Zonation and habitat selection on a reclaimed coastal foredune

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Geomorphic / floristic variables are useful as general habitat indicators on coastal foredunes. Variables used in this study were vegetation cover, plant community structure and sand movement. Three distinct zones, four habitats and six subhabitats were identified. Zonation and habitat selection appeared to be related to cover for two small mammal species. The arthropod orders were less susceptible to zonation and strict habitat selection, although some of the species showed selection. The normally unfavourable edaphic habitat, the transition dune, was the most populated, dominated by the marine isopods.

Vir die algemene uitkenning van habitatte op kusduine is geomorfologies / floristiese veranderlikes bruikbaar. Veranderlikes wat in hierdie studie gebruik is, is plantbedekking, plantgemeenskappe en sandbeweging. Drie sones, vier habitatte en ses subhabitatte is geïdentifiseer. Die twee klein soogdiersoorte het sonasie en habitatseleksie getoon. Sonasie en habitatseleksie was minder opmerklik by die Artropoda-ordes. Die meeste individue is in die sone naaste aan die see aangetref.

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Sand is characterized by a number of physical properties which contribute to its uniqueness as an ecological environment. The more important of these characteristics which profoundly affect the fauna are its extreme dryness, its wide temperature variations and the movement of the particles of which it is composed (Callan 1964). Sand dunes are distinctive, geographically widespread habitats, while remarkably similar in general characteristics and appearance (Brown 1973).

The fundamental premise of species distribution is that species are more abundant in some habitats than in others (Morris 1987). The number of species that occur in a particular habitat depends on the interactions between ecological, biogeographic and evolutionary processes (Brown 1973), and the structure and dynamics of a population represent the outcome of the interactions between the life histories of its individuals and the spatial and temporal variations in its environment (Zeng & Brown 1987).

Central to the study of animal ecology is the use which an animal makes of its environment; specifically, the kinds of food it consumes and the variety of habitats it occupies (Johnson 1980). A species's habitat is the sum of the environments in which it occurs. A habitat is therefore a concept of distribution as opposed to niche, which describes the role of a species within a community. A habitat can therefore be described as patches of varying utility with an individual's genetic fitness being greater in the better patches (Melton 1987). Habitat selection refers to the use of a particular habitat, whereas habitat selectivity describes the amount of selection for a number of habitat types (Melton 1987). Differential habitat selection is one of the principal relationships which permit species to coexist and optimal habitat selection is a function of population densities (Melton 1987). Habitat structure and diversity have been correlated with species diversity of birds (MacArthur & MacArthur 1961) and of small mammals (Rosenzweig & Winakur 1969).

Coastal foredunes show distinct geomorphological and floristic zonation (Masson 1988; 1990a). Sand movement has been shown to be a major factor which determines the distribution of plant communities on foredunes (Moreno-Casasola 1986), while interactions between aerial vegetation cover, sand movement and rodents as well as arthropods are evident (Masson 1990b). The aim of this article is two-fold: first, zone / habitat and subhabitat structure is defined in terms of geomorphic / floristic characteristics; second, zone, habitat, and subhabitat selectivity is quantified for two small mammal species and four arthropod orders.

Study area

An artificially reclaimed foredune on the South African coast (22°50′E / 34°S), Wilderness, was selected as study site. The coast is exposed to strong winds and waves, and consists of a barrier dune system (Tinley 1985), backing an exposed (*sensu* McLachlan 1980) beach. The foredune is 100 m wide, and three geomorphic / floristic zones are present. The area was reshaped and artificially stabilized with *Ammophila arenaria*, marram grass, tufts and seeded with indigenous species, five years prior to the study. The environment is considered to be a functional ecosystem in a pioneer stage, yet vulnerable and impoverished (Masson 1990c).

