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Predictability of two moisture sources in the Namib Desert

R.D. Pietruszka and M.K. Seely

Desert Ecological Research Unit, P.O. Box 1592, Swakopmund, 9000, Namibia.

We use autocorrelation analyses to examine the temporal predictability of two moisture sources in the Namib Desert, fog-water precipitation and rainfall. Although longitudinal gradients in the predictability of both sources were apparent, fog was more predictable than rainfall. Because of the greater predictability and lower variability of fog-water precipitation, it is a more reliable moisture source. This may have been a major factor in the evolution of the unusual biota of this desert.

Ons pas outokorrelasieanalises toe om die tydvoorspelbaarheid van twee vogbronne in die Namibwoestyn, naamlik die presipitering van water uit mistigheid en die reënval, toe ondersoek. Hoewel daar klaarblyklik lengtegradiënte by die voorspelbaarheid van albei bronne was, was mistigheid voorspelbaar as reënval. Vanweë die beter voorspelbaarheid en kleiner veranderlikheid van die presipitering van mistigheidsvog, is dit 'n betroubaarder vogbron. Dit kon 'n belangrike faktor by die evolusie van die woestyn se ongewone biota gewees het.

Compared to other terrestrial habitats, deserts present organisms with harsh and unpredictable conditions. Moisture is often acknowledged as the 'master limiting factor'[1] to biota inhabiting arid regions owing to its comparative scarcity.[1-6] Yet, the timing and reliability of moisture availability are at least as important to desert organisms as the restriction of absolute quantities of water. When water occurs predictably in time, as through predictable rainfall events, natural selection may result in some degree of periodic environmental tracking by organisms. This is particularly likely where the predictability of moisture inputs is great relative to generation length,[7-9] thereby ameliorating environmental conditions. The precision of such tracking, however, may decline rapidly as this predictability decreases, resulting in an increased importance of plasticity in the responses of organisms (= opportunism[10,11]), a pattern often observed among desert inhabitants.[4]

Despite the temporally and spatially uneven moisture regimes that characterize deserts,[6] degrees of uncertainty in moisture inputs can be discerned within desert systems.[12] In an autocorrelation analysis of precipitation events in North American deserts, Pianka[1] found considerable variation in the degree of stochasticity in rainfall among the Great Basin, Sonoran, and Mojave deserts. Interestingly, the least predictable rainfall regime (Great Basin) in that analysis also exhibited the lowest long-term annual variability in precipitation, while the reverse was true of the most predictable rainfall pattern (Mojave).

In contrast to North American deserts, the Namib Desert is considerably more arid, averaging only about 10 – 30% of the annual rainfall seen in the North American system. Moreover, in the central Namib water from two sources, rain and fog-water precipitation, is extensively utilized by the desert biota,[12-20] suggesting that one or both of these moisture sources may be predictable enough to be tracked. Our purpose here is to examine the patterns of rainfall and fog-water precipitation along a longitudinal gradient in the central Namib and in doing so to gain some insight into the degree of predictability of these sources of water.

Methods and materials

Data on rainfall and fog-water precipitation were gathered from three locations within the central Namib (Fig. 1). At this latitude fog extends approximately 100 km inland. Fog-water precipitation is not measured at Walvis Bay, and only rarely occurs as far inland as Ganab.[21] Thus, the three sites examined were all well within the fog belt, excluding its westernmost and easternmost parts. Fog-water precipitation data were taken from Lancaster *et al.*,[21] and from more recent records. These data were obtained from autographic rain gauges fitted with cylindrical wire mesh screens. The record lengths of monthly fog-water precipitation for the three sites were as follows: Rooibank, 192 months; Swartbank, 156 months; Gobabeb, 216 months. Where monthly total values were missing from the record, mean monthly values were substituted for use in subsequent calculations. For Rooibank a total of 17 such estimates were made, while 12 were made for Swartbank and 19 for Gobabeb. In no case was the total fog-water for a given month estimated more than three times during the entire record.

