LONG TERM POPULATION DYNAMICS OF TENEBRIONID BEETLES IN THE NAMIB DESERT

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Running title: Namib beetle populations

[] indicates comments to authors, not part of text

Raymond Peters

Single genus counts

Abstract

Desert animals are believed to have highly variable, unpredictable populations, that are mainly influenced by episodic events, especially precipitation, rather than by community processes. We tested this for darkling beetles (Coleoptera: Tenebrionidae) in the hyper-arid Central Namib. The sources of surface water in this desert are frequent advective fog along the Atlantic coast (CV=43%), highly sporadic summer rain from Indian Ocean monsoons (mean=11.3mm per annum; CV=250%), winter rain from the Atlantic Ocean (mean=4.0mm; CV=217%), and runoff in ephemeral rivers (mean=18 days annually; CV=150%). We monitored tenebrionid populations by pit trapping in five habitats continuously for 22 years (1976-1998), 1976 beginning with a heavy monsoon rain (>100mm) and continuing to the next heavy monsoon that occurred in 1997. There were gradual changes in species richness (22-31 per habitat; CV=14-37%) and total abundance (72-5280 individuals per trap per annum; CV=34-108%), increasing for several years and declining thereafter. Different species had different abundance patterns in response to various water sources. These responses are grouped into five models, namely, long-lived species responding gradually to heavy monsoons and often using fog water, irruptive species linked to all monsoons, seasonal species tied to winter rains, species responding to general precipitation, and those that depend on river floods. Our analyses confirm the hypothesis that rain is fundamental to population processes for most tenebrionid species in this desert. This study is contributing to our understanding of the ecological processes that may be affected by climate change, resource availability and desertification in southern Africa.

I: Introduction

Long-term patterns of population change provide insights into driving forces in ecology. This has served as the fundamental rationale of long-term ecological research (LTER), which has set the following objectives (Franklin *et al.,* 1990; Risser, 1995; Gosz, 1996): 1) to further the understanding of long-term ecological phenomena; 2) to study the role of episodic events that may be important despite their rarity; 3) to contribute to the scientific basis of ecosystem management; 4) to provide data for predictive modeling at large spatial and temporal scales; 5) and to identify and understand the ultimate environmental changes resulting from human activities.

Population ecologists have paid much attention to temperate insects especially to understand factors that regulate abundance patterns ranging from stable to cyclical or fluctuating irregularly. Andrewartha & Birch (1954) suggested abiotic explanations as main causes of population dynamics, but currently, density-dependant factors, especially competition, predation and disease are usually invoked (Myers, 1988; Shorrocks, 1993). Patterns and their underlying factors may, however, differ in the tropics, where long-term records are scarce (Wolda, 1978).

Comparable data from deserts are even more rare, where climatic-event explanations of population dynamics have been suggested (Wolda, 1978). Deserts are viewed as environments that are not at biotic equilibrium (Westoby *et al*., 1989) and population dynamics may thus be unstable. A better understanding of population ecology in deserts may, however, be crucial to facilitate the survival of particular biotic communities in environments of increasing aridity (le Houérou, 1990) and desertification (___).

A seasonal level of resolution of patterns of population change provides information on the kinds of phenology underlying population changes. The degree to which animal populations are strongly pulsed, seasonal or aseasonal (annual) may reflect their degree of dependence on particular climatic conditions that can be expected during the course of a year. By contrast, patterns of life history of arthropods usually become apparent on an annual level of resolution. Year-to-year changes may indicate to which degree populations follow equilibrium patterns that change little or only gradually (possibly cyclical) and differ fundamentally from the long-term strategies of opportunistic species. Desert populations can show both kinds of strategies (e.g., Louw & Seely, 1982; Polis & Farley, 1980; Polis, 1991).

The hyperarid Namib Desert is ideal for studying desert populations. The Desert Ecological Research Unit at Gobabeb, Namibia (DERU; part of the Desert Research Foundation of Namibia), has enabled ecologists to study many environmental parameters over the past 35 years and has ensured the institutional continuity necessary to study long-term processes (Seely, 1990). This provides an invaluable opportunity for LTER to integrate much of the knowledge derived from short-term studies into the understanding of long-term ecological processes.

The present study concerns a long-term monitoring programme of darkling beetles (Coleoptera: Tenebrionidae) in the Central Namib Desert. We focus on the hypothesis that water availability controls tenebrionid populations. Hydrology has previously been suggested to be fundamental for the population dynamics of Namib biota (Holm, 1970; Seely, 1973, 1989, 1991; Seely & Louw, 1980; Nel, 1983; Yeaton, 1988; Berry & Siegfried, 1991; Brain, 1993; Günster, 1993; Kok & Nel, 1996; Southgate *et al*., 1996). Long-term studies are required to confirm this.

The Central Namib has three sources of fresh water, namely, fog, rainfall and ephemeral river floods (Lancaster *et al*., 1984; Jacobson *et al*., 1995). Annual river floods originate from rains in the distant highlands of the Namibian interior. Regular fog comes from moisture over the Benguela upwelling system of the Atlantic Ocean. Sporadic rain comes from Indian Ocean monsoons in summer and Atlantic lows in winter. In an area with a median annual rainfall of 14 mm, years with >100 mm are extremely rare. Two rains of this magnitude did, however, fall only two years apart in the mid-1970s, providing not only an ideal opportunity to examine the immediate effects of such episodic events (Seely & Louw, 1980), but also an opportunity to monitor the long-term effects (present study). The availability of various water sources combine into a complex mosaic of pulse and reserve. This may provide insights into the question of what some of the expected ecological consequences of changing climate in southern Africa may be. Does Wolda's (1978) prediction that desert organisms are more variable in abundance than temperate and tropical species apply to all desert species, and, if not, what characters may exempt organisms from being ephemeral in an unpredictable climate? We examined these questions in five different habitats over periods of 16-23 years. We compared characteristics of the beetle community with incidents of water availability (rain, fog and river flooding) and their direct and secondary effects with respect to seasonal and annual timing.

Tenebrionids are ideal model organisms for investigating population dynamics in the Namib Desert. Their great diversity and abundance make them a conspicuous feature of this desert (Koch, 1962a). These beetles are relatively large, apterous, readily captured in pitfall traps and easy to identify. Furthermore, tenebrionids are good indicators of environmental conditions because their populations integrate several environmental factors, namely, food resources (e.g., detritus, leaves, dung), biophysical factors such as the availability of shelter (e.g., vegetation cover), soil conditions (e.g., hardness, moisture, stability) and water availability.

Our study can draw from a wealth of background knowledge. Taxonomic studies have devoted much attention to the Tenebrionidae (e.g., Koch 1962a, b; Schulze, 1974; Penrith, 1977, 1979; Endrödy-Younga, 1982) and it is the best-known major insect group in the Namib. Many ecological studies have focused on Namib tenebrionid communities (e.g., Holm & Scholz, 1980; Wharton & Seely, 1982; Seely, 1983, 1991; Crawford & Seely, 1987), while important physiological parameters have also enjoyed attention (e.g., Seely *et al.*, 1983; Seely, in prep [larval paper]; Roberts, 1991; Naidu, 1992), as have key elements of the reproductive biology (e.g., de Villiers, 1984; Seely, 1986; Enders *et al.*, 1998; Rössl, in prep). Similarly, studies elsewhere on tenebrionid and carabid beetles provide us with a useful baseline for comparison (e.g., Mitchell, 1963; Greenslade, 1964; Rickard & Haverfield, 1965; Ericson, 1979; Faragalla & Adam, 1985; Wise, 1981, 1982). Finally, where our study fails to explain some portentous parameters of the population dynamics of Namib tenebrionids, we suggest further avenues of investigation that may have fruitful bearing on issues being examined in this ongoing study.

I. Materials and Methods

Date Convention

Data years start in July and end in June so as to encompass the entire austral growth season. To avoid confusion, data years are written in the form: "92/93", sometimes shortened to "92", for the year beginning in July 1992 and ending in June 1993. Written calender years start with "19".

Abbreviations

Study Sites: KR = Kuiseb River
GP = Gravel Plains
IV = Interdune Valley
DS = Dune Slope
SF = Slipface

A. Trapping methods

1. Locations and Habitats

(Figure IIA1.1-2a-e: map & illustrations of habitats)

Gravel Plain (GP)

Location – Quartz Hill, 2 km N of Gobabeb (23°32'S; 15°02'E).
Habitat – (Wharton & Seely, 1982). Gently undulating gravel plains, interspersed with small rocky outcrops. The grasses *Stipagrostis ciliata* and *S. subacaulis* occur briefly after little rainfall and for several years after heavier rain. At other times the ground is bare except for sparse perennial *Salsola tuberculata*, a woody dwarf shrub. The ground is relatively firm, with a ca.15-cm thick gravel-sand layer overlying a hard crust of gypsum. Cracked rock surfaces and burrows provide shelter.
Food – Detritus trapped between stones.

Interdune Valley (IV)

Location – 1-2 km SSE of Gobabeb (23°35'S; 15°02'E).
Habitat – (Robinson & Seely, 1980). Near the edge of a gently sloping, 2-km-wide valley between 100-m high linear dunes. Scattered *Salsola tuberculata* occur on high ground, but the rest of the area is devoid of living plants except for periods after rains, when *S. gonatostachys* grows (Seely & Louw, 1980). The ground consists of firm sand, gravel, course stones, broad sheets of sandstone and very occasional rocky outcrops. Arthropods penetrate the surface by burrowing or by entering crevices.

Dune Slope (DS)

Location – Kahani dune, 10 km SSW of Gobabeb (23°39'S; 15°01'E).
Habitat – (Robinson & Seely, 1982). The dune slope is divided into three major zones, the dune base, the lower plinth and the upper plinth. The two adjacent zones, the interdune valley and the slipface, are here treated separately, as they are distinct and were monitored separately. Grasses are more persistent on the dune slope than in other habitats. Their cover generally decreases from the bottom upwards, except for *S. sabulicola*, which increases (Seely, 1990). Plants on the dune base of the study area are the perennial grass *Cladoraphis spinosa* and the leaf succulent *Trianthema hereroensis*, which dominated. Another typical feature of the dune base, the large Nara cucurbit *Acanthosicyos horridus*, was absent at the study site. After rains, tubers *Monsonia ignorata*, lilies *Hexacyrtis dickiana* and grass *S. gonatostachys* grew, the latter being more persistent here than on the interdune valley. The lower plinth was typified by perennial *S. sabulicola* and *T. hereroensis*, which both could form relatively large hummocks. On the upper plinth, typically only *S. sabulicola* remained. Steepness of the slope and its variability increased from the dune base upwards to the upper plinth, while the firmness of its purely sandy substratum decreased. Besides the green flush immediately after the big rains, *S. sabulicola* and *T. hereroensis* seedlings that arose then, developed substantially for at least 6-11 years thereafter (Seely, 1990).

Food – Seeds and flowers produced by resident plants and detritus trapped by them forms the basis of the detritivorous food web.

Slipface (SF)

Location – Kahani dune, 10 km SSW of Gobabeb (23°39'S; 15°01'E).

