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**NAMIB DESERT TENEBRIONID BEETLE POPULATION RESPONSES TO
IRREGULAR RAINFALL PULSES**

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1 *Abstract.* The hyper-arid Namib Desert (median annual rainfall 12 mm) is far richer in
2 arthropod species diversity and patterns of adaptation to the environment than other extreme
3 deserts. Populations of 33 flightless detritivorous Namib Desert tenebrionid (Tenebrionidae)
4 beetle species were pit trapped for 18-25 yrs. Mean abundance of Tenebrionidae captured per
5 trap day was: duneless gravel plains (0.2), interdune plains (0.6), dune slopes (0.8) and dune
6 slipfaces (9.3). Abundance in all habitats tracked a rainfall index incorporating magnitude
7 and time.

8 Sporadic rainfall triggered annual population increases of up to three orders of
9 magnitude. For 31 of 33 species rare heavy rainfall (>25 mm) and resultant plant growth
10 produced population increases lasting for one to three years. Slow population declines of
11 several orders of magnitude followed, lasting up to 17 yrs (until the next heavy rainfall).
12 Minimum grass producing rainfall events (>10 mm) triggered smaller population increases by
13 some species, beginning zero to 19 mos later. Seventeen species were triggered by winter
14 rainfall and 18 by summer rainfall. Only one species had a relatively stable population.
15 Range of variability of tenebrionid populations was as great as extremes previously recorded
16 for all other arthropods species in any habitat anywhere.

17 Some observations and conclusions reported here were possible only after long-term
18 monitoring captured several exceptional heavy rainfalls including winter and summer events,
19 sometimes decades apart. Following long-term population patterns after repeated triggers
20 allowed us to identify highly significant distinctive population signatures common to clusters
21 of two to five study species in each habitat. Most cluster member species had similar diel
22 rhythms but differing phylogenetic affinities.

23 *Key words:* *Tenebrionidae; Namib Desert; long-term monitoring; population signature;*
24 *irruption; seasonality; rainfall; fog; detritus; life history.*

INTRODUCTION

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3 The hyper-arid Namib Desert is one of the least productive areas in the world (Seely and
4 Louw 1980). Nevertheless the Namib Desert arthropod assemblage is far richer in both
5 species diversity and patterns of habitat adaptation than other extreme deserts (<50 mm
6 annual precipitation) such as the Sahara, the Empty Quarter and the Atacama (Koch 1961,
7 Louw and Seely 1982). There are >200 species of tenebrionids (Coleoptera: Tenebrionidae)
8 in the Namib Desert, all dependent upon various components of plant detritus and seeds
9 (Crawford and Seely 1993). Wolda (1978) predicted that climatic variability would explain
10 population fluctuations in deserts and Noy-Meir (1980 p.15) suggested that "...individual
11 species responses to the environment can serve as a good approximation to the understanding
12 and prediction of a great many ecological phenomena in some deserts, for the study of which
13 the integrated ecosystem concept is not necessary. This might be particularly true in extreme
14 deserts". Polis (1991) concurred with the view that populations in arid environments are not
15 at biotic equilibrium and respond opportunistically to favorable conditions.

16 How do particular species respond to hydrological pulses (Weltzin and Tissue 2003)?
17 Are there systematic and species-specific patterns of response to pulses of irregular rainfall
18 and if so what are their correlates and their adaptive values? Are populations of desert species
19 more variable than their counterparts in more mesic areas (Wolda 1978)? To address these
20 questions we examined population responses to precipitation events and correlated them with
21 phylogeny, biome derivation, seasonality, diel rhythmicity and relative abundance.

22 Namib tenebrionids are flightless and readily captured in pitfall traps. We measured
23 fluctuations in their abundance and species composition between 1976 and 2000. Long-term
24 monthly and annual patterns of abundance were related to seasonal timing and magnitude of
25 rainfall.

1 STUDY SITE

2

3 Observations were made near Gobabeb (23°33'S, 15°02'E), at the center of the Namib
4 Desert, about 1000 km from its southern and northern extremes, and 60 km from its western
5 and eastern boundaries. At Gobabeb the ephemeral Kuiseb River separates the 40,000-km²
6 Namib Sand Sea dune field from the 40,000-km² Central Namib Desert gravel plains.

7 Four habitats were monitored (Henschel et al. 2003): dune slopes (DS), dune slipfaces
8 (SF), interdune plains (IP; Holm and Scholz 1980, Robinson and Seely 1980, Seely 1991) and
9 gravel plains (GP; Wharton and Seely 1982; Fig. 1). DS flanks a 100 m high linear dune,
10 supporting scattered small vegetation hummocks (11 ha⁻¹, cover <1%). Sand and vegetation
11 at DS trap wind blown detritus. SF is the steep, vegetationless lee slope at the dune crest,
12 comprised of unconsolidated, mobile sand. Wind blown allochthonous detritus accumulates
13 there and may be buried by avalanching sand. IP is on a 2-km wide linear plain between
14 dunes, bare except for a few months after rainfall. The sandy gravel substrate is less firm than
15 GP. GP ground is flat, firm, and bare of grass except after effective rain. Detritus is trapped
16 under stones and in rock crevices, places favored by tenebrionids.