The foredune in the study area consists of the hummock dune zone adjacent to the beach, the incipient foredune zone and the seaward slope of the foredune zone. The hummock dune zone consists of the hummock dunes themselves and embryo dunes characterized by true strandplants, *Agropyron distichum* and *Actotheca populifolia*, with high aeolian activity. The incipient foredune or 'created' littoral dune is characterized by pioneer species such as *Scaevola plumieri*, *Gazania rigens* and *Hydrophylax carnosa* with a few mature shrub plants, eg. *Passerina rigida*. This zone has medium aeolian activity. The seaward slope of the foredune zone contains *Ammophila arenaria* and other shrub species, with almost negligible aeolian activity.

Methods

Data collection

Four transects, at right angles to the beach, were surveyed across the reclaimed area with metal rods positioned at 5-m intervals. Subsequent monthly sand depositional values were recorded from sand levels against these rods. For each of the measuring rods the mean erosion / accretion value and the percentage of occurrence of changes in the levels were determined.

Vegetation belt transects were run along the survey lines. The dominant species in terms of cover was identified for each running m^2. These data were grouped and communities along the transects identified, i.e. pioneer community, shrub community, marram community and a mixed community. The mixed community consisted of marram and shrubs which were dominant in alternate 1-m^2 plots. The percentage aerial cover along these transects was noted.

Sherman aluminium live-traps (230 × 80 × 90 mm), baited with a mixture of rolled oats and peanut butter, were used to enumerate the small mammal populations. The traps were set along the transect lines in late morning, and checked the following morning. Each trap was set with its back to the prevailing wind, since even a light breeze caused them to clog with sand. Squares of closely woven material were provided as nesting material, after two striped mice appeared to have died of exposure in the traps. The location of each capture was noted and the mammal released, unmarked, at the point of capture. The traps were placed at 15-m intervals, each sample period consisting of two consecutive 24-h periods, for a total of 679 trap nights. For each trap station the trapping success was calculated.

Pit traps arranged along the transects were used to sample the arthropods. The sample period consisted of two consecutive 24-h periods for a total of 1 200 trap days. Organisms were identified to the order level. The relative contribution of each order to the total number of organisms captured, was noted. Profiles of the transects with the position of stations and habitat types are shown in Figure 1.

Data analysis

Habitat structure

Three levels of habitat structure were identified: (i) three zones; consisting of (ii) four habitat types; consis-

