8961

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Niche separation in Namib Desert dune Lepismatidae (Thysanura: Insecta): detritivores in an allochthonous detritus ecosystem

R. T. Watson*† 1989

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Strong spatial and temporal niche separation exists among seven dune dwelling Lepismatidae. Lepismatids are divided spatially into two groups occupying the slipface and vegetation clump habitats respectively. Variation in spatial use may be explained as a response to the physical environment and may be related to species' morphological adaptations to physical parameters within dune habitats. Temporal use is divided into diurnal and crepuscular, nocturnal, and dawn active groups. Variation in temporal activity patterns may be explained as a response to specific weather conditions and may be related to species' physiological adaptations that allow activity under specific weather regimes.

Introduction

At least seven lepismatid species occur sympatrically in parts of the main sand dune sea of the Namib Desert. They occupy distinctly different parts of the dune habitat and are active at different times of day (Watson & Irish, 1988), suggesting a spatial and temporal niche differentiation consistent with hypotheses of interspecific competition (MacArthur & Levins, 1967; May, 1973). Although competition between detritivores is theoretically probable (Hairson *et al.*, 1960), the general importance of interspecific competition as a mechanism causing niche separation has been questioned (Connor & Simberloff, 1979; Simberloff, 1983), and interspecific competition is thought to be rare among desert organisms in particular (Wiens, 1977; Noy-Meir, 1979/80).

Noy-Meir (1979/80) suggested that, under desert conditions, a sufficient explanation of population and community dynamics may consist of the autecological responses of each species to the weather, without considering interspecific interactions such as competition and predation. This implies that avoidance of interspecific interaction may not be an evolutionary force in deserts and should not be invoked to explain niche separation in closely related species. To what extent then, can the observed spatial and temporal distribution patterns among the seven Namib lepismatids be explained by their autecological responses to the weather and their abiotic environment in general?

Lepismatids are generally well adapted to xeric conditions, and are found in many arid regions of the world (Edney, 1971; Crawford, 1979), yet there are few studies of their field ecology. Despite the paucity of rainfall, they can be relatively abundant in the sand dunes of the Namib Desert (Watson, 1987), where their role as detritivores may represent an important component of this detritus based ecosystem. The dune dwelling species *Ctenolepisma pauliani* Wygodzinsky, *Hyperlepisma australis* Wygodzinsky, *Namibmormisma muricaudata* (Irish), *Mormisma wygodzinskyi* Irish, *Sabulepisma multiformis* Irish and

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* Desert Ecological Research Unit, P.O. Box 1592, Swakopmund 9000, S.W. Africa/Namibia.
† Present address: 165 Stanford Drive, Westwood, MA 02090, U.S.A.

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6 spp

Swalepisma mirabilis Irish are endemic to the Namib Desert, while *Ctenolepisma terebrans* Silvestri is also found in the Kalahari Desert (Watson & Irish, 1988).

The Namib Desert sand dunes are unique among deserts of the world because of the high animal species diversity associated with the vegetationless dune slipfaces and crests, and a high degree of endemism (Seely, 1978). This coastal desert is characterized by a relatively cool, moderate climate with little seasonal variation of mean temperatures, water input in the form of advective fog, and a supply of allochthonous as well as some autochthonous detritus. The southern dunes occupy an area of 34,000 km^2 and are sparsely covered with spatially separate clumps of vegetation, mainly perennial grasses of the genus *Stipagrostus* and the succulent *Trianthema hereroensis* Schinz (Seely, 1978).

The aims of this paper are fourfold. First, I hypothesize that the spatial and temporal distribution of the seven lepismatid species that occupy the dune habitat at the study site represents strong niche separation between them. Second, I propose that a significant amount of the variations in the use of space and time may be explained as a response to the abiotic environment. Third, I suggest that spatial variation is probably related to species-specific morphological adaptations to microhabitats within the dune environment, and lastly, I discuss the potential for interspecific competition to occur among species occupying the same microhabitat.

