Second beetle B

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PULSED RAINFALL EVENTS TRIGGER RESPONSES OF NAMIB DESERT TENEBRIONID BEETLES

JOH R. HENSCHEL[1], MARY K. SEELY[2]

WILLIAM J. HAMILTON III[3]

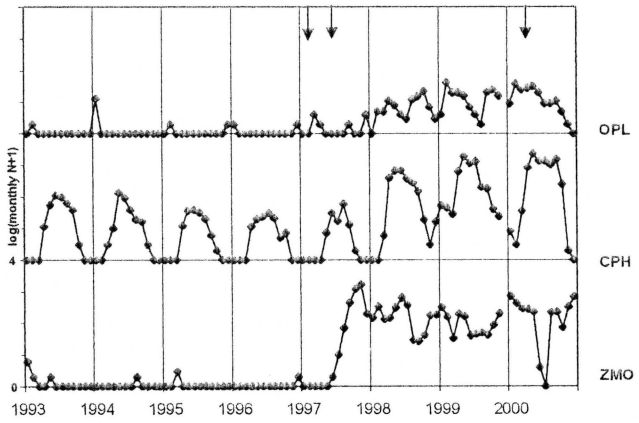
Abstract. Triggers for population increases and correlates with abundance were examined. Sporadic rainfall triggered annual increases up to three orders of magnitude. For 31 species rare heavy rainfall (>25 mm) and the flush of plant growth that followed produced population increases lasting from one to three years. Slow declines of several orders of magnitude persisted for decades until the next heavy rainfall. For some species minimum grass producing rainfall events (>10 mm) triggered smaller population increases beginning zero to 19 mos later. Seventeen species were triggered by winter rainfall and 18 by summer rainfall.

WINTER RAINFALL 17 SPECIES, 18.

Our conclusions were possible only after long-term monitoring captured several rare heavy rainfall and winter and summer rainfall events, sometimes decades apart. Long-term population patterns after repeated triggers allowed us to identify different population signatures common to two to five study species with different phylogenetic characteristics.

Lepidochora discoidalis	35	crepuscular	S	212%	late summer	51%
Lepidochora kahani	68	nocturnal	S	114%	aseasonal	
Lepidochora porti	47	nocturnal	S	118%	early summer	61%
Stips dohrni	47	nocturnal	N	157%	aseasonal	
Stips stali	56	nocturnal	S	253%	aseasonal	
Namibomodes serrimargo	33	nocturnal	C	171%	winter	60%
Parastizopus armaticeps	160	nocturnal	C	255%	aseasonal	
Carchares macer	34	nocturnal	C	329%	aseasonal	
Rhammatodes tagenesthoides	3	crepuscular	N	208%	aseasonal	
Zophosis amabilis	36	diurnal	N	112%	aseasonal	
Zophosis damarina	32	diurnal	N	182%	aseasonal	
Zophosis devexa	12	diurnal	N	163%	aseasonal	
Zophosis fairmaerei	3	diurnal	S	158%	aseasonal	
Zophosis hamiltonuli	2	diurnal	S	114%	early summer	63%
Zophosis hereroensis	16	diurnal	C	372%	winter	98%
Zophosis moralesi	33	diurnal	C	162%	late summer	71%
Zophosis orbicularis	62	diurnal	C	284%	early summer	

Time-series of monthly abundance [log(N +1)] and effective rainfall (arrows) between 1993-2000 of *Zophosis moralesi* (ZMO), *Cauricara phalangium* (CPH) and *Onymacris plana* (OPL)



D/K?

16/11/02	sat	20.00	2	4	97	0	0	0	0	2	23	5
17/11/02	sun	8.00	1	1	97	0	0	0	0	1	31	3
17/11/02	sun	14.00	2	2	97	0	0	0	0	2	23	6
17/11/02	sun	20.00	2	4	95	1	6	0	0	3	13	2
18/11/02	mon	8.00	2	5	97	0	0	0	0	2	0	0
18/11/02	mon	14.00	0	0	99	0	0	0	0	0	31	5
18/11/02	mon	20.00	3	5	97	0	0	0	0	3	23	2
19/11/02	tue	8.00	8	6	90	0	0	0	0	8	31	3
19/11/02	tue	14.00	0	0	99	0	0	0	0	0	23	4
19/11/02	tue	20.00	0	0	96	0	0	2	4	2	23	3
20/11/02	wed	8.00	0	0	99	0	0	0	0	0	0	0
20/11/02	wed	14.00	1	3	97	0	0	0	0	1	23	3
20/11/02	wed	20.00	0	0	99	0	0	0	0	0	23	6
21/11/02	thu	8.00	0	0	99	0	0	0	0	0	31	3
21/11/02	thu	14.00	2	3	97	0	0	0	0	0	31	5
21/11/02	thu	20.00	2	2	97	0	0	0	0	2	31	8
22/11/02	fri	8.00	0	0	99	0	0	0	0	0	31	2
22/11/02	fri	14.00	1	2	98	0	0	0	0	1	23	2
22/11/02	fri	20.00	0	0	99	0	0	0	0	0	23	6
23/11/02	sat	8.00										
24/11/02	sun	8.00										
24/11/02	sun	14.00										
24/11/02	sun	20.00	0	0	99	0	0	0	0	0	31	8
25/11/02	mon	8.00	6	5	93	0	0	0	0	6	05	6
25/11/02	mon	14.00	0	0	99	0	0	0	0	0	31	6
25/11/02	mpo	20.00	0	0	99	0	0	0	0	0	31	5
26/11/02	tue	8.00										
26/11/02	tue	14.00										
26/11/02	tue	20.00										
27/11/02	wed	8.00	7	5	93	0	0	0	0	7	09	2
27/11/02	wed	14.00	5	2	95	0	0	0	0	5	31	2
27/11/02	wed	20.00	1	5	94	3	7	0	0	4	23	3
28/11/02	thu	8.00	7	5	94	0	0	0	0	7	31	2
27/11/02	thu	14.00	1	3	97	0	0	0	0	1	23	2
28/11/02	thu	20.00	0	0	99	0	0	0	0	0	13	2
28/11/02	fri	8.00	0	0	99	0	0	0	0	0	0	0
29/11/02	fri	14.00										
29/11/02	fri	20.00										
30/11/02	sat	8.00										
30/11/02	sat	14.00										
30/11/02	sat	20.00										
01/12/02	sun	8.00										
01/12/02	sun	14.00										
01/12/02	sun	20.00										
02/12/02	mon	8.00	7	9	92	0	0	0	0	7	31	2
02/12/02	mon	14.00	5	9	94	0	0	0	0	5	31	2
02/12/02	mon	20.00	4	5	95	0	0	0	0	4	23	2
03/12/02	tue	8.00	3	4	96	0	0	0	0	3	31	2
03/12/02	tue	14.00	3	3	96	0	0	0	0	3	23	6
03/12/02	tue	20.00	2	4	97	0	0	0	0	2	13	5
04/12/02	wed	8.00	2	4	96	0	0	0	0	0	nw	2
04/12/02	wed	14.00	6	2	96	0	0	0	0	0	nw	6

