# First Approximation of the Ecophysiology of Fog and Dew – A Tribute to Gideon Louw



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**ABSTRACT**

Since his first visit to the Gobabeb Training & Research Centre in 1966, Professor Gideon Louw was interested in how Namib Desert fog and dew affected survival of desert organisms. This prominent South African ecophysiologist subsequently made substantial contributions to this field. In March 2004, Professor Louw passed away, and it is appropriate to examine how he broadened our understanding of fog and dew in desert ecosystems. Louw reported extraordinary behaviour that enabled Namib animals to obtain water from fog; for instance, the sidewinder adder, *Bitis peringueyi*, drinks fog water that has condensed on its cold body. His extensive work on water relations and economy, which includes osmoregulation in desert plants and animals, such as grass, beetles, and springbok, established a foundation that inspired numerous studies by colleagues and students. Louw's important reviews on ecophysiology in which he examined observations concerning the importance of desert fog and dew in a wider context stand as milestones.

## 1. INTRODUCTION

In hyperarid areas such as the Namib Desert the occurrence of fog and dew plays an important role in the water economy of many desert organisms.

This fact was known, particularly through the works of Walter (1936) and Koch (1961), by the time that Louw first visited the Gobabeb Training & Research Centre in the Namib Desert in 1966. Louw (1971, 1972) soon recognised that ecophysiological mechanisms were a key towards understanding the relationship between atmospheric moisture and desert organisms. Extensive contributions of this doyen of desert ecophysiology range from water, energy, and salt balance, to thermal biology, conjunctively in terms of physiology, behaviour and ecology. He inspired a generation of students and colleagues to elucidate these mechanisms and their consequences, and later reviewed some of these insights (Louw & Seely 1982; Louw, 1990, 1993).

In the current paper we present examples of Gideon Louw's observations and perspectives on atmospheric water uptake, relevant to this conference theme. We also indicate how this knowledge has been used and further developed. Here we pay tribute to the late Professor Gideon Nel Louw, of the University of Stellenbosch and later University of Cape Town, who, for many years, actively served as Board Member of the Gobabeb Training & Research Centre. Gideon Louw died in March 2004.

## 2. ATMOSPHERIC MOISTURE SOURCES

### 2.1 Rain

The Namib Desert annually receives less than 50 mm of rainfall, and in its western half generally between 0-12 mm. Although rain water is rarely available on the surface, the effects of rain are extremely important for many life forms (Seely & Louw, 1980). After rainfall, plant biomass increases by an order of magnitude and then gradually declines over the course of the following dry years. Louw (1972) emphasised that the ability to secure atmospheric moisture during the long periods between rainfalls is a key for survival of many Namib organisms.

### 2.2 Fog

Low stratocumulus clouds frequently enter the western part of the Namib Desert from the Atlantic Ocean (Lancaster *et al.*, 1984) and deposit 0.1-1.0 $l.m^{-2}.day^{-1}$ of fog water at particular sites (Henschel *et al.*, 1998). This water is of low salt content (Shanyengana 2002) and its low osmolality of 14-38 m-osmole facilitates drinking (Louw, 1972). Fog water thus represents a relatively predictable, though temporary, source of free water for biota (Louw, 1971; Seely, 1979; Shanyengana 2002).

### 2.3 Humidity & Dew

The prevailing winds for most of the year are relatively cool SW-NW sea breezes that bring moist air into this area and reach saturation during at least some days of each month of the year (Lancaster *et al.*, 1984). This moisture is absorbed by or condenses on surfaces during cool hours (Stone, 1957) and vapour pressure facilitates its penetration into the soil during hot hours (Seely & Mitchell, 1987). Moisture conditions are therefore favourable for small animals on the surface by night and in burrows by day (Louw, 1993).

## 3. ATMOSPHERIC WATER ACQUISITION

### 3.1 Location in Damp Desert Micro-habitats

Moisture penetrates and lingers in sheltered micro-habitats under stones. Louw (1972) described how fog water deposition and dew condensation on stones trickles down the sides to below the stones where it supports the growth of Fensteralgen (Rumrich *et al.*, 1989) and of a small community of invertebrates and micro-organisms. This micro-environment is even moist enough and has sufficient algal food to support snails *Xerocerastus minutus* (Hodgson *et al.*, 1994).

### 3.2 Drinking from Wet Surfaces

Louw & Holm (1971) noted the inability of southern slipface lizards, *Meroles anchietae*, to maintain condition solely on dry seeds alone, their normal diet. They recorded that these lizards drink water from wet surfaces and store it in an abdominal bladder. They concluded that the occurrence of fog explains the survival of these lizards. Drinking of water drops from wet sand or vegetation has since been observed for many small animals (Seely *et al.* 1998) such as beetles (Seely, 1979), scorpions (Polis & Seely, 1990), and termites (Grube & Rudolph, 1995). Tenebrionid beetles, *Lepidochora* spp., take this one step further and construct trenches on the dune surface that enhance the amount of fog water collected (Seely & Hamilton, 1976). Although water imbibition has often been demonstrated (either gravimetrically or using tritiated water), the mechanism of drinking water from the sand is poorly understood (Nicolson, 1990).

Plants can also absorb fog water from the sand surface. Using tritiated water, Louw and Seely (1980) demonstrated that roots of the spiny dune grass *Stipagrostis sabulicola* took up water sprayed thinly on the dune surface adjacent to the plants (akin to fog), and transported this water up into the stem and leaves.