Methods

This study was conducted in the driest portion of the central Namib (Seely & Louw, 1980) on the northern edge of the main Namib sand dune sea, near Gobabeb (23°37′S, 15°01′E), between August 1985 and July 1986. Four habitats have been identified within the dune environment, namely the interdune gravel plains, dune base, dune plinth, and slipface (Robinson & Seely, 1980). Only lepismatids dwelling on the slipface and dune slope (base and plinth combined) were considered in this study, but two alternative microhabitats were distinguished on the dune slope, namely bare sand and vegetation clumps (Seely & Louw, 1980; Watson & Irish, 1988).

Pit-fall trapping was used to sample the normally surface-active lepismatids. Traps were set in five clusters (10 m apart) of four traps (1 m apart) in each of the three dune habitats. Trapping was conducted for two periods of 24 h, each 24 h apart, at bi-monthly intervals for a year, thus incorporating a selection of seasonally variable environmental conditions. The number of each lepismatid species in every pit-trap was recorded at bi-hourly intervals throughout the 24-h period.

Quadrat sampling was used for aspects of this study in which a sampling method that was independent of lepismatid surface-activity was required. The quadrat consisted of a $0{\cdot}5$ m $\times$ $0{\cdot}5$ m^2 $\times$ $0{\cdot}4$ m deep, open-ended steel box that was pushed into the sand to a depth of $0{\cdot}3$ m. The contents were then extracted and sieved through a $0{\cdot}75$-mm mesh sieve to separate the biotic components from the sand, and the number of each lepismatid species was recorded. Quadrats were placed randomly within each of the three habitats using a stratified random sampling design.

The spatial distribution of the seven lepismatid species was determined from pit-fall trapping data because this method generally yielded higher sample sizes than quadrat sampling. However, pit-fall trapping yielded few *H. australis*, so its spatial distribution was verified using quadrat sampling, in which its relative abundance was much greater. Spatial niche overlap was calculated between all pairs of species using Hurlbert's overlap index L (Hurlbert, 1978), which provided a measure of the degree of specialization of resource use as well as overlap between two species. Values of $L > 1$ indicate overlap and high specialization of resource use, $L < 1$ indicates little overlap but high specialization of resource use, while $L = 1$ indicates overlap and no resource use specialization. Resource states were taken to be the number of sampling units in each habitat. Schoener's (1970) overlap index C_{xy} is also reported because it is a commonly used but less useful (Hurlbert, 1978) measure of species distributional similarity (Goodall, 1973).

The influence of the physical environment on lepismatid spatial distribution was determined from correlation analysis of the number of each species per quadrat and measurements of six physical parameters made in or adjacent to each quadrat. The parameters measured were: detritus biomass per quadrat (weighed after drying at 60°C), sand density and per cent pore space (Foth & Turk, 1972), per cent water content (Foth & Turk, 1972), mean sandgrain size and sandgrain sorting (Folk, 1966). Data were ranked to meet the assumption of normality required by the Pearson product moment correlation test (Zar, 1984)

Temporal activity patterns were determined from pit-fall trapping by assuming that the number of each lepismatid species recorded in the pit-fall traps per 2-h period was proportional to the degree of surface activity within each species' population. Temporal niche overlap was calculated for all species pairs using Hurlbert's L and Schoeners C_{xy}, assuming equal resource states.

The influence of weather on temporal activity was determined by correlation analysis of the number of each species captured in pit-fall traps with five weather parameters recorded simultaneously with trapping data. The weather parameters (solar radiation, ambient humidity, ambient temperature, surface temperature and windspeed), were measured at minute intervals, averaged over hourly intervals and, along with time of day, were recorded by a Campbell data logger. The instruments were located in an exposed position on the dune slope. Data were ranked to meet the assumption of normality (Zar, 1984).

Results

Surface or sub-surface activity?