17 Late summer (January-April) is relatively hot, with occasional fog (9.4 l.m⁻² of vertical
18 fog screen) and has the highest rainfall (mean 15.5 mm). In winter (May-August) ground
19 temperatures fall, and there is occasional fog (11.1 l.m⁻²) alternating with warm spells of dry
20 berg wind and little rain (4.2 mm). Early summer (September-December) is cool to warm,
21 with the highest incidence of fog (16.1 l.m⁻²) and least rainfall (2.4 mm).

22 Minimum effective rainfall (10-12 mm) within a week allows grasses to germinate and
23 seed (Seely 1978, Günster 1995, Jacobson 1997). Most primary productivity is generated
24 within 2 mos by ephemeral plants on the GP (6.9±5.3 g.m⁻²) and IP (4.8±1.6 g.m⁻²) with less
25 on the DS (0.8±2.3 g.m⁻²) and SF (0.0±0.0 g.m⁻²) (Henschel et al. 2003). Heavier rainfall had

1 greater and more enduring effects, producing 5-44 g.m⁻² of detritus on DS and SF (Seely and
2 Louw 1980). Five years after rainfall, detritus declined to 0.7-5.6 g.m⁻² in these habitats.

3 Between 1962 and 2000 mean annual rainfall at Gobabeb was 22.1±26.9 mm (1.0-
4 125.0 mm; median 12.2 mm). Annual rainfall was highly variable (*CV*=122%), characterized
5 by short episodic pulses (Pietruszka and Seely 1985), and followed no detectable multiyear
6 pattern (Table 1; autocorrelation with lags of 3-15 yrs: $r < 0.05$, $P > 0.1$). Effective late summer
7 rain occurred at intervals ranging from 2-9 yrs and effective winter rain at intervals of 2-16
8 yrs (Table 1). A relatively dry interval between 1963-1976 preceded the study, followed by
9 wet years at the start of our study (Table 1). Heavy rains (26-117 mm) in 1976, 1978 and
10 1997, provided an opportunity to examine immediate (Seely 1978, Seely and Louw 1980) and
11 long-term (Southgate et al. 1996, present study) population responses to them.

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METHODS

14 *Trapping protocol.*—Pitfall traps 15 cm in diameter were deployed from March 1976
15 onward. Specimens were identified at traps, and then released. Henschel et al. (2003)
16 describe frequency of trapping and trap layout.

17 Tenebrionid monitoring was continuous in the relatively stable substrates of GP and
18 IP, but intermittent in the mobile SF and DS habitats. Traps were maintained at the original
19 location throughout the study, however the slipface disappeared in 1998, which affected
20 subsequent data. In SF, avalanching sand often filled traps and traps were cleared hourly.
21 Monitoring was twice daily on the DS and less frequent at IP and GP.

22

Abundance data analysis

23 Abundance data encompassing the period 1976 - 2000 were standardized to captures per 1000
24 trap-days (Henschel et al. 2003) to compare habitats. Of 57 tenebrionid species recorded, we
25 examined 33 species with a total abundance of >120 during 25 years. There were eight to 14

1 study species per habitat. Five species were sufficiently abundant to be examined in two
2 habitats and four species qualified in three habitats. To characterize differences in abundance
3 between successive years, we applied a gradation coefficient ($GC = \log(N_j) - \log(N_{j-1})$, where N_j
4 is $N + \frac{1}{2}$ in yr j) and annual variation coefficient ($AV = \text{variance of } GC$) to abundance data
5 following Wolda (1978). GC and AV were determined for all study species within each yr and
6 for all yrs in each habitat. We also quantified annual changes by calculating the cumulative
7 percent deviation of annual abundance from the mean ($C\%D$). Species were compared by
8 correlation of $\log(N)$ and of GC , and grouped accordingly.

9 A population was identified as being triggered when N increased by ≥ 10 and GC by
10 ≥ 0.05 ($\approx 10\%$ increase in N). The initial response is the time period (months) before a
11 sustained population increase was detectable after a triggering rainfall. To account for larval
12 maturation we also tested for one-year lags in the same way. Various types of rainfall that
13 triggered population increases were heavy rainfall (> 25 mm), effective rainfall (> 10 mm) in
14 winter or summer, and light rainfall (< 10 mm). Population irruptions are defined as year-to-
15 year increases in abundance of over 200% ($GC > +1.3$), and population crashes as decreases of
16 $GC > -1.3$.