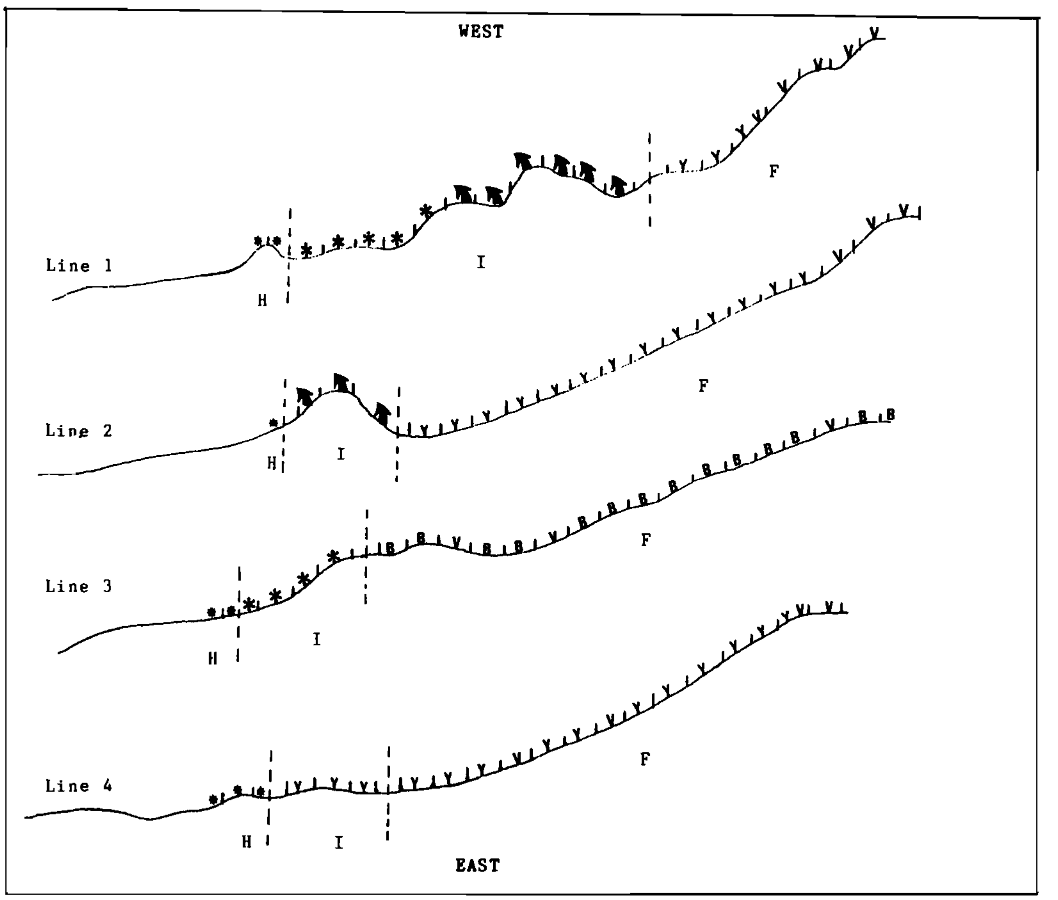

Figure 1 Habitat structure along four transect belts. Microhabitats (1) ★ Hummock; (2) ▲ active IF; (3) ∗ stable IF; (4) B — boardwalk; (5) Y — shrub and grass comm.; (6) V — marram grass. H = hummock dune zone, I = Incipient foredune zone; F = Foredune zone.

ting of (iii) seven subhabitats. The three zones were distinguished on the grounds of position, local topography, aeolian activity and floristic community (Masson 1988). The hummock dune zone is closest to the sea, composed of strandplants (*sensu* Tinley 1985) occurring on embryo and hummock dunes. The incipient foredune zone consists of the littoral dune with pioneer plant communities. The foredune zone comprised the seaward slope landward of the littoral dune ridge rising up to the plateau with secondary (*sensu* Tinley 1985) shrub species and marram grass.

The hummock dune (H-I) (Habitat type I) and incipient foredune (H-II) zones were considered separately. The foredune zone, however, showed distinct vegetation changes (Masson 1988) with the shrubs (H-III) (Habitat type III) dominating the lower reaches and the marram grass (H-IV) the upper reaches. The hummock dune zone was regarded a subhabitat (SH-1) (subhabitat type 1) while the incipient foredune was divided into two subhabitats. An aeolian active, high relief dune with *Scaevola plumieri,* subhabitat (SH-2) and a more stable low relief subhabitat (SH-3). Subhabitat (SH-4) is the area beneath a raised boardwalk, crossing over the foredune zone, while the lower reaches of the foredune zone, a pure shrub community is another subhabitat (SH-5). The upper reaches dominated by marram grass consist of two subhabitats, a mixture of marram grass and shrubs (SH-6), and a pure stand of marram grass (SH-7). The habitat and subhabitat types are schematically illustrated in Figure 1.

Habitat selectivity

Habitat selection was quantified at three spatial scales: (i) selection for broad zones, (ii) selection for habitat types, and (iii) selection for subhabitats. Selection was investigated using 1986–7 data (Masson 1988). Overall selectivity was quantified using the index S (McNaughton 1978) where

$$S = PO\ /\ PA$$

where PA = proportion of traps in the i th habitat and
PO = proportion of captures of the j th species/order in the i th habitat.