H. australis and *N. muricaudata* were rarely caught in pit-fall traps, yet they were abundant in quadrats from the vegetation clump habitat (Fig. 1). This means that, in contrast to the other dune lepismatids that were relatively abundant in the pit-fall traps, *H. australis* and *N. muricaudata* were not frequently surface active. Only *M. wygodzinskyi* was sampled equally by the pit-fall traps and quadrats. *S. multiformis* was rare in quadrat samples but abundant in pit-fall traps, suggesting that this species was sparsely distributed but frequently surface active.

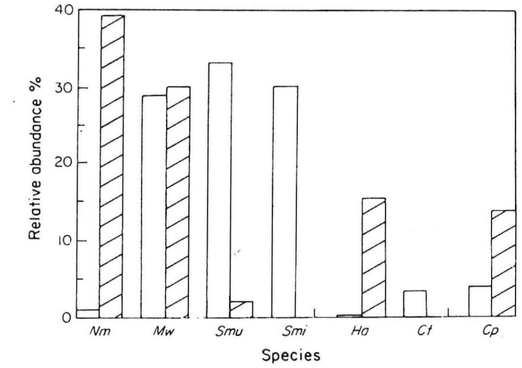

Figure 1. Relative abundance of Namib lepismatids caught in pit-fall traps ($n = 1877$) and quadrats ($n = 121$) in the same locality. Species name abbreviations as follows: Nm, *N. muricaudata*; Mw, *M. wygodzinskyi*; Smu, *S. multiformis*; Smi, *S. mirabilis*; Ha, *H. australis*; Ct, *C. terebrans*; Cp, *C. pauliani*. □, pit-fall traps; ▨, quadrats.

Spatial niche

Indices of spatial overlap (L) were either >1 or <1 (Table 1), demonstrating that all species exhibit extreme specialization of space use. The seven species separated into two distinct groups, each of which overlapped spatially with members of its own group (L > 1), but hardly at all with members of the other group (L < 1; Table 1). The groups were, first, *M. wygodzinskyi*, *S. multiformis* and *S. mirabilis* occupying the slipface habitat, and second, *N. muricaudata*, *H. australis*, *C. terebrans* and *C. pauliani* occupying the vegetation clump habitat on the dune slope. Sample size for *H. australis* was low ($n = 3$), so niche overlap indices between this and all other species were verified using quadrat sample data (Table 1).

Spatial separation of the lepismatids into mainly slipface or mainly vegetation clump habitats with general avoidance of the bare sand slope habitat suggested that the distribution of each species may be related to one or more physical parameters that also varied between these habitats. Of the six physical parameters measured, significant differences were found between habitats in four of them (Table 2). Detritus biomass was high in vegetation clumps, which produce their own detritus as well as act as windblown detritus traps. Although detritus was present on the slipface, which is also a trap for windblown detritus (Robinson & Seely, 1980), the random sampling method rarely intersected the sparsely distributed detritus pads. Detritus biomass was generally low in bare sand on the slope. Sand density and the sandgrain sorting index were significantly lower in the slipface than the other two habitats, and per cent pore space was significantly lower in the slipface habitat compared with the vegetation habitat (Table 2).

If lepismatid distribution was affected by the physical environment as suggested above, then significant correlations would be predicted between physical parameters and the numbers of each lepismatid species wherever they occurred in quadrat samples (Table 3).