17 To identify any connection between abundance and rainfall, years when populations of
18 each species began to increase were compared with effective rainfall in that and the previous
19 year. Positive correlation of $\log(N)$ with a hydrological index ($C\%D_{\log(x)}$, where $x =$ all rain, or
20 summer rain, or winter rain) allowed us to relate population increases to particular features of
21 rainfall. In 1987 and 1997, when effective rainfall occurred in both late summer and winter,
22 responses were attributed to summer rainfall if a response started before the winter rainfall.
23 Later responses in those years were of ambiguous origin and could not be used to classify
24 triggering rainfall events. Decreases in abundance by one or more orders of magnitude, over
25 a period of from one to 17 years, marked the end of responses. Sometimes it was not possible

1 to determine duration of an effect because new population increases were initiated by rainfall
2 when a population was still declining and before a potential population low was reached.

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RESULTS

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Total abundance

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Capture rate.—During this 25 yr study we captured 229,585 individual animals.

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Tenebrionid beetles comprised 88.7% of the catch, ranging from 399 to 25,034 individuals

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per year. The highest tenebrionid capture rate was on SF. During November 1978, a 108 mm

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rainfall year, 3229 tenebrionids were captured in 50 traps during a single day. The lowest

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capture rate was on GP in 1994 when only a single tenebrionid was captured in 15

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continuously deployed traps during 309 da.

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Trend with time.—In all habitats the long-term (>15 yr) trend was for abundance to be

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less than the mean for each habitat from the early 1980s until 1997. The cumulative per cent

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deviation from mean log annual rainfall ($C\%D$) increased steeply from 1976 to 1979, then

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declined, with minor increases in 1982, 1987, 1997, and 2000 (Fig. 2). Small fluctuations in

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total annual abundance were superimposed upon a long-term decline. Increases in abundance

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in IP followed a grass-producing rainfall in all habitats in 1987. In GP, DS and SF increases

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in abundance also occurred in 1982 and 1984 (Fig. 2). There was a sustained increase in

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abundance in all habitats following the 1997 rains. Overall, total annual log abundance of all

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species tracked cumulative percent deviation from mean log rainfall ($C\%D_{\log(\text{rain})}$) in all

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habitats (Pearson's correlation $r=0.60-0.89$, $P<0.02$). In most years abundance was below the

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mean, which was 0.2 ± 0.5 in GP, 0.6 ± 1.2 in IP, 0.8 ± 1.8 in DS, and 9.3 ± 23.1 in SF (Fig. 2).

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Population characteristics

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Diel rhythm.—Study species were active above the surface during three periods:

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diurnal (19 species), nocturnal (12) and crepuscular (2). There was no difference in relative

1 proportions of large and small beetle species that were diurnal or nocturnal/crepuscular
2 (median test, $\chi^2=0.81$, $df=1$, $P>0.05$). Most individuals (78%) trapped in GP, IP, and DS
3 were diurnal. *Lepidochora discoidalis*, a crepuscular species (Hanrahan and Kirchner 1997),
4 dominated abundance in SF.

5 *Seasonality*.—Eighteen species were seasonal, and most of these occurred in IP and
6 SF. In IP several common species followed different seasonal activity schedules. *Cauricara*
7 *phalangium* was abundant during winter and scarce in mid-summer. *Zophosis moralesi* and
8 *Onymacris plana* peaked in the summer.

9 *Cyclicality*.—There were no strong cyclical changes in abundance by any population in
10 any habitat. Autocorrelations between years decreased with increasing time lags ($r<0.22$).

11 *Biogeographic distribution*.—The study area covered the boundary between two
12 biomes. Twenty study species were at the edge of their biogeographic distribution in the
13 study area. Of these, 13 occurred exclusively on the dunes and seven only on the gravel
14 plains.

15 *Annual abundance*.—Population fluctuations yielded species *AV* values ranging from
16 0.171 to 3.009 (Table 2), and mean *AV* values per habitat of from 0.823 to 1.093. Despite
17 these fluctuations, 15 of 57 species, including the nine most abundant species, were trapped or
18 observed in our study area every year. These 15 species accounted for 96.6% of all
19 individuals captured.

20 *Grouping based on abundance patterns*.—In each habitat there were clusters of from
21 two to five species for which the time-series trends of $\log(N)$ and *GC* were highly correlated
22 ($P<0.001$, Fig. 3). Species within clusters agreed with each other in terms of long-term
23 abundance trends or some parameters of population response and differed ($P<0.001$) from all
24 other study species in that habitat. There were two or three such clusters in each of the four

1 habitats. In addition there were from one to five species in the four habitats with population
2 signatures not in agreement with any other species ($P>0.001$, Fig. 3).
3 Species within clusters shared little morphologic and no consistent phylogenetic (tribal level),
4 biogeographic or seasonality affinities. However, 23 of 27 species within clusters had the
5 same diel rhythm as other group members ($\chi^2=9.10$, $df=1$, $P<0.01$).

6 *Responses to trigger events*

7 *Timing of population responses.*—Sometimes adults became active and were detected
8 during the month or months immediately following an event. Most population responses
9 were initiated within six mos, but some species responded only 12-19 mos after a triggering
10 event (Table 2). Most population peaks occurred during the year after the event but five
11 peaks occurred three years later, following steady population increases in the years after the
12 trigger.