The three sites from which rainfall data were obtained were distributed almost equidistant across the desert (Fig. 1). Rainfall data for Walvis Bay (456-month record) were obtained from the long-term records of the Weather Bureau, Department of Transport. Data for Gobabeb (252-month record) and Ganab (180-month record) were recorded on autographic gauges. Missing monthly totals for Gobabeb (19) were taken from Weather Bureau records for that locality. Missing values for Ganab (12) were extrapolated from values in Nel[22] or from values recorded at Zebra Pan, 45 km to the south.

To investigate the predictability (in an ecological rather than a climatological sense) of these two moisture sources, autocorrelations were calculated from the monthly totals of fog-water and rainfall from each of the recording sites.[1] Lag periods (constant time intervals between sample points) of 0 – 36 months were used in the analyses, allowing the calculation of autocorrelations for a series of increasingly more distant points in time. For each autocorrelation series, 1.96 sigma bounds were calculated as $1.96n^{-1}(n-h)^{1/2}$, where n represents the number of months in the sample and h is the lag period.[28] These bounds allow a distinction to be made between a real time series and a sequence of random events. Thus, if an original time series were really a sequence of uncorrelated random variables, then only about 5% of the estimated autocorrelations would be expected to fall outside the 1.96 sigma bounds (i.e. the probability of difference from random, P_d, = .05).[23]

Results and discussion

In the central Namib, rain occurs mainly in the form of convective summer storms[24] and decreases towards the coast. Effective rainfall,[17] therefore, occurs mainly near the eastern edge of the desert, whereas fog-water precipitation is more abundant in the west.[21,25]

Advective fog originates over the Benguela Current and cold-

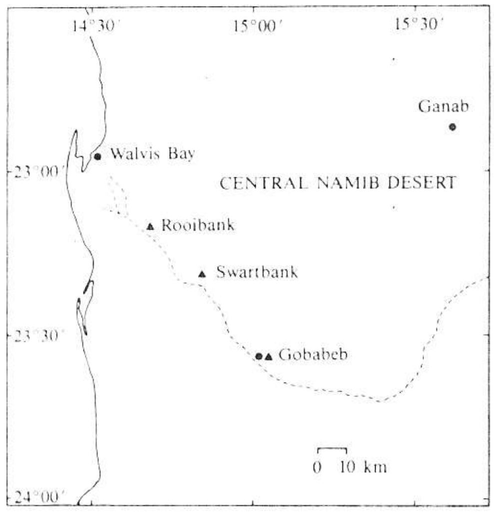

Fig. 1. Sites in the central Namib Desert from which fog-water precipitation records (▲) and rainfall records (●) were used.

water upwelling along the coast,[26] and the number of fog-days is greatest near the coast (e.g. at Rooibank[21]). The main fog bank, however, develops at an elevation of 300 – 600 m[12,21] at the base of the inversion layer,[27] resulting in greater fog-water precipitation inland (e.g. at Swartbank). Further inland, Gobabeb lies within the Kuiseb river valley and does not receive as much fog-water as do other sites located the same distance from the coast but at higher elevations.[21]

Mean monthly fog-water totals (Fig. 2) show that fog may occur during any month of the year and that the amount of precipitation from fog may be relatively high at some locations. Inspection of minimum and maximum annual totals for the three sites over the periods of record (Rooibank, 49 – 158 mm; Swartbank, 88 – 271 mm; Gobabeb, 8 – 48 mm) indicates that the amount of moisture received from fog-water precipitation varies only by a factor of approximately 3 to 6 at the three sites.

In contrast, rainfall is very limited at all recording sites throughout most of the year (Fig. 3). Moreover, the range of annual rainfall totals over the period of record (Walvis Bay, 0 – 80 mm; Gobabeb, 4 – 127 mm; Ganab, 9 – 374 mm) shows extreme variability in this form of moisture input.