Table 1. *Spatial niche use and overlap indices L (Hurlbert, 1978) and C_{xy} (Schoener, 1970) based on pit-fall trapping data in three dune habitats. Indices based on quadrat sampling data are provided for* H. australis *in brackets ( ) because of the low pit-fall trap sample size for this species.* n = *sample size*

Species		*N. muricaudata*	*M. wygodzinskyi*	*S. multiformis*	*S. mirabilis*	*H. australis*	*C. terebrans*	*C. pauliani*
N. muricaudata	L	–	0·01	0·07	0·06	2·86 (4·07)	2·94	2·39
$n = 21$ (49)	C_{xy}		0·01	0·09	0·11	0·76 (1·00)	0·82	0·73
M. wygodzinskyi	L		–	3·04	3·38	0·02 (0)	0·02	0·09
$n = 538$ (33)	C_{xy}			0·92	0·84	0·01 (0)	0·01	0·05
S. multiformis	L			–	3·07	0·12 (0)	0·11	0·17
$n = 619$ (3)	C_{xy}				0·86	0·07 (0)	0·09	0·13
S. mirabilis	L				–	0·15 (0)	0·13	0·13
$n = 561$ (8)	C_{xy}					0·08 (0)	0·09	0·13
H. australis	L					–	2·76 (0)	1·96 (2.29)
$n = 3$ (20)	C_{xy}						0·95 (0)	0·64 (0·56)
C. terebrans	L						–	2·05
$n = 61$ (8)	C_{xy}							0·67
C. pauliani	L							–
$n = 74$ (16)	C_{xy}							

Table 2. *Comparison of physical parameters between dune habitats, using the Kruskall–Wallis test (H), with significant multiple comparisons (critical values calculated at Alpha = 0·05, df. = 2; Zar, 1984)*

Habitat	n		Detritus biomass (g/m^2)	Water content (%)	Sand density (g/ml)	Pore space (%)	Mean sandgrain size (phi)	Sandgrain sorting (index)
A Vegetation	22	$\bar{X}$	280	0·225	1·677	36·4	2·231	0·599
		SD	232	0·046	0·027	1.1	0·192	0·071
B Slope	25	$\bar{X}$	3·2	0·203	1·676	36·5	2·176	0·593
		SD	7·6	0·035	0·047	2·1	0·210	0·107
C Slipface	7	$\bar{X}$	0	0·230	1·626	38·0	2·280	0·440
		SD	0	0·028	0·037	1·4	0·190	0·049
H			39·8	4·8	7·7	5·8	2·7	13·3
P			<0.05	>0·05	<0·05	<0·05	>0·05	<0·05
Multiple comparisons			A–B A–C	– –	A–B B–C	A–C –	– –	A–C B–C

Table 3. *Significant correlations (Pearson product moment correlation coefficient,* r, *at* p < *0·05, df. = 79) of the number of lepismatid species recorded in quadrats and sand properties*

Species		Detritus mass	Water content	Sand density	Pore space	Mean sandgrain size	Sandgrain sorting
N. muricaudata	*r*	0·69			−0·25		
$n = 49$	t	8·4			2·3		
M. wygodzinskyi	*r*	−0·26		−0·35			−0·41
$n = 33$	t	2·4		3·3			4·0
S. multiformis	*r*						−0·22
$n = 3$	t						2·0
S. mirabilis	*r*			−0·51	0·43		−0·31
$n = 8$	t			5·2	4·2		2·9
H. australis	*r*	0·43					
$n = 20$	t	4·2					
C. terebrans	*r*	0·60					0·28
$n = 8$	t	6·6					2·6
C. pauliani	*r*		−0·37				
$n = 16$	t		3·5				

Detritus biomass correlated positively with species associated with vegetation clumps, and negatively with mainly slipface dwelling species, although three species showed no correlation with detritus biomass. The numbers of *M. wygodzinskyi* and *S. mirabilis* correlated negatively with sand density and sorting but positively with pore space. Considering the significant differences in these parameters between habitats, these correlations could be predicted to occur with a strictly slipface dwelling species. Only *C. pauliani* showed any correlation with soil water content, and that was negative.

Temporal niche

Graphs of daily activity times (Fig. 2) showed three general patterns of activity. First, there were the mainly (>60%) diurnal to crepuscular species, *N. muricaudata*, *M. wygodzinskyi*, and *S. multiformis*. Second, there were the mainly nocturnal species that were active in the first half of the night, *C. terebrans* and *C. pauliani*, and third, one species, *S. mirabilis*, became active mainly in the hours just before or around dawn. *H. australis* was not included in this analysis because it was rarely surface active.