Habitat – (Robinson & Seely, 1982). Vegetationless, steep leeward slope of the dune, sloping down at an angle of ±33° from the crest to the avalanche base. The sand is unconsolidated, enabling animals to penetrate it by sand-swimming.

Food – Wind-blown detritus, comprising mainly grass seeds and stalks, accumulates on and within the changeable slipface and represents a stored resource for detritivores. It is re-exposed in greatest quantities at the avalanche base (Seely & Louw, 1980).

Kuiseb River (KR)

Location – 1 km stretch along river, 0.5 km S of Gobabeb (23°32'S; 15°02'E).

Habitat – (Theron & van Rooyen, 1980; Seely *et al.*, 1980; Jacobson *et al.*, 1995). The ca. 200-m wide riparian habitat comprises a central flood channel bordered by a forest dominated from the centre outwards by *Faidherbia albida*, *Tamarix usneoides*, *Salvadora persica*, *Euclea pseudebenus* and *A. erioloba* trees. The understorey is sparse and consists mainly of the perennial grass *Cladoraphis spinosa*, the shrub *Pechuel-loeschea leubnitziae* and alien shrubs, including *Datura innoxia*, *Nerium oleander* and *Nicotiana glauca*. The substratum comprises mostly very fine angular sand grains and silt.

Food – Flowers and leaves of *F. albida*, *A. erioloba*, and *C. spinosa* form the staple for detritivorous beetles (Hanrahan & Seely, 1990). The river did not flood at Gobabeb between 1978 and 1985. Ground water levels dropped, leading to drought-stress and death of *F. albida* trees (Ward & Breen, 1983). Besides loss of habitat, this probably meant less food for some tenebrionid beetles. Another major factor that probably affected food availability was domestic livestock (goats, donkeys and cattle) that regularly traversed much of the study area where they consumed and trampled the indigenous undergrowth and seedpods and deposited dung as a potential food source.

2. Traps

Round tin cans (15.0 cm diameter, 25.0 cm deep), that were dug into the ground, served as pitfall traps at GP, IV and KR. Small plastic buckets (14.5 cm diameter, 15.5 cm deep) were used at DS. At SF, modified conical steel lampshades served as traps.

3. Trapping protocol (Table IIA3)

GP

Period: 10 March 1976 - 31 March 1998 continuous

Placement: Fifteen can traps were placed in five groups of three. Groups were 50-200 m apart and traps in groups were 0.4-6.75 m apart. Two groups were next to low rocky outcrops, two were on the open plain >20 m from any rocks and one was on a quartz hillock.

Procedure: Traps were initially emptied thrice a week and later once a week. Animals were identified and released at the capture site.

IV

Period: 31 January 1977 - 31 March 1998 continuous.

Placement: Twenty-five traps were distributed in two sets, separated by 1 km north to south. Set A, located on relatively high ground, contained thirteen traps, placed 20 m apart in a line running parallel to a dune situated 250 m further east. Set B contained twelve traps placed 20 m apart in a triangle in a low part of the valley, 50-100 m from a dune to the east.

Procedure: Traps were initially processed thrice a week and later once a week. Some traps were sometimes filled with sand, giving incomplete sets. All traps were closed during short, irregular periods when it was not possible to process them.

DS

Period: 240 days between 2 July 1978 - 31 March 1998

Placement: Fourty traps were arranged into four sets, ten to each zone (upper plinth, lower plinth, dune base and interdune plain), placed in two parallel rows per zone. Within each zone, traps were 10 m apart.

Procedure: Traps were deployed at about 17h00 and were cleared at 08h00 the next morning and again at 17h00 in the afternoon. Traps were monitored for at least three consecutive days, but the annual trapping protocol was irregular. From 1993 onwards trapping was conducted on a bi-monthly basis.

SF

Period: 135 days between 15 February 1978 – 31 March 1998

Placement: Fifty traps were set out at the avalanche base of the SF at places where they were not filled too quickly with cascading sand. The length of the avalanche base being trapped at any one time was ±100m. In winter, when the slipface was badly formed, traps were set out on either the E-facing or W-facing slope, or both.

Procedure: The traps were set out at 07h00 before the diurnal beetles became active. The time of the last collection was between 18h00 and 22h00, depending on the decline of the numbers of *Lepidochora discoidalis* and *Onymacris laeviceps*, that were more active during wind (Seely, 1983). A normal trap day was 14 hours. Traps were cleared of captured animals and sand at intervals of 1-2 hours. Captured animals were taken to the nearby camp to be counted, identified and sexed. The animals were kept in buckets until after the last collection of the day, when they were returned to the slipface and released. Traps were monitored for 1-4 consecutive days with an irregular annual trapping protocol until 1993 when a bi-monthly protocol was adopted.

KR

Period: 4 August 1982 - 31 March 1998 continuous

Placement: Twenty traps were arranged in four sets that were 100-400 m apart. The five traps within each set were 8-30 m apart (x=14.9±5.6). Each trap was near or under a tree. One set was under a high canopy of *Acacia albida* trees along the river's flood channel, an area frequented by domestic goats. Another set was under a canopy of *Acacia erioloba* and *Tamarix usneoides* trees situated in a fenced area that excluded livestock on the upper river bank, ca.100 m from the channel. A third set was located along the border of the flood channel with traps in the open or sparsely shaded by small *T. usneoides*. The fourth set was under or adjacent to the low canopies of *A. erioloba* and *T. usneoides* trees on the upper river bank, 50-100 m from the channel.

Procedure: Trap contents were usually processed thrice a week. Animals were taken to the laboratory for identification and were usually all released on the day of capture at a single place, situated approximately mid-way along the study area.

4. Fieldwork limitations

Pitfall traps are a convenient method of catching some types of epigaeic cursorial arthropods. The number of trappable animals actually captured may depend on the population density, activity pattern, walking speed, and small-scale distribution (randomly dispersed or aggregated) of particular species (Mitchell, 1963). On annual time scales, short-term activity patterns make no difference and trapping can reliably reflect the population density of cursorial arthropods that move independently of each other (Jansen & Metz, 1979).

Pitfall traps can, however, have drawbacks. This includes trap avoidance by some species, the ability of others to escape, and consumption of trapped animals by predators (Mitchell, 1963; Luff, 1975). Male tenebrionids following females (Polis *et al.*, 1998) violate the assumption of independent movements. Furthermore, it is not possible to translate data into density (but see Gist & Crossley, 1973). Nevertheless, in field experiments, pitfall traps have been considered reliable within these limits for some animals, like beetles (e.g., Carabidae, Mitchell, 1963; Rickard & Haverfield, 1965; Luff, 1975; Baars, 1979; Ericson, 1979; Faragalla & Adam, 1985; Greenslade, 1964), or unreliable for other animals, like ants (Marsh, 1984), or wandering spiders (Henschel, 1991).

Our present use of pitfall traps is consistent with previous use in studies of Namib tenebrionid ecology (e.g., Holm & Scholz, 1980; Wharton & Seely, 1982; Crawford & Seely, 1987). Namib tenebrionids are easily trapped and, unlike some carabids (Luff, 1975), cannot escape from the large traps that we used. During laboratory studies, beetles could not escape from open smooth-walled buckets, similar to the ones used by us in the field. Furthermore, Henschel & Seely (unpubl.) obtained good correlations of pitfall captures and direct censuses along transects at one site. We thus conclude that the greatest power of expression of the results we obtained from pitfall traps in the present study lies in the relative numbers of various tenebrionids we caught over space and time. The relative numbers of taxa captured may, however, depend on their duration of activity, distance moved and home range. Pitfall traps may not accurately reflect the relative abundance of different major taxa, e.g. when comparing different tribes of Tenebrionidae. Nevertheless, even in this respect they may indicate changes within each group and enable qualitative comparisons between groups.

Another complication is that our data base differs for each habitat (Table IIA3). The number of traps used, though nearly constant within a habitat, ranges from 15 in GP to 50 in SF. Traps were deployed in different configurations in each habitat (see above). Consistent monitoring of various habitats began in different years between 1976 and 1982. Furthermore, monitoring was usually continuous for GS, IV & KR, but irregular or bi-monthly for DS & SF. These differences are due to the history of the development of this project, differences in habitat configuration (i.e. uniform on SF and increasingly more complex on IV, GP, DS and KR), varying manpower availability, and the dictates of circumstances prevailing in various habitats. For example, monitoring SF is highly labour-intensive, requiring each pitfall trap to be cleared hourly, compared to daily on DS, and only every few days in other habitats.

Nevertheless, each pitfall trap represents a consistent sampling unit. We compared abundance among habitats by expressing data as captures.trap^{-1}.day^{-1} (trap-days), or, arbitrarily, per 1000 trap-days. It was, however, not necessary to convert data on diversity or variability indices (R, AV, CV, %D) derived from abundance.

5. Specimen preservation and identification

A reference collection was kept to facilitate identification. Insects were pinned and other animals were preserved in 70% alcohol. Identity of voucher specimens was confirmed by consulting curators of entomology of the National Museum of Namibia.

Where possible, tenebrionids were identified to species level (see Appendix A). Several congeneric tenebrionid species were sometimes confused by assistants in the field and are thus analyzed collectively, referred to as *Genus* spp.. These were: *Namibomodes maculicollis*, *N. serrimargo* and *N. zarcoi*; *Vernayella delabati*, *V. ephialtes* and *V. pauliani*; *Pachynotelus albonotatus*, *P. comma* and *P. machadoi*; *P. lineatus* and *P. albostriatus*. By contrast, we kept apart records for the two subspecies *Onymacris rugatipennis rugatipennis* and *O. r. albotesselata*, as these non-waxy and waxy forms were easily recognized, although Hauffe (1989) and Hauffe & Seely (1995) consider their subspecific status as indistinct.

Field assistants may have experienced some uncertainties in identifying rare tenebrionids that they did not expect to find. We can obtain some indication of the degree of uncertainty by comparing the tenebrionids recorded by us with published lists (Appendix A). We did not record 14 (17%) of the 81 tenebrionid species found near Gobabeb. Of those, nine are rare. Four of the five common species not recorded by us are from the river bed. Within each habitat, we missed 6-25% of the total number of species recorded in that habitat.

Some differences may be due to our very localized records that did not encompass all landscape features of the Central Namib and our reliance on only one method of capture. On the other hand, our data set encompasses most of the climatic variability to be experienced in the vicinity of Gobabeb since research began there 35 years ago. Our long-term traps should therefore have had the opportunity to capture most of the trappable species, either as residents or tourists. We conclude that although we may have missed or misidentified some of the species that do occur in the area, they are not expected to be abundant enough to have changed our data set substantially. Furthermore, we have no reason to doubt that whatever deficiencies in our diversity data there might be, these were randomly distributed over the years of monitoring and do not affect our conclusions.

Our records of taxa other than tenebrionids are less consistent at species level, compounded by the problem that some of the fauna is less well described than the tenebrionids.

