Fog and fauna of the Namib Desert: past and future

DUNCAN MITCHELL,1,2 JOH R. HENSCHEL,3,4,5 ROBYN S. HETEM,1,6 THEO D. WASSENAAR,4,7 W. MAARTIN STRAUSS1,8 SHIRLEY A. HANRAHAN,6,10 AND MARY K. SEELY4,6,9

1Brain Function Research Group, School of Physiology, Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, South Africa
2School of Human Sciences, University of Western Australia, Perth, Western Australia, Australia
3South African Environmental Observation Network Arid Lands Node, Kimberley, South Africa
4Gobabeb Research Institute, Gobabeb, Namibia
5Centre for Environmental Management, University of Free State, Bloemfontein, South Africa
6School of Animal Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa
7Namibia University of Science and Technology, Windhoek, Namibia
8Nature Conservation Programme, Department of Environmental Sciences, UNISA, Florida, South Africa
9Desert Research Foundation of Namibia, Windhoek, Namibia

Citation: Mitchell, D., J. R. Henschel, R. S. Hetem, T. D. Wassenaar, W. M. Strauss, S. A. Hanrahan, and M. K. Seely. 2020. Fog and fauna of the Namib Desert: past and future. Ecosphere 11(1):e02996. 10.1002/ecs2.2996

Abstract. The future of fog-dependent habitats under climate change is unknown but likely precarious; many have experienced recent declines in fog. Fog-dependent deserts particularly will be threatened, because, there, fog can be the main water source for biota. We review the interactions between fog and fauna of the Namib Desert, about which there is 50 yr of research. We resynthesize the data, seeking patterns and mechanisms that could provide a framework for predicting outcomes of changes in fog regime in other fog-dependent deserts. In the Namib, fog constitutes the most-predictable form of free water. At least 48 Namib animal species consume free water from fog, or are likely to do so, employing both liquid and vapor phase. Fog also sustains plants that form the base for metabolic water production and wets the diet to provide pre-formed water. So fog provides or underpins all the water intake of Namib fauna. Only a few species are active fog-harvesters, though. Among Namib beetles, two species are unique in that they fog-bask; they assume stereotyped postures in wind-driven fog and droplets deposit on their carapaces. Some Namib beetle species construct surface ridges that trap fog water, which they consume. Some arthropods emerge from their subsurface habitats, or occupy its wet top layers, to access fog water, at times and in conditions outside their usual surface activity. Many more taxa, including vertebrates, use fog water opportunistically. They do not actively seek it out but use it when available. Acquiring fog water from droplets requires overcoming spherical surface tension so is possible only for animals heavier than ~100 mg. Smaller animals extract water from films or acquire it in the vapor phase. Some Namib animals use hygroscopic surfaces to extract vapor from unsaturated air, at ambient humidities attained in fog or sometimes between fogs. Rapid acquisition of water during episodic fog events creates problems for storage and osmoregulation, which some Namib animals have solved in enterprising ways, including long-term internal storage of water and sequestering of osmolytes. Although not yet comprehensive, the body of research reviewed, and the principles that we have elucidated underlying fog usage, should inform future research on fauna throughout fog-dependent deserts.

Key words: Desiccation; fog-basking; fog water harvesting; fog-dependent desert; Lepidochora; spp. osmoregulation; tenebrionid beetles; Onymacris; spp. water vapor pressure.

Received 16 August 2019; accepted 11 October 2019. Corresponding Editor: Robert R. Parmenter.

Copyright © 2020 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
INTRODUCTION

In a single year, just more than 40 yr ago, two papers on the fog and fauna of the Namib Desert featured on the covers of *Nature* and *Science* (Hamilton and Seely 1976, Seely and Hamilton 1976). They reported remarkable behavior in Namib Desert tenebrionid beetles by means of which the beetles accessed fog water directly, and they remain icons of research on animal biology related to fog. That remarkable behavior drew attention to a more general phenomenon, the dependence of so many of the Namib Desert’s animals on fog as their source of free water (Seely 1978, Seely and Pallett 2008). The swirling of fog around the high dunes of the Namib sand sea is a spectacular event (Fig. 1) and, if the fog deposits, it heralds an outbreak of animal activity accessing the water (for the meteorological properties and chemistry of Namib fog, see Appendix S1). Though interest accelerated after those high-profile papers were published, the importance for Namib fauna of depositing fog (historically often referred to as “precipitating” fog; for differences between depositing fog and condensing dew, see Appendix S2) as a source of free water actually may have been recognized as long as 40 yr earlier (Walter 1936). Well before the two landmark papers on tenebrionid beetles appeared, in his plea for a permanent research station in the Namib, Reginald Lawrence (1959) of the Natal Museum, Pietermaritzburg, South Africa, eloquently related how “with the sinking of the sun and the coming of the cold dank mist which blows in from the sea and deposits a thin mantle of moisture on the sands, a new and different set of life forms arises from the unending sand to pass the night feeding and preying upon each other.”

Fig. 2 is a diagrammatic map of the Namib Desert, indicating the geography that will appear in the text, and Table 1 summarizes the fog characteristics of the Desert in the 1960s and 1970s, the last period, until the present, during which those characteristics were measured systematically along a transect from the coast to the inland. The Namib Desert is a long and narrow coastal desert, stretching from southern Angola to just north of Cape Town, South Africa, and centered on the Namib Desert sand sea, in the dunes of which Fig. 1 was photographed. The sand sea is a UNESCO World Heritage Site (Seely 2012). Those measurements in the 60s and 70s showed that there was a non-linear gradient of fog across the width of the Desert, with mean annual fog precipitation reaching nearly 200 mm at some inland sites, and declining to near zero about 100 km from the coast. Fig. 2 shows an estimated boundary of the fog belt, east of which fog occurred on <25 d/yr. Nearly half the Desert is located outside the fog belt, but little biological research has been conducted outside the belt. The mean number of fog days per year reached a maximum of 87 at 33 km from the coast, implying a mean interval between fogs of four days, but the maximum interval between fogs at that site was 40 d. It is the interval between fogs, not the fog volume, that is important for fog-dependent animals; each depositing fog event produces surplus water. Though more predictable than that of rain (Pietruszka and Seely 1985), the interval between fogs is highly stochastic, and Namib animals that rely on fog cannot predict when the next fog will occur. That unpredictability has shaped the evolution of their body fluid physiology.

Not enough research has been carried out in other foggy deserts to know how widespread fog dependency of animals is. There are other coastal foggy deserts, for example, the Atacama, Baja California, Omani, and Yemeni Deserts. None of those has housed the vast body of research on the relationship between fog and desert animals that has been forthcoming from the Namib, mainly, but not only, from its Gobabeb Research Institute, the permanent station envisaged by Lawrence (Henschel and Lancaster 2013; Fig. 2).

At the time that the earlier landmark research was done, there was no inkling that the fog regime in the Namib, and indeed in any other fog-dependent desert, could be a transient phenomenon. That no longer is the case. With climate change, fog regimes are changing, but it is extraordinarily difficult for climatologists to
predict how a particular fog regime will change (Koračin et al. 2014, Torregrosa et al. 2014). There were early predictions that off-shore fog might increase because global warming would intensify ocean upwellings (Bakun 1990); in the early years of this century, fog was much more prevalent off the shore of Namibia than over the land (Cermak 2012). There now is compelling meteorological evidence, however, that fog over land is declining, and substantially so (Johnstone and Dawson 2010). The declines are widespread geographically. They have been recorded at multiple sites in Europe, North America, South America, and Asia (Klemm and Lin 2016), and at Cape Town airport, on the west coast of southern Africa just south of the Namib (Fig. 2; Van Schalkwyk 2011). Only in a band along the Himalayas has there been a measured widespread increase in fog (Klemm and Lin 2016). The little specific modeling that has been done predicts that fog will decline in the inland Namib too (Hänsler et al. 2011). If fog declines, so too, we expect, will the fog-dependent biota. If we are to predict the fate of fog-dependent animals, and potentially to contribute to their conservation, when a change in regime is imminent or upon us, we need an understanding of the current relationship between those animals and the fog regime that extends beyond the descriptive.

By reviewing and synthesizing the vast body of research from the Namib (and it will be for the first time that such a task has been attempted, for any foggy desert), we hope to contribute to such an understanding.

We begin by summarizing the mechanisms through which Namib animals access water, of which fog forms the most important ultimate source, at least for those that occur in the main fog zone (Fig. 2). We then traverse the spectrum of Namib species that have adapted to access fog water either opportunistically or through highly specialized adaptations that allow them to make
Fig. 2. Geography of the Namib Desert. The extent of the Namib Desert was reproduced from Henschel and Lancaster (2013). In Namibia, the fog line follows the contour delineating the eastern edge of the zone receiving about 25 d of fog per year, based on data from Mendelsohn et al. (2002). Less-frequent fog occurs east of this line.
up a significant part of their water budget from fog. Those species that cannot acquire sufficient water from the other possible sources, metabolic water and pre-formed water in the solid diet, are perhaps the most at risk from predicted future declines in fog water events. We also discuss the adaptations of these organisms to the consumption of low-osmolality fluid, which brings a set of physiological challenges that must be overcome. Finally, we discuss the most critical gaps in knowledge and point out potentially fruitful lines of investigation for an improved understanding of species- and ecosystem-specific risks related to climate change and possible future decreases in fog.

### How Namib Fauna Access Fog Water

To contextualize the mechanisms by which fog sustains the Namib’s fauna, we first identify how Namib animals can acquire water. Multicellular animals access water via three avenues, metabolic water (water produced as one end product of the oxidation of fuel), pre-formed water (water in and on food), and free water (liquid or vapor). If metabolic water and pre-formed water are insufficient to balance an animal’s water budget, the animal will need free water. In the Namib, though, all three avenues are dependent on fog, immediately or ultimately (Henschel et al. 2001). As we shall see, fog sustains much of the

**Table 1. Fog characteristics of the Central Namib in the 1960s/1970s (reconstructed from Lancaster et al. 1984).**

| Distance from coast (km) | Elevation (m) | Annual fog precipitation (mean mm) | Number of fog days per year (mean) | Maximum interval between fog days (mean) | Years of data collection |
|-------------------------|--------------|------------------------------------|-----------------------------------|------------------------------------------|-------------------------|
| 2                       | 20           | 34                                 | 65                                | 134                                      | 6–9                     |
| 22                      | 63           | 80                                 | 76                                | 46                                       | 12–15                   |
| 33                      | 340          | 184                                | 87                                | 40                                       | 8–12                    |
| 51                      | 407          | 36                                 | 38                                | 77                                       | 5–8                     |
| 56                      | 407          | 31                                 | 37                                | 63                                       | 13–15                   |
| 60                      | 500          | 183                                | 77                                | 33                                       | 2–4                     |
| 100                     | 780          | 15                                 | 16                                | 118                                      | 2–4                     |
| 112                     | 1000         | 3                                  | 3                                 | 772                                      | 10–14                   |

**Table 2. Examples of desert vertebrates that can survive without free water.**

| Species | Ecophysiology | Reference |
|---------|---------------|-----------|
| Arabian oryx *Oryx leucoryx* | Saudi Arabian desert, free water available only a few weeks per year, ambient temperatures regularly exceed 40°C | Hetem et al. (2010) |
| Springbok *Antidorcas marsupialis* | Namib Desert resident, survive without drinking | Nagy and Knight (1994), Skinner and Louw (1996) |
| Some Namib rodent species | Survive eating only dry seeds | Louw (1972), Withers et al. (1980), Buffenstein et al. (1985) |
| Some Namib lark species | Survive without drinking | Willoughby (1971), Cox (1983), Williams (1999) |
| Grant’s golden mole *Eremitaupa granti* | Namib sand-swimmer, insectivorous | Fielden et al. (1990) |
vegetation that provides metabolic fuel. Plant material and the detritus formed from its decomposition provide pre-formed water best when they have been wet, which usually will be by fog.

There are desert taxa of many sizes that can survive on metabolic and pre-formed water alone (examples listed in Table 2). A dramatic example at the high-mass end of the spectrum is the Arabian oryx. In the Namib, springbok *Antidorcas marsupialis* can survive on metabolic and pre-formed water alone and other antelope species probably can do so too. The gemsbok *Oryx gazella*, iconic in the Namib, may be one of those (King et al. 1975) but its water dependency in the Namib does not seem to have been investigated formally. However, many Namib animal species, of all sizes, are unable to meet their water demands from metabolic and pre-formed water. They need free water, either from rain or from one of the sources of non-rainfall water that present themselves in the desert. In the Namib’s fog belt (Fig. 2), fog in droplet or vapor form is the most-reliable source of that free water (Pietruszka and Seely 1985).

Rain occurs on so few days in the average year (Figs. 3, 4; Lancaster et al. 1984) that rain water and the standing water that may follow rainfall are not reliable sources for Namib taxa needing free water to balance their water budgets. The soil moisture dynamics of the mobile sand dunes are not determined by rainfall (Li et al. 2016). Moreover, though decadal rainfall at Gobabeb actually doubled between 1979 and 2009, the number of days on which rain fell declined by 29% (Fig. 4), and it is the interval between events, rather than their magnitude, that is important for Namib animals. Namib species have adapted well to accessing available water from sources other than rain, sometimes in very novel ways. Free water can be available as liquid water from fog and dew (Fig. 5; Appendices S1, S2). Dew forms less frequently than fog occurs (see Fig. 3). A recent year-long record of precipitation at five sites along a 45 km east-west transect originating near Walvis Bay (Fig. 2) revealed that 92% of all precipitation at those sites occurred as depositing fog (Gottlieb et al. 2019). Dew usually forms around dawn, when it condenses on solid surfaces such as the plants of Fig. 5, but not on the dune sand (see Appendix S2). The water in air that will form dew is in the vapor phase, so invisible. The water in fog is in both vapor and liquid phases, and it is the liquid droplets that make fog visible (Fig. 5). The fog droplets may stay in the air, or, in the right circumstances, may deposit on a surface, leaving residual droplets on whatever it deposits after the fog cloud clears. Dew cannot form on any surface under fog (see Appendix S2), but can form after fog has lifted, so dew and residual fog droplets can coexist. In other deserts, dew may be more important to the resident animals than is fog (Broza 1979, Wang et al. 2017), especially if those animals are active around dawn. In the Namib, more dew forms per year on dew-measuring instruments than

![Graph showing frequency of days per month with various types of precipitation in 2001 at Gobabeb Research Institute.](image)

Fig. 3. Number of days per month, in 2001 at Gobabeb Research Institute (Fig. 2), with relative humidity >97% (shaded bars), dew (open bars), fog (black bars), and rain >0.1 mm (hatched bars). (Redrawn from Henschel and Seely 2008).
collects in fog gauges at the same sites (Soderberg 2010), but what the instruments measure does not translate into water available to biota (Kaseke et al. 2012a). We do not believe that dew is as important to the Namib animals as fog is, though we concede that the topic is under-researched (see Appendix S2).