Indices of temporal overlap for every species pair (Table 4) qualified these subjective groups as follows. The mainly nocturnal species *C. terebrans* and *C. pauliani* overlapped with each other (L = 1·8), and to an extent with the crepuscular species *S. multiformis* and *S. mirabilis* (L > 1·38), although the latter pair did not overlap with each other (L = 0·39). All these species exhibited specialization of time use (L > 1 or L < 1). The comparisons of *N. muricaudata* with *M. wygodzinskyi* and the latter species with *S. multiformis* had overlap values (L) close to 1, indicating that they overlapped in time use with little specialization between them. Most other species' pair-comparisons exhibited low overlap but with

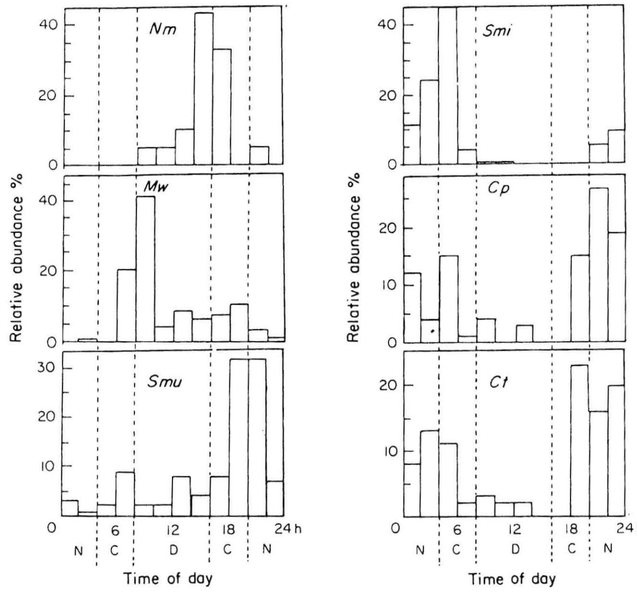

Figure 2. Temporal activity patterns of Namib lepismatids shown as the relative abundance of each species caught in pit-fall traps at bi-hourly intervals through the 24-h diel cycle. N, nocturnal; C, crepuscular; D, diurnal. Species name abbreviations as follows: Nm, *N. muricaudata*; Mw, *M. wygodzinskyi*; Smu, *S. multiformis*; Smi, *S. mirabilis*; Ct, *C. terebrans*; Cp, *C. pauliani*.

Table 4. *Temporal niche use and overlap indices L (Hurlbert, 1978) and C_{xy} (Schoener, 1970) from pit-fall trap data.* n = *sample size*

Species		*N. muricaudata*	*M. Wygodzinskyi*	*S. multiformis*	*S. mirabilis*	*H. australis*	*C. terebrans*	*C. pauliani*
N. muricaudata	L	–	0·95	0·77	0·02	2·29	0·14	0·21
n = 21	C_{xy}		0·32	0·29	0·03	0·48	0·11	0·12
M. wygodzinskyi	L		–	0·99	0·12	2·20	0·58	0·55
n = 538	C_{xy}			0·46	0·08	0·47	0·22	0·22
S. multiformis	L			–	0·39	0·55	1·59	1·58
n = 619	C_{xy}				0·17	0·14	0·59	0·56
S. mirabilis	L				–	0·01	1·38	1·42
n = 561	C_{xy}					0·00	0·44	0·42
H. australis	L					–	0·20	0·27
n = 3	C_{xy}						0·05	0·07
C. terebrans	L						–	1·80
n = 61	C_{xy}							0·80
C. pauliani	L							–
n = 74	C_{xy}							

Table 5. *Significant correlations (Pearson product moment correlation coefficient,* r, *at* $p < 0.05$, *df.* = *139) between the number of each lepismatid species recorded in pit-traps and ambient weather conditions*