6. Number of individuals and species (Table IIA6)

We captured 468350 individuals of 242 species. Tenebrionids made up 92.3% of the catch, but only 33.5% of the species. On the dune slope, tenebrionids comprised only 63% of the catch, due to the many ants, solifugids, Thysanura and weevils occurring there. In other habitats, the tenebrionid proportion was higher (82-99%).

As tenebrionid imagoes are the best-known group of arthropods in the Central Namib and comprised most of the catch, we concentrate our analyses on this taxonomic group.

7. Standardization (Table IIA3)

Calculations with abundance took into consideration that monthly records were of unequal duration. Recorded month was based on the date that the traps were emptied. Duration of trapping months varied for GP, KR and IV from 15-40 days, for DS from 1-19 days and SF 1-9 days. A 40-day 'month' occurred when traps that were emptied at the beginning of a month included captures from the last week of the previous month.

Standardized results (e.g., Appendices C-G) are expressed as integers, i.e. animals were units, not fractions. To avoid "losing" species after standardization, data less than 1 were made equal to 1. Singletons remained 1. To avoid introducing rounding errors through the summing of monthly data to yearly data, raw data were summed and monthly and yearly sets were standardized separately. Similarly, summed raw data for groups of taxa, e.g., total for Tenebrionidae as a family, were standardized; standardized data for each species were not summed. Thus, the figures given for "Tenebrionidae" and "Total" in Appendices C-G are not exactly the same as the sum of standardized abundance of all the subsets of each group.

Duration of standard periods (Table IIA3) was based on the normal trapping protocol at each site. Trapping effort varied much for DS and SF: to avoid unrealistic distortions, short standard periods were selected. During the 3 initial years in IV, only 4 traps were used (normal=25) over 6-10 months, wheras in the subsequent 14 years, 25 traps were used continuously. Data for the first three years were standardized to the subsequent protocol. In the dune habitats (SF, DS & IV), when $\leq$50% of the traps were filled with wind-blown sand, each trapping day was standardized based on data for the open traps; data for <50% open traps were discarded.

B. Weather

1. Recording stations and instruments

Rain and fog were recorded at two autographic weather stations situated at Gobabeb Station and along High Dune, 8 km S of Gobabeb (23°38'S; 15°02'E). Continuous recording began at Gobabeb in 1962 and at High Dune in 1980. Data from the latter station were used as a backup and for spatial comparison of local events (e.g., patchy rain showers). Quantity and time of precipitation were recorded graphically on a recording drum. Data (±0.1 mm of precipitation) were extracted manually from the plots and summed up per day, month and year.

Periods (days) when the river flowed have been recorded manually since 1962. The maximum height of floods against a depth gauge in the river's central flood channel was noted. River-flooding events were also monitored at a weir situated 20 km downstream of Gobabeb; from these records we could deduce incidents of overbank flooding.

2. Significant events

Besides monthly and annual totals of rain, we took special note of heavier rainfall events, or effective rain, that succeeded in stimulating grass growth. The amount required for this may vary depending on the soil and plants involved. Jacobson (1993) and Günster (1993) noted that rainfall events of 10-12 mm sufficed for ephemeral grasses to sprout and complete their life cycles; Seely (1978a, b) calculated a zero-intercept of standing crop at 11 mm of rain. Based on this, we refer to >10 mm rain falling during one week in the growth season (September-April) as effective rain. Within the range of low annual rainfall occurring in this part of the desert, grass standing crop increases steadily with rain quantity (Seely, 1978; Jacobson, 1993).

In winter (May-August), 10-20 mm of rain did not appear to elicit germination of ephemeral grasses and succulents, while >20 mm did (pers.obs.). Water from winter rains did not appear to evaporate as quickly as that from summer rains and developed a moist subsurface layer of sand that could last for a long time (Gut, 1989; pers.obs.). This could benefit beetle larvae directly (Seely *et al.*, in prep.; Rössl, in prep., pers.obs.). We examined whether >10 mm of winter rain were significant events that may affect tenebrionid populations.

Fog is a relatively predicable water source on the annual time scale (Pietruszka & Seely, 1985; Henschel *et al.*, 1998). All fog precipitation can potentially benefit Namib Desert organisms directly (Seely & Hamilton, 1976; Seely, 1979; Seely, 1983; Seely *et al.*, 1983) and we used all fog data to compile monthly and annual totals.

Among the various effects of river floods, events of overbank flooding may have the potential for greatest effects on riparian biota (Jacobson *et al.*, 1995). During overbank flooding, water, detritus and nutrient-rich silt is transported beyond the confines of the central flood channel and penetrates the flanking forest, where much of it is deposited. Jacobson (THESIS) determined the presence or absence of overbank flooding near Gobabeb from regressions of river height measured at a weir 20 km from Gobabeb. We used his data to test for effects on beetle populations.

3. Characterization and Derivations

Rainfall in the Namib is highly variable and characterized by short episodic pulses (Pietruszka & Seely, 1985). These instantaneous events may, however, affect desert biota for long periods thereafter (Seely, 1973; Seely & Louw, 1980; Wharton & Seely, 1980; Seely 1990). An index is required that reflects this prolonged influence. This can be achieved by the cumulative percent deviation (C%D) of rainfall, which incorporates historical effects of surplus and deficit rainfall. We calculated C%D for all rain, effective rain, winter rain, river flow days and overbank flooding.

Another way of incorporating historic effects was to calculate the year-to-year change in total rainfall:

(quantity in year)/(quantity in previous year)

This is the same as R, the gradient coefficient (Benedek 1970 in Wolda 1978).

4. Seasonality

Based on previous observations of wind, fog, rain and temperature regime (Lancaster *et al* 1984), we divided the year up into three seasons of four months each. At Gobabeb, early summer (September-December) is a cool to warm period, with a high incidence of fog; late summer (January-April) is relatively hot, with less fog; winter (May-August) is characterized by a decrease in ground temperature, due to the sun's lower angle of incidence, and cool, calm periods with occasional fog alternating with warm, stormy periods of very dry berg winds. These climatic factors can vary much within seasons and between years, but form a general pattern (Lancaster *et al.*, 1984).

5. Limitations of rainfall records

Locations of rain gauges and pitfall traps did not correspond. Our two rain gauges were positioned 8 km apart, 0.5-2 km from each trapping site. The Gobabeb Station gauge recorded 0.2±1.7 mm more rain than the High Dune gauge, an insignificant amount (Wilcoxon's signed rank test: Z=1.2, P=0.13). In the winters of

1982 and 1987, much more rain fell at one than at the other gauge; the differences (8.0 vs 11.4 mm and 11.4 vs 5.1 mm at Gobabeb Station and High Dune respectively) could affect conclusions on beetle responses. We thus consider both values for each trapping site. In all other cases, heavy rain fell at both gauges and we use the amount recorded at Gobabeb Station.

C. Analyses of diversity and population dynamics (Table IIB)

1. Diversity and Community Components

From our raw data of species abundances, we determined tenebrionid species richness (S) with or without singletons for each habitat, overall and per year. We calculated the Shannon-Wiener index (H') and derived the index of evenness, J' (also called equitability; Pielou, 1975). We describe results for J' in preference to H', as J' expresses only the relative distribution of abundance among species without the complicating effect of S. S and J' were calculated for the grand total on annual data, as well as for each year on monthly data. The latter were used to calculate the percent deviation from the mean (%D) and the gradation coefficient (R).

We distinguished various components of the tenebrionid community, namely, common residents, common migrants, rare residents, and rare tourists. The latter were species that strayed from another habitat or region and did not form self-sustaining populations in the study area. Apart from drawing on previous knowledge, we could recognize the different categories by comparing species between habitats. Common residents are in the core area of the species range; apart from being abundant, at least in some years, they can occur exclusively in a specific habitat, or are abundant in one habitat and rare elsewhere, or are found commonly in several habitats. By contrast, common migrants are species that are known to be much more abundant elsewhere (> order of magnitude) and that venture into the studied habitat in especially good years. When such migrants are rare, they fall into the tourist category, i.e., it is assumed that all such individuals originated elsewhere. Rare residents are not known to be common at another place or at another time.

On species-effort curves for each habitat, we determined when species from various categories were captured for the first time. From the asymptotic species-effort curve, we determined various parameters and the species found in each: the number of species recorded on the first day of trapping, the first month, half year, and year. We noted the period it took to record 50% of all species, 95% and 100% and whether or not the curve reached asymptote. From square-root-transformed data, the slope of the main, linear part of the curve, from after the initial month of capture until there was a marked departure from this line was calculated. This middle part spanned 50-90% of the species-effort curve and was used to characterize the principal rate of capture within each habitat.

2. Abundance

Data were standardized (see section IIA6) to examine trends in abundance. Months were the smallest units of time considered, but most of the determinations were derived from annual abundance (see Appendices D-G).

The ten most abundant tenebrionid species were selected to characterize the community in each habitat. These were termed the focal species. Other taxa (Coleoptera families, insect and arachnid orders, lizard families) were included in more general analyses if ≥ 100 were captured.

We characterized focal species by their degree of variability in abundance within each year. Based on our knowledge of taxa and subjective examination of monthly abundance curves, we classified species as pulsed, if they were abundant in only some years depending on the timing of rains or floods, seasonal, if they were more abundant in a few months per year, and annual, if they were present all year long (see Louw & Seely, 1982; Polis, 1979). We quantified this in three ways. The first method was to calculate the coefficient of variation of monthly abundance for each year; consistent high CV values over several years were indicative of strong seasonality. Other indices were based on the monthly totals over all years. Wolda & Broadhead's (1985) seasonal maximum, SM, presents the percent abundance found in the month of maximum abundance, but gives no indication of the spread of data around this maximum. As an index of the spread of abundance over the months of the year, we calculated annual evenness, J', substituting "12 months" for "S". By visual comparison, we have found that J', applied in this way, appears to provide a good reflection of degree of seasonality; J' near 1.0 indicates a balanced spread of abundance over all months while J' < 0.7 shows seasonality. The latter can be separated from event-related pulses by examining CV for different years. J' provides a less erratic index for those species that are abundant in only a few months each year than does CV.

To characterize variability in abundance between years, we applied the gradient coefficient, R, on abundance data transformed to log, with 0 changed to ½, following Wolda (1978; Table IIB). We applied this to all values (NS=0; i.e., the smaller N of a pair could be zero), omitting pairs for which neither exceeded 1. Wolda's (1978) recommendation of NS≥5 is too restrictive for our data because a major characteristic of many Namib tenebrionids is their propensity to irrupt and crash (Seely & Louw, 1980; pers.obs.). To make our data comparable with Wolda's Table 2 (1978; pp.1025-1031), we did, however, apply NS≥5 for that purpose, but used NS=0 to compare our species and habitats. Furthermore, we used every pair of years (i.e., Year2:Year1, 3:2, 4:3...), as Wolda's (1978) use of only every second pair results is a reduction in sample size without actually circumventing the problem of using interdependent data. From R, we derived the annual variation, AV, or variance of R (Wolda, 1978), and mean R for each focal species. These two parameters were also determined for all focal species within each year, as well as for all years and focal species in a habitat. Another method of quantifying annual changes was to calculate the percent deviation of annual abundance from the mean. The average absolute deviation characterized variability of species.