For the surprisingly many days of each year that free water is available in the form of droplets on the Namib substrate, usually after fog but sometimes from dew, a spectrum of Namib animal species accesses free water from those droplets. We have tabulated, for the first time, all the Namib species (48 in total) known or highly likely to use free fog water, how they do so, and when (Appendix S3: Table S1). Accessing free water from droplets requires animals to have sufficient physical strength to overcome water’s spherical surface tension forces, so the water in fog and dew droplets will be unavailable to small animals. The workers of southern African termite species weigh no more than a few milligrams (Ferrar 1982). When pseudergates of the Namib termite Psammotermes allocerus were offered droplets in the laboratory, they could not access the water; they drowned “tangled in the water film” (Grube and Rudolph 1995). So the smallest animals of the Namib are precluded from using fog droplets, a principle apparently not stated explicitly previously. Their source of free water, if they need it to balance their water budgets, has to be water not subject to high surface tension forces. That could be capillary water in the soil, as it is for P. allocerus (Grube and Rudolph 1995), and, perhaps surprisingly for a desert, also water in its vapor phase when ambient humidity is high (see Acquisition of free water in vapor form), as it is in both depositing and non-depositing fog. Even

Fig. 4. Annual rainfall (mm) and days of rain per annum (including the median and 95% confidence intervals) at Gobabeb Research Institute for the decades between 1980 and 2010. Decadal rainfall tended to increase but remained <30 mm while days of rain tended to decrease, to below 5 d/yr in 2000–2009. High variability arose mainly from isolated years of unusually heavy rain. Data from Eckardt et al. 2013, replotted.
Fig. 5. Fog and dew of the Namib Desert. Left to right top to bottom: fog rolling across the dunes; low fog in valley between dunes; fog lifting off a dune; less dense fog on lower dune slope; dune crest wet after fog; drop of fog water collected on !Nara plant; dew drops collected on grass; grassy interdune plain wet with dew. (Photos: Joh Henschel).
in dense fog, there is much more water contained in the fog’s vapor component than in its droplets (Fig. 6).

**Acquisition of free water from fog droplets**

The vast majority of Namib animal species observed to acquire free water from fog do so opportunistically, from droplets (Appendix S3: Table S1), behavior not unique to the Namib (Broza 1979). They will drink deposited fog if they encounter it while going about their other duties, or if the circumstances are right for it to form near them. The deposited fog may be on the sand or stone, on detritus, on plants, or on the bodies of the animals themselves. Though insects are the best-known fog-harvesters, other fog-harvesting taxa include arachnids, reptiles, and mammals.

By contrast to the many species that acquire free water from fog by opportunistic fog-harvesting, a few Namib tenebrionid beetle species deliberately seek out to capture and drink fog. They are active fog-harvesters. A compelling criterion for classifying a fog-harvester as active is that it seeks liquid fog on the ground surface outside its normal time of day for surface activity, and in a temperature regime that it normally would avoid (Henschel and Seely 2008). Fig. 7 shows an array of tenebrionids that includes three active fog-harvesters. One of those is rare among Namib tenebrionids in that its elytra are white not black. For fog-harvesting, the important feature of the carapace is not the color, though, or the overall shape, but whether the carapace is grooved, a characteristic of the two species *Onymacris unguicularis* and *Onymacris bicolor* that employ fog-basking (Hamilton and Seely 1976). The grooves may be essential for capturing the water droplets or conveying them to the beetles’ mouths (Henschel and Seely 2008). Fog-basking is the behavior that reached the cover of *Nature* and is illustrated in Fig. 8. Only the subspecies *Onymacris unguicularis unguicularis*, which inhabits the sand sea of the central Namib (Lamb et al. 2013), has been studied formally, although the species (subspecies unknown) has been observed using the same behavior in the northern Skeleton Coast dunes (Fig. 2). Beetles of these two species will emerge from the dune sand, in which they spend most of their lives, before fog arrives. In their habitat, it arrives typically from a few hours before midnight to shortly after midnight (Appendix S1) and lasts for about three hours (Seely et al. 1983). In the absence of fog, the beetles never emerge onto the surface at that time. They are thermophilic and normally active diurnally only. Ahead of the arriving fog, they clamber, clumsily because they are cold, to the dune crest or just below it, parts of the dune where fog deposits best (Robinson and Seely 1980), not on the slip face as drawn by Cloudsley-Thompson (2001), and assume a head-stand posture with the elytra facing the wind bringing in the fog. This posture allows fog droplets to deposit on the dorsal carapace, provided that the wind and droplets are suitable; the beetles abandon fogs if the wind is too strong or the fog not dense enough (Seely 1979). The droplets run down the hydrophobic carapace to the

---

**Fig. 6.** Vapor and liquid components of dense fog, at different air temperatures. (Redrawn from Eugster 2008).
mouth parts under gravity, where they apparently are consumed. *Onymacris unguicularis* has unusually high concentrations of glycerol and the sugar trehalose in its body fluids, molecules which may act as cryoprotectants when the thermophilic beetles are exposed at night to temperatures that may be close to 0°C in fogs (Naidu 2008), though air temperatures below 0°C are very rare in the Namib (Schulze 1969, Lancaster et al. 1984) and frost is almost unknown (Goudie 1972).

Unlike the beetles that use fog droplets opportunistically, the fog-baskers emerge in advance of visible droplet formation (Seely 1979). The beetles are obsessive about their fog-basking. They do not react to human observers nearby, and there is no turnover of beetles present during the event (Seely et al. 1983). Because they are cold and lethargic, they would be very vulnerable to nocturnal predators during fog-basking, if such predators were prevalent. The evolution of their fog-basking behavior, and indeed the behavior of other active fog-harvesters, may have depended on low risk of predation, and especially of nocturnal predation (Seely 1978, 1985, Polis et al. 1998). Fog-basking is not a universal attribute of the genus *Onymacris*. The genus is widespread in, but virtually confined to, the Namib, and phylogenetic analysis has confirmed that fog-basking is likely to have evolved independently in
Fig. 8. Active fog-harvesters. (a–d) Fog-basking *Onymacris unguicularis*; (e, f) *Lepidochora kahani* on its complex fog-collecting trench; (g, h) *Lepidochora discoidalis* on its straight fog-collecting trench. (Photos: Joh Henschel).
Onymacris unguicularis and O. bicolor (Ward and Seely 1996). Fig. 9 is a diagrammatic phylogenetic tree showing the relatedness of 14 species of the genus. O. bicolor is related more closely to O. langi, O. candidipennis, O. marginipennis, and O. brainei, which are not fog-baskers, than to the other fog-basker O. unguicularis. The two fog-baskers are more closely related to each other, though, than either is to the non-basking active fog-harvester O. plana. Beetle researchers from Gobabeb and elsewhere have spent enough time in Namib fog, over more than fifty years, for us to be sure that the absence of reported fog-basking in O. langi, O. candidipennis, O. marginipennis, and O. brainei is not because the behavior has been overlooked (Ward and Seely 1996). Some Onymacris species that are not fog-baskers are opportunistic fog-harvesters. They will drink fog that has deposited on vegetation or other nearby surfaces (Appendix S3: Table S1; Seely 1979, Nørgaard and Dacke 2010). O. laeviceps (Fig. 7), more distantly related to the active fog-harvesters than they are to each other (Fig. 9), is an opportunistic fog-harvester. This beetle normally is active first well after sunset and again after dawn (Holm and Edney 1973) and so will encounter residual fog droplets on vegetation regularly. O. plana (Figs. 7, 9), however, normally is active diurnally (Holm and Edney 1973), preferring surface temperatures between 20°C and 50°C, but will emerge at surface temperatures below 10°C to drink droplets off vegetation, and so qualifies as an active fog-harvester (Bartholomew et al. 1985), but not a fog-basker.

Not all tenebrionids with a grooved dorsal carapace fog-bask. Although Holm and Scholtz (1980) claimed that Onymacris laeviceps “lacks the grooves on the elytra which seem to assist with fog basking,” the species does have grooves (see Fig. 7) but, in spite of its carapace being equipped to do so, does not fog-bask. The grooved beetle carapaces of the fog-basking beetles are not as efficient at collecting fog, though, as is the fog-collecting dune grass Stipagrostis sábulicola (Ebner et al. 2011, Nørgaard et al. 2012, Roth-Nebelsick et al. 2012), which begs the question of why the two Onymacris species engage in energetically expensive and potentially

---

**Fig. 9.** Phylogeny of fog-basking in Onymacris beetles. Open circles denote the “white” tenebrionids (Lamb and Bond 2013). Fog-basking is not a trait of the genus and appears to have evolved independently twice (or has been lost by four “white” species). (Redrawn from Ward and Seely 1996, Lamb and Bond 2013).
dangerous fog-basking, rather than taking droplets off the grass, as do some other tenebrionid beetles (Appendix S3: Table S1). It may be that they have a predilection for water of very low osmolality (see Physiological challenges associated with fog-harvesting and Appendix S1), but it also is possible that evolving fog-basking allowed them to occupy vegetationless dunes, from which they would have been excluded if they had evolved to take water only off vegetation. This paradox deserves study.

Devising and constructing artificial surfaces to collect fog and dew, purported to mimic, or be inspired by, the structure and chemistry of Namib beetle carapaces, has become a major international industrial enterprise. The enterprise has been misguided. The carapaces that have been mimicked have been bumpy not grooved and have belonged to beetles that do not collect fog or dew. The species usually mimicked was identified incorrectly (see Hamilton et al. 2003), but neither the mistaken species nor the true species fog-bask. Indeed, both those species are species active only at times at which fog and dew never form, so whatever determined the evolution of their carapaces, it was not capacity to collect fog or dew. Those were not the carapaces to mimic. For a more-detailed account of the misidentification and misunderstanding of natural history that have led to the misguided enterprise, see Appendix S4.

Fog-basking is not the only mechanism used by Namib beetles to capture fog actively. Beetles of the genus Lepidochora, which at times virtually cover the dune slipfaces (Lawrence 1959, Hanrahan and Kirchner 1997), make structures to capture fog (Seely and Hamilton 1976). Three species (Appendix S3: Table S1) of that genus bulldoze trenches on Namib sand dunes when fog is imminent (Fig. 8, lower panels). Unlike that of the Onymacris species, the normal activity period of the Lepidochora species extends into the night; Lepidochora discoidalis is crepuscular and L. kahani and L. porti are nocturnal (Seely et al. 1983, 2005). So Lepidochora beetles may still be active on the dune surface when early fog arrives, but if they have buried already, they will emerge ahead of a suitable fog (Seely 1979). Trench-diggers do not emerge, though, if a fog begins after dawn (Seely 1979). L. discoidalis dig their trenches when neither the ambient temperature nor the wind regime suits their normal surface activity (Seely 1979). The ridges at the edges of their trenches concentrate fog moisture up to six times above that of the surroundings, and the beetles extract that moisture, even in the absence of visible droplets. Indeed, Lepidochora are active not just in fog that is depositing, but also on nights when there is non-depositing fog (Seely et al. 1983), so, presumably, their trench ridges can capture water from the vapor phase. How they extract the water from the moist sand is not known yet, but it is not the “ingestion of fog-soaked sand” that Wharton and Richards (1978) mistakenly reported it to be (Seely 1979). They need to be cool to take up the water; in the laboratory, they will do so at 10°C but not at usual laboratory temperatures (Seely 1979). They can extract water from the sand as long as it is moist enough to maintain a water potential above –0.03 MPa; they do not increase their water uptake if the sand is wetter and re-bury in the sand long before all surface water droplets evaporate (Seely 1979).

Because it occurs in such a small proportion of Namib tenebrionid species (see Table 3 for the numbers), fog-harvesting cannot be considered a general adaptation of Namib tenebrionids, and active fog-harvesting even less so. The tenebrionid beetle species Metriopus depressus, resident in Table 3. Fog-harvesting tenebrionid beetles form a small proportion of Namib tenebrionid species.

| Tenebrionid beetles                              | Number of species | Reference                                      |
|--------------------------------------------------|-------------------|------------------------------------------------|
| In the Namib                                      | 200               | Koch (1961), Cloudsley-Thompson (2001)        |
| Dune sea specialist species restricted to Namib biome sand dunes | 61                | Seely (2012), this paper, Appendix S1: Table S3 |
| Fog-harvesters                                   | 26                | This paper, Appendix S1: Table S3             |
| Known active fog-harvesters                      | 10                | This paper, Appendix S1: Table S3             |
| Known active fog-harvesters on dune slipfaces    | 5                 | This paper, Appendix S1: Table S3             |

www.esajournals.org 13 January 2020 • Volume 11(1) • Article e02996
rocky crevices and other dark areas on gravel plains (Seely 1985), adds confusion because its activity increases massively during depositing fog but the beetle has not yet been reported to drink the fog droplets (Wharton and Seely 1982), though it is large enough to do so (Appendix S3: Table S1). How active fog-harvesters detect that a fog is imminent was earmarked as unknown in 1979 (Seely 1979) and remains so today. Some insect species seem to be able to sense atmospheric humidity (Barton-Browne 1964), but humidity is unlikely to be a good cue in the Namib because it often is very high on fogless nights (Fig. 3), and the beetles are buried too deep to sense surface humidity. Before a fog arrives, Onymacris unguicularis typically will be buried 100 mm below the sand surface and Lepidochora discoidalis up to twice that depth (Seely et al. 1985), seemingly out of contact with surface temperature and humidity. In a heroic study in which the researchers themselves responded, often in the early hours of the morning, to all 66 fogs that the researchers themselves responded, often in the early hours of the morning, to all 66 fogs that occurred in one year, the only factor identified that correlated significantly with beetle surface activity ahead of an imminent fog, for both O. unguicularis and L. discoidalis, was the minimum air temperature on the day of the fog (Seely et al. 1983). That minimum temperature usually would occur around dawn, typically well after the fog had arrived, and would be a variable difficult for the beetles to predict, especially from 100 mm or more below the surface. All active fog-harvesting species seem to know when fog is imminent, and the Onymacris species that fog-bask actually seem to know whether it will be depositing fog. At Gobabeb, O. unguicularis beetles emerged in 97% of depositing fogs but only 76% of non-depositing fogs (Seely et al. 1983). A possible cue might be related to changes in wind direction, which is North-northeast when the fog is on the ground around Gobabeb, rather than the prevailing South-southwest on fogless days (Appendix S1; Seely and Henschel 1998, Spirig et al. 2019). The noise created by wind-blown sand on sand dunes penetrates well into the substrate, and beetles buried in the substrate use that noise to interpret surface events (Hanrahan and Kirchner 1994). They may even be able to detect events as small as individual beetles walking on the surface (Hauffe et al. 1988). So, the beetles will be able to detect, and may well be able to interpret, the direction change of wind preceding fog, and there may be a cue related to direction, wind speed, or turbulence that allows the beetles to distinguish between imminent depositing and non-depositing fog.

There is evidence that fog-harvesting, and particularly active fog-harvesting, bestows measurable survival advantages. Near Gobabeb populations of tenebrionid beetles erupted following the heavy rainfalls of 1976/1978. Over the drier 18 yr that followed, the populations of dune-dwelling species that are not fog-harvesters plummeted; 17 of the 19 species declined to <1% of their mean abundance (Seely et al. 2005). Populations of fog-harvesting beetles were sustained much better. Tenebrionid species that are active harvesters sustained their populations much better than did even the opportunistic fog-harvesters in the same environment (Seely et al. 2005). But the survival advantage of active fog-harvesting can be over-ridden. The persistence of several species of opportunistic fog-harvesters, especially of the genus Zophosis, was better than that of the active fog-baskers and trench-diggers (Seely et al. 2005). The anomalous success of opportunistic over active fog-harvesters was likely to have resulted from better access to resources other than water. The fog-baskers and trench-diggers lived on dunes, whereas the opportunistic fog-harvesters tended to live in better-vegetated areas. In a riverine habitat, relatively well vegetated, 12 species of tenebrionid beetle maintained their abundance well, in spite of none being fog-harvesters (Seely et al. 2005). So better access to food, which provides metabolic and pre-formed water as well as other nutrients, seems to be more important than fog-harvesting in improving beetle survival, and fog-harvesting may become critical only in poorly vegetated habitats, like dunes.