13 *Responses to rainfall.*—A population response to heavy rainfall (four events) was
14 detected for 31 species. *Vansonium bushmanicum* and *Cauricara eburnea* responded only to
15 winter rainfall, not to heavy rain. The other 15 species that responded to winter rainfall also
16 responded to heavy summer rain (Table 2). Summer rain of 10-25 mm triggered 14 species.
17 The five most abundant species responded to effective summer rains (Table 2). Four species
18 responded to the light rain (<10 mm) in February 1984, December 1993 and November 1996
19 (Table 1). Only *Zophosis amabilis* responded to every rainfall event, although several species
20 (*Onymacris laeviceps*, *Stips stali*, *Lepidochora porti*), responded to every category of rain on
21 some occasion.

22 *Population irruptions.*—In all habitats there were fewer years with increases than
23 decreases in abundance (Wilcoxon one-tailed $t=0$, $n=4$, $P<0.1$). Short pulses of population
24 irruption, typically lasting 1-3 yrs (Table 2), were interspersed by long intervals of population
25 decline, usually between five and 10 yrs. However, there were more irruptions than crashes

1 (>200% increase and decrease respectively), and crashes were less extreme than irruptions.
2 Of 19 irruptive species, 11 irrupted faster than they crashed (deviation from 1:1, $t=4.57$,
3 $P<0.001$), while for seven the rates were not different. Only *Zophosis hamiltonuli* crashed
4 faster than it irrupted. SF, a habitat with mobile and shifting substrate, was an exception, but
5 irruptions and crashes there may be an artifact of our sampling method. The 19 irruptive
6 species were more prone to crashes than species that did not irrupt ($r=-0.49$, $P<0.001$).
7 Fourteen species neither irrupted nor crashed.

8 Irruptive species tended to be small (<46 mg median size, $\chi^2=4.76$, $df=1$, $P<0.05$) and
9 most (74%) were diurnal ($\chi^2=3.91$, $df=1$, $P<0.05$). Some irruptive species occupied all
10 habitats. Irruptive species had no particular biogeographical affinity ($\chi^2=2.26$, $df=2$, $P>0.05$).
11 Six of seven (85%) late summer species were irruptive, compared to 50% of the remaining
12 species, but the difference was not significant ($\chi^2=2.94$, $df=1$, $P>0.05$). There also was no
13 significant difference between summer-cued and winter-cued species in tendency to irrupt
14 ($\chi^2=0.76$, $df=1$, $P>0.05$).

15 *Population decline.*—Only three species did not fall below 1% of their maximum abundance
16 (*C. phalangium* 1.2%, *Z. amabilis* 1.3%, *Z. fairmairei* 1.4%). For gradually declining species,
17 GC values ranged between -0.1 and -0.8 (20-85% annual decline). During population lows
18 species common at some time were not trapped for long intervals (>10 years). In GP an
19 interval of low density began between 1988 and 1990 for *Rhammatodes tagenestoides*, *Z.*
20 *damarina*, *Epiphysa arenicola* and *Stips dohrni*, and continued through to the end of the
21 analysis in 2000 (Fig. 3). We increased the trapping effort in GP from 15 to 75 traps for eight
22 mos in 2002 to search for these species, and detected one or more individuals of all but *S.*
23 *dohrni*. From direct observation, *Onymacris unguicularis*, *Cauricara velox*, *C. eburnea*,
24 *Vernayella noctivaga* and *V. delabati* were found to be present, but were not trapped during

1 this interval. *Parastizopus armaticeps* was unrecorded for 12 consecutive yrs, but reappeared
2 on GP and IP in 1997 after heavy rain (Fig. 3, Table 1).

3 *Population changes within and between habitats*

4 Magnitude and temporal patterns of population change differed between habitats. The
5 abundance of individual species that occurred in more than one habitat showed both similar
6 and divergent patterns (Table 2). In GP vegetation was gone a year after rain, but grass
7 remained in IP where the sandy soil retained moisture.

8 In GP, occasional years having a flush of ephemeral plants contrasted strikingly with
9 most years when the habitat was barren (Fig. 1). One species, *Z. amabilis*, fluctuated only
10 slightly, while other species varied widely (e.g. *Metriopus depressus*, Fig. 3).

11 In IP, most species had highly variable populations, but populations of some species,
12 including the highly seasonal *C. phalangium*, changed gradually and then irrupted after heavy
13 rainfall (Fig. 3). The high rainfall yrs of 1976 and 1978 resulted in growth of a 100-150 mm
14 stand of ephemeral grass across the IP. The grass trapped sand blowing across the interdune
15 plain, and sand accumulation submerged the pebbles of the interdune surface by up to 30 mm.
16 By 1979 the annual grass had withered and the accumulated sand had blown away. This
17 distinctive structural change initially attracted *O. plana*, *O. rugatipennis* and *S. stali* from the
18 adjacent DS between 1976 and 1978 (Fig. 3). These species were not found again in
19 comparable numbers in IP during the next 21 yrs (Fig. 3).