We compared tenebrionid species in terms of their abundance and variability thereof and how this compares with some other characteristics of species: e.g., body mass vs. N; N vs. CV; N vs. J'; N vs. AV; N vs. mean R; CV vs. AV; body mass vs. CV; body mass vs. AV.

To test the hypothesis that Namib tenebrionids are dependant on episodic rains or floods to increase their productivity, we compared abundance with rainfall and river flood patterns. We began our assessment with a visual comparison of abundance histograms on tables and graphs depicting tenebrionid abundance (monthly or annual) versus water events: total annual rain and fog, effective rain and winter rain events, and river flood events (e.g., Fig.IIIA1.2).

We regarded a "response" as an increase in the monthly captures of tenebrionids following a "stimulus" (water event) if these increases followed a recognizable pattern. Since our study did not cover the years before the >100 mm rains, we took a general decline of a species during the following years without such rains as indicative that a response to those big rains had occurred. Other responses were judged on a case-by-case basis for each rain event. In the case of a summer and winter rain following each other in successive seasons (this occurred thrice), responses that followed such pairs were classed according to their consistency with previous single events (e.g., winter for species that had previously responded to isolated winter rains). "Response time" was the period (months) it took for a response to begin. A strong drop in abundance marked the end of a response, giving "response duration" (years). The proportion of total abundance contained within each response period indicated its relative importance. To evaluate the strengths of these apparent associations, we correlated each of the water events with the year-to-year increases in abundance (R>0), and lagged by 1 year.

Finally, we compared the outcome of the above analyses between the five habitats (GP, IV, DS, IV & KR), between three different kinds of phenology (pulsed, seasonal, aseasonal balanced) and life history patterns (opportunistic, equilibrium, intermediate), between different tenebrionid tribes and body size classes. These comparisons are based on indices that summarize the various parameters of abundance.

I.

II.

III. Results

A. Precipitation and river flow

(Table IIIA1; Figs IIIA1.1 & IIIA1.2)

1. Rain

Over the 23-year study period, an annual mean rainfall of 23.0±33.1 mm (2.0-115.1 mm; median 11.6 mm) was recorded at Gobabeb. The annual rainfall was very variable and followed no discernable pattern over years. Most (73%) of the rain fell in late summer (January-April), and very little (5%) in early summer (September-December), while 22% of the rain fell in winter.

Two wet years occurred when > 100 mm fell in the late summers of 1976 and 1978. These are the only rainfalls of this magnitude to have fallen in the western central Namib since 1934 (Walter, 1936). We recorded effective summer rains twice more in 1987 and 1990 and heavy winter rains four times in 1979, 1982, 1987 and 1989.

The pattern of C%D of rain was relatively simple. Towards the beginning of the study, there was a strong increase in C%D, followed by a steady decline between 78/79 and 92/93 (Fig. IIIA1.2).

2. Fog

The broad trend of fog precipitation was very different to that of rain, as it decreased between 75/76-78/79 and increased between 85/86-92/93 (Fig. IIIA1.2). Annual precipitation of fog was 40.6±17.6 mm (14-77), and followed a cyclical pattern of 9 years (Table IIIA1; autocorrelation with lag=9: 0.161 ±S.E. 0.296). After an initial increase in fog from 75/76 to 80/81, it decreased again until 85/86. Maximum recorded fog precipitation occurred in the years 89/90-92/93. The seasonal pattern was quite consistent, with 49% of fog occurring in early summer (September-December), 21% in late summer, and 30% in winter. On monthly and annual time scales, fog is the most predictable water source available to Namib biota (Pietruszka & Seely, 1985; Table IIIA1).

3. River flow

The river usually flowed annually for days to months in response to rainfall on the Khomashochland (Huntley, 1985), but there was a prolonged period without river flow from 79/80-84/85. From 85/86 onwards, annual floods resumed, with overbank flooding occurring in six of the subsequent eight years (Table IIIA1).

B. Summary Data Presentation (Appendix C-G)

Standardized abundance data, pertinent details about the tenebrionid species captured and summaries of derivations and indices for each habitat are listed in Appendices C-G. Details are outlined below.

C. Diversity and Evenness

1. Species Representation

In each habitat, we captured most of the species recorded in previous studies (Appendix A; see section IIA5). Species richness recorded by us did not differ much from that expected from the literature (Table IIIC1), except in IV, where we found 38% more species than recorded previously. This discrepancy may be due to different study areas, capture procedures and time periods. We conclude that our records are representative of the fauna found in each habitat.

2. Species-effort (Table IIIC1)

***The rate of appearance of new species in our records differs markedly between habitats. Species were recorded fastest in SF and DS and slowest in GP and KR. This is probably not merely an artefact of the much lower effort in DS and SF, as is evidenced by the rapid attainment of asymptote of the species-effort curve in those two habitats and the similarity of our species richness values to previous records. [DO PAIRWISE COMPARISON: SAME TRAP DAYS_]

The order of appearance of species was inversely related to the relative abundance (Kendall's Tau: rank analysis__). The ten most abundant species were all represented within the first few effort-days in SF and DS, and within 3 months in KR, but took over a year to appear in IV and over three years in GP. These differences may be due to different events in time that played significant roles in various habitats (see section IIIC6 below).

About once per year, rare species (i.e. <10 individuals total) appeared for the first time in GP, IV and KR. Effort was too low to analyze rarity in SF and DS.

3. Species overlap between habitats (Table IIIC3)

Most species (59%) were not unique to one habitat. Of the 56 tenebrionid species recorded by us, 9% were in all five habitats (these were *Onymacris plana*, *O. rugatipennis*, *Zophosis moralesi*, *Z. hereroensis*, and *Namibomodes maculicollis*), 16% were in four habitats, 21% in three and 11% in two (Appendix H). [STATS___]

Only in GP were more than one-third (42%) of the tenebrionids unique to that habitat; all except one of the other species in GP were also found in IV (the exception was *Stips dohrni* that occurred in KR, Appendix H). The least overlap was of GP with DS and SF. Many species were recorded in all habitats of the dunefield, namely SF, DS and IV, explaining the low degree of uniqueness in terms of species present in these regions. IV also had many species in common with the adjacent KR.

4. Diversity (Table IIIC4; Fig.IIIC4)

Total species richness of tenebrionids was highest in GP and KR and lowest in DS and SF. On an annual basis, KR had more species than the other habitats, which were similar to each other. SF and KR had fewer singletons than other habitats. Maximum annual S was similar among habitats, but the range was narrower in IV and especially KR.

DS and GP had the highest evenness (J'), i.e., more species were numerically co-dominant than in other habitats. This effect was less obvious on an annual time scale. IV had the lowest evenness on both accounts. Monthly species richness and evenness were least variable (coefficient of variation) in KR and most variable in IV.

5. Diversity trends over time (Fig.IIIC5.1-4)

Species richness fluctuated a lot over the years at all sites except KR; timing and magnitude of fluctuations often differed between habitats (Fig.IIIC5.1; Table IIIC4). S increased in the four open habitats until 78/79 and then converged in 81/82. After that, trends diverged: IV, DS and SF decreased in 83/84 and 88/89 while GP increased. In general, S decreased towards the end of the study period, except in KR, where it remained relatively constant. This overall decrease in S from 79/80 to 92/93 is even clearer for mean monthly S (Fig.IIIC5.2).

The number of singletons (species of which only one individual was recorded in a habitat per year) may reflect trends for rare species: they may be tourists, last individuals of declining populations or rare resident. We found that the occurrence of singletons in various habitats was sporadic, with highest frequencies recorded in 76/77, 78/79-81/82, and 88/89-90/91 (Fig.IIIC5.3).

Trends in annual evenness, J', differed between habitats (Fig.IIIC5.4). In GP, J' increased much from 75/76-79/80 and then remained high throughout. This indicates that only few species dominated abundance in the early years, and that abundance was more evenly spread among the declining number of species in later years. Fluctuating J' in other habitats is more difficult to interpret. Only in SF did J' exceed 0.6 in the early '80s, indicative of several co-dominants. IV experienced a sharp decrease in J' during the late '70s and again during the late '80s. In general, J' was low in IV, indicative of dominance by one or two species. The strongest trend for DS was a drop in J' towards the end, coinciding with a drop in S. In KR, J' decreased until 86/87 after which it increased; thus, fewer species dominated stronger numerically between 84/85-88/89 than during other years.

6. Diversity in relation to rain and drought

a. Statistics: Can extreme deviations from mean or decreasing diversity/time of drought be recognized statistically? --> autocorrelation statistics?

b. Statistics to test month-to-month or year-to-year differences in S or J': ANOVA of mean monthly or yearly S/J' (12 months x number of years)

D. Abundance (Appendices C-G)

1. Capture Rate (Table IIID1)

The mean monthly abundance of tenebrionids different significantly between all habitats besides IV and DS (t-test; $P<0.05$). In GP there was once a period of 6 months (2730 trap units) in which no beetles were captured. This was also the habitat with the lowest overall abundance. Mean monthly abundance was much higher in SF than in other habitats.

The average size of beetles was larger in KR and DS than in other habitats. This explains why the total mass of tenebrionids captured each month in SF was similar to that in KR, despite the differences in abundance [paired t-test_]. Conversely, the total monthly mass of beetles in DS was much more than in IV, despite the similar numbers of beetles captured.

Variability of monthly abundance, as indicated by CV, was highest in IV. This could be due to seasonal fluctuations in numbers or periodic pulses. CV was lowest in KR. The high mean CV of species was not matched by a relatively high CV of all tenebrionids; this would indicate that, although some species fluctuated in different seasons, total numbers of tenebrionids did not. On an annual basis, tenebrionid abundance deviated most from the mean in GP and least in KR; individual species did, however, also deviate much in IV and DS.

The mean gradation coefficients, R, were <0, reflecting longer periods of population decline than increase. The grand means of annual variability of R, AV, were moderately high (0.3-0.9; Wolda, 1978). Mean AV was highest in SF and IV, intermediate in GP and DS, and lowest in KR.

2. Total tenebrionids: abundance trends with time (Fig.IIID2)

Total numbers of tenebrionids declined from the beginning of the study to the end in all habitats (Fig.IIID2.1). Abundance dropped permanently to below the mean for that habitat in 79/80 in GP, 80/81 in SF, 81/82 in IV, 83/84 in SF and 88/89 in KR (Fig.IIID2.2). Superimposed on this general trend, abundance fluctuated a little, with increases evident for DS in 79/80, SF in 82/83, for SF, DS and IV in 87/88 and GP in 76/77, 83/84 and 88/89. These patterns were in most cases mirrored in biomass. Notably, the increases in abundance did not show up in biomass at GP, except for the initial irruption. This is because the beetles that increased in abundance at GP after 77/78 were relatively small. The relative positions of the biomass curves from various habitats differed from those of abundance, probably due to differences in beetle size alluded to above.