Among the ~1500 known invertebrates in the Namib Sand Sea World Heritage site (Seely 2012), there are other Namib invertebrates that behave in a way that makes them likely to qualify as fog-harvesters, but for which we do not yet have recorded observations of them acquiring fog water (Appendix S3: Table S1). The snail Xerocerastus minutus lives in the Hamilton Range of hills inland from Walvis Bay, Namibia (Fig. 2), normally in crevices or under rocks. However, it emerges from those refuges and is active on the moist surfaces during depositing fog. It may be
that it feeds only during fog events (Hodgson et al. 1994). Presumably it is accessing fog water, but that presumption has not been confirmed.

South of Gobabeb, a burrowing snail *Trigonephrus* sp., has been reported anecdotally to become active on the surface on foggy mornings (Dallas et al. 1991). Apart from incidental observations that spiders or spiderlings of at least three species cling to wet web and trapdoors on foggy mornings (Fig. 10; Henschel 1997; Appendix S3: Table S1), there has been no investigation of the relationship between fog and Namib spiders, of which there are many species (Lawrence 1962, Griffin 1998). The dancing white lady spider *Leucorchestris arenicola* needs free water. It does not survive in the laboratory if given food but not water (Henschel 1990). Spider webs may collect fog droplets. The web of the cribellate spider *Uloborus walckenaerius*, not found in the Namib but widespread in North Africa, Europe, and Asia, seems to be structured to do so (Zheng et al. 2010). The chemistry of the silk lining the burrows of *Ariadna* spiders changes across the Namib fog belt, apparently making the web more hydrophilic inland (Conti et al. 2015). Fog condensing on the trapdoor web of *Leucorchestris arenicola* can make the trapdoor so clammy that the spiders then are reluctant to exit to forage (Henschel 1990). If the spiders or spiderlings do access fog water, then an earlier contention (Seely 1993) that no burrowing animals in the Namib harvest fog is not valid.

There may be fog-harvesters among the wealth of other invertebrate taxa in the Namib, unknown because fog-related behavior simply never has been studied. Just as there is spider diversity, so there are many ant species even just in the central Namib (Marsh 1986); some are carnivorous and some eat honeydew, but whether all can survive on metabolic and pre-formed water, or whether they need free water, is unknown. The scorpion assembly in the Namib

---

**Fig. 10.** *Carparachne aureoflava* spiderlings on a trapdoor moist with residual fog droplets. Normally these spiderlings would be deep down in the maternal burrow at this time. The spiderlings depicted are Stage 2 nymphs, pre-dispersal, with estimated masses of 10–20 mg, probably too small to access water directly from fog droplets. (Photo: Joh Henschel).
is abundant and rich in species (Lamoral 1979, Prendini 2005), but, apart from a single opportunistic observation of Parabuthus villosus drinking fog droplets off plants (Polis and Seely 1990), the relationship between scorpions and fog appears not to have been explored. P. villosus, though, may be unique among Namib scorpions in drinking fog, because it can regulate its hemolymph (see Physiological challenges associated with harvesting fog) whereas most scorpion species cannot do so (Robertson et al. 1982).

What appears to be harvesting of fog or dew has been reported not just for invertebrates but for some Namib vertebrate species (Appendix S3: Table S1). For most of the vertebrate species, the reported harvesting has been opportunistic, but for two burying snake species in the genus Bitis not normally on the surface at the low temperatures that occur during fogs, it appears to be active (Appendix S3: Table S1). The snakes drink water droplets that collect on their bodies during fogs. They use dorsoventral flattening to form a channel which conveys the water to the mouth. The sidewinder Bitis peringueyi, resident in the Namib sand sea, will adopt the flattened posture if water is sprayed on it in captivity (Louw 1972, Robinson and Hughes 1978). Two diurnally active gecko species, in the genus Rhoptropus, are listed in Appendix S3: Table S1 as fog-harvesters because analysis of their water budgets has shown them to be obligate fog users (see Obligate fog users), though no one actually has seen them accessing free water. No Namib lizard has been seen capturing atmospheric water on its integument, as some lizard species elsewhere do (Sherbrooke 1990, Peterson 1998).

Likewise, no Namib frog has been seen condensing atmospheric water on to its body, as green tree frogs Litoria caerulea do in Australia (Tracy et al. 2011). In the Namib, there are at least 15 species of frog, some of which have no aquatic stages in their life cycles (Seely and Griffin 1986). One such species, Breviceps macrops, inhabits a narrow strip of beach and white coastal dune in the southern Namib and has the common name “desert rain frog,” a misnomer because it clearly is fog-dependent and not rain-dependent. It occurs only at sites where there is fog on at least 75 d/yr (Channing and Wahlberg 2011). It is active on the surface at night, from well after sunset, and that is when the fog occurs too. At other times, it lives in burrows in visibly moist sand, where it also lays its eggs. The sand moisture derives mainly from fog, at least when the frog is distant from the beach (Channing and Wahlberg 2011). There is no experimental evidence that the frog accesses free water directly from fog (though it may well do, including through its skin). The habitat of Breviceps macrops characteristically is damp, but that is not true for the habitats of other amphibian species that inhabit the central Namib gravel plains and river beds (Channing 1976). Two of these species, Bufo vertebralis hoeschi and Phrynomerus annectens, live on granite inselbergs on the arid gravel plains and use ephemeral pools only for laying eggs. Those ephemeral pools form after light rain, but also could form from fog, and more frequently. The possibility that these frogs use fog-filled pools for egg-laying requires confirmation. P. annectens is active only nocturnally, but B. vertebralis hoeschi can be active at any time of day or night, including “on bare granite in full sunlight” (Channing 1976). As do other members of the genus Bufo, this Namib Bufo may spread substrate moisture over its skin by capillary action, so implementing evaporative cooling without depleting body fluids (Channing 1976). The most-reliable source of that substrate moisture would be fog but using fog would require water to be acquired and stored until the ambient heat load necessitates evaporative cooling. However, once again there is no experimental evidence yet that either B. vertebralis hoeschi or P. annectens drinks free water from fog.

In summary, many Namib animal species, invertebrate and vertebrate drink liquid water from fog droplets. For most, accessing fog water is opportunistic; they may drink deposited fog if they encounter it or if it happens to form near them. Some Namib animals, like the famous fog-basking beetles, are active fog-harvesters though. They will compromise other functions so as to access deposited fog. In other fog-dependent deserts, we should expect to find many opportunistic harvesters of deposited fog. Active fog-harvesters will be rare or absent, we expect.

Acquisition of free water in vapor form

Namib animals too small to acquire water from droplets still can acquire free water from
water vapor in the atmosphere, even if the atmosphere is not saturated. Historically, research on water vapor acquisition by Namib animals and research on their fog dependency have proceeded as separate enterprises. But most, if not all, Namib animals that acquire water vapor directly can do so only if their habitat is wet by fog or dew, or has high relative humidity in adjacent air. The Namib has high relative humidity in the absence of fog or dew, at least for part of the day, surprisingly often for a desert (Fig. 3; Appendix S1). The animals could be on the surface when they access that water vapor, or in the superficial layers of the substrate, which is where many Namib animals, vertebrate and invertebrate, spend most of their lives (Seely 1978, 2012, Seely and Pallett 2008).

The research literature on water vapor acquisition by animals is not easy to comprehend, at least partially because there are two different ways by which animals can acquire water vapor from air, down a vapor pressure gradient, or into a hygroscopic surface. For neither does the air have to be saturated (that is 100% relative humidity), although biologists tend to regard acquisition of water from unsaturated air as counterintuitive (e.g., Cloudsley-Thompson 1975). The first way, down a vapor pressure gradient, conforms to a basic principle of mass transfer: If the ambient water vapor pressure exceeds the water vapor of the animal’s tissues, irrespective of what the ambient relative humidity is, water vapor will be driven to enter the animal (Edney 1971). The same process moves water vapor from the atmosphere into the Namib soil, where it is a major source of adsorbed water (Kaseke et al. 2012b). Though acquisition of water down a vapor pressure gradient is common in arthropods generally (Chown and Nicolson 2004) and has been proposed for some Namib plants (Henschel and Seely 2008), absorption of water vapor by that process appears not to be investigated in Namib animals. What has been investigated in the Namib is the consequence of vapor pressure gradients between the animals and their surroundings, for decisions of sand dune beetles to bury and emerge (Seely and Mitchell 1987).

If the ambient water vapor pressure is less than the water vapor of the animal’s tissues, water vapor will be driven to leave the animal, and the animal may desiccate. To counter the desiccation threat, adult tenebrionid beetles, and probably other taxa, use a highly impermeable integument to impede water vapor loss (Beament 1961, Cloudsley-Thompson 1975, Nicolson et al. 1984). The intrinsic impermeability of the integument does not appear to depend on the beetle being alive (Beament 1964) and having an impermeable integument may not be unique to arid-adapted insects (Seely 1989). Some Namib tenebrionids decrease permeability further by coating that integument with a waterproof wax bloom when in desiccating environments, making them virtually immune to the desiccating effects of vapor pressure gradients (McClain et al. 1985). If the animals are to acquire water vapor from the atmosphere when the vapor pressure gradient is in the opposite direction, how do they overcome the problem posed by impermeable integuments? Beament (1964) proposed that insect integments have a valve sub-served by active transport, such that they can be impermeable to outward flow of water but permeable to inward flow. Whether or not it is by active transport, some form of control of rate of water vapor absorption, when the gradient favors it, appears essential. An animal with an uncontrolled permeable integument may not be able to limit vapor absorption. For example, if the larvae of the tenebrionid beetle *Tenebrio molitor*, which indeed have a permeable integument, are exposed to high ambient water vapor pressure, they absorb sufficient water to interfere with metabolic processes (Mellanby 1932). *Tenebrio molitor* does not occur naturally in the Namib. At the other extreme, two desiccation-resistant species of tenebrionid beetle from the arid southwest of the United States did not acquire any water when placed in a chamber at 30°C, 97% relative humidity for 24 h (Ahearn and Hadley 1969), so provided no evidence of Beament’s valve.

Water vapor pressure is determined by a number of physical properties of whatever holds the vapor, with the most important here being temperature and relative humidity. Inspection of a psychometric chart will reveal that, arguably, temperature is more important than is relative humidity. Water vapor pressure increases linearly with relative humidity but more steeply with temperature. The relative humidity of
tissue water typically is 99% (Cloudsley-Thompson 1975), or, more properly, its water activity is 0.99 (O’Donnell and Machin 1988). So a functional water vapor pressure gradient between atmosphere and tissues at the same temperature, directed toward the tissues, cannot be created by a relative humidity difference; the maximum difference in relative humidity would be 1%. A functional gradient can be created if the animal’s water vapor pressure will decrease if its temperature decreases, even if relative humidity stays the same. Psychrometric calculations will show, for example, that a beetle with permeable integument that has managed to cool itself to 20°C (water vapor pressure = 2.3 kPa) in an environment with an air temperature of 25°C will be able to absorb water vapor from the surrounding air as long as the relative humidity of that air is higher than 73%, because the vapor pressure of 25°C air is higher than 2.3 kPa at all relative humidities higher than 73%. Although it is a hyper-arid desert, high relative humidities are reached frequently in the Namib, at some time of the day, all the way from the coast to about 50 km inland (Appendix S1; Fig. 3), and as long as the wind is blowing onshore, persistent periods of very low relative humidity (<20%) of ambient air are uncommon (Schulze 1969, Lancaster et al. 1984). So, Namib animals with permeable integuments, in theory, could acquire water down a vapor pressure gradient by cooling themselves below ambient air temperature at the time at which relative humidity is high, for example by contact with a cold substrate or by losing heat by radiation to the night sky. Some Namib animals indeed do cool themselves in fogs (see Appendix S3: Table S1) so that droplets are sustained, but whether they then also absorb water vapor is unexplored. There is a pressing need to measure the surface temperatures of desert animals at times of high ambient water vapor pressure, to see whether they can cool themselves, and not just Namib animals.

There is a theoretical way, other than by body cooling, of creating a vapor pressure gradient favoring water acquisition, and that is by presenting a tissue surface with high osmolality to the air. Vapor pressure decreases with increasing osmolality. At 20°C, the saturated vapor pressure of pure water is 2.4 kPa. One kilograms of water contains 56 mol of water, and adding 1 mol of solute (creating a solution approximately equivalent to the osmolality of sea water) will drop water vapor pressure by \(2.4 \times \frac{1}{56} = 0.04\) kPa (Natelson and Natelson 1975, O’Donnell and Machin 1988), that is by <2%. An animal would have to present a tissue surface at 16,000 mOsmol/L, much higher than the highest urine osmolality of any vertebrate (Beuchat 1990), to create a water vapor deficit equal to that created by dropping its surface temperature by 5°C. Beament (1961) pointed out more than 50 yr ago that proposals for water vapor absorption dependent on high tissue osmolality sometimes required osmolalities not achievable physiologically. Also, osmotic acquisition of water vapor requires anatomical structures supporting fluid flow (Machin 1983) and requires energy, both to create the surface of high osmolality and subsequently to release that water to the animal’s tissues (Beament 1964).

Despite the physiological challenges, osmotic acquisition actually is feasible, in some tenebrionid beetle larvae. The rectal (or cryptonephridial) complex first discovered in \(Tenebrio molitor\) larvae provides the anatomical substrate for such a mechanism. The complex comprises the distal portions of six Malpighian tubules wrapped around the rectal sheath and is likely to have evolved to recover water from the excreta of beetles living in arid areas (Ramsay 1964). Given that it can be exposed to ambient air by rectal pumping (Coutchié and Machin 1984), the complex serves equally well to absorb ambient water vapor, and there is excellent agreement (Machin 1983) between the osmolality of the fluid (probably just a solution of inorganic chlorides) generated by the complex, 6700 mOsmol/kg, and the minimum ambient relative humidity (88%), determined experimentally, from which \(Tenebrio molitor\) can acquire ambient water vapor \([1000 \times 56 \times (100 – 88)/100 = 6720\) mOsmol/kg]. A rectal complex similar, but neither anatomically nor functionally identical, to that of \(Tenebrio molitor\) larvae, occurs in \(Onymacris marginipennis\) larvae (Machin and O’Donnell 1991). Based on allometric arguments and on actual measures of ion concentrations, Coutchié and Machin (1984) proposed that the \(Onymacris\) rectal complex might provide a surface with sufficiently high osmolality, higher
than that in _Tenebrio molitor_, dependent on the Malpighian tubules producing supersaturated potassium chloride (Machin and O’Donnell 1991). However, neither the massive osmolality required nor the experimental evidence (Coutchié and Crowe 1979a) point to absorption of water down an osmotically generated water pressure gradient being the mechanism of vapor acquisition in _Onymacris_ larvae. Indeed, though the tissue osmolality necessary for _Tenebrio molitor_ to absorb water vapor down a vapor pressure gradient can be achieved physiologically, Mellanby (1932) concluded that even _Tenebrio molitor_ larvae do not employ a vapor pressure gradient, but rather use the alternative means to acquire water vapor. They behave like a hygroscopic substance.