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DISCUSSION

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23 Studies of tenebrionid beetles in arid America, Australia and the Middle East report
24 that population fluctuations and their differences between species are largely attributable to
25 variations in rainfall (e.g., Rickard and Haverfield 1965, Faragalla and Adam 1985, Parmenter

1 et al. 1989, Stafford-Smith and Morton 1990, Ayal and Merkl 1994, Krasnov and Ayal 1995,
2 Deslippe et al. 2001). This conclusion agrees with the findings of our study, with the caveats
3 that population responses are also strongly modified by rainfall schedules and life history
4 characteristics of the component species, including diel rhythmicity and seasonality. Patterns
5 of population responses to precipitation were either species-specific or characteristic of
6 clusters of species independent from phylogeny and biogeography.

7 *Population Responses to rainfall*

8 In the past 120 yrs, rainfall exceeding 100 mm occurred in the Namib in 1934, 1976,
9 1978 and 2000 (Meteorological Services; Weather@iafrica.com.na). Rainfall, the most
10 important trigger of Namib Desert tenebrionid population irruptions, acts on populations in
11 several different ways. It increases soil moisture (Besler and Gut 1997, Jacobson 1997), thus
12 favoring larval development (Rasmussen et al. 1991), and it increases primary productivity by
13 generating detritus, the basis for detritivorous beetle productivity (Seely 1973). Light
14 effective rainfall briefly stimulates growth of ephemeral plants (Seely 1978), whereas many
15 perennial plants require heavy rainfall to become established (Walter 1936, Seely and Louw
16 1980, Seely 1989, Southgate et al. 1996, Hachfeld 2000). Total tenebrionid abundance
17 tracked cumulative percent deviation from mean of log annual rainfall ($C\%D_{log(rain)}$; Fig. 2).
18 This cumulative index also reflected the flush and decline of detritus and minor increases of
19 the detritus pool following small effective rains. The amount of grass on the desert surface
20 declined steadily after vegetation flushes (Henschel et al. 2003). Renewal of detritus on the
21 surface depends on wind driven mobilization of a declining store of subsurface detritus.
22 All but two tenebrionid species responded to heavy rainfall. After the 1976 and 1978 rains
23 tenebrionid abundance declined by nearly two orders of magnitude (25,034 to 399 for all
24 tenebrionid species and habitats combined between 1977 and 1995; Fig. 3). The 1994-1996
25 population low was followed by an interval of increasing abundance after the 1997 rains (to

1 21,495 in 2000). Relatively heavy rain at Gobabeb in 1997 confirmed the identity of triggers
2 to patterns of responses to exceptional events (Fig. 3). Lighter and less frequent winter
3 rainfall was important for several species (Table 2), perhaps because near-surface moisture
4 lasts longer in winter due to reduced evaporation and persistent moisture in 5-8°C cooler soil
5 (Besler and Gut 1997). The population responses of different tenebrionid species were
6 triggered by specific rainfall schedules and amounts. Timing and magnitude of irruptions and
7 declines differ among species and habitats. While year-to-year changes in abundance of some
8 species are highly variable (maximum $AV=3.01$, *L. discoidalis*), others change gradually
9 (minimum $AV=0.171$, *C. phalangium*, Table 2).

10 Populations of most species responded to triggering events within the same year or the
11 following year and, for most species the irruption lasted more than three years. Thirteen
12 species responded slowly and persisted for more than three years. For the quick-and-short
13 response group of 11 species, such as slipface-dwelling *O. unguicularis* and *O. laeviceps*, the
14 population peak occurred during the brief pulse of soil moisture suitable for larval
15 development and when large amounts of detritus were available. Seven species responded
16 quickly and persisted while only two species responded slowly and did not persist.

17 *Life history effects upon recruitment*

18 Timing of rainfall strongly influences the timing and magnitude of responses. Rain
19 preceding summer-active species such as *Z. moralesi* allows the residual population of adults,
20 eggs and larvae to reproduce, develop and metamorphose in 75 da or less (Rössl 2000). Thus
21 it is possible to recruit a fresh cohort of adults within the time constraints of the annual
22 breeding season and irrupt again. By contrast, its strict seasonality explains failure of *C.*
23 *phalangium* to irrupt in IP in 1997. That year rainfall followed its breeding season and it
24 responded the following winter during its usual breeding season. Population responses to
25 triggers of some species operate within the constraints of differing phenology and larval

1 longevity. Other species respond to the extremes of rainfall with a myriad of different
2 combinations of life history characteristics.

3 *Population variability*

4 Wolda (1978) summarized a widespread search for correlates and principles
5 concerning variability, evaluating the relationship between stability and biome derivation. He
6 considered the significance of mean *AV* values for 138 groups of temperate and tropical insects
7 (Wolda 1978, Table 2 of that paper). Namib Desert tenebrionid populations are highly
8 variable. Mean *AV* values (0.823-1.093) for all tenebrionid species per habitat from our study
9 lie above Wolda's upper quartile of values (minimum, lower quartile, median, upper quartile,
10 maximum: 0.018, 0.206, 0.412, 0.666, 5.250; smallest abundance number: *NS* = 0-4 or
11 greater). Only nine of Wolda's values were higher than our highest value. Only seven Namib
12 species lie below Wolda's median. Only *C. phalangium* falls within Wolda's lower quartile.