The above summaries suggest that fog-water precipitation, in particular, may occur fairly predictably through time. Autocorrelation analysis of these data (Fig. 4) confirms that this is the case. Autocorrelations are positive when a precipitation value, x, is positively correlated with x at an earlier time (= lag). Values near zero indicate independence of any two x-values and thus also indicate unpredictability. Among the three recording stations, Rooibank (Fig. 4*a*) exhibited the most predictable pattern, with an annual cycle of negative and positive correlations at six-month intervals that continued to show similar amplitude and periodicity throughout the maximum lag period. Thus, if a certain amount of fog-water precipitation occurs in a given month, it is probable that a similar amount will not be available 6 months hence but will again be present in 12 months. Over the maximum lag period more than 55% of autocorrelations lie outside the 1.96 sigma bounds and it is unlikely that the pattern reflects a random series of events (probability of difference from random, $P_d > .50$). The great predictability of fog-water at Rooibank probably results from the proximity of this site to the coast.

Farther inland, at Swartbank, the mean annual amount of fog-water precipitation is more than twice that at Rooibank, yet the predictability of receiving it is not as great (Fig. 4*b*), although it is still unlikely to be a reflection of a random series ($P_d > .20$). As with Rooibank, positive correlation follows roughly a 12-month periodicity, although at this site this pattern disappears when the lag period is increased to 36 months. The location of this site, 11 km farther inland and 240 m higher than Rooibank, most likely results in its being subjected less to the maritime climate and influenced more by continental climatic elements, resulting in a less predictable fog regime.

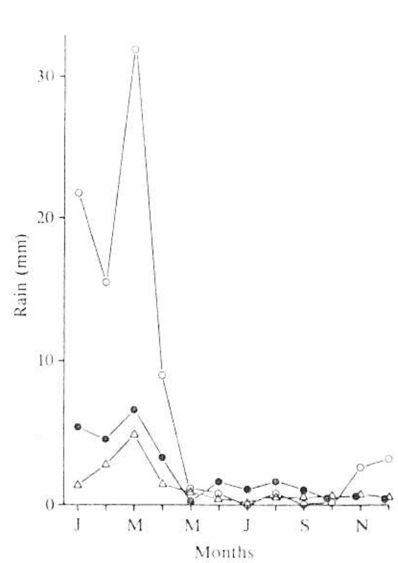

Fig. 3. Mean monthly rainfall totals for Walvis Bay (△), Gobabeb (●) and Ganab (○).

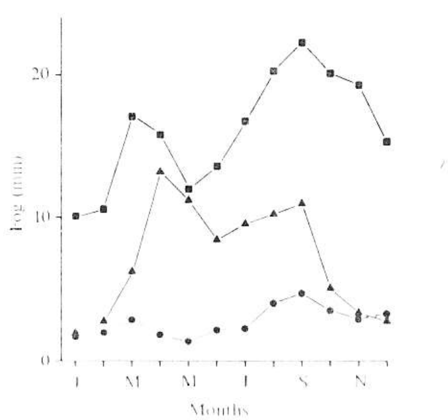

Fig. 2. Mean monthly fog-water precipitation totals for Rooibank (▲), Swartbank (■), and Gobabeb (●).

Average annual fog-water precipitation at Gobabeb is considerably less than at either of the sites nearer the coast. The predictability of fog at this location (Fig. 4*c*), however, is quite similar to that at Swartbank and is distinctly different from that expected for a random series ($P_d > .25$). As with Swartbank the probability of fog-water precipitation is generally positive at lags of 1 – 3 months and 11 – 13 months. Unlike Rooibank, neither of the more inland sites exhibited any strong negative autocorrelations, suggesting that at these sites there is seldom a predictable decrease in the amount of fog-water precipitation.

When examined in the same way, however, rainfall was much less predictable. In the east, Ganab exhibited the clearest and most regular pattern (Fig. 5*a*). There the strongest positive predictability was apparent at 1 – 2 months lag and again at 23 – 26 months lag with somewhat lower positive autocorrelations at lags of 11 – 13 months and 34 months. Overall, the pattern of precipitation is different from that expected for random series ($P_d > .19$) and is quite similar to that found for the North American Mo-