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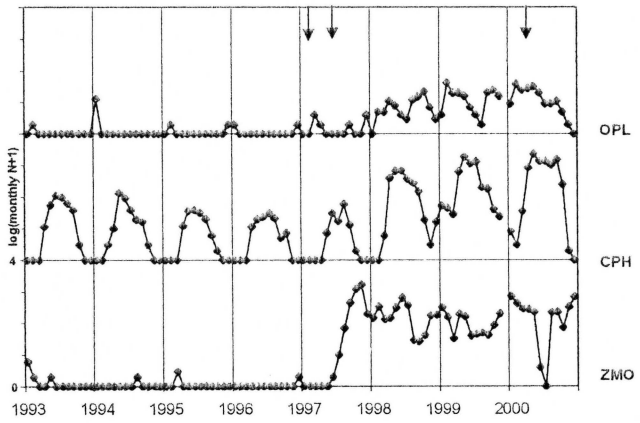

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17/11/02	sun	20.00	2	4	95	1	6	0	0	3	13	2
18/11/02	mon	8.00	2	5	97	0	0	0	0	2	0	0
18/11/02	mon	14.00	0	0	99	0	0	0	0	0	31	5
18/11/02	mon	20.00	3	5	97	0	0	0	0	3	23	2
19/11/02	tue	8.00	8	6	90	0	0	0	0	8	31	3
19/11/02	tue	14.00	0	0	99	0	0	0	0	0	23	4
19/11/02	tue	20.00	0	0	96	0	0	2	4	2	23	3
20/11/02	wed	8.00	0	0	99	0	0	0	0	0	0	0
20/11/02	wed	14.00	1	3	97	0	0	0	0	1	23	3
20/11/02	wed	20.00	0	0	99	0	0	0	0	0	23	6
21/11/02	thu	8.00	0	0	99	0	0	0	0	0	31	3
21/11/02	thu	14.00	2	3	97	0	0	0	0	0	31	5
21/11/02	thu	20.00	2	2	97	0	0	0	0	2	31	8
22/11/02	fri	8.00	0	0	99	0	0	0	0	0	31	2
22/11/02	fri	14.00	1	2	98	0	0	0	0	1	23	2
22/11/02	fri	20.00	0	0	99	0	0	0	0	0	23	6
23/11/02	sat	8.00										
24/11/02	sun	8.00										
24/11/02	sun	14.00										
24/11/02	sun	20.00	0	0	99	0	0	0	0	0	31	8
25/11/02	mon	8.00	6	5	93	0	0	0	0	6	05	6
25/11/02	mon	14.00	0	0	99	0	0	0	0	0	31	6
25/11/02	mpo	20.00	0	0	99	0	0	0	0	0	31	5
26/11/02	tue	8.00										
26/11/02	tue	14.00										
26/11/02	tue	20.00										
27/11/02	wed	8.00	7	5	93	0	0	0	0	7	09	2
27/11/02	wed	14.00	5	2	95	0	0	0	0	5	31	2
27/11/02	wed	20.00	1	5	94	3	7	0	0	4	23	3
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28/11/02	thu	20.00	0	0	99	0	0	0	0	0	13	2
28/11/02	fri	8.00	0	0	99	0	0	0	0	0	0	0
29/11/02	fri	14.00										
29/11/02	fri	20.00										
30/11/02	sat	8.00										
30/11/02	sat	14.00										
30/11/02	sat	20.00										
01/12/02	sun	8.00										
01/12/02	sun	14.00										
01/12/02	sun	20.00										
02/12/02	mon	8.00	7	9	92	0	0	0	0	7	31	2
02/12/02	mon	14.00	5	9	94	0	0	0	0	5	31	2
02/12/02	mon	20.00	4	5	95	0	0	0	0	4	23	2
03/12/02	tue	8.00	3	4	96	0	0	0	0	3	31	2
03/12/02	tue	14.00	3	3	96	0	0	0	0	3	23	6
03/12/02	tue	20.00	2	4	97	0	0	0	0	2	13	5
04/12/02	wed	8.00	2	4	96	0	0	0	0	0	nw	2
04/12/02	wed	14.00	6	2	96	0	0	0	0	0	nw	6

WIND_S	VISIBL_	VISIBL_	WCOND	TEMP_[	TEMP_\	TEMP_M	TEMP_M	TEMP_I	TEMP_M	TEMP_TI	HUMID_I
	Visibi		Wea	Temperature							Humid
	mx	mn	cond	dry	wet	max	min	max	min	thermo	hygr
knt			prsnt					reset	reset		
6	74	72	02	11.9	10.8	32.4	11.2	12.3	11.9	10.0	72
6	84	82	02	21.4	14.8		11.9		21.5	20.0	333
4	80	78	02	18.3	14.2	26.4				17.0	44
0	82	80	02	12.7	11.2	26.4	12.3	13.2	12.9	11.0	66
10	82	80	02	25.4	15.5		12.8		26.5	23.8	29
12	80	78	02	18.7	13.8	29.3				17.4	42
4	74	72	02	12.0	10.7	29.3		12.7		10.0	68
6	84	82	02	23.5	15.2					21.9	28
12	80	78	02	18.8	12.7	25.2				17.7	28
0	82	80	02	12.0	9.8	25.2	9.5	12.3	12.0	10.0	63
10	84	82	02	26.3	15.8		11.8		26.5	25.8	72
12	78	76	02	18.3	12.2	27.5				17.8	32
6	82	80	02	11.0	8.8	27.5	7.51	11.6	11.2	10.0	60
6	82	80	02	28.2	16.0		11.0		28.4	27.2	18
14	74	72	02	23.7	12.5	30.5				22.5	18
16	84	82	02	23.3	10.2	30.5	19.0	23.4	23.3	22.3	14
10	84	82	02	34.5	14.8		15.8		35.0	34.0	6
14	78	76	02	29.7	13.0	36.9				29.0	5
18	82	80	02	27.7	13.8	36.9	23.7	27.8	27.8	27.2	7
6	81	80	02	38.4	19.2		27.6		38.6	38.5	5
12	80	78	02	30.9	20.8	38.8				30.0	8
4	80	78	02	16.3	13.0	38.8	18.4	16.5	16.3	16.0	54
6	84	82	02	38.5	19.3		16.3		35.6	35.0	15
6	80	78	02	30.2	17.7	37.3				30.0	18
4	74	72	41	12.3	12.0	37.3	11.3	12.6	12.3	11.0	74
6	84	82	02	35.0	20.1		12.3		35.6	34.0	12
6	80	78	02	29.5	1808	36.7				28.8	12
0	80	78	02	16.7	14.3	36.7	12.5	17.9	16.8	16.0	50
10	84	82	02	29.4	20.2		16.7		29.4	28.0	20
10	78	76	02	23.0	17.8	32.0				22.8	31
4	38	36	43	10.6	10.0	32.0	9.01	10.7	10.3	9.8	76
10	82	80	02	26.3	16.2		10.2		26.3	26.0	22
4	80	78	02	22.0	14.4	28.8				22.0	23
4	67	65	45	10.0	9.6	28.8	9.4	10.2	9.9	9.0	87
0	84	82	xx	27.4	16.1		10.0		27.5	26.4	24
0	82	80	xx	21.5	15.0	28.5				21.0	28
0	82	80	x	12.5	11.4	28.2	10.0	29.5	12.5	11.9	66
4	84		82	28.4	17.2		10.0		28.5	27.0	19
10	80		78	23.5	15.0	29.6				23.0	21
0	82		80	15.2	11.8	29.6	9.8	16.4	15.3	14.0	27
10	84	82	01	34.3	18.8		15.2		20.3	33.1	12
6	80		78	28.2	15.8	36.4				28.0	12
4	84	82	02	16.6	13.5	36.4	14.0	17.0	16.7	15.8	44
8	84	82	02	28.9	19.2		16.6		28.8	28.0	22
6	80	78	02	24.4	16.2	30.0				24.0	24
0	80	78	02	13.7	13.0	30.0	11.5	13.8	13.6	13.0	600
10	80	78	02	30.0	19.2		13.7		30.3	29.4	14