Acquisition of water vapor by hygroscopic surfaces is the second way that animals may acquire water vapor from ambient air (Beament 1961, Wharton and Richards 1978). Movement of water vapor into and out of hygroscopic surfaces differs fundamentally from movement in and out of surfaces with high osmolality in that it depends not on a vapor pressure gradient but on a relative humidity gradient. The hygroscopic surface may be a saturated salt solution. Saturated solutions have a critical relative humidity; if the air adjacent to the solution has a relative humidity higher than that critical relative humidity, water vapor will move out of the air and into the solution (Winston and Bates 1960). Conversely, if the air has a relative humidity less than the critical relative humidity, water vapor will leave the salt solution. If the saturated salt solution is placed in a sealed container containing an air space, the air reaches and maintains a constant relative humidity, a principle used in the calibration of hygrometers. That some insects operate such hygroscopic surfaces was demonstrated experimentally in the 1930s; living insects placed in a sealed container generated and sustained a species-specific relative humidity in the air of that chamber just as a saturated salt solution would do (Beament 1961, 1964). The critical relative humidity of a salt varies with temperature, but also varies massively with a chemical composition of the salt. Known salts cover the range from near 0% to near 100% (Greenspan 1977). As with water vapor acquired by virtue of high tissue osmolality, water acquired at hygroscopic surfaces requires energy both for creation of the hygroscopic surface and for water recovery, although surprisingly little energy is required for recovering water (Henschel and Seely 2008). In larvae of two _Onymacris_ beetle species, it is only 1.2% of their metabolic energy (Coutchié and Crowe 1979a).

Salt solutions are not the only possible hygroscopic surfaces. Cuticle in the vapor-absorbing mouthparts of the desert cockroach _Arenivaga investigata_, resident in the sand dunes of the deserts of the western United States and Mexico, is hydrophilic without being coated with salts (O’Donnell 1982a, b, O’Donnell and Machin 1988). The driving force for water movement to or from the hydrophilic surface remains the relative humidity gradient. This type of hygroscopic surface has not yet been discovered in Namib species.

Though Beament (1964) proposed that the whole insect integument could be involved in water vapor acquisition, in all insect species, not just Namib species, that acquire ambient water vapor via a specialized absorbing surface, the absorbing surfaces that have been identified, whether hygroscopic or osmotically active, have been located in the gastrointestinal tract (Wharton and Richards 1978). They can be at the mouth end of the tract, as they are in the desert cockroach _Arenivaga investigata_ (O’Donnell 1977). Absorbing surfaces in insects more commonly are at the anal end, though, and that is where they are in the Namib insects known to have them, like the rectal complex of the tenebrionid beetle larvae. Researchers at the University of California Davis exposed fasted larvae of two Namib tenebrionid beetle species, _Onymacris plana_ and _O. marginipennis_, to an array of relative humidities, and ambient temperatures up to 37°C (Coutchié and Crowe 1979a). At higher humidities, the larvae accumulated water vapor at rates that reached nearly 100% of their body mass per day, the highest recorded for any insect (Henschel and Seely 2008), but not at a uniform rate, implying some kind of feedback (O’Donnell and Machin 1988). The feedback was related to the amount of water absorbed rather than the rate of uptake (Coutchié and Machin 1984); individual larvae with very high water content gained no further mass. Accumulation in the larvae ceased at ecdysis, implying the need for an intact cuticle for water acquisition. That does not exclude absorption via the...
gastrointestinal tract since the rectum is lined with cuticle (Coutchié and Crowe 1979a). The rate of water accumulation demonstrably depended not on the ambient vapor pressure but on relative humidity, implying hygroscopic accumulation. The atmospheric relative humidity, determined experimentally, below which water accumulation into a hygroscopic surface ceases in an animal (86% for Onymacris plana larvae and 83% for O. marginipennis larvae) is designated as that animal’s critical equilibrium humidity (O’Donnell and Machin 1988, not to be confused with the critical relative humidity of a salt solution). The critical equilibrium humidities of the Namib Onymacris beetle larvae were very similar to that of the desert cockroach Arenivaga investigata (see Table 4 for critical equilibrium humidities of different species).

Another Namib insect, the zygentoman (=thysanuran) Ctenolepisma terebrans, has a much lower critical equilibrium humidity; dehydrated C. terebrans can acquire water vapor from air hygroscopically as long as the air is at a relative humidity of 47.5% or higher (Table 4). That low critical equilibrium humidity does not seem to be an adaptation to aridity, though. It is identical to that of another zygentoman, the firebrat Thermobia domestica, which is ubiquitous, though not yet recorded in the Namib (Irish 2018). It also is not the lowest critical equilibrium humidity on record. The cigarette beetle Lasioderma serricorne, a worldwide pest of tobacco, has a critical equilibrium humidity of 43%. Though Heeg (1967) thought the site was the integument, in the zygentoman the site of water vapor absorption appears to be the lower gastrointestinal tract (Noble-Nesbitt 1970), as expected for Namib insects.

For larvae of both Onymacris species to absorb water vapor hygroscopically, atmospheric relative humidity would have to be above 86%. That certainly would be the case in fog, but even in the absence of fog, depending on the year, sufficiently high relative humidity was reached on more than half the days of most months (Fig. 3), probably more than sufficient to balance the water budgets of the insects that use hygroscopic absorption. Indeed, with episodes of high relative humidity being more frequent than episodes of depositing fog, it is surprising that so few Namib animals capable of absorbing water hygroscopically have been reported. They may well be there, waiting to be discovered. They would need to be on or near the surface to benefit from the higher humidity. Even the moisture from depositing fog typically does not penetrate more than about 30 mm below the sand surface (Soderberg 2010), compared to the 1000 mm or more to which water may penetrate after heavy rain (Southgate et al. 1996).

Namib beetles and zygentomans spend most of their lives not on the soil surface but buried below it. Eckardt et al. (2013) claimed that “recent short-term monitoring of sub-surface soil humidities in the Namib suggests an ample supply of water, at least in the gaseous form,” but measurements of soil water content at 200 mm depth, near Gobabeb, do not support that claim.

Table 4. Critical equilibrium humidities of some invertebrates.

| Species             | Type/conditions                                      | Critical equilibrium humidity (%) | References                        |
|---------------------|------------------------------------------------------|-----------------------------------|-----------------------------------|
| Onymacris plana     | Namib tenebrionid                                    | 86                                | Coutchié and Crowe (1979a)        |
| larvae              |                                                      |                                   |                                   |
| O. marginipennis    | Namib tenebrionid                                    | 83                                | Coutchié and Crowe (1979a)        |
| larvae              |                                                      |                                   | O’Donnell (1982b)                 |
| Arenivaga           | Desert cockroach                                     | 81                                |                                   |
| investigate         |                                                      |                                   |                                   |
| Ctenolepisma        | Ubiquitous zygentoman                                | 60                                | Heeg (1967)                       |
| longicaudata        |                                                      |                                   |                                   |
| C. terebrans        | Namib zygentoman, previously dehydrated to 80% of    | 45–47.5                           | Edney (1971)                      |
|                     | normal body mass                                     |                                   |                                   |
| Thermobia           | Ubiquitous zygentoman                                | 45                                | Noble-Nesbitt (1969, 1975)        |
| domestica           |                                                      |                                   |                                   |
| Lasioderma          | Cigarette beetle, ubiquitous                         | 43                                | Knülle and Spadafora (1970)       |
| serricorne          |                                                      |                                   |                                   |
(Henschel et al. 2003), and nor do the few opportunistic measurements that have been made of relative humidity below the sand surface. In a relatively wet year, relative humidity 100 mm below the surface varied between 25% and 46% at one site (Robinson and Seely 1980) and was <20% at another (Seely and Mitchell 1987), well below the critical equilibrium humidity even of Ctenolepisma terebrans. So neither C. terebrans nor the Onymacris larvae could acquire water vapor hygroscopically when the surrounding sand has its usual relative humidity. They could do so only when sand relative humidity is elevated, which it will be when fog deposits or penetrates, though measurements of subsurface humidities during fogs have not been made yet. How readily the zygentomans, at least, achieve their water demands is a crucial research question, because they are so important in the biological economy of the dunes (Lawrence 1959, Watson and Irish 1988, Watson 1989, Irish 1990), and their body water could sustain the water balance of their predators.

Could the three Namib species demonstrated to be able to acquire water vapor (the zygentoman Ctenolepisma terebrans and the larvae of the tenebroid beetles Onymacris plana and O. marginipennis) theoretically acquire the vapor down a vapor pressure gradient created by a surface with high osmolality in the lower intestinal tract, rather than hygroscopically? For O. marginipennis larvae, with the lower critical equilibrium humidity of the two species at 83%, the osmolality of that surface would have to be about 9500 mOsmol/kg [1000 × 56 × (100−83)/100], much higher than the 6700 mOsmol/kg generated by the Tenebrio molitor rectal complex (Machin 1979), making that an unlikely primary mechanism in our opinion, though O’Donnell and Machin (1988) disagree. For C. terebrans, with a critical equilibrium humidity of 47.5%, that surface would have to have an osmolality of 29,400 mOsmol/kg, physiologically inconceivable. So the theoretical calculations of the osmalalities that would be required confirm the experimental observations of Coutchï and Crowe (1979a) for the larvae: The mechanism has to be hygroscopic not osmotic.

The rectal (cryptonephridial) complex first described for Tenebrio molitor is widespread among Coleoptera (O’Donnell and Machin 1988), and there probably are other beetle species in the Namib the larvae of which could absorb water vapor. The larvae of three other tenebroidids are alleged to do so, but the research remains unpublished (Appendix S3: Table S1; Coutchï and Machin 1984). O’Donnell and Machin (1988) considered that only animals with mass <100 mg could acquire water in vapor form, though the larvae of Onymacris marginipennis are somewhat larger (125–300 mg, Coutchï and Crowe 1979b). For the reasons that we have given related to surface tension, we believe that that mass limit should not be regarded as a ceiling above which the phenomenon of water vapor absorption cannot occur. Rather, it should be regarded as a mass boundary below which animals cannot access free water from droplets, and so have to access it either from water vapor or from water films that are not subject to the high surface tensions of spherical droplets. The termite Psammotermes allocerus has special anatomical structures used to access water from films (Appendix S3: Table S1; Grube and Rudolph 1995). Adults of Zaphosis species of tenebroid beetle weighing <100 mg exploit fog water (Appendix S3: Table S1); the fog water that they acquire is water from fog-moistened sand, not fog droplets. Whether they have special structures to acquire the water is not known. Both developing special structures and acquiring water vapor are energetically costlier than is acquiring water from droplets and therefore are unlikely to be used by animals big enough to be able to access water from droplets.

Just as there are likely to be other beetle larvae that absorb water vapor, there are likely to be Namib zygentoma, other than the two species that happen to have been investigated, that absorb water vapor. It is a phenomenon common in acarines (Beament 1961), but no one appears to have looked for it in Namib ticks and mites, nor investigated their dependency on fog. Ticks cannot always rely on blood to provide their body water. Some may spend 98% of their lives off hosts (O’Donnell and Machin 1988). The African ixodid tick Amblyomma variegatum (not found in the Namib or other arid environments) absorbs water vapor via the mouthparts. The mechanism proposed originally was absorption down a gradient produced by high osmolality generated by a salt produced in the saliva (Rudolph and Knülle...
1974), a method similar to that claimed later for the Pscoptera, a taxon of free-living lice, and for members of the Amblycera and Ischnocera, taxa of avian chewing lice (Rudolph and Knülle 1982). Subsequent measurements (23 yr later), though, demonstrated that the actual osmolality of the salivary salt solution in Amblyomma variegatum was not high enough to produce the necessary vapor pressure gradient, so an alternative hystroscopic mechanism was advanced, similar to that of Arenivaga investigata, based on physical capture of water by hydrophilic cuticle lining the hypostome, a component of the tick’s mouthparts (Gaede and Knülle 1997). In some members of the Amblycera and Ischnocera, the critical equilibrium humidities are in the range 43–55%. Members of the Pscoptera, Amblycera, and Ischnocera occur in the Namib, but their water budgets have not been investigated.

In the future exploration of water vapor acquisition by not just lice but all desert animals, our analysis shows that the working hypothesis should be that the mechanism is more likely to be creation of a water vapor pressure gradient by body surface cooling, or creation of a relative humidity gradient by employment of a hydroscopic surface, probably in the gastrointestinal tract, rather than by osmotic processes. So we would need to look for situations in which ambient vapor pressure is high and animals can cool below air temperature, or for animals that have hydroscopic collecting surfaces. Animals with masses <100 mg are likely candidates to be users of water vapor, because they are too weak to extract water from droplets. So we need to seek out small invertebrates, like zygentomans. A fruitful place to search for any new vapor-absorbing invertebrates in the Namib might be on sand dunes as air water content increases in front of an advancing fog, or on those fogless days in which relative humidity is very high (Fig. 3).

**Generation of metabolic water**

Animals are obliged to acquire free water, vapor, or liquid, only if the water available from their diet does not fulfill their needs. One source of dietary water is metabolic water, which arises from the oxidation of physiological fuels (Schmidt-Nielsen 1990:333). For starch, for example, the oxidation equation is \( \text{C}_6\text{H}_{12}\text{O}_6 + n\text{O}_2 \rightarrow 6\text{nCO}_2 + 5\text{nH}_2\text{O} \). The mass of metabolic water produced, per kJ of energy oxidized, varies a little with the fuel being oxidized. For starch, it is 31 mg/kJ, and for fat, 26 mg/kJ (Schmidt-Nielsen 1990:333). The rate of fuel oxidation and therefore the rate at which metabolic water is produced usually are determined by the rate of turnover of the energy necessary for other physiological functions. Because mass-specific resting metabolic rate (mL \( \text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \)) increases as animal mass decreases, mass-specific metabolic water production also increases as mass decreases. So, allometrically, the smaller the animal, the greater is the contribution of metabolic water to its water budget. However, small ectotherms in the Namib do not conform to the allometry because they have extraordinarily low resting metabolic rates for their mass (Lighton et al. 2001). For example, metabolic rate is as low as 0.044 mL \( \text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \) in the tenebrionid beetle Onymacris unguicularis (Fig. 7) at rest (Louw et al. 1986), which, if the beetle were combusting fat, would generate only 23 mg \( \text{H}_2\text{O} \cdot \text{g}^{-1} \cdot \text{h}^{-1} \) of metabolic water, a tiny contribution to its water budget. Metabolic rate also is very low in the larvae of the beetles *O. plana* and *O. marginipennis* (Coutchié and Crowe 1979a). On the other hand, metabolic rate, and so too the production of metabolic water, is high when Namib animals are exercising. For example, when the athletic tenebrionid beetle *O. plana* (Fig. 7) ran, its metabolic rate increased 64-fold (Bartholomew et al. 1985, Nicolson 1990a) and metabolic water production proportionally, though much of the water generated in running was wasted because it was lost as water vapor in the increased respiration induced by the exercise.

The prolific Namib arthropod fauna is dominated by apterous tenebrionid beetles (Wharton and Seely 1982), excluded from flight, a form of exercise with energy turnover and therefore metabolic water production potentially so high that metabolic water has to be dumped, as has been observed in some bee species (Nicolson 1990b, 2009). Rather than ever dumping metabolic water, some Namib species deliberately increase metabolic water production, even at rest, when desiccated. To combat hyperosmolality, some Namib beetle species, notably *Onymacris plana*, increase combustion of body fat stores, which increases the rate of metabolic water production (Nicolson 1980, Cooper 1982).
However, in most species studied, rate of fat metabolism is not sufficient to compensate for desiccation (Table 5). Also, metabolizing fat, like exercise, requires increased respiration and, in some insect species in dry environments, the consequential increased respiratory water loss may exceed the rate of generation of metabolic water, so making futile the combustion of fat to generate water (Cloudsley-Thompson 2001).