The proportion of selectivity for each sub-category of habitat was calculated as a quantification of selectivity.

$$\text{Prop. select.} = \frac{\text{overall selectivity value of spp.}}{\text{sum of overall selectivity}} \times 100$$

Prop. select. = Proportional selectivity
= quantification of habitat selectivity.

Results

Habitat structure

The three zones showed distinct geomorphic / floristic features and can be considered to be separate geomorphic / floristic environments (Table 1, Column 1). The division of the third zone, the foredune zone, into two separate habitat types is also geomorphic / floristically justified. The lower reaches (H-III) recorded lower sand movement values and subsequently higher cover values than the upper reaches (H-IV) (Table 1, Column 2). The hummock dune (SH-1) is a distinct subhabitat. The incipient foredune zone, a transition zone, is divided into two distinct geomorphic / floristic subhabitats, the aeolian active, high relief dune (SH-2) and a more stable low relief dune (SH-3). From the data the division of the boardwalk (SH-4) and the shrub subhabitat (SH-5) is not justified. However, on the basis of vegetation type the obvious difference should be indicative of selection for vegetation type rather than cover. The division between the pure shrub (SH-5) and the mixed community (SH-6) is geomorphic / floristically unjustified, with the only difference being plant species. There is, however, a pronounced difference between the mixed stand (SH-6) and the marram grass (SH-7).

There are three distinct geomorphic / floristic zones on the coastal foredune at the study site. The hummock dune zone is one geomorphic / floristic subhabitat, and the incipient foredune zone two subhabitats. The foredune zone consists of two habitats, the area beneath the boardwalk and the secondary plant community habitat.

Table 1 Geomorphic / floristic data for the zones, habitats (H-) and subhabitats (SH-). H = Hummock dune zone, I = Incipient foredune zone and F = Foredune zone

Zone	Habitat	Subhabitat
Plant community composition		
H strandplants	strandplants	strandplants
I pioneer spp.	pioneer spp.	*S. plumieri*
		G. rigens
	other	boardwalk
		shrubs
F secondary spp.	marram grass	grass/shrubs
		A. arenaria
Plant cover (%)		
H 2,0 ± 4,5	2,0 ± 4,5	2,0 ± 4,5
I 42,2 ± 1,6	42,2 ± 24,6	41,1 ± 27,6
		43,3 ± 21,6
	78,5 ± 14,4	80,0 ± 5,0
		76,9 ± 14,4
F 71,4 ± 10,9	64,4 ± 19,6	73,0 ± 17,7
		55,7 ± 21,5
Sandlevel changes (mm/month)		
H 189 ± 69	189 ± 69	189 ± 69
I 173 ± 158	173 ± 125	285 ± 205
		61 ± 45
	15 ± 14	16 ± 11
		14 ± 17
F 19 ± 14	24 ± 23	8 ± 7
		39 ± 39
Occurrence of sandlevel changes (%)		
H 100 ± 0,0	100 ± 0,0	100 ± 0,0
I 73,8 ± 19,3	73,8 ± 19,3	87,4 ± 20,5
		60,1 ± 26,9
	29,6 ± 14,2	33,6 ± 7,9
		25,5 ± 20,5
F 29,9 ± 14,2	30,3 ± 15,6	24,4 ± 13,6
		36,3 ± 17,6

The latter consists of two subhabitats (Table 2). Data are displayed in Table 3 according to the three zones, four habitats and six subhabitats.

Habitat selectivity

Small mammals

Two rodent species (206 individuals) were trapped on the foredune with a total capture of 61 in 283 trap nights, i.e. 21,5% capture rate in summer and 145 in 396 trap nights, i.e. 36,6% capture rate in winter. *Rhabdomys pumilio* was the most abundant rodent with a proportional selectivity value of 75,8% and 85,5% on the foredune zone in summer and winter respectively. It appears as if *R. pumilio* favours neither of the habitat types (H-III and H-IV) probably indicative of cover preference. In summer the boardwalk (SH-4) and shrub–grass (SH-5) subhabitats were preferred while in winter the marram grass (SH-6) subhabitat was preferred (Table 4).