Introduction

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

Mean annual rainfall at Gobabeb between 1962 and 2000 was 22.1±26.9 mm (1.0-125.0 mm; median 12.2 mm). Annual rainfall was highly variable (CV=122%), characterized by short episodic pulses (Pietruszka and Seely 1985), and followed no detectable multiyear pattern (Table 1; autocorrelation with lags of 3-15 yrs: $r<0.05$, $p>0.1$). Effective late summer rain of 33.6 ±SD 39.5 mm occurred every 3.2±2.3 yr (2-9 yrs), and effective winter rain of 16.1±6.8 mm at intervals of 6.8±5.6 yr (2-16 yrs; Table 1). A relatively dry interval between 1963-1976 preceded the study, followed by wet years at the start of our study (Table 1). Heavy rains in 1976, 1978 and 1997, provided an opportunity to examine immediate (Seely 1978, Seely and Louw 1980) and long-term (Southgate et al. 1996, present study) population responses to them.

22/04/03	tue	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	4.00
22/04/03	tue	20.00	no fig	no fig	no fig.	no fig.	no fig.	no fig.	no fig.	no fig.	23.00	5.00
23/04/03	wed	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
23/04/03	wed	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00
23/04/03	wed	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	3.00
24/04/03	thu	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	13.00	2.00
24/04/03	thu	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	27.00	2.00
24/04/03	thu	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	13.00	2.00
25/04/03	fri	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25/04/03	fri	14.00										
25/04/03	fri	20.00										
26/04/03	sat	8.00	3.00	2.00	96.00	0.00	0.00	0.00	0.00	3.00	13.00	5.00
26/04/03	sat	14.00	2.00	2.00	98.00	0.00	0.00	0.00	0.00	2.00	31.00	3.00
26/04/03	sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00

To determine whether abundance depended on episodic rainfall, we identified the first year when N increased by $\geq$10 and GC by $\geq$0.05 ($\approx$10% increase in N), then looked for the first month of increase. A population was identified as triggered if an increase started any month after rainfall and continued to increase to a peak greater than monthly abundance the year before the initial increase. To account for larval maturation we also tested for one-year lags in the same way.

Diel rhythm.— Study species were active above the surface during three periods: diurnal (19 species), nocturnal (12) and crepuscular (2). There was no difference in the relative proportions of large and small beetle species that were diurnal or nocturnal/crepuscular (separated by median, χ^2=0.81, df=1, p>0.05). Most individuals (78%) trapped in GP, IP, and DS were diurnal (Archive 5). L. discoidalis, a crepuscular species, dominated abundance in SF.

Seasonality.— Eighteen species were seasonal, and most of these occurred in IP and SF (Archive 5). In IP several common species followed different seasonal activity schedules. Cauricara phalangium was abundant during winter and scarce in mid-summer. Zophosis moralesi and O. plana peaked in the summer (Archive 6). SF was characterized by small-scale and short-term fluctuations in beetle abundance between trapping events.

05/04/03	sat	8.00	3.00	3.00	95.00	0.00	0.00	0.00	0.00	3.00	31.00	3.00
05/04/03	sat	14.00	2.00	3.00	95.00	2.00	6.00	0.00	0.00	4.00	31.00	5.00
05/04/03	sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
06/04/03	sun	8.00	2.00	3.00	95.00	1.00	6.00	0.00	0.00	3.00	0.00	0.00
06/04/03	sun	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	6.00
06/04/03	sun	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00
07/04/03	mon	8.00	4.00	3.00	95.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
07/04/03	mon	14.00	5.00	3.00	94.00	0.00	0.00	0.00	0.00	5.00	31.00	6.00
07/04/03	mon	20.00	2.00	4.00	96.00	2.00	6.00	0.00	0.00	4.00	23.00	5.00
08/04/03	tue	8.00	1.00	4.00	93.00	5.00	7.00	0.00	0.00	6.00	0.00	0.00
08/04/03	tue	14.00	1.00	4.00	95.00	1.00	4.00	0.00	0.00	2.00	23.00	3.00
08/04/03	tue	20.00	1.00	4.00	96.00	2.00	6.00	0.00	0.00	3.00	13.00	3.00
09/04/03	wed	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
09/04/03	wed	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
09/04/03	wed	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	13.00	3.00
10/04/03	thu	8.00	2.00	3.00	97.00	0.00	0.00	0.00	0.00	2.00	31.00	2.00
10/04/03	thu	14.00	0.00	0.00	97.00	2.00	6.00	0.00	0.00	2.00	31.00	5.00
10/04/03	thu	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11/04/03	fri	8.00	1.00	1.00	98.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
11/04/03	fri	14.00										
11/04/03	fri	20.00										
12/04/03	sat	8.00	3.00	9.00	94.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00
12/04/03	sat	14.00	2.00	3.00	97.00	0.00	0.00	0.00	0.00	2.00	23.00	3.00
12/04/03	sat	20.00	4.00	5.00	96.00	0.00	0.00	0.00	0.00	4.00	13.00	5.00
13/04/03	sun	8.00	4.00	5.00	96.00	0.00	0.00	0.00	0.00	4.00	0.00	0.00
13/04/03	sun	14.00	4.00	9.00	94.00	2.00	7.00	0.00	0.00	6.00	5.00	5.00
13/04/03	sun	20.00	4.00	5.00	96.00	0.00	0.00	0.00	0.00	4.00	5.00	10.00
14/04/03	mon	8.00	1.00	4.00	98.00	0.00	0.00	0.00	0.00	1.00	5.00	3.00
14/04/03	mon	14.00	1.00	1.00	98.00	0.00	0.00	0.00	0.00	1.00	13.00	2.00
14/04/03	mon	20.00	1.00	4.00	98.00	0.00	0.00	0.00	0.00	1.00	13.00	3.00
15/04/03	tue	8.00	5.00	5.00	94.00	0.00	0.00	0.00	0.00	5.00	5.00	11.00
15/04/03	tue	14.00	5.00	5.00	94.00	0.00	0.00	0.00	0.00	5.00	5.00	10.00
15/04/03	tue	20.00	3.00	4.00	96.00	0.00	0.00	0.00	0.00	3.00	5.00	4.00
16/04/03	wed	8.00	2.00	5.00	93.00	4.00	7.00	0.00	0.00	6.00	0.00	0.00
16/04/03	wed	14.00	1.00	3.00	94.00	5.00	7.00	0.00	0.00	6.00	5.00	6.00
16/04/03	wed	20.00	5.00	9.00	93.00	0.00	0.00	0.00	0.00	5.00	5.00	8.00
17/04/03	thu	8.00	0.00	0.00	94.00	6.00	7.00	0.00	0.00	6.00	5.00	7.00
17/04/03	thu	14.00	2.00	2.00	97.00	0.00	0.00	0.00	0.00	2.00	5.00	6.00
17/04/03	thu	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
18/04/03	fri	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	13.00	3.00
18/04/03	fri	14.00	1.00	1.00	97.00	0.00	0.00	0.00	0.00	1.00	31.00	2.00
18/04/03	fri	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
19/04/03	sat	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
19/04/03	sat	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
19/04/03	sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	18.00	2.00
20/04/03	sun	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
20/04/03	sun	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	27.00	2.00
20/04/03	sun	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	3.00
21/04/03	mon	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
21/04/03	mon	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	13.00	2.00
21/04/03	mon	20.00	3.00	4.00	97.00	0.00	0.00	0.00	0.00	3.00	23.00	3.00
22/04/03	tue	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Timing of population responses.—Population responses were sometimes detected during the month or months immediately following an event as adults became active. Most population responses were initiated in six mos, but some only 12-19 mos after a triggering event (Table 3). Most population peaks occurred during the year after the event but five peaks occurred three years later, following steady population increases in the years after the trigger.