13 What is the significance of the wide range of *AV* values we found for individual
14 tenebrionid species (0.17-3.01, Table 2)? An answer to this question requires a species by
15 species analysis of the correlates of similarities and differences in *AV* values. *L. discoidalis*, a
16 high (3.01) *AV* species, is an extreme specialist, confined entirely to detritus pads on slipfaces
17 and irrupting after heavy rainfall (Fig. 3). The high *AV* of this and another SF species,
18 *O. unguicularis* (*AV*=2.24) is the result of long intervals between rainfall, producing pulses of
19 detritus followed by irruptions. The number of active individuals of these species found
20 along a particular stretch of dune varies temporarily and spatially as patches of wind-
21 mobilized detritus develop. *O. laeviceps*, a SF and DS resident, supplements its diet by
22 climbing the tall perennial grass, *Stipagrostis sabulicola*, to obtain seeds. Its low *AV* (1.21) is
23 explained by this adaptation to obtain a perennial food source other species do not routinely
24 access. The lowest *AV* value (0.17) was recorded for *C. phalangium*, a highly seasonal winter-

1 active species on IP. This small long-legged species is highly mobile, searching large areas of
2 IP for widely scattered relatively abundant detritus.

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CONCLUSIONS

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6 Detritivorous tenebrionids persist in the hyperarid Namib because detritus produced
7 by rainfall events prolongs the presence of their populations. Most detritus is unavailable to
8 detritivores most of the time. It becomes available when daily wind uncovers or imports fresh
9 detritus. Adults are long-lived and maintain a bet-hedging reproductive strategy, and may use
10 fog to overcome water limitations during enduring rainless intervals, allowing them to irrupt
11 after the next pulse of rainfall. Not all species increase with every flush of vegetation.

12 Many species respond to particular kinds of rainfall: e.g., summer rainfall with its
13 flush of primary productivity, or winter rain with its lingering soil moisture, or require
14 different intensities of such events to respond at all. Despite the wide range of triggers, initial
15 response times and rates of population change, species show several discrete nodes defining
16 common population signatures of abundance patterns. Population signatures show categorical
17 differences among species in how they respond to rainfall of different magnitudes in different
18 seasons. Nevertheless, nearly all population changes can be related to hydrological pulses.

19 Our observations of the fundamental importance of hydrological triggering events
20 concur with Noy-Meir's (1980) autecological perspective. Population changes of individual
21 species in the study area are driven by hydrological events but are species specific,
22 multifaceted and affected by several environmental or antecedent conditions besides rainfall.
23 By responding selectively to alternative triggering events, sympatric species show temporal
24 patterns and magnitudes of population fluctuation (Fig. 3) that are more diverse than predicted
25 by Noy-Meir's (1980) original model.

1 Our answer to Wolda's (1978) and Noy-Meir's (1980) question about the relative
2 variability of groups of species inhabiting desert biomes is that most Namib tenebrionids
3 species fluctuate more widely than most species inhabiting more mesic habitats.

4 We made some findings and developed some novel interpretations of Namib Desert
5 tenebrionid populations only after we had obtained >20 years of data. The identification of
6 clusters of species with similar population signatures required such long data sets including
7 several population fluctuations by several species. Identification of the triggers to population
8 increases required replicated observation of infrequently observed (3 times in 25 years)
9 events. Long-term observations capturing temporary increases in abundance allowed
10 identification of population characteristics of some species that were rare for long intervals.
11 In the case of the heavy rains in 1976, 1978, 1997 and 2000 there are several intervals when a
12 10-yr study would have observed the response to no or only one such event.

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3

4

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1 TABLE 1: Annual rainfall (mm) at Gobabeb 1963-2000 showing effective rainfall events during early summer
 2 (e), late summer (l), winter (w), or none (o). Effective rains in parenthesis were light, but triggered some beetle
 3 population responses.

4

Year, begin study in habitat	rain (mm)	effective rain (mm)	effective rain season
1963	37.9	10.2, 12.8	lw
1964	5.4	0	o
1965	36.5	12.7, 11.9	le
1966	8.1	0	o
1967	26.0	18.4	l
1968	4.9	0	o
1969	28.9	13.2	l
1970	1.0	0	o
1971	38.5	10.9	l
1972	8.5	0	o
1973	9.3	0	o
1974	24.2	0	o
1975	6.6	0	o
1976 GP	125.0	117.0	l
1977 IP	12.8	0	o
1978 SF, DS	108.6	107.6	l
1979	34.5	22.7	w
1980	9.7	0	o
1981	4.6	0	o
1982	19.7	11.4	w
1983	11.6	0	o
1984	8.0	(6.8)	l
1985	6.8	0	o
1986	2.0	0	o
1987	24.3	12.6, 11.4	lw
1988	7.8	0	o
1989	16.1	11.7	w
1990	12.3	10.1	l
1991	18.3	0	o
1992	1.2	0	o
1993	12.2	(7.8)	e
1994	15.0	0	o
1995	23.0	11.2	l
1996	10.6	(6.6)	e
1997	72.7	28.2, 26.6	lw
1998	2.6	0	o
1999	7.6	0	o
2000	36.8	27.7	l
Mean	22.1		
SD	26.9		
Min	1.0		
Median	12.2		
Max	125.0		
CV _{yr}	122%		
CV _{mo}	333%		