Mus minutoides selected the incipient foredune zone in summer (92,7%) and in winter (80,3%). The aeolian stable dune subhabitat form (SH-3) was preferred (48%) to the aeolian active form (SH-2) (34,6%) with no captures in any of the other subhabitats other than the grass (SH-6) in summer. In winter the stable form (SH-3) was preferred (46,8%) with insignificant captures in the other subhabitats (Table 4). No captures were made in the hummock dune zone.

Table 2 Geomorphic / floristic zones, habitats (H-) and subhabitats (SH-) on a reclaimed coastal foredune

Zone	Habitat	Subhabitat
Hummock dune (H)	Hummock (H-I)	hummock (SH-1)
Incipient foredune (I)	Incipient (H-II)	active (SH-2)
		inactive (SH-3)
	Boardwalk (H-III)	boardwalk (SH-4)
Foredune (F)	Foredune (H-IV)	mixture (SH-5)
		marram (SH-6)

Table 3 Geomorphic / floristic data based on the classification from Table 2. The zones are shown as H, I and F

Zone	Habitat	Subhabitat
Plant community composition		
H strandplants	strandplants	strandplants
I pioneer spp.	pioneer spp.	*S. plumieri*
		G. rigens
	boardwalk	boardwalk
F secondary spp.	secondary spp.	grass/shrubs
		A. arenaria
Plant cover (%)		
H 2,0 ± 4,5	2,0 ± 4,5	2,0 ± 4,5
I 42,2 ± 1,6	42,2 ± 24,6	41,1 ± 27,6
		43,3 ± 21,6
	80,0 ± 5,0	80,0 ± 5,0
F 71,4 ± 10,9	65,3 ± 18,0	75,0 ± 14,6
		55,7 ± 21,5
Sandlevel changes (mm/month)		
H 189 ± 69	189 ± 69	189 ± 69
I 173 ± 158	173 ± 125	285 ± 205
		61 ± 45
	16 ± 11	16 ± 11
F 19 ± 14	25 ± 18	11 ± 12
		39 ± 39
Occurrence of sandlevel changes (%)		
H 100 ± 0,0	100 ± 0,0	100 ± 0,0
I 73,8 ± 19,3	73,8 ± 19,3	87,4 ± 20,5
		60,1 ± 26,9
	33,6 ± 7,9	33,6 ± 7,9
F 29,9 ± 5,9	30,6 ± 16,3	24,9 ± 17,1
		36,3 ± 17,6

Arthropods

Only arthropods which were present in significant numbers were studied and these represented four orders; namely, the Hymenoptera (ants and wasps) and Coleoptera (beetles), both in the class Insecta, the Araneae (spiders) in the class Arachnida, and the Isopoda, class Crustacea. A total of 14 orders was recorded. The order Hymenoptera was studied under two broad groups, the wasps and the ants. One species of the Coleoptera, the spotted maize beetle, was studied.The order Isopoda was represented by two species; namely the marine isopod *Tylos capensis,* sea louse, and the terrestrial isopod *Armadillium vulgare*, the pill bug. In summer a total of 4 611 invertebrate organisms was captured and in winter 2 324. However, in summer 78,9% of the captures were *T. capensis* individuals and in winter 50,8%.