Responses to rainfall. —A population response to heavy rainfall (26-117 mm) was detected for 31 species. Vansonium bushmanicum and Cauricara eburnea responded only to winter rainfall, not to heavy rain. The other 15 species that responded to winter rainfall also responded to heavy summer rain (Table 3). Summer rain of 10-25 mm triggered 14 species. The five most abundant species responded to effective summer rains (Tables 3). Four species responded to light rain (<10 mm) in February 1984, December 1993 and November 1996 (Table 1). Only Zophosis amabilis responded to every rainfall event, although several species (Onymacris laeviceps, Stips stali, Lepidochora porti), responded to every category of rain on some occasion.

Discussion

Studies of tenebrionid beetles in arid America, Australia and the Middle East report that population fluctuations and their differences between species are

18/03/03	tue	20.00	1.00	4.00	95.00	4.00	7.00	0.00	0.00	5.00	18.00	2.00
19/03/03	wed	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	36.00	2.00
19/03/03	wed	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	27.00	2.00
19/03/03	wed	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	3.00
20/03/03	thu	8.00	1.00	6.00	90.00	0.00	0.00	0.00	0.00	1.00	36.00	2.00
20/03/03	thu	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	27.00	5.00
20/03/03	thu	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	27.00	4.00
21/03/03	fri	8.00	8.00	6.00	93.00	0.00	0.00	0.00	0.00	8.00	27.00	4.00
21/03/03	fri	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	NW	4.00
21/03/03	fri	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	W	2.00
22/03/03	sat	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	9.00	4.00
22/03/03	sat	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00
22/03/03	sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	13.00	5.00
23/03/03	sun	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	0.00	0.00
23/03/03	sun	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	13.00	2.00
23/03/03	sun	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
24/03/03	mon	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24/03/03	mon	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	5.00
24/03/03	mon	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	6.00
25/03/03	tue	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25/03/03	tue	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	2.00
25/03/03	tue	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	SW	2.00
26/03/03	wed	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
26/03/03	wed	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	W	5.00
26/03/03	wed	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	W	2.00
27/03/03	thu	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	9.00	2.00
27/03/03	thu	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	W	2.00
27/03/03	thu	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00
28/03/03	fri	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	E	2.00
28/03/03	fri	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	SW	6.00
28/03/03	fri	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	SW	4.00
29/03/03	sat	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	2.00
29/03/03	sat	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	W	3.00
29/03/03	sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	4.00
30/03/03	sun	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	0.00	0.00
30/03/03	sun	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00
30/03/03	sun	20.00	0.00	0.00	94.00	4.00	5.00	0.00	0.00	4.00	23.00	3.00
31/03/03	mon	8.00	3.00	1.00	94.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00
31/03/03	mon	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	W	4.00
31/03/03	mon	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	5.00
01/04/03	tue	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	31.00	2.00
01/04/03	tue	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	3.00
01/04/03	tue	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00
02/04/03	wed	8.00	3.00	1.00	93.00	0.00	0.00	0.00	0.00	3.00	31.00	2.00
02/04/03	wed	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
02/04/03	wed	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	18.00	3.00
03/04/03	thu	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
03/04/03	thu	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	4.00
03/04/03	thu	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	18.00	2.00
04/04/03	fri	8.00	4.00	5.00	95.00	0.00	0.00	0.00	0.00	4.00	0.00	0.00
04/04/03	fri	14.00	4.00	2.00	95.00	0.00	0.00	0.00	0.00	4.00	31.00	5.00
04/04/03	fri	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	18.00	2.00

largely attributable to rainfall variations (e.g., Rickard and Haverfield 1965, Faragalla and Adam 1985, Parmenter et al. 1989, Stafford-Smith and Morton 1990, Ayal and Merkl 1994, Krasnov and Ayal 1995, Deslippe et al. 2001). This conclusion agrees with the findings of our study with the caveats that population responses are also strongly modified by rainfall schedules and life history characteristics including diel rhythmicity. We observed that patterns of population responses to precipitation were either species-specific or characteristic of clusters of species independent from phylogeny and biogeography. Despite the wide range of triggers, initial response times and rates of population change, species clustered by population fluctuation and abundance patterns show several discrete nodes expressing population signatures in common.

Rainfall, the most important trigger of Namib Desert tenebrionid population irruptions, acts on populations in several different ways. It increases soil moisture (Besler and Gut 1997, Jacobson 1997), thus favoring larval development (Rössl 2000), and it increases primary productivity by generating detritus, the basis for detritivorous beetle productivity (Seely 1973). Light effective rainfall briefly stimulates growth of ephemeral plants (Seely 1978), whereas many perennial plants require heavy rainfall to become established (Walter 1936, Seely and Louw 1980, Seely 1989, Southgate et al. 1996, Hachfeld 2000).