Trends differed among habitats for the degree of month-to-month fluctuations in abundance, as represented by annual CV (Fig.IIID2.4). In GP, it decreased from high (>80%) in 75/76-77/78 to low over all years until 89/90, after which usually <1 tenebrionid was captured per month. In IV, the CV fluctuated at a high level, except during 79/80-81/82. CV started low in DS, but was high between 80/81-84/85. In SF, CV was high except during 82/83 and 92/93.

The gradation coefficient, R, indicated in which years there was an increase or a decrease in annual abundance over the previous year (Fig.IIID2.5). R was stable and close to 0 in KR. Substantial increases (R>0.1) occurred in various other habitats during eight years (76/77, 78/79, 79/80, 82/83, 83/84, 86/87-88/90 and 91/92). In all other year, strong decreases were evident in one or the other habitat. Details of increase or decrease events differed among habits (see below).

3. Tenebrionid species: abundance trends with time (Fig.IIID3)

Temporal patterns of mean abundance-trend indices (CV and R) for focal species were somewhat different from those seen for total tenebrionids. Mean CV values were high (Fig.IIID3.1). CV remained fairly steady in KR in all years and in GP from 75/76 to 85/86, after which they increased. In IV, the general trend of gradual increase was interrupted by drops in 78/79, 83/84 and 87/88-88/89. DS showed a year-to-year fluctuation (this may not be a real pattern, but could be an artefact of the ad-hoc sampling protocol). In SF, mean CV first increased, then gradually decreased towards the end, indicating either that seasonal influences on abundance declined over the years or that species that responded to seasonal factors were less important in later years.

Trends in year-to-year changes of annual abundance differed between species, making the pattern of the mean gradation coefficient (Fig.IIID3.2) difficult to interpret. This notion is supported by the high annual variability of log R, AV, seen in one or the other habitat during most years (Fig.IIID3.3). Our high values of AV could be partly due to our acceptance of a low NS and relatively small number of focal species per annum per habitat (7-18; Appendix C-G; see Wolda, 1978). They do, however, reflect that different species varied differently in abundance over the years (e.g., some increased, while others decreased) and that the year-to-year changes in the abundance of various species were sometimes strong (see below). The highest values of AV for each habitat (except KR, where monitoring started only late) were attained prior to 82/83.

4. Gradation coefficient (Fig.IIID4, Table IIID4)

Frequency of log R values for focal species of each habitat followed a normal distribution (Fig.IIID4.1 [test for normality]). The tails of the distribution at either end beyond R>1 and R<-1 reflect year-to-year changes in the abundance of focal species of over an order of magnitude. In SF, as many as 31% of the values were in these tails, with the proportion decreasing in DS, IV and GP, to a minimum of 5% in KR (Table IIID4).

We calculated annual variability, AV, in two ways: annual AV, for each year over all focal species and, species AV, for each species over all years. Most species AV (56%) were $\geq$0.5 (Wolda, 1978 considers an AV of 0.5 to be high), while 32% exceeded 1. Annual AV was, however, usually <0.5 (60%) and relatively seldom >1 (11%). From this we infer that, although the abundance of many species was highly variable, the strongest fluctuations took place in only few years.

Maximum log R for a species correlated significantly with minimum log R (r=-0.43; P<0.01; Fig.IIID4.3; leaving out an extreme outlier for *Psammogaster malani* in KR whose numbers increased, but did not decrease). This relationship indicates that populations of those species that have the capacity to irrupt quickly (high positive log R), can also crash quickly (low negative log R). The furthest outliers of this relationship are for four species on the left bottom of Figure IIID4.3. These species came from IV and SF, where monitoring began with high numbers of each of these species established (details given in next section). Our records may thus have missed possible irruptions by these species, which would have placed these outliers closer to the general curve. In general, the relationship indicated that the maximum rate of population increase for a species was about 1.7 times higher than the maximum rate of year-to-year decline [test for significant difference from parity: how? one of them is not a measure; e.g. count species above or below the 1:-1 line and run chi-square??]. It thus appears that factors controlling tenebrionid populations have a stronger influence on population increases than they have on their decreases.

Some populations were increasing during all years of our study, although their frequency varied much (Fig. IIID4.4). Many species increased in several non-river habitats between 76/77-83/84 and 86/87-88/89, with maximum numbers of increasing populations occurring in GP in 79/80, in IV during 86/87, DS in 79/80 and SF in 77/78. In KR, the number of growing populations increased between 85/86-88/89 and again in 91/92.

E. Population trends of species

1. Annual abundance

(Fig.IIIE1.1-5: log N of 10 focal species per habitat, Appendix H)

Abundance of species varied differently. The thirteen most abundant species in all habitats declined from peak abundances early in our study period (ca.76/77-77/78); rate of decline of these species varied from gradual (minimum logR=-0.4) to very rapid (logR=-3.1; over a thousand-fold decline from one year to the next). Other species increased or made their first appearance only in later years, notably in 82/83 or 83/84 and in 86/87 or 87/88.

We compared annual abundance with a number of other characteristics of each species (Table IIIE1). [need to do stats____]

[classify species into quartiles by relative abundance: see Appendix H]

abundant (25% of all species with > mean N)
intermediate abundances (25-75%)
rare (25% with <mean N)

2. Population changes within years: pulsed, seasonal or annual

[how many and what kind of species fall into various categories]

quartile definitions: see ranks in Appendix H
    pulsed (25% of all species with >CV & MJ')
    seasonal (25-75%)
    annual (25% with <CV & MJ')
concurrently inspect monthly data to assign phenology categories:
    among upper 75% of values, look for non-annual increases
for seasonal category: how strongly associated maximum month & %N
    (see Wolda & Broadhead, 1985)

3. Population changes between years: opportunistic, equilibrium or intermediate

quartile definitions for AV & %D, see Appendix H, and assign from data

4. Are there characteristics that such classes share?

are consistently different dynamics a function of:
a. Abundance: e.g., do rare & abundant species fluctuate more seasonally, yearly classes: rare vs abundant
b. Phenology: classes: pulsed, seasonal, present all year
c. Life history: opportunistic, equilibrium
d. Body size: classes: large, small species
e. Location: classes: river, plains, interdune, dune slope, slipface

F. Population trends versus water regime

- Data: monthly lag response to certain rains (Appendix H)
  from this we can determine: length of larval life
- Data: proportion of population that can be explained by rain events

[Notes: The big table Appendix H (parts of which could be incorporated into figures and tables of results), contains a lot of information that allows us to home in close to what each species is up to and go to town with plenty of cross-comparisons. To summarise some of the pertinent points of the Appendix H table:

- Species are ranked by their average abundance over all habitats; that is why it is total N/5000 traps, the sum of the following five habitat columns; so, for instance, although *L.discoidalis* was only ever found in 3 habitats, the total represents an average over all habitats (zero for the remaining other 2 habitats). With this we have a balanced overview of overall abundance
- Besides abundance (N/1000traps), data are shown for the main habitat only, i.e., the habitat in which species were most abundant
- Beetle sizes were obtained from direct measurements
- "Mass/Cal" is a morphology index of unknown usefulness: it is the ratio of actual mean mass of that species vs. its calculated mass from the Namib teneb length-vs-mass curve (Henschel & Seely, in prep); perhaps more compact beetles (heavier than expected) have different tolerance of drought periods -- this we can test with other data on the table (similar for other size parameters)
- to explain some of the other indices [we should think how best to make this load palatable]
    - CV=mean coefficient of variation for that species from CVs calculated for each year
    - %D is the annual mean absolute percent deviation of abundance from the mean
    - maxR is the maximum gradation coefficient for that species: what is its capacity to irrupt? (positive R)
    - minR: tendency to crash? (negative R)
    - %A is the percent of total abundance (including non-tenebrionids) that the given species represents in its main habitats (e.g., *L.discoidalis* were 65.5% of all captures on the slipface)
    - AR is the abundance rank of the species in its main habitat
    - SR=seasonal representation (Wolda & Broadhead, 1985); number of months of "total" year that a species was present; for us, this is not much use, as it is usually 12 or close to it
    - SM=seasonal maximum: percent of abundance in maximum month in "total" year (one way of indicating seasonality; strong if SM>>10%)
    - MJ' is the index of evenness or evenness applied to months, as explained in methods: if MJ' is lower than 0.7, species is pulsed
    - ELW=123; season of maximum abundance in "total" year;
      E=1=early summer; L=2=late summer; W=3=winter
    - BIP=123; within-year abundance distribution (from MJ')
    - more indices could be summarized in a similar fashion as ELW and BIP to allow us to run ANOVA's
    - the columns under "Responding to" indicate the rainfall/flood events for which I have recorded responses
        - 100L=>100mm rain in late summer (2 events)
        - 10L=>10mm in late summer (1 event)
        - 10W=>10mm in winter (4 events)
            - HYDRO should actually be "negative hydrology" as it is indicated by the steady decrease in numbers the longer the river does not flow

    - FLOOD includes
    - please note that the linkage of abundance with rain events is subjective and based on the logic explained towards the end of "methods"
    - at the time of ploughing through this part, I was no longer able to ponder at ease on how to support these assessments with statistics (not for want of searching in lit and trying out ad nauseam; Gary, your suggested index of "cumulative percent deviation" for rain and abundance gives very funny monkey-tail patterns on plots that make little sense to me, with data straight or lagged)
  - "beg (mon)" and "dur (yrs)" indicate the beginning of a response and its duration in months and years respectively; in some cases, both of these are approximations, e.g., for some species that are already present when a stimulus arrives, the beginning is when monthly abundance increases well beyond the normal monthly fluctuation; duration of responses to 100L in study areas that were opened only well beyond was taken as "as from 21 Jan 1976" (the first big rain) if the species was most abundant at the beginning of the study
  - Ranking shows the relative rank of various indices and factors, such as abundance (N: sorted by that), etc.; this may be useful in visual interpretations of the table, for designating quartiles and for conducting rank correlations; some ranks are from biggest to smallest (e.g., abundance, size), while others are from smallest to biggest (e.g., CV, R) depending on circumstance
  - Order in Habitat indicates the abundance rank that the species had in each habitat; note that *Z.moralesi* was No.1 in 2 habitats.
- Some of the "bottom lines" that emerge:
  - Fog does not appear to contribute to population growth, although it may help to decrease rate of population decline for some species
  - Rare, big summer rains explain the patterns of total abundance and of the most abundant species in each habitat
  - Big summer rains may be crucial for some species: how do they bridge the long gaps between? some enter egg- or larval dormancy (adults disappear), while other declining adult populations continue egg production e.g., *P.globosa, O.rugatipennis, O.plana*; note that the latter species were not affected much by smaller rains
  - Winter rains appear to be important for many other species (some of which don't respond to summer rain -- see Appendix H); one can count on winter rains roughly every 4-5 years, making this more reliable than any effective summer rains (look at 30-year record)
  - River floods, especially overbank floods appears to be important for a few species; where this was not the case (in the immediate sense), interpretation becomes "fuzzy"; the river is quite complex and was monitored for relatively short periods only (11 yrs out of 18-year study); thus, any statements concerning causes are less certain; a big question mark hangs over *P.globosa*, as its abundance patterns did not tie up with river flow patterns in an obvious way, although we know that it feeds so much on river flowers (Hanrahan *et al.*, 1990; Crawford, *et al.*, 1990) [my bet is that big rains are ultimately

involved, but we lack concrete evidence for this]; similar for *O. rugatipennis*, although there we do know from the interdune that big rains are involved