The tenebrionid beetles that rely on metabolic water production to combat desiccation are herbivorous. Even when Namib animals themselves are carnivorous, like scorpions, their prey tends to be herbivorous. So, the fuel that is combusted to produce metabolic water ultimately comes from plants, and many of those plants are sustained by fog between infrequent rainfall events. The typical ecological consequences of precipitation events in the Namib are shown in Table 6. Intermittent heavy rainfall pulses are crucial for Namib biota. Arising from their consequences for vegetation, they bring about irruptions in herbivorous beetle populations (Seely 1989, Seely et al. 2005) and allow migration of mammal species (Seely and Griffin 1986). Also, the pulses may fill endorheic pools that harbor a surprising array of fauna, dormant when the pools dry up (Curtis et al. 1998). Small rainfall events do occur between the heavy pulses, usually as convective thunderstorms, but the rainfall is slight and spatially and temporarily highly variable (Eckardt et al. 2013). It is the more-predictable fog that sustains plants between the pulse years, and some Namib plants have specialized adaptations that enable them to enhance their exploitation of fog water (Seely et al. 1977, Louw and Seely 1980, Ebner et al. 2011, Nørgaard et al. 2012, Gottlieb et al. 2019).

In summary, propagation of the vegetation that Namib animals combust, so forming metabolic water, seems to require large rainfall events, which are rare. Between those events, the vegetation is sustained by fog. The contribution of metabolic water to the water balance of those animals at rest is constrained, though, by their typical low metabolic rates, which may or may

---

Table 5. Do Namib tenebrionids metabolize fat to produce body water during desiccation?

| Species            | Fat metabolism                                                                 | Reference                  |
|--------------------|--------------------------------------------------------------------------------|----------------------------|
| Onymacris plana    | So efficient that body water content, as a fraction of body mass, does not decrease during desiccation | Nicolson (1980)            |
| O. unguicularis    | Metabolizes too little to maintain body water content.                            | Naidu (2008)               |
| Physadesmia globosa| Metabolizes too little to maintain body water content. Shade-seeking diurnal forager. | Naidu and Hattingh (1988)  |
| Stenocara gracilipes| Metabolizes too little to maintain body water content. Shade-seeking diurnal forager. | Naidu (2001a)              |
| Stips stali        | No fat metabolism. Slow-moving nocturnal forager.                                | Naidu and Hattingh (1986)  |

Table 6. Ecological significance of precipitation events on Namib vegetation.

| Precipitation event | Frequency                                                                 | Significance                                                                 | Reference                                                                 |
|---------------------|----------------------------------------------------------------------------|------------------------------------------------------------------------------|---------------------------------------------------------------------------|
| Heavy rainfall pulses| About every 40 yr, typically 100 mm in a year                                | Germination of plants, Generate biomass, especially detritus, Decompose buried plant material | Seely and Louw (1980), Seely (1978), Southgate et al. (1996), Henschel et al. (2007), Aushiku et al. (2015), Jacobson and Jacobson (1998), but see Jacobson et al. (2015) |
| Small rainfall events| Every 2–9 yr, annual median 12 mm (95% CI 10–21 mm) at Gobabeb Research Institute (1963–2010) | Allow germinated grass to grow, in most years                                 | Henschel et al. (2003)                                                    |
| Fog                 | Up to 1 L m$^{-2} d^{-1}$ (equivalent to 1 mm/d)                            | Sustains plant growth                                                        | Robinson and Seely (1980), Pietruszka and Seely (1985), Seely and Griffin (1986), Soderberg (2010) |
not prevail in the animals of other fog-dependent deserts.

**Consumption of pre-formed water**

The other source of water from the diet is pre-formed water, liquid water within solid food. The plant fuel responsible for the generation of metabolic water also brings in pre-formed water, in the living plant, or in its decomposition products. Fragmented plant material forms detritus that is distributed widely by wind, even to the vegetationless dunes (Seely 1978, Robinson and Seely 1980). Detritus mass can exceed above-ground living biomass in deserts (Hadley and Szarek 1981), and detritivory is common among Namib invertebrates (Seely and Griffin 1986, Seely 1993). Pioneering desert entomologist P. A. Buxton discovered, in the Palestinian desert, the extraordinary capacity of detritus to accumulate water from ambient air at night, provided that ambient relative humidity exceeded 80% (Buxton 1924), as it would on foggy Namib nights. Tschinkel (1973) demonstrated similar accumulation of water on detritus in simulated Namib fog. So, in the case of detritivores, it is the nocturnally feeding species that ought to be able to benefit best from pre-formed water (because the plants and detritus dry during the day), and they should benefit most when their food has absorbed fog water (Henschel and Seely 2008). Anomalously, though, in fogs when *Lepidochora* beetles have detritus available that has a water content of 60%, they do not eat it. Rather, they eat detritus at dry times of the day, when its water content is only about 2% (Seely and Hamilton 1976). Indeed, no Namib fog-harvesting beetle species eats during fogs (Seely 1979, 1993). That may be because most of the known fog-harvesting beetles normally are diurnally active foragers; some nocturnally active beetle species elsewhere do consume droplets from fog or dew and eat hygroscopic detritus at the same time (Broza 1979).

In contrast to the tenebrionid beetles, some herbivorous vertebrates do benefit from the pre-formed water that is provided by fog (Table 7). Carnivorous animals generally have far more pre-formed water available to them than do herbivorous animals, in the body fluids of their prey. The dune lizard *Meroles anchietae* has a very sophisticated adaptation for storing fog water (see *Physiological challenges associated with fog-harvesting*), but its ability to acquire and store fog water may contribute little to its routine water budget in the field (Cooper and Robinson 1990), which implies that the adaptation may have evolved only to deal with emergencies.

So pre-formed water makes a variable contribution to the water intake of Namib animals. For herbivorous animals, having plant material wet by fog enhances pre-formed water intake. However, some beetles that have access to fog-sodden detritus shun it, for reasons still unknown.

**Obligate fog-harvesters**

Though animals that do not acquire sufficient metabolic and pre-formed water have to acquire free water, that an animal consumes free fog water when it is available does not necessarily mean that the animal needs fog water to balance its water budget (Cooper 1982). Indeed, in the laboratory, the iconic fog-basking beetle *Onymacris unguicularis* can survive perfectly well on metabolic and pre-formed water obtained from a

| Table 7. Examples of Namib animals benefitting from consuming pre-formed water. |
|-----------------|-------------------------------------------------|-----------------|
| **Species**     | **Benefit**                                    | **Reference**   |
| Ostrich *Struthio camelus* | Feed in the early hours of the morning on grass containing 27% water; the same grass at solar noon contains 13% water | Louw (1972) |
| Giraffe *Giraffa camelopardalis* | Evening fog increases the water content of *Commiphora* spp. and other plants, which are consumed | Fennessy (2009) |
| Elephant *Loxodonta africana* | Does not need to store fog water when eating water-rich beetle larvae or moist plant ovules | Cooper and Robinson (1990), Nagy and Shemanski (2009) |
| Lizard *Meroles anchietae* | Acquires water in excess of its needs from termite diet | Murray et al. (2014) |
| Lizard *Pedioplanis husabensis* | | |
dry seed diet (Cooper 1982), though they may not be able to sustain maximum surface foraging activity or egg production (Seely 1979). A similar situation prevails for the sidewinding adder *Bitis peringueyi*, which harvests water droplets from fog and drinks them, but can function perfectly well without free water if it has access to its usual prey of lizards (Robinson and Hughes 1978). Compelling evidence for a need for fog water would be the inability of an animal to survive if deprived of that water; such evidence has not been forthcoming in the field, but when tenebrionid beetle larvae were deprived experimentally from access to water vapor, they perished (Henschel and Seely 2008). Though taking such laboratory studies to the field is extraordinarily difficult, those field studies need to be done. The decline in populations of tenebrionid beetles that are not fog-harvesters, relative to the decline in fog-harvesters (Seely et al. 2005), is good circumstantial evidence, obtained in the field, of the need for fog water in some species.

Another way of establishing if an animal needs fog water is to analyze its water budget formally, an analysis best accomplished with the doubly labeled water technique, which uses isotope dilution to measure energy turnover rate (and consequently rate of generation of metabolic water) and total water turnover. Diet analysis allows estimation of pre-formed water consumption, so that the deficit, if any, between total water turnover and water available from metabolic water and pre-formed water can be calculated. Cooper (1982) used doubly labeled water to analyze the water budget of *Onymacris unguicularis* active on the dunes and concluded that fog water contributed half of that budget, with the implication that *Onymacris unguicularis* would be unlikely to survive on the dunes in the absence of fog. Individuals can survive without free water in benign environments (laboratory temperature, controlled 75% relative humidity, partly crushed bird seed available ad libitum). The implication that *O. unguicularis* would be unlikely to survive in its natural habitat is supported by its geographic distribution. It is confined to the fog belt, extending 60–70 km from the coast, even though otherwise-suitable dune habitats extend at least 50 km further inland (Fig. 2; Seely 1979). Its distribution coincides with that of the succulent plant *Trianthema hereroensis*, and the only content of the crops of Cooper’s beetles caught in the field was the seeds of *T. hereroensis* (Cooper 1982). *T. hereroensis* depends on absorbing water directly through its leaves (Seely et al. 1977), an attribute not unique to Namib plants (Mooney et al. 1980). Cooper’s analysis, though, assumed, without attempted justification, that the doubly labeled water technique overestimated rate of energy consumption by 25% and did not explain how he quantified the rate of absorption of water vapor by the beetle.

Murray and his colleagues recently used the doubly labeled water technique, without the overestimate assumption, to analyze the water balance of the endemic rock-dwelling diurnal gecko *Rhoptropus bradfieldi* (Murray et al. 2015). They concluded that their population of this gecko species needed free water to balance its water budget. They identified fog as the likely source of that free water, though no one actually has seen *R. bradfieldi* consuming fog water. Though Murray and colleagues did not address the possibility, *R. bradfieldi* may acquire its fog water from the tissues of its ant prey if the ants increase body water content in fog. Using the data of Nagy et al. (1993), Murray and his colleagues concluded that, like *R. bradfieldi*, to balance its water budget another diurnal species of *Rhoptropus*, *R. afer*, also rock-dwelling but on different kinds of rock, needs free water, usually fog water because it is available more frequently (Fig. 3), but also potentially dew because the lizard lives on solid rock on which dew can condense (see Appendix S2; Murray et al. 2015). Though it lives in equally arid environments and has a higher body mass than does *Rhoptropus*, the sand-burying lizard *Gerrhosaurus skoogi*, resident in the northern Namib dune sea (Mitchell et al. 1987, Lamb and Bauer 2013), does not require free water, according to doubly labeled water analysis, because it acquires so much pre-formed water from the plant! *Nara (Acanthosicyos horridus)*, the mainstay of its diet (Nagy et al. 1991). Similarly, the Husab sand lizard *Pedioplanis husabensis*, sympatric with *R. bradfieldi* at some locations, is able to acquire sufficient pre-formed water from its preferred termite prey so as not to require free fog water (Murray et al. 2014), which does not preclude the lizard using fog water opportunistically, if it is available.
PHYSIOLOGICAL CHALLENGES ASSOCIATED WITH FOG-HARVESTING

Reliance on free water from irregular fogs, as a source of body water, creates at least three physiological problems for the fog-harvesters. The first problem is how to survive without lethal dehydration between one fog event and the next. Even though fog is more regular than is rain, when the next fog will occur cannot be predicted. How does the interval between fogs compare with how long beetles can survive without free water? Measurements of the intervals between depositing and non-depositing fogs (for example Table 1; Appendix S1) show that animals that rely on depositing fogs may need to survive for months without drinking. Those that can access atmospheric water in other ways may need to survive only weeks. How long they may need to survive also depends on where they are in the Namib (Table 1), with the shortest interval between fogs occurring well inland. At the eastern edge of the fog belt, where intervals between fogs can exceed two years (Table 2; Appendix S1), specialist beetles that rely on fog-basking are absent.

Surviving desiccation between fogs requires avoiding hyperosmolality, either by maintaining body water content by synthesizing water from lipids as some beetles do (Nicolson 1980, Cooper 1982), or by removing osmolytes as body water declines as many other beetle species do (Hatttingh et al. 1984, Henschel et al. 2001, Naidu 2001b). Not all Namib tenebrionid beetle species, though, have effective osmoregulation during dehydration (see Table 8 for hemolymph properties during desiccation), and some species defy the rules for surviving desiccation, apparently tolerating the hyperosmolality and other consequences of desiccation. The trench-digger *Lepidochora discoidalis* exhibits substantial concentration of its hemolymph when it is dehydrated, but survives desiccation well (Louw and Hamilton 1972); how it does so physiologically has not been examined. Subjected to desiccation in the laboratory, half of a sample of *L. discoidalis* survived for 34 d and half of a sample of *Onymacris unguicularis* for 78 d, but at the higher relative humidities of their natural habitats, they could survive longer (Seely et al. 1983). If there are phylogenetic, or ecological, or physiological principles distinguishing those beetles that withstand desiccation and those that do not, and or underlying what mechanisms those that withstand desiccation use, those principles have not emerged yet.

The second physiological problem for fog-harvesters that acquire free water from episodic fogs is where to store that water. That is not a trivial problem for animals that can consume more than a third of their mass during a single fog event (Table 9; Hamilton and Seely 1976), especially if they have a hard carapace preventing expansion of body tissues, although tenebrionid beetles with hard carapaces could use their subelytral cavity as an expansion space (Slobodchikoff and Wismann 1981). The third physiological problem is how to deal with the consequences for osmoregulation of admitting fog water with very low osmolality (Appendix S1) into the body fluid space. That third problem may not be as grave for insects as for other taxa, because the ability of some Namib insects to tolerate wide variations in body fluid osmolality (Table 8) apparently is not a rare phenomenon among insects (Barton-Browne 1964). The problem of finding space to store fluid consumed is not nearly as serious for fog-consumers as it is for blood-sucking invertebrates (Machin 1981), but blood does not have the low osmolality of fog water. One solution to both the second and third problems would be to consume fog water only after desiccation, when body water is decreased, and consequently, there is available volume and an excess of osmolytes.

Table 8. Hemolymph volume and osmolality changes of Namib tenebrionids during desiccation.

| Species               | Hemolymph volume decrease (%) | Hemolymph osmolality increase (%) | Reference                  |
|-----------------------|-------------------------------|----------------------------------|----------------------------|
| *Stenocara gracilipes*| 72                            | 5                                | Naidu (2001a)              |
| *Onymacris plana*     | 66                            | 13                               | Nicolson (1980)            |
| *Lepidochora discoidalis* | -                           | 27                               | Louw and Hamilton (1972)   |
| *Physadesmia globose* | -                             | 34                               | Naidu and Hatttingh (1988) |

*Hyphen: hemolymph volume decreases not reported.*
There is circumstantial evidence that some tenebrionid beetles indeed reject available fog water if they are not in water deficit. There was high individual variability in the amount of water gained during fogs by both *Onymacris unguicularis* (Hamilton and Seely 1976) and *Lepidochora discoidalis* (Seely 1979), and fewer beetles emerged if the fog events were repetitive (Seely 1979), when, presumably, any relative water deficit has been resolved.

The strategy of drinking fog water only when thirsty, that is when in body water deficit, relies on there being a tolerable interval between fog events (Pietruszka and Seely 1985), and may be effective currently, but the strategy will lose effectiveness if fog events become less regular under climate change (Hansler et al. 2011), or fog distribution across the landscape changes (Cermak 2012). A safer strategy would be to consume as much fog water as possible whenever a fog occurs, so building up as big a reserve of water as is possible, and it is that strategy that will have difficult-to-manage consequences for space and osmoregulation. When offered water after being dehydrated in the laboratory, the beetle *Sips stali* over-compensated such that its hemolymph volume was much greater than normal, and hemolymph osmolality decreased significantly (Naidu and Hattingh 1986). The species has not (yet) been observed harvesting fog, though, and may have evolved not to do so. It is nocturnal, surface-active at the times at which fogs occur, but is far more common in river beds, away from the depositing fog, than on dune slopes (Wharton 1983, Seely et al. 2005).