01/03/03	sat	14.00	1.00	2.00	97.00	0.00	0.00	0.00	0.00	1.00	31.00	4.00
01/03/03	sat	20.00	2.00	4.00	96.00	0.00	0.00	0.00	0.00	2.00	23.00	3.00
02/03/03	sun	8.00	7.00	5.00	92.00	0.00	0.00	0.00	0.00	7.00	5.00	3.00
02/03/03	sun	14.00	2.00	2.00	97.00	0.00	0.00	0.00	0.00	2.00	31.00	3.00
02/03/03	sun	20.00	3.00	4.00	96.00	0.00	0.00	0.00	0.00	3.00	27.00	5.00
03/03/03	mon	8.00	7.00	2.00	92.00	5.00	7.00	0.00	0.00	7.00	0.00	0.00
03/03/03	mon	14.00	2.00	5.00	93.00	4.00	7.00	0.00	0.00	6.00	23.00	2.00
03/03/03	mon	20.00	3.00	4.00	96.00	0.00	0.00	0.00	0.00	3.00	23.00	2.00
04/03/03	tue	8.00	1.00	5.00	93.00	5.00	7.00	0.00	0.00	6.00	31.00	3.00
04/03/03	tue	14.00	2.00	5.00	92.00	5.00	7.00	0.00	0.00	7.00	23.00	2.00
04/03/03	tue	20.00	1.00	4.00	93.00	6.00	7.00	0.00	0.00	7.00	23.00	2.00
05/03/03	wed	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	13.00	2.00
05/03/03	wed	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	5.00
05/03/03	wed	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00
06/03/03	thu	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	31.00	5.00
06/03/03	thu	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	7.00
06/03/03	thu	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	5.00
07/03/03	fri	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	31.00	4.00
07/03/03	fri	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	27.00	3.00
07/03/03	fri	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	18.00	3.00
08/03/03	sat	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	5.00	3.00
08/03/03	sat	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	3.00
08/03/03	sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	5.00
09/03/03	sun	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	5.00	5.00
09/03/03	sun	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
09/03/03	sun	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	3.00
10/03/03	mon	8.00	1.00	1.00	95.00	0.00	0.00	0.00	0.00	1.00	36.00	3.00
10/03/03	mon	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	6.00
10/03/03	mon	20.00	0.00	0.00	95.00	3.00	8.00	0.00	0.00	3.00	23.00	2.00
11/03/03	tue	8.00	0.00	0.00	95.00	3.00	8.00	0.00	0.00	3.00	31.00	3.00
11/03/03	tue	14.00	1.00	1.00	97.00	0.00	0.00	0.00	0.00	1.00	31.00	3.00
11/03/03	tue	20.00	6.00	7.00	93.00	0.00	0.00	0.00	0.00	6.00	27.00	6.00
12/03/03	wed	8.00	2.00	4.00	93.00	4.00	7.00	0.00	0.00	6.00	31.00	4.00
12/03/03	wed	14.00	3.00	2.00	96.00	0.00	0.00	0.00	0.00	3.00	31.00	5.00
12/03/03	wed	20.00	1.00	4.00	95.00	0.00	0.00	0.00	0.00	1.00	SW	6.00
13/03/03	thu	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	31.00	2.00
13/03/03	thu	14.00	1.00	2.00	97.00	0.00	0.00	0.00	0.00	1.00	23.00	3.00
13/03/03	thu	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	18.00	3.00
14/03/03	fri	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
14/03/03	fri	14.00	1.00	2.00	97.00	0.00	0.00	0.00	0.00	1.00	31.00	2.00
14/03/03	fri	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	3.00
15/03/03	sat	8.00	5.00	1.00	94.00	0.00	0.00	0.00	0.00	5.00	31.00	2.00
15/03/03	sat	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	27.00	6.00
15/03/00	sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	27.00	2.00
16/03/03	sun	8.00		6.00	90.00	0.00	0.00	0.00	0.00	8.00	31.00	3.00
16/03/03	sun	14.00	1.00	1.00	97.00	0.00	0.00	2.00	4.00	6.00	31.00	5.00
16/03/03	sun	20.00	4.00	5.00	94.00	0.00	0.00	0.00	0.00	4.00	27.00	2.00
17/03/03	mon	8.00	1.00	1.00	96.00	0.00	0.00	2.00	1.00	4.00	31.00	2.00
17/03/03	mon	14.00	0.00	0.00	98.00	0.00	0.00	3.00	1.00	3.00	31.00	5.00
17/03/03	mon	20.00	0.00	0.00	98.00	0.00	0.00	4.00	6.00	4.00	W	2.00
18/03/03	tue	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	36.00	1.00
18/03/03	tue	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	27.00	4.00

Responses to rainfall.— In the past 120 yrs, rainfall exceeding 100 mm occurred in the Namib in 1934, 1976, 1978 and 2000 (Namibian Meteorological Service). All but two tenebrionid species responded to heavy rainfall. After the 1976 and 1978 rains tenebrionid abundance declined by nearly two orders of magnitude (25,034 to 399 for all tenebrionid species and habitats combined between 1977 and 1995; Figs. 2 & 4). The 1994-1996 population low was followed by an interval of increasing abundance after the 1997 rains (to 21,495 in 2000). Relatively heavy rain at Gobabeb in 1997 confirmed the identity of triggers to patterns of responses to exceptional events (Figs. 3& 4). Lighter and less frequent winter rainfall was important for several species (Table 3), perhaps because near-surface moisture lasts longer in winter (Besler and Gut 1997) due to reduced evaporation and persistent moisture in 5-8°C cooler soil.

Life history effects upon recruitment

Timing of rainfall strongly influences the timing and magnitude of responses. Rain preceding summer-active species such as Z. moralesi allows the residual population of adults, eggs and larvae to reproduce, develop and metamorphose in 75 da or less (Rössl 2000). This recruits a fresh cohort of adults within the time constraints of the breeding season and with fresh resources, made possible a second breeding effort and the irruption of this species. By contrast, seasonality of activity explains the failure of C. phalangium to irrupt in IP in 1997. The 1997 winter rainfall followed the main activity season

