Long-term data show behavioural fog collection adaptations determine Namib Desert beetle abundance

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Long-term (25 yr) measures of weather and populations of the 28 most frequently trapped Namib Desert Tenebrionidae (darkling beetles) revealed a population-sustaining effect of fog for eight species using specialized behavioural mechanisms to collect fog water. During a prolonged (18 yr) low-rainfall interval, populations of these fog-collecting species maintained more of their relative abundance than all but one species that does not collect fog. Fog-collecting adaptations include complete change in diel activity period, sand trench and sand parapet building, and fog basking. All eight fog-collecting species persisted during the dry period, whereas 17 of the 19 species lacking fog-collecting adaptations disappeared or declined to less than 1% of their mean abundance. Populations of two species reported to collect fog facultatively during their usual diel rhythm declined as rapidly as species lacking fog-collecting adaptations. These demographic comparisons of fog-collecting species and species that do not do so depended upon monitoring highly variable population fluctuations under the particular climatic events that occurred during this study. The population consequences of adaptations to collecting fog water could not have been identified by any study lasting less than 17 years.

Introduction

Here we relate differences in long-term population changes by diverse Namib Desert Tenebrionidae to an array of behavioural adaptations for collecting fog water. During a 25-year study of abundance of these flightless darkling beetles begun at the time of heavy rainfall in 1976 and 1978, there occurred an extended interval with little or no rainfall. Initially abundant species declined to low numbers or disappeared. But eight species with specialized behavioural adaptations to collecting fog declined less rapidly than all but one species lacking comparable behaviour patterns. The conclusion that behaviour determines persistence of populations could not have been made without data on the abundance of multiple species collected for at least 17 years. Riverine species with access to a persistent supply of fresh vegetation also resisted population decline.

Namib Desert Tenebrionidae are extraordinarily species rich and diverse in their morphological,[1] behavioural[2–4] ecological[5] and physiological[6] adaptations to their desert environment. Mechanisms used by Namib Desert tenebrionid beetles include the ability of adults of some species to secure fog water by becoming active at night and on cool early mornings when they would ordinarily be buried and inactive. To secure fog water, they collect it on their dorsal surface (fog basking[2,7]), extract it from wet sand (directly or by forming ridges to enhance fog water precipitation[3,4]), or suck moisture from fog-wetted detritus and vegetation.[8,9]

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Materials and methods

This study was conducted at Gobabeb, 56 km inland from the Atlantic coast of Namibia. Median annual rainfall was 12.2 mm. This outpost, at the inland edge of the fog system,[10] is better positioned to measure year-to-year changes in fog frequency and deposition than are stations along the almost continuously foggy coast. Fog deposition has been recorded daily since 1966 with cylindrical wire mesh and a 1-m^2 flat plastic standard fog screen collector.[11]

We monitored tenebrionid populations with pitfall traps beginning in 1976. We established pit traps in five habitats:[12] a gravel plain (GP), three dune habitats [an interdune plain (IP), a dune slope (DS) and a dune slipface (SF)], and in the Kuiseb River riparian corridor (RE) separating the dune fields from the gravel plain. Beetles were identified to species in the field or laboratory, then released near the capture site. Monitoring was continuous in the relatively stable substrates of RE, GP and IP, but intermittent in the mobile DS and SF habitats. Traps were maintained at their original location throughout the study. The slipface disappeared in 1998, affecting subsequent SF data. In the slipface, avalanching sand often filled traps, necessitating hourly processing. The contents of traps were counted and the traps emptied twice daily on the DS, less frequently at IP and GP. Pit traps in the RE were maintained for 19 years including the four comparison years, 1992–95.

We analysed data for 27 focal species from desert habitats, defined as each species captured during the first three study years and at least 120 times during 25 years. There were five to 11 focal species per habitat. Some species were sufficiently abundant to qualify as focal species in two or more habitats but we confine our analysis here to the demographic response of species in the habitat where they were most common. These desert species were compared with 12 species from the ephemeral Kuiseb River.