- [in an aside: our data on Appendix D & E indicate that *O.r.albotessellata* is present after big rains only for a short time, and then "evaporates", probably into the non-waxy *O.r.r.*; I am inclined to combine this waxy phase with *O.r.rugatipennis* --see Hauffe 1989, Hauffe & Seely, 1995]
- A lot of valuable detail on individual species emerges from these patterns; we can relate some of them to species accounts from previous studies
- It is difficult to perform correlations with our abundance data against rainfall in the normal fashion, as the time scales (duration) differ so much -- i.e., population increases or decreases can occur over several years in response to several days of rain; the scales also differ: thus the plot of cumulative percent deviation of rain, floods and fog (Fig.IIIA1.2) does not resemble similar plots for abundance (but it could for transformed data), although the general response pattern does support the notion of rain-driven populations

DISCUSSION

<u>Topics</u>

- water availability pattern: compare to other descriptions and effects in deserts and relate to previous Namib literature (e.g. Seely & Stuart, 1976; Stafford-Smith & Morton, 1990); also outline Central Namib rainfall in relation to main winter-rainfall zone in south and main summer-rainfall zone north
  - historical patterns: how often can big rains be expected? According to Seely (1989), no big rains have occurred in the Namib since the big rain of 33/34 reported by Walter (1936)
- seasonal climate (general pattern: compare early summer, late summer and winter)
- phenology of Namib tenebrionids and the ways in which it could affect population dynamics
  - reproductive biology of females (see de Villiers, 1984 and others)
  - patterns of egg-production, including "bet-hedging" (first discussed for Namib tenebs by Seely, 1983): consequences -> capacity to increase is ready when conditions get favourable & schedules of fecundity and juvenile mortality need not be coupled
  - egg-laying
  - ecophysiology of larvae
  - longevity of larvae [pers.comm. info: Mary?]
  - longevity of adults [Pietruszka pers.comm., marked beetles appearing in our own sets: such info was not recorded in the normal data books]
  - site fidelity, home range and dispersion of adults (Roer, 1985; Hamilton & Seely, 1976; Crawford *et al.*, 1990; Pietruszka pers.comm.)
- pertinent info on foraging behaviour and diet: what, how and when Namib beetle adults and larvae eat and drink
- consequences of water availability pattern for Namib biota [see notes]
- phenology and life history patterns that can be deduced from current study
  - seasonality (CV & J')
  - adult population response time of growth after water-events could reflect longevity of larvae

  - dormancy in non-adult stages (inferences)
    - none, if adults are year-round and always present; R does not get very high
    - possibly none or <1yr, if seasonal adults appear every year; R does not get very high
    - likely if population has capacity to boom suddenly (i.e. not build-up via increasing reproductive output of population, but abrupt appearance of many adults from none or very few before); R high in some years
- diversity patterns and change of tenebrionid population composition in relation to episodic rain/flood events
    - explain our patterns
    - local diversity over time: why so high (82 tenebrionid species near Gobabeb): time-niches?
- population dynamics of individual species and overall: kinds of patterns seen on annual and seasonal scales: summarize results
  - seasonality: pertinent info on that season (note: season of appearance of adults may not be due to optimal conditions for them then, but could be due to optimal conditions for eggs or larvae previously; survival of critical stage)
  - community composition over time: different phenologies and life-history pattens lead to community changes over time: discuss separately for most abundant species, common and rare
  - annual variability: how do desert population dynamics compare with insects in other regions (Wolda, 1978, Wolda & Broadhead, 1985)
  - comparison with beetles elsewhere: especially tenebrionids & carabids (e.g. Mitchell, 1963; Rickard & Haverfield, 1965; Wise, 1981, 1982; Parmenter & MacMahon, 1984; Parmenter *et al.*, 1989; Faragella & Adam, 1985; [we have lots more: I have not yet rooted deeply]
- discuss other factors that may relate to dynamics of individual species in Namib
  - size
  - habitat occurrence
  - phenology & life-history pattern: longevity & egg-production patterns: when, how many & hatching protocol: eggs used as "storage" or constantly put in as "bet-hedging" material
  - geographical distribution (& origin?): is centre of distribution here or north (summer rain) or south (winter rain)?
- other important factors that could influence current habitats but were not examined in detail (this could also be mentioned under "future studies" part
  - east wind
    - variation in availability of allochthonous detritus
    - possibly only significant on slipface
  - livestock
    - consumes food that can no longer become detritus (e.g., *C. spinosa* has nearly disappeared near Gobabeb)
    - disturbs the soil, changing it for larvae
    - denudes the area, removing beetle shelter
    - provides dung as food
    - goat numbers and their effects on the habitat have increased in recent years

- [annual censuses by veterinary services]
- what are our most puzzling patterns? Which of our explanations are still very speculative and need substantiation? Are any of these important, e.g. *P. globosa*? What to do about these in future (see Appendix _)?
- conclusions of present study

Water Availability

1. Possible kinds of effects of water availability or drought on beetles [could make a table to sum up these factors; differentiate between eggs/larvae and adults]
    a. Primary
        i. Free water
            (1) Rain: rarely available and penetrates quickly; unreliable source in desert; it may be difficult for animals to drink water once it has penetrated the sand (absorption is possible, see below)
            (2) Fog: frequently availabe; many species have behavioural strategies to gain fog water at the surface; [note: only dehydrated beetles fog-bask, Seely *et al.*, 1983]; fog water typically does not penetrate far into the ground and disappears rapidly when the surface heats up in the sun; water of this kind has been shown to increase egg production (e.g. *O. unguicularis*, de Villiers, 1984)
            (3) River: rarely available and usually only in a narrow belt; risk of drowning when trying to drink
        ii. Moisture
            (1) Rain: penetrates into substratum, providing a humid environment for chthonic animals; this could be particularly important for eggs and larvae, and would provide an amenable haven for adults; it has been shown that some animals (e.g., Thysanura, Edney, 1971) can absorb moisture from moist sand, thus gaining free water. Similary, sand moisture appears to benefit beetle larvae directly (Coutchie & Crowe, 1979, Seely *et al.*, in prep.; see also Coutchie & Machin, 1984, Machin & O'Donnell, 1991; [also osmoregulation papers by Naidu and others).
                - Water from summer rain may not be available for a long time, as it disappears from top 15 cm of sand within 1 month (Yeaton, 1988; see also Gut, 1988).
                - Moisture near surface of sand may last longer in winter (Gut, 1988; pers.obs.) because of reduced evaporation in 10°C cooler ground (Lancaster *et al.*, 1984), a result of the sun's lower angle of incidence.
            (2) Fog: increases humidity at the surface, enabling larvae to be active in this otherwise hostile region; surface activity may be necessary to gain access to food (e.g., easier to collect at surface)

        - (3) River: overbank flooding may penetrate under shady canopies, moisten sand and provide nutrients for an extended period (months?)
        - (4) Drought: desiccation: ability to osmoregulate (see Naidu, 1992); some beetles such as *O. rugatipennis* and *S. gracilipes* have good ability to osmoregulate, sustaining water losses of over 70%; *P. globosa* regulates H2O poorly; *O. unguicularis* and *S. stali* are intermediate with regulation breaking down as dydration progresses; poor osmoregulation may explain disappearance of some species of some tenebrionid species during drought
- b. Secondary
    - i. Primary production & detritus generation
        - (1) Rain: when enough rain falls in a short period of time (>10mm in a week), this can stimulate germination (winter rain may not be as effective) or greening and growth of perennial plants; this produces food for herbivores and, later the seeds and plant remains are available for consumption by detritivores (allochthonous effects may also arise when detritus is wind-blown from relatively rain-rich areas into the desert; such detritus accumulates particularly on slipfaces; in that case local rains are no guide to food availablity)
        - (2) Fog: desert perennial plants obtain water from the fog (Walter, 1936; Seely *et al.*, 1977; Louw & Seely, 1980; Seely, 1981; Nott, 1985); this can provide green food for herbivores and also results in the production of seeds and flowers that feed detritivores
        - (3) River: river flow, particularly overbank floods, stimulate germination of tree, grass and herb seedlings, including aliens; may cause flowering of smaller plants (subsurface flow may influence tree flowering patter, but that is not clear)
        - (4) Drought: lack of green leaves, reduction in quantity detritus after prolonged drought, possible reduction in quality of detritus [any data on quantity/quality with time?]
    - ii. Palatability
        - ◦ some foods, particularly detritus, may only become palatable to some beetles when soaked with water; fog would have this effect more frequently on the surface only, while rainwater may penetrate the ground and soak detritus reserves there
    - iii. Fungus & Bacteria
        - ◦ Some arthropods may feed on fungi and bacteria (e.g., Thysanura, Watson *et al.*, 1990) [NB: this could be a major food source and may explain effect of winter rain?]

- Microbial activity in near-surface wind-blown sand is very low (le Roux, 1970), but relatively high in interdune and detritus patches on dune slope; the latter were comparable to desert soils elsewhere; the potential for microbial productivity to increase with rain does thus exist [note that le Roux found very few fungi in 1968, in dry sand during a dry period; negated by recent evidence, see below]
- Particularly rain, but also fog and river flow stimulates growth of fungi and mycorrhizae in dunes (Jacobson, 1992; pers.comm.).
- fungi could facilitate access by consumers to tough fiber or seedpods by weakening/softening such structures?
- [look for more examples, e.g., any evidence that any Coleoptera larvae anywhere live on micro-fungi or bactria?]
- [what happened to Crawford & student investigation on Namib tenebs?]
- [any evidence for plains?]