12/02/03 wed	8.00										
12/02/03 wed	14.00	1.00	2.00	94.00	5.00	7.00	0.00	0.00	6.00	23.00	3.00
12/02/03 wed	20.00	2.00	4.00	95.00	4.00	7.00	0.00	0.00	6.00	23.00	5.00
13/02/03 thu	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	31.00	5.00
13/02/03 thu	14.00	1.00	2.00	96.00	2.00	6.00	0.00	0.00	3.00	31.00	7.00
13/02/03 thu	20.00	2.00	4.00	97.00	0.00	0.00	0.00	0.00	2.00	31.00	3.00
14/02/03 fri	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	31.00	5.00
14/02/02 fri	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	6.00
14/02/03 fri	20.00										
15/02/03 sat	8.00										
15/02/03 sat	14.00										
15/02/03 sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	6.00
16/02/03 sun	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
16/02/03 sun	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	13.00	3.00
16/02/03 sun	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	13.00	5.00
17/02/03 mon	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
17/02/03 mon	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	2.00
17/02/03 mon	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	5.00
18/02/03 tue	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	31.00	2.00
18/02/03 tue	14.00	1.00	1.00	97.00	0.00	0.00	0.00	0.00	1.00	23.00	3.00
18/02/03 tue	20.00	3.00	5.00	96.00	0.00	0.00	0.00	0.00	3.00	25.00	5.00
19/02/03 wed	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
19/02/03 wed	14.00	2.00	2.00	97.00	0.00	0.00	0.00	0.00	2.00	23.00	3.00
19/02/03 wed	20.00	2.00	4.00	97.00	0.00	0.00	0.00	0.00	2.00	23.00	5.00
20/02/03 thu	8.00	7.00	5.00	97.00	0.00	0.00	0.00	0.00	7.00	31.00	5.00
20/02/03 thu	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	5.00
20/02/03 thu	20.00										
21/02/03 fri	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	31.00	6.00
21/02/03 fri	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	6.00
21/02/03 fri	20.00	2.00	4.00	97.00	0.00	0.00	0.00	0.00	2.00	31.00	3.00
22/02/03 sat	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	31.00	5.00
22/02/03 sat	14.00	2.00	1.00	97.00	0.00	0.00	0.00	0.00	2.00	31.00	4.00
22/02/03 sat	20.00										
23/02/03 sun	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	0.00	0.00
23/02/03 sun	14.00	2.00	2.00	97.00	0.00	0.00	0.00	0.00	2.00	31.00	2.00
23/02/03 sun	20.00										
24/02/03 mon	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	23.00	2.00
24/02/03 mon	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	3.00
24/02/03 mon	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	6.00
25/02/03 tue	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	5.00	2.00
25/02/03 tue	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
25/02/03 tue	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	6.00
26/02/03 wed	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	5.00	2.00
26/02/03 wed	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
26/02/03 wed	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
27/02/03 thu	8.00	0.00	0.00	96.00	3.00	8.00	0.00	0.00	3.00	31.00	3.00
27/02/03 thu	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
27/02/03 thu	20.00	1.00	4.00	97.00	0.00	0.00	0.00	0.00	1.00	13.00	5.00
28/02/03 fri	8.00	2.00	2.00	96.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00
28/02/03 fri	14.00										
28/02/03 fri	20.00	1.00	4.00	97.00	0.00	0.00	0.00	0.00	1.00	23.00	3.00
01/03/03 sat	8.00	3.00	8.00	94.00	2.00	8.00	0.00	0.00	5.00	0.00	0.00

of C. phalangium, so it only responded the following winter during its usual adult activity season (Archive 6). Population responses to triggers operate within the constraints of different life history parameters such as phenology and larval longevity.

Detritivorous tenebrionids persist in the hyperarid Namib because detritus prolongs the effects of episodic rainfall events. Most detritus is unavailable to detritivores most of the time. It becomes available when daily wind uncovers or blows in fresh detritus. Imagoes are long-lived and maintain a bet-hedging reproductive strategy that may use fog to sustain water limitations during enduring rainless intervals, allowing them to irrupt after the next pulse. Not all species increase with every flush of vegetation. Many species respond to particular kinds of rainfall: e.g., summer rainfall with its flush of primary productivity, or winter rain with its lingering soil moisture, or require different intensities of such events to respond at all. There are categorical differences among species in how they respond to rainfall of different magnitudes in different seasons. Nevertheless, nearly all population changes can be related to hydrological pulses.

Our interpretation of the fundamental importance of hydrological triggering events thus concurs with Noy-Meir's (1980) autecological perspective. Population changes in the study area are driven by hydrological events. However, population responses to the environment are multifaceted and affected

25/01/03 sat	20.00	0.00	0.00	96.00	2.00	7.00	0.00	0.00	2.00	23.00	6.00
26/01/03 sun	8.00										
26/01/03 sun	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	3.00
26/01/03 sun	20.00	1.00	4.00	97.00	0.00	0.00	0.00	0.00	1.00	31.00	5.00
27/01/03 mon	8.00	1.00	2.00	97.00	0.00	0.00	0.00	0.00	1.00	5.00	3.00
27/01/03 mon	14.00	1.00	1.00	97.00	0.00	0.00	0.00	0.00	1.00	31.00	6.00
27/01/03 mon	20.00	2.00	4.00	97.00	0.00	0.00	0.00	0.00	2.00	31.00	7.00
28/01/03 tue	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
28/01/03 tue	14.00	2.00	3.00	96.00	0.00	0.00	0.00	0.00	2.00	27.00	6.00
28/01/03 tue	20.00	2.00	4.00	94.00	2.00	8.00	0.00	0.00	4.00	13.00	3.00
29/01/03 wed	8.00	2.00	5.00	93.00	4.00	8.00	0.00	0.00	6.00	31.00	7.00
29/01/03 wed	14.00	2.00	2.00	92.00	0.00	0.00	0.00	0.00	2.00	31.00	5.00
29/01/03 wed	20.00	0.00	0.00	97.00	0.00	0.00	0.00	0.00	0.00	31.00	3.00
30/01/03 thu	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	5.00
30/01/03 thu	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
30/01/03 thu	20.00	4.00	7.00	96.00	0.00	0.00	0.00	0.00	0.00	31.00	6.00
31/01/03 fri	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	5.00	4.00
31/01/03 fri	14.00	2.00	3.00	94.00	3.00	6.00	0.00	0.00	5.00	31.00	6.00
31/01/03 fri	20.00	1.00	4.00	95.00	3.00	8.00	0.00	0.00	4.00	31.00	6.00
01/02/03 sat	8.00	3.00	5.00	94.00	5.00	8.00	0.00	0.00	7.00	0.00	0.00
01/02/03 sat	14.00	1.00	3.00	95.00	3.00	8.00	0.00	0.00	4.00	31.00	6.00
01/02/03 sat	20.00										
02/02/03 sun	8.00										
02/02/03 sun	14.00										
02/02/03 sun	20.00	2.00	4.00	97.00	0.00	0.00	0.00	0.00	2.00	23.00	2.00
03/02/03 mon	8.00	2.00	2.00	97.00	0.00	0.00	0.00	0.00	2.00	6.00	2.00
03/02/03 mon	14.00	2.00	2.00	94.00	1.00	6.00	0.00	0.00	3.00	23.00	3.00
03/02/03 mon	20.00										
04/02/03 tue	8.00	1.00	4.00	92.00	6.00	7.00	0.00	0.00	7.00	0.00	0.00
04/02/03 tue	14.00										
04/02/03 tue	20.00										
05/02/03 wed	8.00	2.00	5.00	95.00	1.00	8.00	0.00	3.00	4.00	5.00	3.00
05/02/03 wed	14.00	3.00	3.00	95.00	2.00	6.00	0.00	0.00	5.00	23.00	5.00
05/02/03 wed	20.00	3.00	4.00	93.00	3.00	8.00	0.00	0.00	6.00	23.00	5.00
06/02/03 thu	8.00	2.00	1.00	97.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00
06/02/03 thu	14.00	2.00	2.00	96.00	0.00	0.00	0.00	0.00	2.00	31.00	3.00
06/02/03 thu	20.00	3.00	5.00	94.00	1.00	6.00	0.00	0.00	4.00	23.00	3.00
07/02/03 fri	8.00	3.00	5.00	94.00	0.00	0.00	0.00	0.00	3.00	5.00	2.00
07/02/03 fri	14.00	2.00	2.00	93.00	4.00	6.00	0.00	0.00	6.00	23.00	4.00
07/02/03 fri	20.00	3.00	5.00	94.00	1.00	6.00	0.00	0.00	4.00	31.00	3.00
08/02/03 sat	8.00										
08/02/03 sat	14.00	2.00	5.00	92.00	5.00	7.00	0.00	0.00	7.00	31.00	3.00
08/02/03 sat	20.00	2.00	4.00	93.00	4.00	7.00	0.00	0.00	6.00	13.00	3.00
09/02/03 sun	8.00	2.00	5.00	93.00	5.00	8.00	0.00	0.00	7.00	0.00	0.00
09/02/03 sun	14.00	3.00	2.00	96.00	0.00	0.00	0.00	0.00	3.00	31.00	7.00
09/02/03 sun	20.00	3.00	5.00	95.00	2.00	6.00	0.00	0.00	5.00	31.00	5.00
10/02/03 mon	8.00	2.00	1.00	94.00	5.00	7.00	0.00	0.00	6.00	0.00	0.00
10/02/03 mon	14.00	3.00	2.00	95.00	2.00	8.00	0.00	0.00	5.00	31.00	3.00
10/02/02 mon	20.00	3.00	5.00	94.00	1.00	7.00	0.00	0.00	4.00	13.00	2.00
11/02/03 tue	8.00	2.00	5.00	96.00	3.00	6.00	0.00	0.00	5.00	31.00	3.00
11/02/03 tue	14.00	2.00	2.00	95.00	2.00	6.00	0.00	0.00	4.00	SW	2.00
11/02/03 tue	20.00	6.00	9.00	94.00	0.00	0.00	0.00	0.00	6.00	13.00	6.00