Species		Time of day	Solar radiation	Temperature	Humidity	Windspeed
N. muricaudata	*r*	0·171	0·329	0·420	−0·405	0.353
	t	2·1	4·1	5·5	5·2	4·5
M. wydogzinskyi	*r*		0·441	0·372	−0·405	0.265
	t		5·8	4·7	5·2	3·2
S. multiformis	*r*	0·385		0·335	−0·405	0.456
	t	4·9		4·2	5·2	6·0
S. mirabilis	*r*	−0·343	−0·306	−0·494	0·516	−0.205
	t	2·9	4·3	3·8	6·7	7·1
H. australis	*r*		0·171	0·173	−0·182	
	t		2·0	2·1	2·2	
C. terebrans	*r*	0·189	−0·175			0.164
	t	2·3	2·1			2·0
C. pauliani	*r*		−0·347	−0·234	0·228	
	t		4·4	2·8	2·8	

generally high specialization of time use (L < 1). Overlap indices for *H. australis* were based on a sample size of only three and therefore were probably meaningless but, in contrast to the other species, *H. australis* and *N. muricaudata* have already been shown to be mainly sub-surface active. Thus, in general, activity periods of the seven species were temporarily separated, or separated by activity mode, that is, surface or sub-surface active.

Daily activity patterns (Fig. 2) were derived from data summed over the whole year. However, day to day variation of activity periods appeared to be related to ambient weather conditions. Significant correlations between weather parameters and the number of each species caught in pit-fall traps (Table 5) showed that weather may have had a facultative effect on lepismatid activity, although few correlations explained more than about 25% of the variation ($r^2 < 0{\cdot}25$). Diurnal species showed a positive correlation with solar radiation, while the correlation with nocturnal species was negative. Only *S. multiformis* showed no correlation with solar radiation, being active during both day and night. The numbers of *N. muricaudata*, *M. wygodzinskyi*, and *S. multiformis* were positively correlated with wind speed, whereas *S. mirabilis* was active under calm conditions. Diurnal species were negatively correlated with humidity, which shows a diel cycle of low diurnal to high nocturnal levels (Lancaster *et al.*, 1984). *S. mirabilis* showed a strong positive correlation with humidity, suggesting that this species was facultatively humidity or fog active. The numbers of *N. muricaudata*, *M. wygodzinskyi* and *S. multiformis* were positively correlated with ambient temperature, whereas *S. mirabilis* and *C. pauliani* were active under generally cool conditions.

Spatial and temporal overlap

Examination of every possible species pair comparison for spatial and temporal overlap separately (Table 6) showed that all but two pairs (9·5%) were separated by either time or space or both these dimensions. The two pairs that showed both spatial and temporal overlap, were *C. terebrans* with *C. pauliani* and *N. muricaudata* with *H. australis*. The latter pair occupied the vegetation clump habitat and were rarely surface active, although *N. muricaudata* was surface active more often than *H. australis* which may represent a source of niche separation between them. *C. terebrans* and *C. pauliani* also occupied vegetation clumps, but *C. terebrans* was rarely caught in pit-fall traps. *C. terebrans* was more abundant in the interdune plain habitat (Watson & Irish, 1988), that was not included in this study, so these two species may be separated spatially to a greater degree than was evident from these results.

Table 6. *Comparison of spatial and temporal overlap between the seven lepismatid species. L > 1 indicates niche overlap between species pairs, L < 1 indicates little niche overlap*

Spatial overlap	Temporal overlap L > 1	Temporal overlap L < 1
L > 1	Nm–Ha Ct–Cp	Nm–Ct Nm–Cp Mw–Smu Mw–Smi Smu–Smi Ha–Cp Ha–Ct
L < 1	Nm–Mw Nm–Smu Mw–Ct Mw–Cp Smu–Ha Smu–Ct Smu–Cp Smi–Ct Smi–Cp	Nm–Smi Smi–Ha Mw–Ha

Species name abbreviations as follows: Nm, *N. muricaudata*; Mw, *M. wygodzinskyi*; Smu, *S. multiformis*; Smi, *S. mirabilis*; Ha, *H. australis*; Ct, *C. terebrans*; Cp, *C. pauliani*.