1 TABLE 2: Abundance measures of study species: trap rate per 1000 trap days per habitat, range of annual trap rate, population variation
 2 expressed as annual variation (AV) and maximum gradation coefficient (GC_{max}). Irruptive species have max $GC > 1.3$.
 3

Species	Code	Traprate Habitat				Traprate Annual		Irruptive		Response				Rainfall Trigger
		GP	IP	DS	SF	min	max	AV	GC_{max}	Initial month med	Peak range	Peak yrs	Duration yrs	
<i>Cauricara eburnea</i>	CEB	1.06				0	4	0.424	1.30	7	0-10	0-1	6	winter
<i>Cauricara phalangium</i>	CPH		236.98	55.26	21.93	12.22	983	0.171	1.32	3	0-14	1-3	6	winter, light
<i>Cauricara velox</i>	CVE	12.41				0.01	140	0.410	2.10	2	0-12	2	5-7	winter, light
<i>Epiphysa arenicola</i>	EAR	2.61	0.06			0.01	11	0.237	1.11	5	0-10	1	5	winter
<i>Eustolopus octoseriatus</i>	EOC	2.04	7.01	1.43	0.58	0	57	1.315	3.01	2	0-3	0-1	1-2	summer
<i>Metriopus depressus</i>	MDE	20.50	330.14	0.01	0.88	0	150	0.459	2.38	4	1-11	1	5	heavy only
<i>Onymacris laeviceps</i>	OLA		1.44	13.93	351.17	2.08	1133	1.208	2.25	2	0-5	0-1	2-3	any
<i>Onymacris plana</i>	OPL	0.12	47.95	195.07	237.72	0.01	1911	0.713	0.79	11	2-15	1-2	6-10	heavy only
<i>Onymacris rugatipennis</i>	ORU	0.06	7.89	7.46	2.05	0.01	67	0.711	1.27	4	0-13	1-3	2-5	heavy only
<i>Onymacris unguicularis</i>	OUN		0.06	6.25	159.65	0.01	906	2.235	2.33	1	0-5	0	2	summer
<i>Physasteria cribripes</i>	PCR	12.10	0.09	0.22	0.29	0	159	0.354	1.30	4	1-7	1-3	3-7	summer
<i>Vernayella delabati</i>	VDE			0.01	77.19	0.01	456	1.469	1.22	2	1-3	0	1	winter
<i>Vernayella noctivago</i>	VNO		0.01	11.29	0.01	0.01	117	0.288	0.32	1	1	0	1	winter
<i>Vansonium bushmanicum</i>	VBU	0.24	1.11	0.22		0	11	1.350	2.31	9	5-13	0-1	1-3	winter
<i>Pachynotelus albonotatus</i>	PAL		2.60	2.08	0.29	0	20	1.972	2.24	3	0-14	1-2	3	summer
<i>Eurychora sp.</i>	EUR	1.56	0.01	0.11		0	16	0.428	0.90	8	1-11	2	2-4	winter
<i>Lepidochora discoidalis</i>	LDI		0.01	2.41	3481.29	0	29094	3.009	3.47	2	0-5	0	3-5	summer
<i>Lepidochora kahani</i>	LKA				108.19	0	444	1.323	2.20	5	0-19	0-2	3-4	summer
<i>Lepidochora porti</i>	LPO		0.03	32.46		0	135	0.545	1.12	2	0-5	0-1	2-3	any
<i>Stips dohrni</i>	SDO	0.89				0	4	0.383	0.90	3	1-5	2	4-5	heavy only
<i>Stips stali</i>	SST		5.46	28.62		0.01	321	0.928	0.57	3	1-5	0-2	3	any
<i>Namibomodes serrimargo</i>	NSE		0.05	11.95	8.48	0	63	0.421	0.70	1	1	0	2	winter
<i>Parastizopus armaticeps</i>	PAR	1.53	0.01			0	16	0.721	1.20	7	5-9	2	7	heavy only
<i>Carchares macer</i>	CMA		1.20	6.91		0	85	1.259	2.31	7	7	1	3	heavy only
<i>Rhammatodes tagenesthoides</i>	RTA	7.97				0	59	0.698	1.58	5	1-7	2	3-5	winter, light
<i>Zophosis amabilis</i>	ZAM	17.43	0.02			0.93	68	0.237	1.00	5	0-10	2	4	all
<i>Zophosis damarina</i>	ZDA	8.55				0	76	0.525	1.56	4	0-8	0	3	winter, light
<i>Zophosis devexa</i>	ZDE	7.64				0	55	0.533	2.13	7	0-17	1	4-7	summer
<i>Zophosis fairmaerei</i>	ZFA		0.03	10.96	922.51	88.89	6156	0.725	0.92	5	1-12	0	3-5	summer
<i>Zophosis hamiltonuli</i>	ZHA		2.20	56.14	9.36	0	202	0.927	1.56	3	1-15	1-3	4	winter
<i>Zophosis hereroensis</i>	ZHE	0.08	10.94	362.39	612.87	5.55	11261	1.295	1.95	3	1-13	0-1	2-3	summer
<i>Zophosis moralesi</i>	ZMO	90.96	358.63	53.62	1.75	0.11	1964	0.557	3.38	4	0-9	0-2	7-8	summer
<i>Zophosis orbicularis</i>	ZOR	0.48	7.98	1.10		0.01	103	1.423	0.65	3	0-12	1-3	4	winter