by several environmental or antecedent conditions besides rainfall. Because of responding selectively to alternative triggering events, sympatric species show diverse temporal patterns and magnitudes of population fluctuation, more so than predicted by Noy-Meir's (1980) original model.

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08/01/03	wed	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
08/01/03	wed	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	6.00
09/01/03	thu	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	5.00	4.00
09/01/03	thu	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	5.00
09/01/03	thu	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	3.00
10/01/03	fri	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	5.00	2.00
10/01/03	fri	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	5.00
10/01/03	fri	20.00	1.00	4.00	98.00	0.00	0.00	0.00	0.00	1.00	23.00	3.00
11/01/03	sat	8.00	8.00	6.00	96.00	0.00	0.00	0.00	0.00	8.00	5.00	3.00
11/01/03	sat	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	6.00
11/01/03	sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	2.00
12/01/03	sun	8.00	7.00	5.00	93.00	0.00	0.00	0.00	0.00	7.00	31.00	3.00
12/01/03	sun	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
12/01/03	sun	20.00	2.00	4.00	97.00	0.00	0.00	0.00	0.00	2.00	23.00	3.00
13/01/03	mon	8.00	2.00	2.00	97.00	0.00	0.00	0.00	0.00	2.00	31.00	2.00
13/01/03	mon	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	4.00
13/01/03	mon	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00
14/01/03	tue	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	5.00	2.00
14/01/03	tue	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	3.00
14/01/03	tue	20.00	2.00	1.00	97.00	1.00	6.00	0.00	0.00	2.00	31.00	3.00
15/01/03	wed	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	5.00	2.00
15/01/03	wed	14.00	1.00	1.00	98.00	0.00	0.00	0.00	0.00	1.00	23.00	4.00
15/01/03	wed	20.00	1.00	4.00	97.00	0.00	0.00	0.00	0.00	1.00	23.00	3.00
16/01/03	thu	8.00	5.00	5.00	94.00	0.00	0.00	0.00	0.00	5.00	5.00	2.00
10/01/03	thu	14.00	3.00	2.00	96.00	0.00	0.00	0.00	0.00	3.00	23.00	4.00
16/01/03	thu	20.00	1.00	4.00	94.00	0.00	0.00	0.00	0.00	5.00	23.00	5.00
17/01/03	fri	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	36.00	2.00
17/01/03	fri	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	3.00
17/01/03	fri	20.00	2.00	4.00	97.00	0.00	0.00	0.00	0.00	2.00	13.00	4.00
18/01/03	sat	8.00	3.00	7.00	96.00	4.00	2.00	0.00	0.00	7.00	0.00	0.00
18/01/03	sat	14.00	3.00	2.00	94.00	0.00	0.00	0.00	0.00	3.00	23.00	4.00
18/01/03	sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	S	2.00
19/01/03	sun	8.00	5.00	5.00	96.00	0.00	0.00	0.00	0.00	5.00	NE	2.00
19/01/03	sun	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	6.00
19/01/03	sun	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	7.00
20/01/03	mon	8.00	2.00	2.00	97.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00
20/01/03	mon	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	27.00	3.00
20/01/03	mon	20.00	2.00	4.00	97.00	0.00	0.00	0.00	0.00	2.00	23.00	3.00
21/01/03	tue	8.00	4.00	5.00	95.00	0.00	0.00	0.00	0.00	4.00	31.00	6.00
21/01/03	tue	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	3.00
21/01/03	tue	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00
22/01/03	wed	8.00	3.00	3.00	97.00	0.00	0.00	0.00	0.00	3.00	31.00	3.00
22/01/03	wed	14.00	0.00	0.00	97.00	3.00	8.00	1.00	1.00	4.00	27.00	5.00
22/01/03	wed	20.00	2.00	2.00	96.00	0.00	0.00	0.00	0.00	2.00	23.00	3.00
23/01/03	thu	8.00	1.00	2.00	95.00	3.00	8.00	0.00	0.00	4.00	0.00	0.00
23/01/03	thu	14.00	1.00	1.00	97.00	0.00	0.00	0.00	0.00	1.00	31.00	6.00
23/01/03	thu	20.00	1.00	1.00	97.00	0.00	0.00	0.00	0.00	1.00	31.00	2.00
24/01/03	fri	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	5.00	4.00
24/01/03	fri	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	6.00
24/01/03	fri	20.00	3.00	4.00	95.00	0.00	0.00	0.00	0.00	3.00	23.00	5.00
25/01/03	sat	8.00	3.00	3.00	95.00	0.00	0.00	0.00	0.00	3.00	31.00	3.00
25/01/03	sat	14.00										