The ants selected the foredune zone in both the summer (438 individuals) and the winter (416 individuals) (Table 5). The secondary vegetation community

Table 4 Small mammal 'proportional selectivity values (%)' for the zones, habitats and subhabitats

Zones		Habitats		Subhabitats	
summer	winter	summer	winter	summer	winter
Rhabdomys pumilio					
(54 individuals in summer, 134 in winter)					
0	0	0	0	0	0
24,2	14,5	14,3	7,0	4,7 .	5,8
				8,1	2,7
		41,2	45,6	34,7	28,6
75,8	85,5	44,5	47,4	36,8	25,7
				16,0	37,0
Mus minutoides					
(7 individuals in summer, 11 in winter)					
0	0	0	0	0	0
92,7	80,3	74,9	66,1	34,6	13,7
				48,0	46,8
		0	22,0	0	13,7
7,3	19,7	25,1	11,9	0	12,2
				17,3	13,7

Table 5 Arthropod 'proportional selectivity values (%)' for zones habitats and subhabitats

Zones		Habitats		Subhabitats	
summer	winter	summer	winter	summer	winter
Ants					
3,3	0	2,1	0	1,3	0
24,2	22,9	15,5	16,3	3,7	19,7
				5,8	1,0
		33,7	23,6	20,4	13,7
75,8	77,1	48,7	60,1	29,2	36,4
				29,7	29,2
Wasps					
24,2	12,8	19,3	7,6	12,1	5,4
30,2	33,3	24,1	19,8	9,7	10,5
				19,6	17,1
		17,3	42,2	10,8	30,1
45,5	53,9	39,3	30,5	25,6	24,7
				22,2	12,4
***Tylos capensis* (marine isopod)**					
59,5	55,4	59,3	57,4	43,1	41,6
38,7	37,9	38,4	39,2	17,7	20,1
				37,1	35,1
		0	0	0	0
1,8	6,7	2,2	3,4	2,1	3,2
				0	0
***Armadillum vulgare* (terrestrial isopod)**					
0	6,5	0	3,1	0	2,1
100	9,5	100	4,5	100	2,6
				0	3,2
		0	54,5	0	37,1
0	84,1	0	37,9	0	24,0
				0	31,5
Melyridae (maize beetle)					
38,9	0	31,7	0	22,6	0
26,5	49,0	21,6	45,3	10,4	0
				19,4	29,7
		16,5	0	11,8	0
34,6	51,0	30,1	54,6	25,0	6,4
				10,8	64,1
Araneae (spiders)					
10,4	11,4	4,7	7,7	3,3	4,7
19,0	35,9	8,6	24,2	5,7	14,9
				6,4	14,7
		59,5	32,0	42,4	19,7
70,6	52,7	27,3	36,1	17,9	21,4
				24,3	24,6

(H-IV) was preferred. In summer selection was similar for shrub–grass (SH-5) and marram (SH-6) while in winter selection was for the shrub–grass (SH-5). The wasps preferred the foredune zone in summer (354 individuals) and in winter (122 individuals). In summer the marram (SH-6) was preferred while in winter the boardwalk (SH-4) was preferred (Table 5).

The marine isopod, *T. capensis*, selected the hummock dune zone (H-I; SH-1). Of the two incipient foredune subhabitats the more stable form (SH-3) was preferred. These organisms occurred as far back as the shrub–grass (SH-5) subhabitat. The terrestrial isopod, *A. vulgare*, preferred the foredune zone. The boardwalk (H-III; SH-4) was selected for as well as the upper marram grass (SH-6) reaches of the foredune zone (Table 5).

The maize beetle was evenly distributed across the foredune complex in summer (203 individuals) while in winter (7 individuals) the hummock dune zone was avoided. The hummock dune (SH-1) and the shrub–grass (SH-5) was selected for. The spiders selected for the foredune zone in summer (79) and the upper two zones in winter (344). In summer selection seems prominent for the upper reaches while in winter selection is less apparent with an even distribution of individuals occurring (Table 4).

Discussion

One of the most important needs of an animal is finding a suitable place to live. Different parts of the environment represent habitats of varying quality in terms of benefits. Habitat quality can affect an individual's ability to survive and reproduce. A distinct geomorphologic / floristic zonation occurs on a coastal foredune. Within each of the three zones, sand movement, plant species and cover are distinct. However, the distribution of plant communities on dunes have been shown to be correlated with the amount of sand movement they can withstand and is thus an important factor that determines their spatial distribution in coastal dunes (Moreno-Casasola 1986).