Results

Rainfall and populations

Most of the focal species (N = 23 of 27) peaked in abundance 1–3 yr after major rainfall events (>100 mm per annum), then steadily declined during ensuing years (Fig. 1), reaching low and often undetectable levels over intervals as long as 12 years. Other species, too infrequently captured to be included in the focal group, reappeared only after an absence of up to 17 years. Effective rainfall (>10 mm per week), that stimulated an increase in primary productivity, was infrequent and occurred in only nine of the 25 study years. After the heavy rainfall events of the 1970s, there was an 18-year interval between heavy rains, coinciding with an interval of more frequent and more moisture-laden fog (Fig. 1).

Fog

Fog was experienced in 88% of 324 months between 1966 and 2000. Fog deposition differed relatively little between consecutive years, but changed markedly over the course of decades. It was relatively sparse between 1966 and 1978 (annual mean = 27.0 l/m^2 of vertical fog screen), intermediate between 1979 and 1988 (38.5 l/m^2), then high between 1989 and 1997 (55.8 l/m^2), followed by a decline. The maximum fog frequency and deposition began 11 yr after the second of two major rainfall events in

Table 1. Population response of 39 Namib Desert Tenebrionidae arranged in order of population resistance to prolonged drought. Activity regularity is compared with activity pattern on days lacking fog.

Desert habitat	Fog-collecting mechanism	Change in diel rhythm?	Species	Tribe	Mean *N*/yr* 1976–2000	%*N*/yr 1992–1995
SF	Sand ridge	Yes	*Zophosis fairmairei*	Zophosini	166.1	57.2
SF	Nocturnal	Yes	*Onymacris laeviceps*	Adesmiini	63.2	26.9
DS	Sand ridge	Yes	*Zophosis hamiltonuli*	Zophosini	26.9	24.1
GP	Nocturnal	Yes	*Zophosis amabilis*	Zophosini	94.1	19.1
IP	0	No	*Cauricara phalangium*	Adesmiini	2133	17.7
SF	Sand trench	Yes	*Lepidochora discoidalis*	Eurychorini	627	12.8
SF	Fog bask	Yes	*Onymacris unguicularis*	Adesmiini	28.7	11.6
SF	Sand trench	Yes	*Lepidochora kahani*	Eurychorini	19.5	6.8
DS	Sand trench	Yes	*Lepidochora porti*	Eurychorini	15.6	6.4
GP	0	No	*Cauricara velox*	Adesmiini	67.0	2.2
IP	0	No	*Pachynotelus albonotatus*	Cryptochilini	23.4	0.2
GP	Facultative	No	*Zophosis moralesi*	Zophosini	491	0.1
DS	0	No	*Zophosis hereroensis*	Zophosini	174	0.1
IP	Facultative	No	*Onymacris plana*	Adesmiini	432	0.1
DS	0	No	*Vernayella noctivago*	Caenocrypticini	5.4	0.1
IP	0	No	*Vansonium bushmanicum*	Calognathini	10.0	0.1
SF	0	No	*Vernayella delabati*	Caenocrypticini	11.8	0.0
GP	0	No	*Eurychora* sp. I	Eurychorini	8.4	0.0
GP	0	No	*Metriopus depressus*	Adesmiini	111	0.0
GP	0	No	*Stips dohrni*	Eurychorini	4.8	0.0
DS	0	No	*Namibomodes serrimargo*	Molurini	5.7	0.0
GP	0	No	*Parastizopus armaticeps*	Opatrini	8.3	0.0
IP	0	No	*Carchares macer*	Scaurini	10.8	0.0
GP	0	No	*Rhammatodes tagenestoides*	Tentyriini	42.0	0.0
GP	0	No	*Zophosis damarina*	Zophosini	46.2	0.0
GP	0	No	*Zophosis devexa*	Zophosini	41.2	0.0
GP	0	No	*Physosterna cribripes*	Adesmiini	65.4	0.0
Riverine habitat					Mean *N* 1982–2000	
RE	0	No	*Pachynotelus lineatus*	Cryptochilini	55.1	144
RE	0	No	*Gonopus tibialis*	Platynotini	1692	114
RE	0	No	*Rammatodes subcostatus*	Tentyriini	746.4	110
RE	0	No	*Gonocephalum* sp.	Opatrini	161.4	94.8
RE	0	No	*Eurychora* sp. II	Eurychorini	105.7	82.3
RE	0	No	*Physadesmia globosa*	Adesmiini	13 240	75.1
RE	0	No	*Namibomodes muscicollis*	Molurini	118.8	58.5
RE	0	No	*Zophosis orbicularis*	Zophosini	296	58.0
RE	0	No	*Stenocara gracilipes*	Adesmiini	298	52.6
RE	0	No	*Epiphysa arenicola*	Adesmiini	35.3	31.9
RE	0	No	*Stips stali*	Eurychorini	406	23.9
RE	0	No	*Onymacris rugatipennis*	Adesmiini	1146	20.2