One way of storing fog water without excess dilution of body fluids is to isolate the fog water internally and then gradually to add osmolytes to it, before allowing it to mix with other body fluids. Such a storage strategy has been reported for *Onymacris unguicularis*, which retains fog water in its gut (Hamilton and Seely 1976, Seely 1979). For animals like *O. unguicularis* that have a rectal complex that recovers water from excreta (Ramsay 1964), the gut is a safe storage site, because any water reaching the complex will be absorbed. Before it was discovered in *O. unguicularis*, physical storage of fog water had been detected in the slipface lizard *Meroles anchietae*, a species confined to the fog belt (Louw 1972), which can retain water in a bladder (Louw and Holm 1972, Cooper and Robinson 1990). In that lizard species, there was residual water in storage for at least eight weeks after a drink (Louw and Holm 1972), remarkably long but well short of the longest interval between depositing fogs (Table 1; Appendix S1). The osmolality of the stored fluid was lower than blood osmolality, but much closer to blood osmolality than to fog osmolality (Cooper and Robinson 1990). Even though absorbing the water would have restored toward normal the plasma osmolality of dehydrated lizards, 35% more than that of lizards captured in the field after a fog, the osmolality of the dehydrated lizards hardly was affected immediately after they drank, confirming obligatory isolation of the water that has been consumed recently (Louw and Holm 1972). Whether the lizards have control on when water is released from storage is not known. It would be an advantage to be able to release some water when they eat prey with an osmolality higher than their own (Louw and Holm 1972).

Whether the other Namib lizard species that are fog-harvesters (Appendix S3: Table S1) have water-storage anatomy similar to that of *Meroles anchietae* is not known. Analogous structures but at the oral end of the gastrointestinal tract, the salivary gland water sacs, allow the termite *Hodotermes mossambicus* to isolate and store water such that its body water content reaches 95% (Mitchell et al. 1993). In other dry areas,

| Species                  | Description   | Mass (mg) | Maximum change of body mass (%) | Water gained (mg) | Reference                  |
|--------------------------|---------------|-----------|---------------------------------|-------------------|-----------------------------|
| *Meroles anchietae*      | Lizard        | 3400      | 11                              | 370               | Louw and Holm (1972)        |
| *Onymacris unguicularis* | Beetle        | 700       | 34                              | 240               | Hamilton and Seely (1976)   |
| *Lepidochora discoidalis*| Beetle        | 80        | 41                              | 33                | Seely and Hamilton (1976)   |
Hodotermes colonies dig shafts downwards until they encounter wet soil, from which they can access water (Picker 1986). Whether Hodotermes can reach subsurface water in the Namib is unknown. The tunnels of another Namib termite Baucaliotermes hainesi seem too shallow for those termites to do so (Tschinkel 2010). Hodotermes has another potential source of water to fill those sacs, though. Although usually considered diurnally active and therefore expected not to encounter fog, at least in the summer H. mossambicus is active on or near the surface both in the day and at night in the Namib (Mitchell et al. 1993, Henschel 1994, Hager 2008). Nocturnal activity would give them access to fog water, but whether they use fog water has not been studied yet.

Those Namib animals that cannot isolate the fog water that they consume face a formidable osmoregulatory dilemma. They will dehydrate during the intervals between precipitation events and that dehydration will be relatively slow, taking days or weeks, potentially allowing compensation. When they drink at an event that makes free water available, such as in or after a fog, they will accumulate substantial amounts of low-osmolality liquid in minutes or hours and, if they do not isolate that water, will need rapid osmoregulatory interventions to prevent tissue osmolality plummeting (Hattingh et al. 1984). That some beetles will consume free fog water off their carapaces, rather than more-abundant and less-dilute liquid that has accumulated on plant material during fogs (Seely and Hamilton 1976, Gottlieb et al. 2019), seems to imply a benefit to consuming low-osmolality water, in spite of the challenges of doing so. What that benefit may be requires further investigation.

How do animals cope physiologically with rapid rehydration? Diuresis (excretion of the excess water) is the most-common physiological response of animals faced with water overload. Adults of the tenebrionid beetle Onymacris plana have the capacity to excrete excess body water through diuretic hormone acting on their Malpighian tubules (Nicolson and Hanrahan 1986, Cloudsley-Thompson 2001). However, one expects desert animals to avoid diuresis. Desert animals need to conserve the water, and so would benefit by manipulating the osmoles, not the water, if water overload threatens osmoregulation. Osmoregulation may not be the only reason for the beetles to conserve water; they may need high body water for egg and sperm production (Seely 1979, Hattingh et al. 1984). Some beetles indeed can sequester excess osmoles temporarily during dehydration and release them into the dilute fluid acquired during rapid rehydration (Nicolson 1980, Naidu and Hattingh 1986, Naidu 2008). Organic molecules, notably amino acids but also unidentified molecules, contribute substantially as osmoles during rehydration in some species (Naidu 1998, 2001a, b), as they do in some invertebrate species away from the Namib, and especially aquatic species (Barton-Browne 1964). Arthropods with trachea are at an advantage over those that have to trade off hemolymph osmoregulation against hemolymph respiratory function (Hadley 1994). Apart from, or addition to, manipulating osmoles, when they consume fog water, beetles could switch off the process of generating metabolic water from fat, which they use to produce metabolic water during dehydration (Nicolson 1980, Cooper 1982), and so both reduce water load and preserve energy stores. Table 10 shows how the Namib tenebrionids that have been studied cope with the physiological challenge of rehydration when consuming fog water. It is highly anomalous that the species best equipped to deal with rapid rehydration is a species that appears not to rehydrate using fog water.

Whether taxa other than tenebrionid beetles have the capacity to osmoregulate if they overhydrate, without dumping water, remains to be investigated. One would expect to find animals able to sequester water, and animals with highly adapted osmoregulation, in other fog-dependent deserts. Accessing fog water without being able to manage it internally would be counteradaptive.

**Namib Fauna and Fog: The Future**

Fog past and present clearly has been influential in the lives of many taxa of Namib animals. What influence it will have in future depends on the yet-unknown answer to a crucial question: What will happen to the Namib fog regime under climate change? In addition, though, to addressing future climate change, there is much to be done before we properly understand the interaction between current fog and fauna of the Namib.
To date, research on the interaction between fog and fauna of the Namib has focused on tenebrionid beetles. As the late and legendary desert fauna expert John Cloudsley-Thompson put it, “not infrequently, the only animal to be seen during the day, if any is visible at all, will be a tenebrionid beetle” (Cloudsley-Thompson 2001). In a long-term pitfall trapping project conducted near Gobabeb, tenebrionid beetles made up 91% of all animals caught (Henschel et al. 2003). According to Lamb and Bond (2013), “tenebrionid species richness and morphological diversity are far greater in southwestern Africa than anywhere else on the continent.” So researchers have concentrated on what has been before their eyes, novel, interesting, and abundant. Concentration on adult tenebrionid beetles necessarily has left gaps (see Table 11 for resulting research opportunities). One only has to review how many other insect species (Neuroptera, Hymenoptera, Orthoptera, Dermaptera, Zygentoma, Collembola, Isoptera) were caught in the long-term pitfall traps (Henschel et al. 2003) and to accept that only ground-dwelling species were caught in the traps, to realize how many gaps there are in studies of insect fog dependency. Just as invertebrate research in the Namib has concentrated on one group, the tenebrionid beetles, so among the vertebrates research on water budgets has concentrated on reptiles, and especially lizards. That

**Table 10. How Namib tenebrionids cope with rehydration when consuming fog water.**

| Species and fog behavior | Mechanism | Efficiency | References |
|--------------------------|-----------|------------|------------|
| Lepidochora discoidalis (Trench-digger) | - | Osmoregulate well during rapid rehydration | Louw and Hamilton (1972), Hattingh et al. (1984) |
| Onymacris marginipennis larvae (Hygroscopic vapor absorber) | - | Osmoregulate well at high hemolymph volumes. Osmolality changes by 13% of the change expected from the change in hemolymph volume | Coutchié and Crowe (1979); Machin (1981) |
| Onymacris plana (Active fog-harvester) | Increase hemolymph [K⁺] and [Cl⁻] when partially restoring hemolymph volume. Use amino acids as osmolytes | Excellent regulation of hemolymph osmolality during rehydration in laboratory | Naidu (2001a) |
| Onymacris rugatipennis (Unlikely to use fog. See Appendix S3) | Require food for osmoregulation during rehydration, perhaps for osmolytes. Rapidly re-synthesizes fat during rehydration. | Expected to cope well | Naidu (2008), Cooper (1982) |
| Onymacris unguicularis (Fog-basker) | Takes in fog water with sodden detritus | In laboratory (no detritus), efficient on the first day of rehydration but collapsed after that, leaving beetles atactic | Naidu and Hattingh (1988) |
| Physadesmia globosa (Opportunist fog-harvester) | Uses amino acids as osmolytes | Tenebrionid best equipped to cope with rapid consumption of fog. In laboratory, previously desiccated for 10 d, increased hemolymph volume 2.5-fold over an hour of drinking; hemolymph osmolality decreased by only 4% | Naidu (2001a) |
| Stenocara gracilipes (Not observed using fog) | - | In laboratory, previously desiccated for 10 d, increased hemolymph volume 2.5-fold over an hour of drinking; hemolymph osmolality decreased by only 4% | Naidu (2001a) |
| Stips stali (Use of fog not studied) | - | In the field, regulation of body water and osmolality much better during rehydration | Naidu (1998) |

*Hyphen: mechanism unknown.*
focus is not surprising. Lizards are the most conspicuous of the Namib vertebrates (Herrmann and Branch 2013). There are huge gaps in our understanding of the fog dependency of other vertebrates. For carnivorous vertebrates, it may well be the fog dependency of their prey that is crucial; in the nearby Kalahari Desert, survival of aardvark *Orycteropus afer*, notably absent from the Namib, is dependent on the water balance of the termites that they eat (Rey et al. 2017).

If we are to engage in new research on the water budgets of under-researched Namib fauna, what kind of research should that be? As we have argued previously, in the context of large
terrestrial mammals (Mitchell et al. 2002), we believe that laboratory studies are not sufficient on their own. For example, the suite of detailed studies on the osmoregulation of beetles desiccated for 10 d and kept at constant laboratory temperature does not tell us whether the osmoregulation of those beetles is adequate for survival when the interval between depositing fogs can exceed 100 d, and the beetles in their natural habitats certainly will not maintain a constant body temperature. We appeal for a greater emphasis on field research. Also, the laboratory studies invariably have investigated a single species in isolation. That is not a realistic reflection of life in a natural habitat, where no single species is isolated from a community. As we have contended, the ability of an insectivorous species, for example, to manage its water budget may depend little on its exchange of water with the physical environment, but rather on the exchange of water between its prey and the prey’s environment.

Included in future field studies must be better measurements not just of the functioning of the animals themselves but of their environments. Measurement of the environmental conditions in the Namib has been, and continues to be, good for above-ground environments, but with many Namib species living much or all of their lives below the ground surface, we need much better measurements of the psychrometric characteristics of subsurface environments. In the context of fog, we especially need measurements of temperature and water vapor pressure over a profile of depths below the surface, across the fog belt. Some such measurements have been made, mainly opportunistically for the purposes of research projects being conducted at the site (Seely and Mitchell 1987, Eckardt et al. 2013), but we need systematic measurements. Even those data that have been gathered systematically for above-ground environments are not yet accessible universally or analyzed fully. For example, there is a pressing need for an update on Table 1, related to intervals between fogs.

So there would still be much to be done on the fog dependency of Namib fauna even if there were no changes in the fogging for its environment. But climate change ensures that its environment is changing (Thuiller et al. 2006) and will continue to do so for the rest of the century at least. Desert-adapted species are particularly vulnerable to the consequences of climate change (Vale and Brito 2015). Modeling predicts that the west of southern Africa, including the Namib, will become hotter and drier (Engelbrecht et al. 2015). Whereas in 2001 one could say “the Namib is not hostile to many of its inhabitants” (Henschel et al. 2001), it may well be hostile to many by 2100. Although we have some information about rain, there is no certainty about what is happening, and will happen, to Namib fog, though a decline seems inevitable. Mainly because its formation and distribution depend on a complex interaction of wind regimes of uncertain future (Torregrosa et al. 2014, Bakun et al. 2015), it is extraordinarily difficult to predict future fog patterns (see Appendix S5). We need to keep working toward a better understanding of the future climatology of Namib fog. As changes in the physical environment occur, we need to monitor the consequences on the Desert’s food webs, beginning with plants (D’Odorico et al. 2009). We need to pick index plant and animal species currently considered fog-dependent and fog-independent, and to track their physiology and ecology over time, as their environment changes. Establishing that a species is fog-dependent, that is an obligate fog-user, will not be easy, since use of fog as a water source does not necessarily imply dependence on fog. We also need to monitor the abundance of animal species considered fog-dependent and fog-independent, and not just the abundance of diurnally active species, nor indeed just of species that emerge on to the surface. Finally, we need to compare changes in the biology of the Namib fauna with concurrent changes in deserts elsewhere, both fog-dependent and fog-independent. Very little is known about the biology of the fauna of foggy deserts other than the Namib and perhaps the Negev Desert in Israel. There has been substantial research on the fog climatology, and the fog-dependent flora and micro-organisms of the Atacama Desert of South America (Rundel et al. 1991, Cáceres et al. 2007) but little or no research on the fog dependency of its multicellular animals.

So the Namib is unique among foggy deserts in the wealth of research conducted on the relationship between its fauna and fog. Is its fog meteorology and its biology also so unique that that wealth of research will not inform our future understanding of the relationship between fauna and fog in other foggy deserts? Certainly, no other
coastal foggy desert has the combination of cool coastal climate, large sand dune mass, and land gently rising from the coast of the Namib (Koch 1962, Seely 1978, 1984). That means that fog meteorology (where and when fog forms and deposits) will be different elsewhere, as will be the relative contributions of rain and fog to the free water intake of animals. Species certainly will be different in other deserts, but will the faunal structures and relationships be different? We know that 60% of tenebrionid beetle species that occur on the sand dunes of the central Namib occur nowhere else in the world (Seely 1993), but the phenomenon of tenebrionid endemicity is not unique to the Namib. Of the tenebrionid species of the Monte Desert of Argentina, 57% are endemic (Roig-Juñent et al. 2001). Of the 359 tenebrionid species and subspecies inhabiting Peru, 60% are endemic to it (Giraldo and Flores 2016). We expect the principles that determine how Namib tenebrionids interact with fog will apply to tenebrionids elsewhere, though those interactions have not yet been discovered elsewhere. We expect, for example, that, as in the Namib, most species (not just tenebrionids) that have adapted to access fog water will do so opportunistically; a few species may have highly specialized adaptations that allow them to make up a significant part of their water budget from fog. We expect that, as in the Namib, invertebrates with masses above about 100 mg accessing fog water will access droplets; those with lower mass will access water vapor and will do so hygroscopically. We expect that, as in the Namib, some fog-dependent invertebrates will have specialized physiological mechanisms for managing body fluid osmolality during dehydration and rehydration. We do believe that the body of research on the animals of the Namib, which we have reviewed and analyzed, is the flagship internationally for research on the fauna of foggy deserts. Buxton’s classical book entitled, *Animal life in deserts; a study of the fauna in relation to the environment*, published in 1923, does not contain the words “fog” or “Namib.” That would not be the case in any similar book published now.