Notes on Namib Literature

- Watson (1990): Namib dune Thysanura eat fungi
- Watson (1989): Namib dune detritus is dense around plinth veg, sparse on open slope and scattered on slipface: no significant difference in moisture among dune levels.
- Edney (1971): Namib Thysanura absorb moisture from air and sand.
- Yeaton (1988): shows graph that illustrates that rain moisture disappears from near-surface dune sand layer (upper 15 cm) within a month (result of April rain on Far East dune); frequency of rainfall increases growth of Namib dune perennials
- Influence of fog on primary productivity: dune perennial plants absorb fog water: Seely, de Vos & Louw (1977); Louw & Seely (1980); Seely (1981); Nott (1985)
- Jacobson (1992), pers.comm.: Fog moisture enhances fungal growth near surface; moisture deeper in sand after rain stimulates fungal blooming [we could connect this to winter rain effect, but this has not been tested]
- Crawford, Hanrahan & Seely (1990): *P.globosa* diet is 50-96% flowers of *A.erioloba* and *A.albida*; litter quality did not affect distribution of *P.g.*; food selection depends on items encountered by beetles, not density of items in field; population may respond to flower availability above a certain minimum threshold, otherwise decline [NB: use this as argument in describing pop pattern]; thermal environment in shady trees may be important for gut symbionts; individual beetle can show fairly high degree of site fidelity, but shift intermittently
- Crawford (1988): tenebrionid gut symbionts need to avoid thermal stress and require optimal temperatures [however, optimal thermal considerations may not be important on annual scale for our study]; "nutritional state...both affects and reflects habitat selection, which is of paramount importance to habitat use and, ultimately, to fitness" p119

General Notes

- Compare rainfall with biota
  - RUE - Rain Use Efficiency Factor (Le Houérou, 1984): ratio of annual primary production (kg DM/ha/year) and rainfall (mm/year); RUE tends to decrease when aridity increases, but is variable, depending on physical parameters; RUE can be index of ecosystem productivity; average RUE=4.0, i.e. 4kg production of dry matter per ha/year per mm of rain (le Houérou *et al.*, 1988)
    see: le Houérou, H.N. 1984. Rain use efficiency: a unifying conept in arid-land ecology. Journal of Arid Environments 7: 213-247.
  - PRVR - Production to Rain variability Ratio (Le Houérou *et al.*, 1988): ratio of CV annual production and CV annual rain; average PRVR=1.5, i.e. production varies 1.5 times more than rainfall
    see: Le Houerou, H.N., Bingham, R.L. & Skerbek, W., 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments*. 15, 1-18.

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- Numerous assistants including volunteers
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- discussion: Cliff Crawford, Bill Hamilton, Kathy & Peter Jacobson, Yael Lubin, Florian Jeltsch, John Mendelsohn, Paco Pinero, Karel Spitzer, David Ward, Christian Wissel, Henk Wolda
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Table IIA3: Trapping protocol

Data	GP	IV	DS	SF	KR
Start	10Mar'76	31Jan'77	2Jul'78	15Feb'78	4Aug'82
Months	208	198	175	180	131
Operational months	206	187	50	57	129
Years (Jul-Jun)	18	17	15	16	11
No. Traps	15	* 25	* 40	* 50	20
Arrangement	triads	2 lines	8 lines	1 line	4 groups
Operational hrs.d^{-1}	24	24	24	±14	24
Trap hrs.d^{-1}	360	600	960	±637	480
Operational days	6150	5131	175	112	3711
Trap days	92250	123689	6691	5264	74212
Std. trap month (d)	30	30	1.5	0.5	30
Std. trap year (d)	365	365	18	6	365

* sometimes fewer traps were deployed or some were filled with sand

Table IIA6: Abundance and number of species of animals captured in pit traps in different habitats [should we present data in % of vertical total? we could combine taxa or leave out habitats]

TAXA	GP	IV	DS	SF	KR	TOTAL
Abundance						
Tenebrionidae	16345	75517	6402	61878	200457	360599
Other Coleoptera	75	104	150	230	1164	1724
Formicidae	757	2000	538	195	124	3614
Isoptera	38	282	34	0	7	361
Orthoptera	17	59	74	6	42	198
Thysanura	42	1855	758	3130	23	5808
Other Insects	0	26	17	6	180	229
Solpugida	706	5336	252	151	8	6448
Araneae	195	154	41	53	171	614
Scorpionida	147	75	3	0	10	235
Reptiles	254	362	130	522	15	1283
Total	18576	85732	8399	66172	201931	380843
Captures.trap^{-1}.day^{-1}	0.2	0.7	1.3	12.6	2.7	1.2
Species						
Tenebrionidae *	31	29	23	22	31	61
Other Coleoptera	7	12	20	18	28	44
Formicidae	6	3	5	1	7	11
Isoptera	1	2	2	0	2	2
Orthoptera	4	4	4	1	2	6
Thysanura	1	1	7	4	1	9
Other Insects	0	2	6	0	8	10
Solpugida	12	7	5	3	3	20
Araneae	15	5	22	6	23	48
Scorpionida	2	3	2	0	4	8
Reptilia	16	8	8	3	7	23
Total	95	76	104	58	116	242

++ crawling invertebrates and reptiles recorded in the vicinity of the study area are listed in Appendices A & B

* species groups of tenebrionids were counted as one

Table IIB: Glossary of properties and calculations applied in this study. Standarized data were used, except where indicated with *

Property	Abbreviation, Equation, Definition	Current Application
Sample size	n	
Mean	$x \pm y$: Mean ± 1 standard deviation	
significance	$P<0.05$, where not stated otherwise	
Abundance	N	
	N_i = quantity in year i	
	$N_{i,m}$ = monthly quantity in year i	
	ΣN = grand total	
	$\tilde{N}$ = grand mean	
Gradation Coeff.	$\log R_i = \log(N_i) - \log(N_{i-1})$	abundance
	exclude pairs 0-0, 0-1, & 1-1	
	if $N=0$, make $N=\frac{1}{2}$	
	also, $R_i = (MM_i) / (MM_{i-1})$	rainfall
	$R_i = S_i / S_{i-1}$	species richness
	$R_i = H'_i / H'_{i-1}$	diversity
Annual Variance	Wolda's AV	as for R
	AV = variance of R	
Coeff. Variation	$CV_i = SD_{i,m} \times 100 / (\text{mean } N_{i,m})$	monthly N
	where SD = standard deviation	rainfall
Seasonal Maximum	SM = % abundance in maximum month or season	
Percent Deviation	from grand mean	
	$\%D_i = (N_i - \tilde{N}) \times 100 / (\tilde{N})$	abundance
	likewise for S & H'	diversity
Cumulative %D	$C\%D_i = \%D_i + \%D_{1...i}$	rainfall, N
	where $\%D_{1...i} = \%D_1 + \%D_2 + ... + \%D_i$	
Species richness	S = number of species	tenebrionids
	also, $S_{-1} = S -$ singletons	
Singleton	$N_i = 1.\text{species}^{-1}.\text{year}^{-1}.\text{site}^{-1}$	tenebrionids
Diversity	variability of taxa	tenebrionids
	Shannon-Wiener index	
	$H' = \text{sum}(P_k \times \log_{10}P_k) \times (-1)$	
	where P_k = proportion of species k	
Evenness	abundance distribution	
	$J' = H' / \log(S)$	tenebrionids
	$J' = mH' / \log(12) \approx mH'$	seasonality
	where $mH' = H'$ on totals for months	
Species-effort	cumulative number of species recorded	tenebrionids

Table IIIA1: Annual quantity of rain and fog precipitation and duration of river flow recorded at Gobabeb between 1962-1992, with an indication of heavy rainfall events (>10 mm) in summer (s) and winter (w) and overbank floods (f) in the river.

Year	Rain (mm)		Fog (mm)	Flood (days)		Begin trapping	Dates of effective rain
62/63	15.8	w	-	68			
63/64	24.0		-	-			
64/65	25.6	s	-	26			
65/66	16.8	w	-	18			
66/67	26.6	s	31.1	22			
67/68	5.3		37.9	11			
68/69	30.3	s	28.6	18			
69/70	3.5		-	1			
70/71	20.5	s	26.8	34			
71/72	24.7		35.9	43			
72/73	7.9		36.3	15	f		
73/74	23.3		18.6	102	f		
74/75	7.0		11.1	10	f		
75/76	115.1	s	26.1	61		GP	21-25Jan, 31Mar-1Apr76
76/77	14.3		14.0	8		IV	
77/78	108.6	s	27.0	7	f	SF	7-9Feb, 28-31Mar, 28Apr78
78/79	31.2	w	18.8	8		DS	1-4Jun79
79/80	5.5		41.7	0			
80/81	11.8		48.0	0			
81/82	6.3		42.4	0			
82/83	19.0	w	35.3	0		KR	1-2Jul82
83/84	4.5		38.8	0			
84/85	7.0		22.7	0			
85/86	2.0		19.6	14	f		
86/87	12.9	s	47.4	7	f		5-6Apr87
87/88	23.8	w	47.3	17			19Jul87
88/89	16.3	w	41.7	8	f		7May89
89/90	11.5	s	77.0	17	f		11Feb90
90/91	10.9		63.5	4	f		
91/92	9.2		52.9	3			
92/93	4.5		67.5	18	f		
93/94	21.4	s	27.5	6	f		12-13Dec'93
94/95	15.4		74.2	17			
95/96	18.6		53.7	3			
96/97	70.0	sw	46.6	33	f		16Jan97, 24May97
97/98				3			
35-yr							
Mean	22.0		38.7	18			
SD	25.6		17.1	22			
Min	2.0		11.1	0			
Max	115.1		77.0	102			
Cvyr	116		44	126			
22-yr							
Mean	24.5		42.4	10			

SD	31.6	17.8	14
Min	2.0	14.0	0
Max	115.1	77.0	61
CVmo	240	83	248
Cvyr	129	42	134

Winter Rain: 4.3±9.1 mm; CV=211.8%, intervals: 5.7yrs
Summer Rain: 11.3±28.3 mm; CV=250.1%, intervals: 4.0yrs

Table IIIC1: Species-effort rates of tenebrionids in various habitats. "Rate" is the slope of the middle of the curve of square-root transformed days versus species number

Parameter	GP	IV	DS	SF	KR
S-literature	32	18	28	19	33
S-current	31	29	23	22	31
Total effort days	6319	5136	176	112	3981
Days for 100% of species	5081	4143	147	40	3912
Days for 95% of species	2653	1791	101	31	3209
Days for 50% of species	458	163	6	2	223
Days for 10 most abundant	1161	377	8	2	84
N: rare (<10)	11	14	9	8	11
Intervals: rare	462±673	296±627	16±17	5±7	356±407
Rate (slope)	0.67	0.91	3.77	7.67	0.65

Table IIIC3: Number of tenebrionid species that were unique to only one habitat or common to several habitats [show mirror-image data? this way it is easy to get all info for habitat in one glance along either row or column, but each item in central table is duplicated; an alternative is to give percent in the mirror image, but that may be confusing]

Habitat	GP	IV	DS	SF	KR	Total
GP	-	17	9	7	15	
IV	17	-	20	15	20	
DS	9	20	-	17	13	
SF	7	15	17	-	11	
KR	15	20	13	11	-	
Unique	13	0	0	1	9	23
S	31	29	23	22	31	56

Table IIIC4: Diversity indices of tenebrionids in various habitats

Parameter	GP	IV	DS	SF	KR
S, total	31	29	23	22	31
S, mean annual	14	12	12	13	17
S, mean monthly	6	4	6	8	11
S, annual range	6-21	9-20	5-18	5-19	15-19
S, monthly range	1-11	2-6	3-12	5-11	9-12
singletons, total	4	4	4	3	2
singletons, annual	3	3	3	1	2
J', total	0.52	0.28	0.50	0.32	0.33
J', mean annual	0.68	0.31	0.47	0.47	0.40
mean annual CVof S	35	37	32	26	14
mean annual CV of J'	46	72	51	33	17

Table IIID1: Standardized abundance (N), mass (mg) and derived indices of tenebrionids trapped in various habitats. Month=30 days; CV=coefficient of variation of monthly N per annum; %D=percent deviation from mean annual N; R=gradation coefficient of annual N; AV=annual variation of R; total=N of all tenebrionids before performing calculation; .species^{-1}=mean index for all focal species