*N is annual pit trap captures per habitat per year for all years excluding the test interval, 1992–95.
SF, slipface; DS, dune slope; GP, gravel plain; IP interdune plain.

1976 and 1978 (Fig. 1). During the latter part of the peak fog period, 1992–95, all indices related to rainfall were low, allowing us to separate possible effects of fog from rainfall upon beetle populations.

Populations of fog collectors versus other species

Ten species are known to respond behaviourally to fog in nature[8] (Table 1). Two of these species, *Onymacris plana* and *Zophosis moralesi,* are facultative responders. They obtain fog water only when heavy late morning fog events wet the soil or the vegetation that they encounter during their normal activity period. The eight other species are specialists, emerging at night and using fog basking or trench and ridge building to collect water. Three of these specialists are *Lepidochora* species, one (*L. discoidalis*) crepuscular, the two others nocturnal. All three respond with the other fog-collecting species to predawn fog events. For the years 1992–95, populations of these eight specialized fog-collecting species are compared with the 19 species that did not collect or facultatively collect fog (Table 1). Comparisons are limited to the habitat where each species was most abundant. The eight specialized fog-collecting species maintained 20.6 ± 16.6 (s.d.)% of their abundance compared with 1.08 ± 4.05% for the other 19 species (Mann-Whitney U test, $Z = 3.97$, $P = 0.00007$). Fifteen of the 19 species not specialized for fog collection declined from as few as two to zero captured individuals between 1992 and 1995. None of the eight fog-collecting species did so ($\chi^2 = 5.49$, d.f. = 1, $P = 0.019$).

In the riverine habitat, a persistent fall of flowers from *Acacia erioloba, Faidherbia albida* and other fresh vegetation less dependent upon climate and more on moist riparian soils, supported a high biomass of tenebrionids. Although not responsive to fog, the 12 focal species there maintained 77.4 ± 44.2 (s.d.)% of their long-term abundance, significantly greater than the fog-dependent species dwelling in the desert dune habitat ($Z = 3.09$, $P = 0.002$).

Discussion

On monthly and annual time scales, fog was the most predictable water source for Namib Desert organisms[13] (Fig. 1). Although fog did not trigger population increases, tenebrionid beetles that collected fog could sustain higher population densities between rainfalls. For tenebrionids, moisture availability may be a crucial factor affecting reproduction[14–16] and offspring survival. Larvae of some species can extract water from satu-