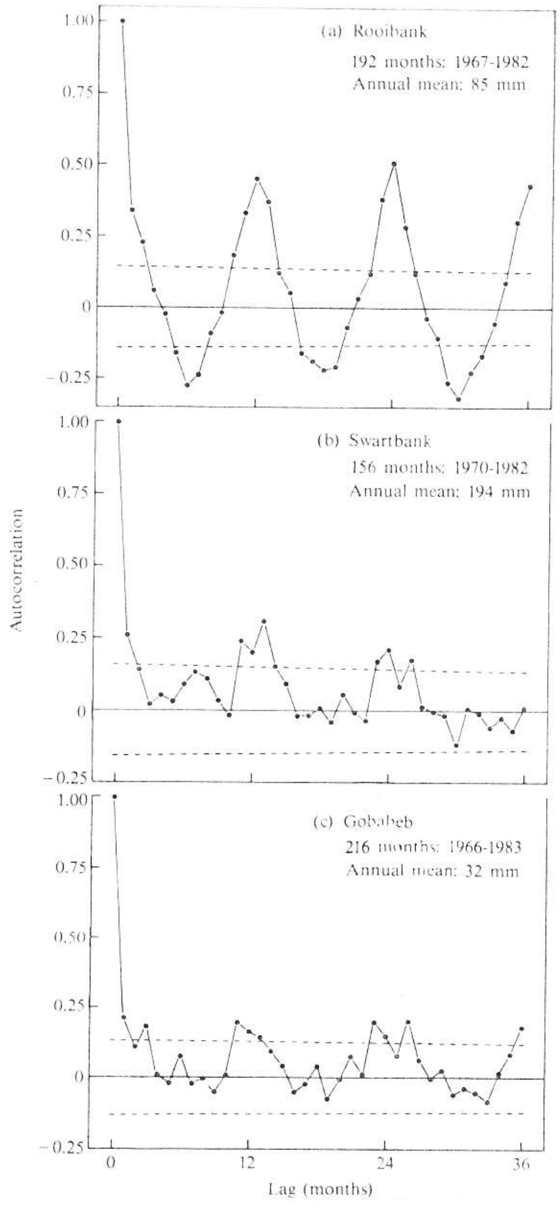

Fig. 4. Autocorrelation of monthly fog-water precipitation for (a) Rooibank, (b) Swartbank, and (c) Gobabeb. Lag periods are from 0 to 36 months. 1.96 sigma bounds are indicated as broken lines. See text for interpretation.

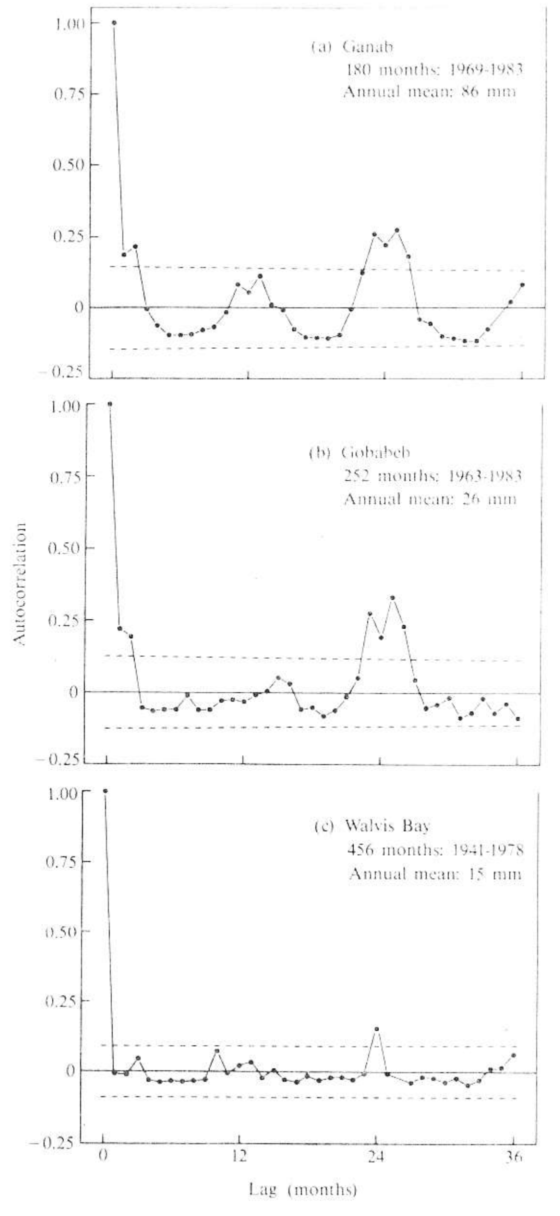

Fig. 5. Autocorrelation of monthly rainfall for (a) Ganab, (b) Gobabeb, and (c) Walvis Bay. Lag periods are from 0 to 36 months. 1.96 sigma bounds are indicated as broken lines.

jave Desert.[1] The pattern seen at Ganab reflects rather clearly the summer rains that typify the eastern part of the Namib.