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22/12/02	sun	8.00	8.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	31.00	2.00
22/12/02	sun	14.00	2.00	2.00	98.00	0.00	0.00	0.00	0.00	0.00	23.00	6.00
22/12/02	sun	20.00	2.00	2.00	98.00	0.00	0.00	0.00	0.00	0.00	S	2.00
23/12/02	mon	8.00	3.00	4.00	98.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
23/12/02	mon	14.00	3.00	4.00	98.00	0.00	0.00	0.00	0.00	0.00	27.00	5.00
23/12/02	mon	20.00	2.00	4.00	97.00	0.00	0.00	0.00	0.00	0.00	27.00	5.00
24/12/02	tue	8.00	8.00	5.00	90.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24/12/02	tue	14.00	8.00	4.00	98.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00
24/12/02	tue	20.00										
25/12/02	wed	8.00										
25/12/02	wed	14.00										
25/12/02	wed	20.00										
26/12/02	thu	8.00										
26/12/02	thu	14.00										
26/12/02	thu	20.00										
27/12/02	fri	8.00										
27/12/02	fri	14.00										
27/12/02	fri	20.00										
28/12/02	sat	8.00										
28/12/02	sat	14.00										
28/12/02	sat	20.00										
29/12/02	sun	8.00										
29/12/02	sun	14.00										
29/12/02	sun	20.00										
30/12/02	mon	8.00										
30.12.02	mon	14.00										
30/12/02	mon	20.00										
31/12/02	tue	8.00										
31/12/02	tue	14.00										
31/12/02	tue	20.00										
01/01/03	wed	8.00										
01/01/03	wed	14.00										
01/01/03	wed	20.00										
02/01/03	thu	8.00										
02/01/03	thu	14.00										
02/01/03	thu	20.00										
03/01/03	fri	8.00	8.00	5.00	90.00	0.00	0.00	0.00	0.00	8.00	36.00	5.00
03/01/03	fri	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	no figur	no figure
03/01/03	fri	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00
04/01/03	sat	8.00	8.00	5.00	90.00	0.00	0.00	0.00	0.00	0.00	no figur	no figure
04/01/03	sat	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	no figur	no figure
04/01/03	sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00
05/01/03	sun	8.00										
05/01/03	sun	14.00	6.00	5.00	94.00	0.00	0.00	0.00	0.00	0.00	27.00	6.00
05/01/03	sun	20.00										
06/01/03	mon	8.00	7.00	5.00	95.00	0.00	0.00	0.00	0.00	7.00	31.00	4.00
06/01/03	mon	14.00	0.00	0.00	96.00	4.00	7.00	0.00	0.00	4.00	27.00	2.00
06/01/03	mon	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00
07/01/03	tue	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	31.00	2.00
07/01/03	tue	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	27.00	7.00
07/01/03	tue	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	3.00
08/01/03	wed	8.00	7.00	5.00	93.00	0.00	0.00	0.00	0.00	7.00	5.00	4.00

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TABLE A5: Characteristics of study species: dry body mass, daily activity pattern, biogeographic distribution (region) relative to Gobabeb (S=southwards, N=northwards, C=N & S), average monthly variation ***cv***, season of highest activity, proportion captured during main season for seasonal species. Degree of seasonality was calculated from the percent abundance in the season of maximum abundance. This was correlated with the variation of monthly abundance (***cv*** r=0.97, p<0.001). For seasonal species this was >50%.

Species	Mass mg	Activity pattern	Region	CV/mo	Seasonality	Season %N
Cauricara eburnea	44	diurnal	N	114%	aseasonal	
Cauricara phalangium	34	diurnal	S	99%	winter	85%
Cauricara velox	35	diurnal	N	249%	winter	74%
Epiphysa arenicola	384	nocturnal	C	139%	early summer	50%
Eustolopus octoseriatus	105	diurnal	C	227%	aseasonal	
Metriopus depressus	54	diurnal	C	160%	late summer	52%
Onymacris laeviceps	253	diurnal	S	96%	late summer	80%
Onymacris plana	328	diurnal	S	56%	aseasonal	
Onymacris rugatipennis	235	diurnal	S	265%	aseasonal	
Onymacris unguicularis	252	diurnal	C	165%	late summer	51%
Physasterna cribripes	402	diurnal	C	271%	late summer	66%
Vernayella delabati	1	nocturnal	S	248%	early summer	76%
Vernayella noctivago	2	nocturnal	S	252%	winter	74%
Vansonium bushmanicum	9	nocturnal	C	215%	early summer	75%
Pachynotelus albonotatus	71	diurnal	S	190%	aseasonal	
Eurychora sp.	70	nocturnal	C	208%	late summer	53%

04/12/02	wed	20.00	6	2	96	0	0	0	0	0	0	0	
05/12/02	thu	8.00	4	5	96	0	0	0	0	4	31	2	
05/12/02	thu	14.00	2	3	97	0	0	0	0	2	31	6	
05/12/02	thu	20.00	0	0	99	0	0	0	0	0	23	3	
06/12/02	fri	8.00	6.00	5.00	97.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
06/12/02	fri	14.00	1.00	2.00	98.00	0.00	0.00	0.00	0.00	1.00	31.00	5.00	
06/12/02	fri	20.00	2.00	4.00	97.00	0.00	0.00	0.00	0.00	2.00	23.00	2.00	
07/12/02	sat	8.00	1.00	1.00	97.00	0.00	0.00	0.00	0.00	1.00	5.00	3.00	
07/12/02	sat	14.00	1.00	2.00	97.00	0.00	0.00	0.00	0.00	1.00	23.00	2.00	
07/12/02	sat	20.00	0.00	0.00	92.00	2.00	4.00	1.00	4.00	3.00	23.00	5.00	
08/12/02	sun	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	5.00	5.00	
08/12/02	sun	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	3.00	
08/12/02	sun	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	3.00	
09/12/02	mon	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	5.00	2.00	
09/12/02	mon	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	6.00	
09/12/02	mon	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	2.00	
10/12/02	tue	8.00	6.00	5.00	93.00	0.00	0.00	0.00	0.00	6.00	31.00	5.00	
10/12/02	tue	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	3.00	
10/12/02	tue	20.00	2.00	4.00	97.00	0.00	0.00	0.00	0.00	2.00	23.00	6.00	
11/12/02	wed	8.00	6.00	2.00	98.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
11/12/02	wed	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	NE	5.00	
11/12/02	wed	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	5.00	8.00	
12/12/02	thu	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	5.00	3.00	
12/12/02	thu	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	18.00	3.00	
12/12/02	thu	20.00	2.00	5.00	97.00	0.00	0.00	0.00	0.00	2.00	23.00	7.00	
13/12/02	fri	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	2.00	
13/12/02	fri	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	31.00	5.00	
13/12/02	fri	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	4.00	
14/12/02	sat	8.00	8.00	6.00	90.00	0.00	0.00	0.00	0.00	8.00	5.00	2.00	
14/12/02	sat	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	6.00	
14/12/02	sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	6.00	
15/12/02	sun	8.00	7.00	5.00	94.00	0.00	0.00	0.00	0.00	7.00	0.00	0.00	
15/12/02	sun	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	5.00	5.00	
15/12/02	sun	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	5.00	5.00	
16/12/02	mon	8.00	8.00	5.00	90.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
16/12/02	mon	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	SW	2.00	
16/12/02	mon	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00	
17/12/02	tue	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	5.00	5.00	
17/12/02	tue	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	NE	5.00	
17/12/02	tue	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00	
18/12/02	wed	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
18/12/02	wed	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	5.00	5.00	
18/12/02	wed	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	4.00	
19/12/02	thu	8.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
19/12/02	thu	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	5.00	
19/12/02	thu	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	23.00	4.00	
20/12/02	fri	8.00	0.00	0.00	90.00	0.00	0.00	8.00	0.00	0.00	0.00	0.00	
20/12/02	fri	14.00											
20/12/02	fri	20.00											
21/12/02	sat	8.00	8.00	5.00	90.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
21/12/02	sat	14.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
21/12/02	sat	20.00	0.00	0.00	99.00	0.00	0.00	0.00	0.00	0.00	18.00	5.00	