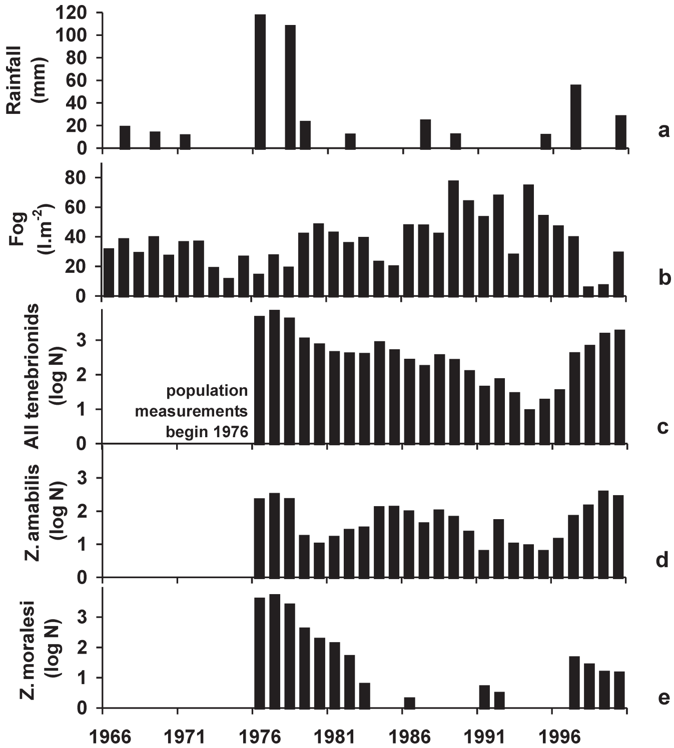

Fig. 1. Annual fog and rainfall between 1966 and 2000 and abundance of all beetle species and two selected species between 1976 and 2000. **a**, Effective rainfall; **b**, fog deposition; **c**, abundance occurrence in pit traps by year for all species inhabiting the same Namib Desert gravel plains habitat; and **d** a species, *Zophosis amabilis*, responding behaviourally and demographically to fog; or **e** not so responding, *Z. moralesi*.

rated atmospheres equivalent to foggy conditions.[17,18] When fog is prevented from reaching these larvae, they die or develop more slowly.[16]

Such observations have previously led to the suggestion that fog-collecting behaviour will ultimately sustain beetle populations,[4,6] and the current study demonstrates that it does so. Half of the species for which fog collection was important are habitat specialists occurring on the slipface, where the surface layer of sand is highly mobile and usually dry,[19] so that there is little available moisture other than that from the atmosphere. There is more subterranean moisture in the relatively stable dune slope,[19] but even there two species collected fog water (Fig. 1). Only the riverine habitat had permanent water available in its alluvial aquifer.

Many animals in the Namib can tap fog water (reviewed in ref. 20). In some cases the mechanisms are complex, such as fog basking; otherwise diurnal tenebrionid beetles emerge from subsurface refugia at night and laboriously climb dunes where they stand head downward to collect fog.[2] In a cladistic analysis, Ward and Seely[7] concluded that fog basking evolved independently in the two species that do so, the white-bodied *Onymacris bicolor* and the all-black *O. unguicularis.* Parker and Lawrence[21] illustrated a paper concerned with fog-collecting mechanisms of Namib Desert beetles with a photograph of *Physosterna cribripes* said, in apparent error, to be a *Stenocara* species[9] and to be fog basking. In the current long-term study, the *P. cribripes* population monitored by us fell from a high of 856 individuals to a singleton recorded during the four-year low of 1992–95. During 40 years of field observations in *P. cribripes* habitat, we have not encountered this species at night or on foggy mornings. We therefore include *P. cribripes* here as a non-fog-behaving and non-fog-responding species.

In a hyper-arid desert, where substantial vegetation-producing events are irregular and often widely separated, long-term comparative studies may be the only way to quantify the population consequences of some adaptations to desertic conditions. For the population responses to fog reported here, a minimum 17-year record for 33 species was needed to identify the relationship of fog-collecting behaviour to population responses. To do so, we monitored 57 tenebrionid species and selected only those sufficiently common to meet our minimum abundance criterion. This demonstrates the value of monitoring populations over long periods of time.

This project is part of the Environmental Observatories Network Programme of the Gobabeb Training and Research Centre, Namibia. We thank Cliff Crawford and Gary Polis for assistance in developing monitoring methods and Phoebe Barnard, Jessica Green and John Pallett for critically reading the manuscript. The Ministry of Environment and Tourism granted permission to conduct research in the Namib-Naukluft Park.

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