Table 3, Louw 1983) and that the functional levels of the communities in these two areas are directly correlated with environmental conditions. Disorderly niche specialization by the ground-living Tenebrionidae of the Namib (see above) augments the view that this area is more fragile than the Kalahari.

OPSOMMING

Verwantskappe tussen die grondlewende Tenebrionidae (Coleoptera) wat in die suidelike Namib en Kalahari ekosisteme versamel is, is ondersoek. Verwantskappe binne elk van die sisteme word aangebied vanuit 'n seisoens- en 24-uurse periodisiteitsoogpunt, laasgenoemde met verwysing na habitatsbesetting. Verwantskappe tussen die twee sisteme is ondersoek, hoofsaaklik vanuit 'n ekologiese ekwivalensie oogpunt. Daar word ook kortliks na filogenetiese skakeling verwys. Die gevolglike resultate, veral wat betref spesialisering en ekologiese ekwivalensie en -suksessie gee aanleiding tot kort besprekings oor die historiese ontwikkeling van die twee gebiede.

ACKNOWLEDGEMENTS

I am grateful to Prof. C.H. Scholtz (Department of Entomology, University of Pretoria), Dr S. Endrödy-Younga (Department of Coleoptera, Transvaal Museum, Pretoria), Mr J. Irish (State Museum, Windhoek) and especially Dr M-L. Penrith (Department of Coleoptera, Transvaal Museum, Pretoria) for critically reading the manuscript and for advice which led to its improvement. Miss Annamé van Rensburg is thanked for assisting with the preparation of the figures.

The Council, Director and Assistant Director of the National Museum, Bloemfontein are thanked for permission to publish this manuscript.

REFERENCES

ANDREWARTHA, H.G. & BIRCH, L.C. 1954. *The distribution and abundance of animals.* Chicago: University Chicago Press.

BUCKLEY, R.C. 1981. Parallel dunefield ecosystems: southern Kalahari and central Australia. *Journal of Arid Environments* 4: 287-298.

CLARK, L.R., GEIER, P.W., HUGHES, R.D. & MORRIS, R.F. 1967. *The ecology of insect populations in theory and practice.* London: Methuen & Co., Ltd.

CLEMENTS, F.E. & SHELFORD, V.E. 1939. *Bio-ecology.* New York: John Wiley & Sons.

KOCH, C. 1955. Monograph on the Tenebrionidae of southern Africa. Vol. I: Tentyriinae, Molurini, Trachynotina, *Somaticus. Transvaal Museum Memoirs* 7: 1-242.

KREBS, C.J. 1972. *Ecology. The experimental analysis of distribution and abundance.* London: Harper & Row Publishers.

LOUW, S. 1979. A partial revision of the subtribes Oxurina and Hypomelina (Coleoptera: Tenebrionidae: Molurini). *Cimbebasia* (A) 5:95-78.

LOUW, S. 1983. The diversity and daily and seasonal activity of ground-living Tenebrionidae (Coleoptera) in the southern Namib and Kalahari ecosystems. *Cimbebasia* (A) 7: 35-56.

LOUW, S. 1984. Comparison of the faunistics and ecological patterns of the ground-living beetle faunas of the Kalahari and Namib desert, pp. 157-159. **In:** Holm, E. (Ed.). *Notes on the Coleopterous fauna of the Kalahari.* Supplement to *Koedoe* 1984.

ODUM, E.P. 1971. *Fundamentals of ecology.* London: W.B. Saunders & Co.

PENRITH, M-L. 1977. The Zophosini (Coleoptera: Tenebrionidae) of western southern Africa. *Cimbebasia Memoir* 3: 1-291.

PENRITH, M-L. 1979. Revision of the western southern African Adesmiini (Coleoptera: Tenebrionidae). *Cimbebasia* (A) 5: 1-94.

PENRITH, M-L. 1984. New taxa of *Onymacris* Allard, and relationships within the genus (Coleoptera: Tenebrionidae). *Ann. Transv. Mus.* 33: 513-533.

PRICE, P.W. 1975. *Insect Ecology.* New York: John Wiley & Sons.

ROSS, H.H. 1962. *A synthesis of evolutionary theory.* New York: Prentice-Hall Inc.

EDITORIAL COMMITTEE

Orders to: National Museum, P.O. Box 266, Bloemfontein 9300, Republic of South Africa.