1 FIG. 1: Photograph of the area near Gobabeb showing the four study habitats: gravel plains
2 (GP) north of the Kuiseb River, the interdune plain (IP) south, and a dune slope (DS) and
3 slipface (SF).

4

5 FIG. 2: Time-series of total log annual abundance of tenebrionids in four habitats in
6 comparison with $C\%D_{\log(\text{rain})}$.

7

8 FIG. 3: Time-series of abundance $[\log(N+1)]$ of tenebrionid species coded according to Table
9 2. Correlated species in each habitat are grouped together (A-I) or are uncorrelated within
10 their habitat (U).

Figure 1

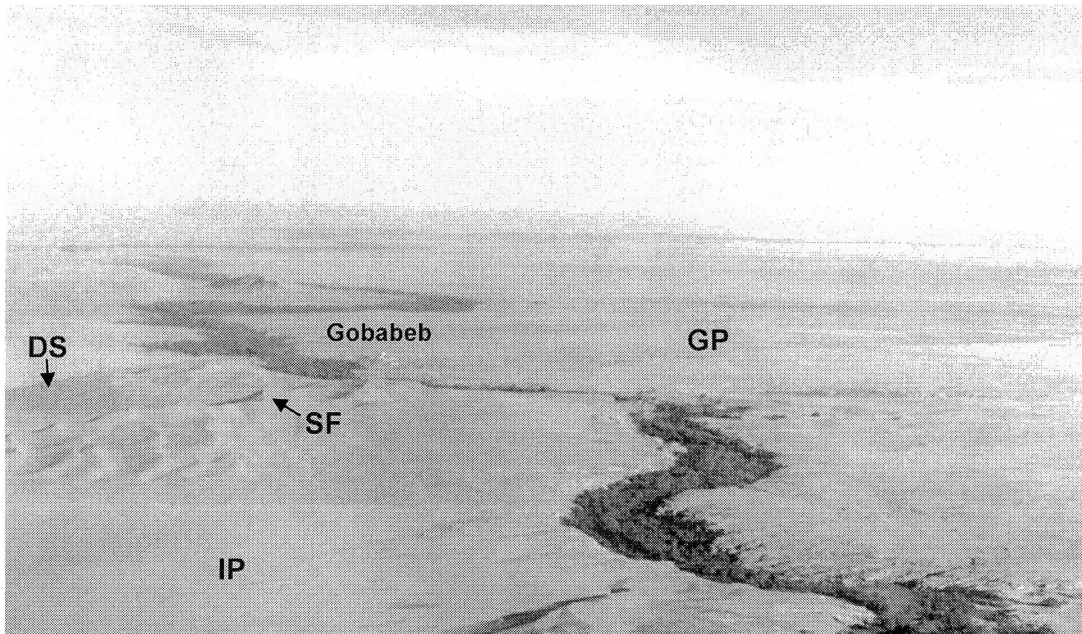


Figure 2

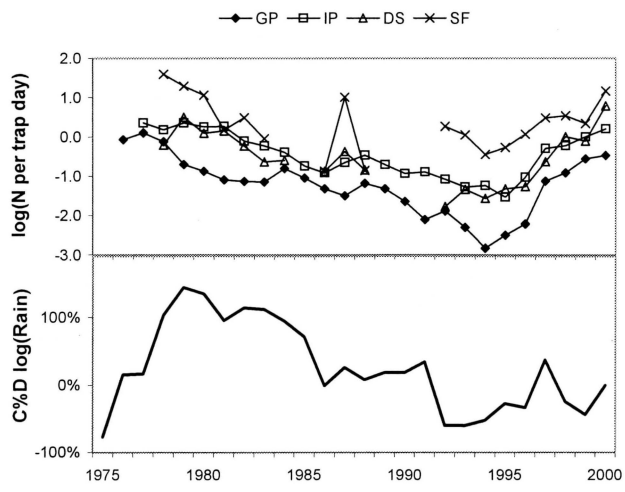


Figure 3