To the west, Gobabeb exhibits a pattern of autocorrelations similar to that seen at Ganab ($P_d > .16$), although it is clearly less regular (Fig. 5*b*). On an annual basis, precipitation at Gobabeb is actually rather unpredictable for lags greater than two months. As many of the major rainfall events in the central Namib may be experienced by both sites,[24] the similarity in their patterns of predictability at long lag periods (e.g. 23 – 26 months) may be derived from more regional events.

Autocorrelation of monthly rainfall totals at Walvis Bay yielded a pattern substantially less predictable than for either of the two inland sites (Fig. 5*c*). Indeed, the only similarity between the coastal and inland locations was the positive peak at 24 months lag, strengthening the interpretation that widespread regional events may be involved in these autocorrelations. Overall, the pattern seen for this location was not distinguishable from that expected by a series of random events ($P_d < .03$).

The above analyses illustrate two separate gradients in the predictability of precipitation occurring in the central Namib. A rather marked decline in the predictability of rainfall is apparent from east to west. This is consistent with the convective origin of rainfall in the Namib, which is generally prevented toward the coast by a layer of cold surface air.[25] Moreoever, it suggests that rainfall may not be sufficiently predictable over most of the central Namib to be tracked on a relatively short-term basis (i.e. within a year), although tracking by some organisms could still occur at longer lag periods. Fog-water precipitation, on the other hand, follows a gradient of decreasing predictability from coastal areas inland. This gradient is not as steep as that for rainfall and appears to depend more on factors that determine the inland penetration of fog rather than the degree of exposure of a site to the fog bank.

When the two water sources are compared overall, predictability of fog-water precipitation is greater than that from rainfall. Moreover, in contrast to Pianka's[1] findings for rainfall in North American deserts, the more predictable fog regime also shows lower annual variability (coefficients of variation for fog: Rooibank, 29%; Swartbank, 29%; Gobabeb, 36%; coefficients of variation for rain: Ganab, 102%; Gobabeb, 123%; Walvis

Bay, 106%). The comparatively greater degree of predictability and lesser degree of variability of fog, even at sites toward the inland limit of penetration, results in greater reliability of fog as a source of moisture.

A number of plants and animals of the Namib take advantage of this somewhat unusual source of moisture, at least as a supplementary water source. The dune succulent *Trianthema hereroensis*, for example, absorbs moisture through its aerial parts,[16] whereas the perennial grass *Stipagrostis sabulicola* produces an extensive network of roots immediately beneath the sand surface to trap fog-water.[19] A variety of tenebrionid beetles[12,14,15,18,20] and other invertebrates[18] are behaviourally adapted to make use of fog. Particularly striking among these adaptations are the fog-basking behaviour of *Onymacris unguicularis*[14] and the trench-constructing behaviour of *Lepidochora* species through which these beetles trap fog.[15] Thus, although a single occurrence of fog-water precipitation may amount to far less moisture being available for an organism than would be from a single cloudburst,[21] it is probably the realibility of fog-water precipitation that has contributed to the evolution of the unusual biota of the Namib Desert.[17,29]