### 3.3 Consumption of Moist Food

The moisture content of grass increases corresponding to air humidity and can reach 27% at a relative humidity of 90% (Louw, 1972; Fig. 1). By feeding during cool, moist hours, particularly during fog or dew, animals as large as ostrich *Struthio camelus* (Louw, 1972) and springbok *Antidorcas marsupialis* (Louw & Seely, 1982; Nagy & Knight, 1994; Skinner & Louw, 1996) gain supplementary water that significantly increase their endurance in otherwise dry areas. This also appears to be the case for some rodents (*Petromyscus collinus, Aethomys namaquensis*, and *Petromus typicus*) living on Namib inselbergs which intercept fog (Withers, Louw & Henschel, 1980). This is different for gerbils (*Gerbillurus* spp.), which balance their daily energy expenditure to daily water turnover rates so efficiently that water freed from oxidation of protein, fats and carbohydrates nearly satisfies their requirements. Together with the available moisture from food (and reduced water loss; Buffenstein *et al.*, 1985), gerbils can survive on air-dried seeds.

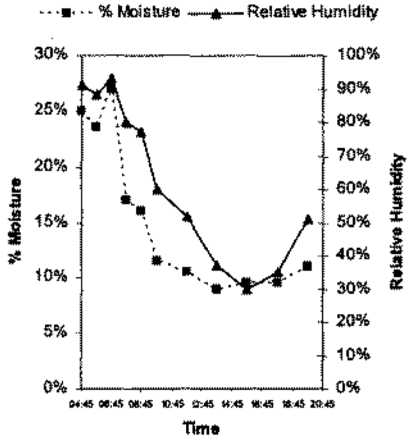


Figure 1: Effect of relative humidity of air at various times on moisture content of the desert grass *Stipagrostis uniplumis* (from Fig.8, Louw, 1972).

### 3.4 Body as Collector

An even more specialised behaviour is fog basking. Louw (1972) first described this behaviour for the sidewinder adder, *Bitis peringueyi*, which was later elaborated by Robinson & Hughes (1978). In fog, this snake flattens its body against the sand surface, thereby increasing the surface area exposed to water deposition. The snake licks water droplets off its body and periodically raises its head to swallow.

Fog basking is also performed by the tenebrionid beetles *Onymacris bicolor* and *O. unguicularis* (Hamilton & Seely, 1976), diurnal species which climb up onto cool fog-swept dunes at night to allow fog to deposit onto their carapaces. Drops run down towards the mouth and the beetles drink. These two species differ from other tenebrionids (Louw & Seely, 1982) in terms of behaviour and surface characteristics of the fog-collecting carapace: they are active during cool periods (Hamilton & Seely, 1976) and the carapace has a hydrophobic coating, a smooth texture and longitudinally ribbing (Shanyengana 2002). Fog basking has to date not been confirmed in nature for any other Namib beetles (Hamilton *et al.*, 2003).

Akin to this behaviour is the fog collection and imbibition of the dune succulent *Trianthema hereoensis* (Seely, de Vos & Louw, 1977). Fog droplets are absorbed through the leaves and translocated to the root system. Furthermore, fog drops that drip onto the surrounding sand can percolate down to the roots, which is a method that also appears to enhance fog utilisation by the dune grass *Stipagrostis sabulicola*.

### 3.5 Absorption of Water Vapour

Louw & Seely (1982) emphasised the importance for desert insects to absorb water vapour even in unsaturated air. Machin *et al.* (1982) demonstrated this for Namib tenebrionid larvae, which come to the surface at night and use a specialised, complex structure of their rectal cavity that uses Malpighian tubule fluid to absorb water vapour. The osmotic pressure in this structure is a biologically extraordinary 9 Osmol, compared to 0.6 Osmol in the haemolymph. Louw (1990) highlighted that this mechanism is indeed 'special' to desert animals. Rössl (2000) found that when fog did not reach larvae of eight species, all larvae of three species died and the others developed more slowly.

Similar to the absorption of atmospheric moisture is the resorption of water from exhaled air by the ostrich, which thus conserves 25% of its daily water turnover (Withers, Siegfried & Louw, 1981).

## 4. SUMMARY AND CONCLUSION

Louw's multifaceted approach towards studying desert organisms was based on the philosophy that "life has evolved largely around the unique properties of water" (p.16 Louw, 1983). Water uptake is one facet, and even in a hyperarid environment, there are a number of ways for organisms to obtain water, namely a) location in moist micro-environments, b) drinking from wet surfaces, c) consumption of moist food, d) collecting water on the body, and e) absorbing water vapour. Both (d) and (e) involve some special adaptations, notably fog-basking, and formation of high osmotic pressure.

Applications for fog- and dew-water collection have already started to make use of some of these biological principles. Examples to improve current technology could be: effectively track moisture the way some organisms do; extract moisture from straw (or other fibre) absorbed from the atmosphere; improve the effectiveness of surfaces to collect and facilitate run-off of fog; finding cost-effective methods to use osmotic pressure to obtain water from unsaturated air.

Louw's legacy leaves us with the portrayal of life as a hydrological process and a broad message concerning its conservation, not least for its invaluable lessons on survival.

## 5. ACKNOWLEGEMENTS

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