The hummock dune zone is an ephemeral habitat, adjacent to a dynamic transient habitat, the beach (Clark 1977). Although the beach / surf zone and dunes comprise two separate ecosystems, they are intimately connected physically, chemically and biologically (McLachlan 1986). The hummock dune zone represents the foremost vegetated area of the beach and the hinterland margin. The vegetation is specialized, while the dominant arthropods are of marine origin. The transition zone between the ephemeral vegetated hummock dunes and the more stable vegetated foredunes is the incipient foredune zone. The majority of the vegetation is specialized, while the arthropods are dominated by the marine species, *Tylos capensis*.

Generally, two geomorphic / floristic habitats occur on coastal foredunes, the hummock dune and the foredune. However, other geomorphic / floristic habitats could occur. The incipient foredune and the boardwalk habitats were identified as such at the study site.

The interrelationships of small mammals and habitat structure, particularly vegetative cover, have been discussed (Birney, Grant & Baird 1976). Vegetation structure is also an indicator of environment and may thus reflect indirect controls such as primary productivity and thus food supply on mammal populations. Resources can be apportioned among species on the basis of extrinsic properties. The greater the distribution of resources, the greater the possibility for subdivision of resources and co-existence of species (Brown 1973). The vegetative cover influences the risk of predation which may cause rodents to shift habitat usage relative to the amount of available cover (Kotler 1984). This explains the high selectivity preference for the boardwalk habitat, where cover was high and vegetation negligible. In the Mojave desert, rodents treat shrubs as patches, and the size and spacing of these shrubs have pronounced effects upon the composition of the assemblage (Thompson 1982).

Rodent taxa differ in habitat utilization and additionally in their degree of association with various habitat components (Hallett 1982). *Rhabdomys pumilio*, a broad-niche species and grassland specialist, selected a broad range of habitats compared with the other species. It seems that only a small proportion of local patches provide suitable conditions for survival and reproduction. It should be borne in mind that organisms themselves are important parts of the habitat of other organisms (Elton & Miller 1954).

The driftline and environs (hummock dune zone), normally an unfavourable permanent habitat for many species, was selected for by the marine isopods. This was the most populated habitat. The Hymenoptera dominated the foredune zone in terms of numbers, and selected for this habitat. While subhabitat separation between the ants and wasps seem evident from results, it is unlikely, as the one crawls and the other flies, and habitat exclusion seems unnecessary. Dune ants have shown distribution patterns related to environmental gradients (Curtis & Seely 1987), and surface arthropods have shown increased surface activity in shaded microhabitats (Smith, Smith & Patten 1987). The maize beetle selects for a specific vegetation composition while the spiders were evenly distributed. Elsewhere habitat structure has been found to influence the spider community, and habitats with the greatest structural variation and floristic richness are also richest in species of spiders (Duffey 1962). The greater part of the study area consisted of marram tufts, and it has been shown that even relatively low values of *A. arenaria* severely depress the diversity of sand burrowing organisms. A general decline in numbers as the percentage of open sand increases has been demonstrated by Slobodchikoff & Doyen (1977).

Conclusion

Geomorphic / floristic variables are useful as general habitat indicators on coastal foredunes. Distinct zones, habitats and subhabitats are apparent on coastal foredunes. Overlap between animal distribution was apparent, partially owing to an animal's ability to move. Because of its capability to move, an animal species can choose favourable conditions at the right moment of day or season. In this way, animal species can exploit their habitat optimally by living and feeding in places where and at times when the micro-climatic conditions are favourable. Alternatively, because of this ability to avoid unfavourable conditions a less strict correlation between preferences and tolerances and observed distribution will be found. Habitat selection is indeed a force for achieving competitive co-existence (Rosenzweig 1981), but increasing density could modify the relationship between habitat structure and dispersal patterns.

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