Variable	GP	IV	DS	SF	KR
Mean±SD N.month^{-1}.trap^{-1}	6±18	21±41	25±29	440±689	83±41
Minimum N.month^{-1}.trap^{-1}	0.0	0.1	0.7	3.0	11.2
Maximum N.month^{-1}.trap^{-1}	176	366	152	3598	224
Mass mg.month^{-1}.trap^{-1}	384	781	4355	20655	17643
Mean mass mg.individual^{-1}	69	63	143	69	217
CV, total	73	108	78	76	34
CV, mean.species^{-1}	190	209	147	138	118
%D, total	107	96	59	99	28
%D, mean.species^{-1}	117	132	109	85	93
R, total	-0.100	-0.109	-0.145	-0.237	-0.054
R, mean.species^{-1}	-0.030	-0.065	-0.182	-0.162	-0.020
AV, total	0.083	0.032	0.063	0.277	0.004
AV, mean.species^{-1}	0.519	0.863	0.654	0.912	0.311
n months	206	187	50	57	128
n years	18	17	10	9	11

Table IIID4: Proportion of values of log R for each species in each habitat each year that were <-1 or >1, indicating increases or decreases of above an order of magnitude

	GP	IV	DS	SF	KR
% < -1	5.6	10.5	16.7	20.5	1.4
% > 1	9.3	9.9	11.1	11.0	3.4
n of log R	216	162	72	73	146

Table IIIE1: Correlation of abundance with other characteristics of tenebrionids [data in Appendix H; Spearman rank correlation or Kendall's T; chi-square for #habitats (1-5) that species occurred in]

	r
Mass	
CV	
%D	
mean logR	
AV	
minimum R	
maximum R	
	Chi-square
Number of habitats	

Table IIIF_: Number of species for which >5% of abundance appeared to be associated with their responses to various water events in each habitat (see Fig.__)

Water Event	GP	IV	DS	SF	KR
Big rain (>100 mm)	18	13	9	15	4
Summer effective rain	4	4	1	4	3
Winter rain	13	7	7	6	4
River flowing	-	-	-	-	9

APPENDIX A: TENEBRIONIDS RECORDED IN THE VICINITY OF GOBABEB

Sources (capital=abundant/common; lowercase=present/rare)
Cc = current
Hh = Holm & Scholtz (1980)
Rr = Robinson & Seely (1980)
Ww = Wharton & Seely (1982)
p = Prinsloo (1990)
e = Penrith (1977, 1979)

Species	GP	IV	DS	SF	KR
ADESMIINI (14/14)					
Cauricara eburnea (Pascoe)	Cwe	.	.	.	.
Epiphysa arenicola Penrith	Cw	c	.	.	Cpw
Epiphysa flavicollis (Fabricius)	c	.	.	.	.
Eustolopus octoseriatus Gebien	ce	CRHe	rHe	cr	c
Metriopus depressus (Haag)	CWe	ce	.	c	c
Onymacris laeviceps Gebien	.	Ch	CRHe	CRH	.
Onymacris plana (Péringuey)	c	Crh	CRHe	CRH	c
Onymacris rugatipennis (Haag)	c	cr	CRHew	cH	CpW
Onymacris unguicularis (Haag)	.	ch	cRHe	CRH	.
Physosterna cribripes (Haag)	CW	c	.	c	c
Physadesmia globosa (Haag)	cW	c	he	.	CpW
Stenocara gracilipes Solier	ce	ce	.	.	CpW
Stenocara (Cauricara) phalangium (Gebien)	ce	CRHe	CRH	C	c
Stenocara (Cauricara) velox (Péringuey)	Cwe	c	.	.	p
CAENOCRYPTICINI (5/6)					
Caenocrypticus peezi Koch	.	.	.	.	cpw
Caenocrypticus phaleroides Koch	.	h	H	.	.
Vernayella delabati Koch	.	.	rH	CRh	.
Vernayella ephialtes Koch	.	.	rh	CRh	.
Vernayella pauliani Koch	.	.	cH	CH	.
Vernayella noctivaga Koch	.	c	CRh	CRh	c
CALOGNATHINI (2/2)					
Calognathus chevrolati Gebien	.	c	c	c	c
Vansonium bushmanicum Koch	cw	Cw	c	.	.
CRYPTOCHILINI (3/5)					
Pachynotelus albonotatus Haag	.	C	c	c	.
Pachynotelus comma Gebien	.	cR	cR	.	.
Pachynotelus machadoi Koch	.	cH	cH	h	.
Pachynotelus albostriatus Haag	.	.	.	.	p
Pachynotelus lineatus Haag	.	.	.	.	Cpw
DROSOCHRINI (1/2)					
Diestecopus histrio Koch	w	.	.	.	.
Nicandra	.	.	.	.	cw
EPITRAGINI (1/1)					
Himatismus sp.	.	.	.	.	cw
EURYCHORINI (8/8)					
Eurychora sp.1	.	.	.	.	CW
Eurychora sp.2	CW	c	.	.	.
Geophanus sp.	.	.	.	.	cW
Lepidochora discoidalis (Gebien)	.	c	cRH	CRH	.
Lepidochora kahani Koch	.	.	cRh	CRH	.
Lepidochora porti Koch	.	c	CRH	crh	.
Stips dohrni (Haag)	Cw	.	.	.	c
Stips stali (Haag)	c	ch	CwRH	.	CpW
MELANIMINI (0/1)					
Cheirodes sp.	w	.	.	.	W

MOLURINI (3/8)					
Namibomodes muculicollis Koch	c	c	C	C	C
Namibomodes serrimargo (Gebien)	.	ch	cRH	cH	.
Namibomodes zarcoi Koch	.	.	w	.	cpw
Phanerotomea sp.	c	.	.	.	.
Psammodes sp.	w	.	.	.	.
Synhimba melancholicum Koch	w	.	.	.	.
Synhimba sp.	.	.	.	.	W
Trachynotidus cf. *rufozonatus*	w	.	.	.	.
OPATRINI (5/9)					
Clitobius sp.	.	.	.	.	W
Ennychiatus fitzsimmonsi Koch	.	.	.	.	c
Gonocephalum sp.	.	.	.	.	Cw
Leubbertia plana Koch	.	.	.	.	pw
Neocaedius sp.	.	.	.	.	W
Parastizopus armaticeps (Péringuey)	CW	c	.	.	c
Planostibes dentipes Koch	.	.	.	.	cpw
Psammogaster malani Koch	.	ch	cwRh	Crh	cpw
Stizopina	w	.	.	.	.
PLATYNOTINI (1/1)					
Gonopus tibialis Fabricius	cw	c	c	.	CW
SCAURINI (2/2)					
Carchares macer Pascoe	w	c	Cwh	.	c
Herpiscrius sp.	.	.	.	.	cw
TENTYRIINI (6/8)					
Archinamibia peezi Koch	.	.	rh	.	.
Asphaltesthes impressipennis Fairmaire	c	.	.	.	cW
Cyphostethe sp.	.	.	.	.	c
Derosphaerius humilis Péringuey	.	.	h	.	w
Rhammatodes aequalipennis Péringuey	cW	.	.	.	cp
Rhammatodes longicornis Haag	cW	.	.	.	pw
Rhammatodes subcostatus Koch	.	.	.	.	Cpw
Rhammatodes tagenesthoides Koch	Cw	.	.	.	.
ZOPHOSINI (14/14)					
Zophosis (Calosis) amabilis Deyrolle	CW	.	.	.	.
Zophosis (Dactylocalcar) caecus Gebien	.	.	Rhe	crhe	c
Zophosis (Occidentophosis) cerea Penrith	CWe	.	.	.	.
Zophosis (Occidentophosis) damarina Pér.	Ce	.	.	.	.
Zophosis (Gyrosis) devexa Péringuey	CWe	.	.	.	cp
Zophosis dorsata Péringuey	Ce	.	.	.	w
Zophosis (Cardiosis) fairmairei Péringuey	.	c	CRhe	CRH	c
Zophosis (Protodactylus) giessi Koch	.	.	e	.	cpw
Zophosis (Cardiosis) hamiltonuli Koch	.	c	CRH	ch	.
Zophosis (Cerosis) hereroensis Gebien	c	CH	CHe	CHe	c
Zophosis (Carpiella) latisterna Koch	cwe	.	.	.	c
Zophosis mniszechi Deyrolle	ce	w	.	.	.
Zophosis (Gyrosis) moralesi (Koch)	CWe	CwRH	CrH	Crh	c
Zophosis (Gyrosis) orbicularis Deyrolle	c	cR	cwrhe	h	CpW
ALL SPECIES	41	35	36	27	51
CURRENT STUDY	34	33	27	25	41

* Several species of *Vernayella*, *Namibomodes* and *Pachynotelus* were not distinguished within the genera. * indicates the species name used in the current study, based on the identity of voucher specimens

APPENDIX B: GROUND-ACTIVE ARTHROPODS (OTHER THAN TENEBRIONIDS) AND REPTILES RECORDED IN THE VICINITY OF GOBABEB [OMIT]

APPENDIX C-G: ANNUAL ABUNDANCE OF TENEBRIONID SPECIES IN EACH HABITAT

APPENDIX H: SUMMARY DATA FOR TENEBRIONIDS

APPENDIX I: POSSIBLE AVENUES FOR RELATED FURTHER STUDIES
(mention also briefly in discussion)

- improvements in current monitoring: what critical info would strengthen our conclusions for future analyses (try to make them least labour-intensive)
    - loop-holes in current protocol that can be changed
    - regular monitoring of dune slope and slipface: ±2 days a month all-year
    - on-site rain guages
    - monitor detritus, e.g.
        - mass of detritus that accumulates in pitfall traps; put small buckets into can traps and throw contents through sieve once a month
        - in river, distinguish between flowers and rest, and between fresh and old flowers
    - monitor on-site primary productivity when this occurs; quantification should be very simple and consistent between observers:
        - ephemeral grasses: distance (by position of closest root bases) and size (number of stalks/seed-heads, maximum height) of 5 grass clumps closest to a fixed point near each trap
        - how to characterize perennials, if at all, e.g.
            - distance from trap of closest individual
            - size of live proportion
            - seed-heads or flower-heads (total or sample)
- consequences of various kinds of rain (big, effective summer & wet winter) in terms of sand moisture pattern, fungal growth: monitor depth distribution of water with time (Gut 1988, Yeaton 1988, Jacobson 1992)
- tree flowering patterns in river: what determines them
- overbank flooding in river: what direct benefits to beetles (carry out specific experiments when this occurs)
- detritus dynamics: change over time in quantity, quality and distribution (how important is allochthonous origin: East Wind material?)
- consumption of fungus by tenebrionids: is it important?
- larval biology: key examples from each of the population dynamic patterns: what are the important factors that can benefit survival of many and cause population growth: these could be food, sand moisture (note: our study did not find much evidence that fog is involved in population growth -- it may merely slow down the decrease)