**ACKNOWLEDGMENTS**

This review paper originated at the FogLife colloquia held in 2014 and 2015 at the Gobabeb Research Institute, Namibia, which brought together researchers and students from Namibia, South Africa, and elsewhere, to discuss the biological impacts of past, current, and future fog in the Namib. The colloquia were funded by the South African National Research Foundation (NRF) and the Namibian National Commission on Research Science and Technology (NCRST), through grants made under the NRF/NCRST Namibia/South Africa Collaborative Research Programme to Gillian Maggs-Kölling, Mary Seely, W. Maartin Strauss, and Duncan Mitchell. We commend the NRF and NCRST for their prescience in supporting the colloquia and thank them for their financial support. We thank Gillian Maggs-Kölling, Director of the Gobabeb Research Institute, and her staff, for hosting the colloquia. For their help in tracking down elusive papers, we also thank Monja Gerber (Gobabeb Research Institute) and Shane Maloney (University of Western Australia). For providing valuable information about termite biology, we thank Rüdiger Wehner (University of Zurich), Mike Picker (University of Cape Town), and Frances Duncan (University of the Witwatersrand). For providing expert information on the formation of Namib fog, we thank Roland Vogt (University of Basle). We are particularly indebted to Trip Lamb (University of East Carolina) for his exquisite array of beetles (Fig. 7), which he generously constructed for our paper.

**LITERATURE CITED**

Ahearn, G. A., and N. F. Hadley. 1969. The effects of temperature and humidity on water loss in two desert tenebrionid beetles, *Eleodes armata* and *Cryptoglossa verrucosa*. Comparative Biochemistry and Physiology 30:739–749.

Aushiku, N. N. L., L. Buschbeck, A. Christian, M. Handjaba, L. Haraes, J. Ithindi, K. Johannes, A. Kandjai, and E. Ndjomba. 2015. Changes in rainfall and biomass in the Namib sand sea dune ecosystem over 52 years. Journal of the Namibia Scientific Society 63:203–221.

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. Science 247:198–201.

Bakun, A., B. A. Black, S. J. Bograd, M. García-Reyes, A. J. Miller, R. R. Rykaczewski, and W. Sydeman. 2015. Anticipated effects of climate change on coastal upwelling ecosystems. Current Climate Change Reports 1:85–93.

Bartholomew, G. A., J. R. B. Lighton, and G. N. Louw. 1985. Energetics of locomotion and patterns of respiration in tenebrionid beetles from the Namib Desert. Journal of Comparative Physiology B 155:155–162.
Barton-Browne, L. B. 1964. Water regulation in insects. Annual Review of Entomology 9:63–82.
Beadent, J. W. L. 1961. The water relations of insect cuticle. Biological Reviews 36:281–320.
Beadent, J. W. L. 1964. The active transport and passive movement of water in insects. Advances in Insect Physiology 2:67–129.
Beech, C. A. 1990. Body size, medullary thickness, and urine concentrating ability in mammals. American Journal of Physiology: regulatory Integrative and Comparative Physiology 258:R298–R308.
Bothma, J. P., J. A. J. Nel, and A. Macdonald. 1984. Food niche separation between four sympatric Namib Desert carnivores. Journal of Zoology 202:327–340.
Broza, M. 1979. Dew, fog and hygroscopic food as a source of water for desert arthropods. Journal of Arid Environments 2:43–49.
Buffensteind, R., W. E. Campbell, and J. U. M. Jarvis. 1985. Identification of crystalline allantoin in the urine of African Cricetidae (Rodentia) and its role in their water economy. Journal of Comparative Physiology B 155:493–499.
Buxton, P. A. 1923. Animal life in deserts: a study of the fauna in relation to the environment. Edward Arnold & Co., London, UK.
Buxton, P. A. 1924. Heat, moisture, and animal life in deserts. Proceedings of the Royal Society of London Series B 96:123–131.
Cáceres, L., B. Gómez-Silva, X. Garró, V. Rodríguez, V. Monardes, and C. P. McKay. 2007. Relative humidity patterns and fog water precipitation in the Atacama Desert and biological implications. Journal of Geophysical Research: Biogeosciences 112. https://doi.org/10.1029/2006JG000344
Cermak, J. 2012. Low clouds and fog along the South-Western African coast - Satellite-based retrieval and spatial patterns. Atmospheric Research 116:15–21.
Channing, A. 1976. Life histories of frogs in the Namib Desert. Zoologica Africana 11:299–312.
Channing, A., and K. Wahlberg. 2011. Distribution and conservation status of the desert rain frog Breviceps macrops. African Journal of Herpetology 60:101–112.
Chown, S. L., and S. Nicolson. 2004. Insect physiological ecology: mechanisms and patterns. Oxford University Press, Oxford, UK.
Cloudsley-Thompson, J. L. 1975. Adaptations of Arthropoda to arid environments. Annual Review of Entomology 20:261–283.
Cloudsley-Thompson, J. L. 1990. Thermal ecology and behaviour of Physadesmia globosa (Coleoptera: Tenebrionidae) in the Namib Desert. Journal of Arid Environments 19:317–324.
Cloudsley-Thompson, J. L. 2001. Thermal and water relations of desert beetles. Naturwissenschaften 88:447–460.
Coineau, Y., and M. K. Seely. 1983. Mise en évidence d’un peuplement de microarthropodes dans les sables fins des dunes du Namib central. Pages 652–654 in P. Lebrun, H. M. Andre, A. de Medts, C. Gregoire-Wibo, and G. Wauthy, editors. New trends in soil biology. Dieu-Brichart, Louvain-la-Neuve, Belgium.
Conti, E., E. Barbagallo, S. Battatiato, A. Marletta, G. Costa, and F. Samperi. 2015. Do habitat features affect the composition of silk proteins by Namibian arid-adapted Ariadna spiders (Araneae: Segestriidae)? Italian Journal of Zoology 82:48–60.
Cooper, P. D. 1982. Water balance and osmoregulation in a free-ranging tenebrionid beetle, Onymacris unguicularis, of the Namib Desert. Journal of Insect Physiology 28:737–742.
Cooper, P. D., and M. D. Robinson. 1990. Water balance and bladder function in the Namib Desert sand dune lizard, Aporosaura archictae (Lacertidae). Copeia 1990:34–40.
Coutchic, P. A., and J. H. Crowe. 1979a. Transport of water vapor by tenebrionid beetles. I. Kinetics. Physiological Zoology 52:67–87.
Coutchic, P. A., and J. H. Crowe. 1979b. Transport of water vapor by tenebrionid beetles. II. Regulation of the osmolarity and composition of hemolymph. Physiological Zoology 52:88–100.
Coutchic, P. A., and J. Machin. 1984. Allometry of water vapor absorption in two species of tenebrionid beetle larvae. American Journal of Physiology: regulatory Integrative and Comparative Physiology 247:R230–R236.
Cox, G. W. 1983. Foraging behaviour of dune lark. Ostrich 54:113–120.
Curris, B., K. S. Roberts, M. Griffin, S. Bethune, C. J. Hay, and H. Kolberg. 1998. Species richness and conservation of Namibian freshwater macro-invertebrates, fish and amphibians. Biodiversity and Conservation 7:447–466.
Dallas, H. F., B. A. Curtis, and D. Ward. 1991. Water exchange, temperature tolerance, oxygen consumption and activity of the Namib Desert snail, Trigonephrus sp. Journal of Molluscan Studies 57:359–366.
D’Odorico, P., et al. 2009. Dryland ecohydrology: research perspectives. Annals of Arid Zone 48:1–29.
Ebner, M., T. Miranda, and A. Roth-Nebelsick. 2011. Efficient fog harvesting by Stipagrostis salicicola (Namib dune bushman grass). Journal of Arid Environments 75:524–531.
Eckardt, F. D., K. Soderberg, L. J. Coop, A. A. Muller, K. J. Vickery, R. D. Grandin, C. Jack, T. S. Kapalanga, and J. Henschel. 2013. The nature of moisture at Gobabeb, in the central Namib Desert. Journal of Arid Environments 93:7–19.

Edney, E. B. 1971. Some aspects of water balance in tenebrionid beetles and a thysanuran from the Namib Desert of southern Africa. Physiological Zoology 44:61–76.

Engelbrecht, F., et al. 2015. Projections of rapidly rising surface temperatures over Africa under low mitigation. Environmental Research Letters 10:85004.

Eugster, W. 2008. Fog research. Die Erde 139:1–10.

FENNERSY, J. 2009. Home range and seasonal movements of Giraffa camelopardalis angolensis in the northern Namib Desert. African Journal of Ecology 47:318–327.

FERRAR, P. 1982. Termites of a South African savanna. IV. Subterranean populations, mass determinations and biomass estimations. Oecologia 52:147–151.

FIELDEN, L. J., M. R. Perrin, and G. C. Hickman. 1990. Water metabolism in the Namib Desert Golden Mole, Eremitalpa granti namibensis (Chrysochloridae). Comparative Biochemistry and Physiology Part A: physiology 96:227–234.

GAEDER, K., and W. KNÜLLE. 1997. On the mechanism of water vapor sorption from unsaturated atmospheres by ticks. Journal of Experimental Biology 200:1491–1498.

GIRALDO, A. E., and G. E. Flores. 2016. Peruvian Tenebrionidae: a review of present knowledge and biodiversity. Annales Zoologici 66:499–514.

GOTTLOB, T. R., F. D. Eckardt, Z. S. Venter, and M. D. Cramer. 2019. The contribution of fog to water and nutrient supply to Arthridaeus leubnitzi in the central Namib Desert, Namibia. Journal of Arid Environments 161:35–46.

Goudie, A. 1972. Climate, weathering, crust formation, dunes, and fluvial features of the Central Namib Desert, near Gobabeb, South West Africa. Madoqua Series II 1:15–31.

Greenspan, L. 1977. Humidity fixed points of binary saturated aqueous solutions. Journal of Research of the National Bureau of Standards A. Physics and Chemistry 81A:90–96.

Griffin, R. E. 1998. Species richness and biogeography of non-acarine arachnids in Namibia. Biodiversity and Conservation 7:467–481.

Grube, S., and D. Rudolph. 1995. Tenebrionidae in arid environments: the water balance of Psammotermes allocaerus Silvestri. Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie 10:665–668.

Hadley, N. F. 1994. Water relations of terrestrial arthropods. Academic Press, San Diego, California, USA.

Hadley, N. F., and S. R. Szarek. 1981. Productivity of desert ecosystems. BioScience 31:747–753.

Hager, F. A. 2008. Das Fouragierverhalten der Ernte- termiten Hodotermes mossambicus. Ruhr University, Bochum, Germany.

Hamilton, W. J. I., J. R. Henschel, and M. K. Seely. 2003. Fog collection by Namib Desert beetles. South African Journal of Science 99:181.

Henschel, J. R. 1997. The effect of wind on foraging activity of the tenebrionid beetle Lepidochora discoidalis in the sand dunes of the Namib Desert. African Zoology 32:136–139.

HÄNSLER, A., J. CERMAK, S. HAGEMANN, and D. JACOB. 2011. Will the southern African west coast fog be affected by future climate change? Results of an initial fog projection using a regional climate model. Erdkunde 65:261–275.

HARRISON, J. G., C. H. SCHOLTZ, and S. L. CHOWN. 2003. A revision of the endemic south-western African dung beetle subgenus Scarabaeus (Pachysoma) MacLeay, including notes on other flightless Scar- baeei (Scarabaeidae: Scarabaeinae). Journal of Natural History 37:305–355.

HATTINGH, J., M. GANHAO, and S. G. NAIDU. 1984. Haemolymph composition in Namib Desert tenebri- onid beetles. Comparative Biochemistry and Physiology Part A: physiology 78:541–545.

HAUFFE, H. C., R. D. PIETRUSZKA, and M. K. SEALY. 1988. Observations on the behaviour of Onymacris laevicaps Gebien (Coleoptera: Tenebrionidae: Adesmini) in the central Namib Desert dunes. Journal of the Entomological Society of Southern Africa 51:183–192.

HEEG, J. 1967. Studies on Thyarsana. I. The water economy of Machiloides delanyi Wygodzinsky and Cheno- lepisma longicudata Escherich. Zoológica Africana 3:21–41.

HENSCHEL, J. R. 1990. The biology of Leucorchestris arenicola (Araneae: Heteropodidae), a burrowing spider of the Namib dunes. Pages 115–127 in M. K. Seely, editor. Namib ecology: 25 years of Namib research. Transvaal Museum Monograph No. 7. Transvaal Museum, Pretoria, South Africa.

HENSCHEL, J. R. 1994. Diet and foraging behaviour of huntsman spiders in the Namib dunes (Araneae: Heteropodidae). Journal of Zoology 234:239–251.

HENSCHEL, J. R. 1997. Psammophil in Namib Desert spiders. Journal of Arid Environments 37:695–707.
Henschel, J., P. Klintenberg, C. Roberts, and M. Seely. 2007. Long-term ecological research from an arid, variable, drought-prone environment. Sêkeressè 18:342–347.

Henschel, J. R., and N. Lancaster. 2013. Gobabeb - 50 years of Namib Desert research. Journal of Arid Environments 93:1–6.

Henschel, J. R., V. Mtuleni, J. Pallett, and M. K. Seely. 2003. The surface-dwelling arthropod fauna of Gobabeb with a description of the long-term pitfall trapping project. Journal of the Namibia Scientific Society 51:65–92.

Henschel, J. R., M. B. Robertson, and M. K. Seely. 2001. Animal physiology in the Namib Desert: coping with little water, scarce food and elevated temperatures. Pages 423–457 in I. Prakash, editor. Ecology of desert environments. Scientific Publishers (India), Jodhpur, India.

Henschel, J. R., and M. K. Seely. 2008. Ecophysiology of atmospheric moisture in the Namib Desert. Atmospheric Research 87:362–368.

Henschel, J. R., T. D. Wassenaar, A. Kanandjembo, M. K. Louw, G. Neef, T. Shuuuya, and K. Soderberg. 2018. Roots point to water sources of Welwitschia mirabilis in a hyperarid desert. Ecohydrology 12: e2039.

Herrmann, H. W., and W. R. Branch. 2013. Fifty years of herpetological research in the Namib Desert and Namibia with an updated and annotated species checklist. Journal of Arid Environments 93:94–115.

Hetem, R. S., W. M. Strauss, L. G. Fick, S. K. Maloney, L. C. R. Meyer, M. Shobrak, A. Fuller, and D. Mitchell. 2010. Variation in the daily rhythm of body temperature of free-living Arabian oryx (Oryx leucoryx): Does water limitation drive heterothermy? Journal of Comparative Physiology B: Biochemical, Systems, and Environmental Physiology 180:1111–1119.

Hodgson, A. N., C. Hanel, and A. J. Loveridge. 1994. The reproductive cycle of the pulmonate snail Xerocerasinus minutus from the Namib desert. Journal of Molluscan Studies 60:355–358.

Holm, E., and E. B. Edney. 1973. Daily activity of Namib Desert arthropods in relation to climate. Ecology 54:45–56.

Holm, E., and C. H. Scholtz. 1979. Revision of the genus Pachysoma M’Leay with an evaluation of the subtribe Pachysomina Ferreira and its genera (Coleoptera: Scarabaeidae). Journal of the Entomological Society of Southern Africa 42:225–244.

Holm, E., and C. H. Scholtz. 1980. Structure and pattern of the Namib Desert dune ecosystem at Gobabeb. Madoqua 12:3–39.