Morphology and niche differentiation

Whatever the selection forces involved, one would expect to find behavioural, morphological and/or physiological adaptations in each species that enable them to inhabit their specific part of the dune and to be active at the time of day and manner that I have observed. Some trends between the species' morphology (body shape and appendages) and their spatial distribution can be deduced as follows.

C. terebrans and *C. pauliani* are similar in body shape to the familiar lepismatids that live commensally in human dwellings (Fig. 3), which is essentially an arid environment but much more stable that the shifting sands of desert dunes. *C. terebrans* and *C. pauliani* therefore, may exploit the more stable parts of the dune environment in an opportunistic manner. Leg spination of psammophilous lepismatids becomes longer, stronger and more numerous, and arranged in a comb structure, as the sand substrate becomes less stable (Irish, 1987; Watson & Irish, 1988). *C. pauliani* has long, strong spines arranged in a comb, and is therefore perhaps better able to survive in a wider range of dune habitats than *C. terebrans* which lacks the definite comb structure. *C. terebrans* is limited to the

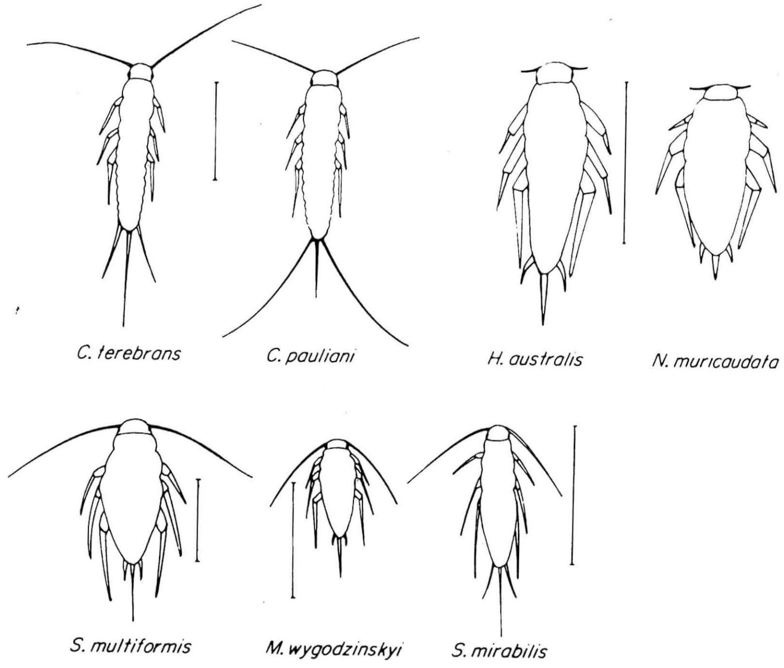

Figure 3. Line diagrams of Namib lepismatids to illustrate body shapes and relative lengths of appendages. Scale-bar beside each species represents 5 mm.

vegetation hummocks and interdune gravel plains, while *C. pauliani* is numerous in vegetation hummocks but also found in compacted bare sand (Watson & Irish, 1988).

Compared with the familiar long, thin-bodied lepismatids, the sub-surface active species *N. muricaudata* and *H. australis* are broad at the head with a tapered humpbacked body and have short appendages (Fig. 3). The resemblance of this body shape to aero- or hydro-dynamic shapes suggests that, for insects of this size, the sand presents a fluid medium through which they 'swim'. Appendages are shortened, possibly to reduce drag in this viscous 'fluid' medium. Additionally, appendages would not serve a useful sensory function below the sand as they would always be stimulated by contact with sand grains.