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1. Pianka E.R. (1967). On lizard species diversity: North American flatland deserts. *Ecology* **48**, 334 – 351.
2. Noy-Meir I. (1973). Desert ecosystems: environment and producers. *Ann. Rev. Ecol. Syst.* **4**, 25 – 51.
3. Noy-Meir I. (1974). Desert ecosystems: higher trophic levels. *Ann. Rev. Ecol. Syst.* **5**, 194 – 214.
4. Seely M.K. and Louw G.N. (1980). First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. *J. Arid Environ.* **3**, 25 – 54.
5. Hadley N.F. and Szarek S.R. (1981). Productivity of desert ecosystems. *BioScience* **31**, 747 – 753.
6. Crawford C.S. and Gosz J.R. (1982). Desert ecosystems: their resources in space and time. *Environmental Conservation* **9**, 181 – 195.
7. Levins R. (1968). *Evolution in Changing Environments.* Princeton University Press, Princeton.
8. Southwood T.R.E. (1976). Bionomic strategies and population parameters. In *Theoretical Ecology. Principles and Applications*, edit. R.M. May, pp. 26 – 48. W.B. Saunders, Phildelphia.
9. Southwood T.R.E. (1977). Habitat, the temple for ecological strategies? *J. Anim. Ecol.* **46**, 337 – 365.
10. Hickman J.C. (1975). Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadense* (Polygonaceae). *J. Ecol.* **63**, 689 – 701.
11. Wiens J.A. (1976). Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* **7**, 81 – 120.
12. Louw G.N. and Seely M.K. (1982). *Ecology of Desert Organisms.* Longman, London.
13. Louw G.N. (1972). The role of advective fog in the water economy of certain Namib Desert animals. *Symp. Zool. Soc. Lond.* No. 31, 297 – 314.
14. Hamilton III W.J. and Seely M.K. (1976). Fog basking by the Namib desert beetle, *Onymacris unguicularis*. *Nature* **262**, 284 – 285.
15. Seely M.K. and Hamilton III W.J. (1976). Fog catchment sand trenches constructed by tenebrionid beetles, *Lepidochora*, from the Namib Desert. *Science* **193**, 484 – 486.
16. Seely M.K., de Vos M.P. and Louw G.N. (1977). Fog imbibition, satellite fauna and unusual leaf structure in a Namib Desert dune plant *Trianthema hereroensis*. *S. Afr. J. Sci.* **73**, 169 – 172.
17. Seely M.K. (1978). Grassland productivity: the desert end of the curve. *S. Afr. J. Sci.* **74**, 295 – 297.
18. Seely M.K. (1979). Irregular fog as a water source for desert dune beetles. *Oecologia (Berl.)* **42**, 213 – 227.
19. Louw G.N. and Seely M.K. (1980). Exploitation of fog water by a perennial Namib dune grass, *Stipagrostis sabulicola*. *S. Afr. J. Sci.* **76**, 38 – 39.
20. Seely M.K., Lewis C.K., O'Brien K.A. and Suttle A.E. (1983). Fog response of tenebrionid beetles in the Namib Desert. *J. Arid Environ.* **6**, 135 – 143.
21. Lancaster J., Lancaster N. and Seely M.K. (1984). Climate of the central Namib Desert. *Madoqua* **14**, 5 – 61.
22. Nel P.S. (1983). *Monitering van die beskikbaarheid, gehalte en benutting van voer op die gruisvlaktes van die kuiseb-studiegebied.* MSc thesis. Universiteit van die Oranje-Vrystaat, Bloemfontein.
23. Fuller W.A. (1976). *Introduction to Statistical Time Series.* John Wiley, New York.
24. Sharon D. (1981). The distribution in space of local rainfall in the Namib Desert. *J. Climatology* **1**, 69 – 75.
25. Besler H. (1972). Klimaverhältnisse und klimageomorphologische Zonierung der zentralen Namib (Sudwestafrika). *Stuttgarter Geogr. Stud.* **83**, 1 – 209.
26. Anon. (1944). *Weather on the coasts of Southern Africa.* Vol. 11, Part 1. Meteorological Services of the Royal Navy and South African Air Force, Cape Town.
27. Taljaard J.J. and Schumann T.E.W. (1940). Upper air temperatures and humidities at Walvis Bay, South West Africa. *Bull. Am. Meteorol. Soc.* **21**, 293 – 296.
28. Logan R.F. (1968). Causes, climates, and distributions of deserts. In *Desert Biology*, edit. G.W. Brown, pp. 21 – 50. Academic Press, New York.
29. Koch C. (1962). The Tenebrionidae of southern Africa XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Ann. Transv. Mus.* **24**, 61 – 106.