M. wygodzinskyi and *S. multiformis* have short, rounded bodies, and the third pair of legs extend beyond the end of the abdomen (Fig. 3). These species are surface active, running rapidly over the unconsolidated sand of the slipface and crest. Their long appendages may serve a useful sensory function on the surface, probably being used to locate windblown detritus and avoid predatory spiders and solifugids. The short, rounded bodies suggest a streamlining function for these species that escape the surface environment by swimming into the soft slipface sand, but body shape may also be related to coping with the strong winds in which they become active.

S. mirabilis occupies the soft sand of the slipface, but it does not have the short, broad, streamlined body shape of the other slipface dwellers (Fig. 3). Rather, its body shape is similar to the *Ctenolepisma* species but is more spindle-like than dorso-ventrally flattened. *S. mirabilis* was the only species to be active during the cold, calm early morning hours when advective fog moved inland and presented a ready source of water to these and other dune dwelling arthropods (Seely *et al.*, 1983). Body shape of slipface dwellers may therefore be more related to the weather conditions under which the species become active than to the fluid medium in which they exist between surface activity periods.

Discussion

Spatial and temporal separation among this Namib dune lepismatid community represent patterns of strong niche separation consistent with hypotheses of biotic interaction, particularly interspecific competition or predation (MacArthur & Levins, 1967; May, 1973; Connell, 1975). However, niche differentiation may also have arisen by chance, the various species having evolved independently into specialists with specialized niches that happen to be different (Connor & Simberloff, 1979). Seely (1985) concluded that the selective value of predation in the Namib was not as marked as the influence of the desert environment. Although little is known of the predation pressure on these lepismatids, potential predators occur in all three habitats, so predation pressures are likely to be similar and not a probable explanation of niche differentiation between these prey species. Thus, the following discussion centers on the possible role of competition versus the influence of the species' autecological response to the abiotic environment.

If competition was an important force in shaping the lepismatid community patterns, then they should conform to three predictions (Begon *et al.*, 1986, pp. 675–676). First, as demonstrated for the Namib dune lepismatids, potential competitors that co-exist should exhibit niche differentiation, in this case, along spatial and temporal dimensions. Second, niche differentiation is likely to manifest itself as morphological differences between species along a continuous scale, such as size or shape. This prediction is only partially applicable to Namib lepismatids, in that morphological differentiation only appears to occur along a continuous scale in three pairs of species, *M. wygodzinskyi* and *S. multiformis* from the slipface habitat, *H. australis* and *N. muricaudata* from the vegetation hummock habitat, and *C. pauliani* and *C. terebrans* from the stable interdunes and vegetation hummock habitats. *S. mirabilis* morphology is anomalous among these three groups. Thus, contrary to the third prediction, that potential competitors with little niche differentiation between them are not likely to co-exist, lepismatid species with least morphological differentiation occupy the same space and do co-exist. This implies that species occupy their habitats in the dune environment because of their morphology, with similar body shapes occurring together in the same habitat, and spatial separation is related to the physical microhabitats in which each species lives. Thus, spatial separation of Namib dune lepismatids is probably the result of chance evolution in response to specialized requirements for specialized microhabitats and resources.

Separation by activity mode and time could be interpreted in the same way, but the role of specialized physiological differentiation for weather conditions experienced at specific times of day may be more important than morphological differentiation. Experiments on water balance indicate habitat related differences between these species (Watson, Unpubl. data).

Except for *S. mirabilis*, species within habitats conform to the first and second predictions, in that niche differentiation manifests itself in morphological differences along a continuous scale. This conformity suggests that, within habitats, competition could occur between lepismatid species, or past selection for the avoidance of competition may have caused the currently observed morphological and temporal differentiation between them.

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Figure 26. After flood of the Kuiseb River the higher levelled terraces are covered with silt which develop a system of mud cracks on drying.

Figure 27. Some fossil loams are compact and indurated especially on the surface.