Holter, P., C. H. Scholtz, and L. Stenseng. 2009. Desert detritivory: nutritional ecology of a dung beetle (Pachysoma glentoni) subsisting on plant litter in arid South African sand dunes. Journal of Arid Environments 73:1090–1094.

Irish, J. 1990. Namib biogeography, as exemplified mainly by the Lepismatidae (Thysanura: Insecta). Pages 61–66 in M. K. Seely, editor. Namib ecology: 25 years of Namib research. Transvaal Museum Monograph No. 7. Transvaal Museum, Pretoria, South Africa.

Irish, J. 2018. Contribution to the knowledge of southern African Lepismatidae (Thysanura, Insecta). Namibian Journal of Environment 2:22–127.

Jacobson, K. M., and P. J. Jacobson. 1998. Rainfall regulates decomposition of buried cellulose in the Namib Desert. Journal of Arid Environments 38:571–583.

Jacobson, K., A. Van Diepeningen, S. Evans, R. Fritts, P. Gemmel, C. Marsho, M. Seely, A. Wenndt, X. Yang, and P. Jacobson. 2015. Non-rainfall moisture activates fungal decomposition of surface litter in the Namib Sand Sea. PLOS ONE 10:e0126977.

Johnstone, J. A., and T. E. Dawson. 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. Proceedings of the National Academy of Sciences USA 107:4533–4538.

Kaseke, K. F., A. J. Mills, R. Brown, K. J. Esler, J. R. Henschel, and M. K. Seely. 2012a. A method for direct assessment of the “non rainfall” atmospheric water cycle: input and evaporation from the soil. Pure and Applied Geophysics 169:847–857.

Kaseke, K. F., A. Mills, K. Esler, J. Henschel, M. K. Seely, and R. Brown. 2012b. Spatial variation of “non-rainfall” water input and the effect of mechanical soil crusts on input and evaporation. Pure and Applied Geophysics 169:2217–2229.

King, J. M., G. P. Kingaby, J. G. Colvin, and B. R. Heath. 1975. Seasonal variation in water turnover by oryx and eland on the Galana Game Ranch Research Project. African Journal of Ecology 13:287–296.

Klemm, O., and N. Lin. 2016. What causes observed fog trends: air quality or climate change. Aerosol and Air Quality Research 16:1131–1142.

Kniolle, W., and R. R. Spadafora. 1970. Occurrence of water vapor sorption from the atmosphere in larvae of some stored-product beetles. Journal of Economic Entomology 63:1069–1070.

Koch, C. 1961. Some aspects of abundant life in the vegetationless sand of the Namib Desert dunes: positive psammophily in Tenebrionid-beetles. Journal of the South West Africa Scientific Society 15:8–34.

Koch, C. 1962. The Tenebrionidae of Southern Africa XXXI. Comprehensive notes on the tenebrionid...
fauna of the Namib Desert. Annals of the Transvaal Museum 24:61–106.

Koracin, D., C. E. Dorman, J. M. Lewis, J. G. Hudson, E. M. Wilcox, and A. Torregrosa. 2014. Marine fog: a review. Atmospheric Research 143:142–175.

Lamb, T., and A. M. Bauer. 2013. To be or not to be Angolosaurus: a multilocus perspective on the phylogenetic position of Africa's desert plated lizard (Gerrhosauridae). Zoologica Scripta 42:381–388.

Lamb, T., and J. E. Bond. 2013. A multilocus perspective on phylogenetic relationships in the Namib darkling beetle genus Onymacris (Tenebrionidae). Molecular Phylogenetics and Evolution 66:757–765.

Lamb, T., R. Pollard, and J. E. Bond. 2013. Genetic variation corroborates subspecific delimitation in the Namib fog-basking beetle, Onymacris unguicularis (Haag) (Tenebrionidae, Coleoptera). ZooKeys 353:47–60.

Lamoral, B. H. 1979. The scorpions of Namibia (Arachnida-Scorpionida). Annals of the Natal Museum 23:497–784.

Lancaster, J., N. Lancaster, and M. K. Seely. 1984. Climate of the central Namib Desert. Madoqua 14:5–61.

Lawrence, R. R. 1959. The sand-dune fauna of the Namib Desert. South African Journal of Science 55:233–239.

Lawrence, R. F. 1962. Spiders of the Namib Desert. Annals of the Transvaal Museum 24:197–211.

Li, B., L. Wang, K. F. Kaseke, L. Li, and M. K. Seely. 2016. The impact of rainfall on soil moisture dynamics in a foggy desert. PLOS ONE 11: e0164982.

Lighton, J. R. B., P. H. Brownell, B. Joos, and R. Turner. 2001. Low metabolic rate in scorpions: implications for population biomass and cannibalism. Journal of Experimental Zoology 286:607–613.

Louw, G. N. 1972. The role of advective fog in the water economy of certain Namib Desert beetles. Symposia of the Royal Society of London 31:297–314.

Louw, G. N., and W. J. I. Hamilton. 1972. Physiological and behavioural ecology of the ultra-psammophilous Namib Desert tenebrionid, Lepidochora argentogrisea (Bocage). Madoqua Series II 1:87–95.

Louw, G. N., and E. Holm. 1972. Physiological, morphological and behavioural adaptations of the ultrasammophilous, Namib Desert lizard Aporosaura anchietae (Bocage). Madoqua Series II 1:67–85.

Louw, G. N., S. W. Nicolson, and M. K. Seely. 1986. Respiration beneath desert sand: carbon dioxide diffusion and respiratory patterns in a tenebrionid beetle. Journal of Experimental Biology 120:443–447.

Louw, G. N., and M. K. Seely. 1980. Exploitation of fog water by a perennial Namib dune grass, Stipagrostis sabulicola. South African Journal of Science 76:38–39.

Machin, J. 1979. Compartmental osmotic pressures in the rectal complex of Tenebrio larvae: evidence for a single tubular pumping site. Journal of Experimental Biology 8:123–137.

Machin, J. 1981. Water compartmentalisation in insects. Journal of Experimental Zoology 215:327–333.

Machin, J. 1983. Water vapor absorption in insects. American Journal of Physiology: regulatory Integrative and Comparative Physiology 244:R187–R192.

Machin, J., and M. J. O'Donnell. 1991. Rectal complex ion activities and electrochemical gradients in larvae of the desert beetle, Onymacris: comparisons with Tenebrio. Journal of Insect Physiology 37:829–838.

Marsh, A. 1986. Checklist, biological notes and distribution of ants in the central Namib Desert. Madoqua 14:333–344.

Marsh, B. A. 1987. Micro-arthropods associated with Welwitschia mirabilis in the Namib Desert. South African Journal of Zoology 22:89–96.

McClain, E., M. K. Seely, N. F. Hadley, and V. Gray. 1985. Wax blooms in tenebrionid beetles of the Namib Desert: correlations with environment. Ecology 66:112–118.

Mellanby, K. 1932. The effect of atmospheric humidity on the metabolism of the fasting mealworm (Tenebrio molitor L., Coleoptera). Proceedings of the Royal Society B: Biological Sciences 111:376–390.

Mendelsohn, J., A. Jarvis, C. Roberts, and T. Robertson. 2002. Atlas of Namibia. A portrait of the land and its people. David Philip Publishers, Cape Town, South Africa.

Mitchell, J. D., P. H. Hewitt, and T. C. K. Van der Linde. 1993. Critical thermal limits and temperature tolerance in the Harvester Termite Hodoterms mossambicus (Hagen). Journal of Insect Physiology 39:523–528.

Mitchell, D., S. K. Maloney, C. Jessen, H. P. Laburn, P. R. Kamerman, G. Mitchell, and A. Fuller. 2002. Adaptive heterothermy and selective brain cooling in arid-zone mammals. Comparative Biochemistry and Physiology Part B 131:571–585.

Mitchell, D., M. K. Seely, C. S. Roberts, R. D. Pietruszka, E. McClain, M. Griffin, and R. I. Yeaton. 1987. On the biology of the lizard Angolosaurus skoogi in the Namib Desert. Madoqua 15:201–216.

Mooney, H. A., S. L. Gulmon, J. Ehleringer, and P. W. Rundel. 1980. Atmospheric water uptake by an Atacama Desert shrub. Science 209:693–694.
Murray, I. W., A. Fuller, H. M. Lease, D. Mitchell, B. O. Wolf, and R. S. Hetem. 2014. The actively foraging desert lizard *Pedioplanis husabensis* (Husab Sand Lizard) behaviorally optimizes its energetic economy. Canadian Journal of Zoology 92:905–913.

Murray, I. W., A. Fuller, H. M. Lease, D. Mitchell, B. O. Wolf, and R. S. Hetem. 2015. Low field metabolic rates for geckos of the genus *Rhoptropus* may not be surprising. Journal of Arid Environments 113:35–42.

Nagy, K. A., B. C. Clarke, M. K. Seely, D. Mitchell, and J. R. B. Lighton. 1991. Water and energy balance in Namibian Desert sand-dune lizards *Angolosaurus skoogi* (Andersson, 1916). Functional Ecology 5:731–739.

Nagy, K. A., and M. H. Knight. 1994. Energy, water, and food use by springbok antelope (*Antidorcas marsupialis*) in the Kalahari Desert. Journal of Mammalogy 75:860–872.

Nagy, K. A., M. K. Seely, and R. Buffenstein. 1993. Surprisingly low field metabolic rate of a diurnal desert gecko, *Rhoptropus afer*. Copeia 11:216–219.

Nagy, K. A., and D. R. Shemanski. 2009. Observations on diet and seed digestion in a sand dune lizard, *Meroselachus anchietae*. African Journal ofHerpetology 58:39–43.

Naidu, S. G. 1998. Haemolymph amino acid, sugar and glycerol levels in the Namib Desert tenebrionid *Stips stali* during dehydration and rehydration. Comparative Biochemistry and Physiology Part A: molecular & Integrative Physiology 119:477–484.

Naidu, S. G. 2001a. Water balance and osmoregulation in *Stenocara gracilipes*, a wax-blooming tenebrionid beetle from the Namib Desert. Journal of Insect Physiology 47:1429–1440.

Naidu, S. G. 2001b. Osmoregulation in *Onymacris rugatipennis*, a free-ranging tenebrionid beetle from the Namib Desert. Comparative Biochemistry and Physiology Part A: molecular and Integrative Physiology 129:873–885.

Naidu, S. G. 2008. Why does the Namib Desert tenebrionid *Onymacris unguicularis* (Coleoptera: Tenebrionidae) fog-bask? European Journal of Entomology 105:829–838.

Naidu, S. G., and J. Hattingh. 1986. Water balance and osmoregulation in *Stips stali*, a nocturnal tenebrionid beetle from the Namib Desert. Journal of Insect Physiology 32:891–896.

Naidu, S. G., and J. Hattingh. 1988. Water balance and osmoregulation in *Physadesmia globosa*, a diurnal tenebrionid beetle from the Namib Desert. Journal of Insect Physiology 34:911–917.

Natelson, S., and E. A. Natelson. 1975. Principles of applied clinical chemistry, volume 1. Maintenance of fluid and electrolyte balance. Plenum Press, New York, New York, USA.

Nicolson, S. W. 1980. Water balance and osmoregulation in *Onymacris plana*, a tenebrionid beetle from the Namib Desert. Journal of Insect Physiology 26:315–320.

Nicolson, S. W. 1990a. Water relations of Namib tenebrionid beetles. Pages 173–178 in M. K. Seely, editor. Namib ecology: 25 years of Namib research. Transvaal Museum Monograph No. 7. Transvaal Museum, Pretoria, South Africa.

Nicolson, S. W. 1990b. Osmoregulation in a nectar-feeding insect, the carpenter bee *Xylocopa capitata*: water excess and ion conservation. Physiological Entomology 15:433–440.

Nicolson, S. W. 2009. Water homeostasis in bees, with the emphasis on sociality. Journal of Experimental Biology 212:429–434.

Nicolson, S. W., and S. A. Hanrahan. 1986. Diuresis in a desert beetle? Hormonal control of the Malpighian tubules of *Onymacris plana* (Coleoptera: Tenebrionidae). Journal of Comparative Physiology B 156:407–413.

Nicolson, S. W., G. N. Louw, and E. B. Edney. 1984. Use of a ventilated capsule and tritiated water to measure evaporative water losses in a tenebrionid beetle. Journal of Experimental Biology 481:477–481.

Noble-Nesbitt, J. 1969. Water balance in the firebrat, *Thermobia domestica* (Packard). Exchanges of water with the atmosphere. Journal of Experimental Biology 50:745–769.

Noble-Nesbitt, J. 1970. Water uptake from subsaturated atmospheres: its site in insects. Nature 255:753–754.

Noble-Nesbitt, J. 1975. Reversible arrest of uptake of water from subsaturated atmospheres by the firebrat, *Thermobia domestica* (Packard). Journal of Experimental Biology 62:657–669.

Nørgaard, T., and M. Dacke. 2010. Fog-basking behaviour and water collection efficiency in Namib Desert Darkling beetles. Frontiers in Zoology 7:23.

Nørgaard, T., M. Ebner, and M. Dacke. 2012. Animal or plant: Which is the better fog water collector? PLOS ONE 7:e34603.

O’Donnell, M. J. 1977. Site of water vapor absorption in the desert cockroach, *Arenivaga investigata* (threshold relative humidity/hygrosopic secretion/insect mouth parts/surface temperatures). Proceedings of the National Academy of Sciences USA 74:1757–1760.

O’Donnell, M. J. 1982a. Hydrophilic cuticle—the basis for water vapor absorption by the desert burrowing cockroach, *Arenivaga investigata*. Journal of Experimental Biology 99:43–60.
O’Donnell, M. J. 1982b. Water vapor absorption by the desert burrowing cockroach, Arenivaga investigata: evidence against a solute dependent mechanism. Journal of Experimental Biology 96:251–262.

O’Donnell, M. J., and J. Machin. 1988. Water vapor absorption by terrestrial organisms. Pages 47–90 in S. H. Wright, editor. Advances in comparative and environmental physiology. Volume 2. Springer, Berlin, Germany.

Parker, A. R., and C. R. Lawrence. 2001. Water capture by a desert beetle. Nature 414:33–34.

Peterson, C. C. 1998. Rain-harvesting behavior by a free-ranging desert horned lizard (Phrynosoma platyrhinos). Southwestern Naturalist 43:391–394.

Picket, M. D. 1986. Burrow and nest characteristics of the harvester termite (Hodotermes mossambicus), and the seed storing activities of the common harvester ant (Messor barbatus). Report PER. Atomic Energy Corporation of SA Ltd., No. 145, 1987, Pretoria, South Africa.

Pietruszka, R. D., and M. K. Seely. 1985. Predictability of two moisture sources in the Namib Desert. South African Journal of Science 81:682–685.

Polis, G. A., J. D. Barnes, M. K. Seely, J. R. Henschel, and M. M. Enders. 1998. Predation as a major cost of reproduction in Namib Desert tenebrionid beetles. Ecology 79:2560–2566.

Polis, G. A., and M. K. Seely. 1990. Inhibition of precipitated fog by Namib Desert scorpions. Journal of Arachnology 18:362–363.

Prendini, L. 2005. Scorpion diversity and distribution in southern Africa: pattern and process. Pages 25–68 in B. A. Huber, B. J. Sinclair, and K.-H. Lampe, editors. African biodiversity: individuals, ecosystems. Springer, New York, New York, USA.

Ramsay, J. A. 1964. The rectal complex of the mealworm Tenebrio molitor, L. (Coleoptera, Tenebrionidae). Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 248:279–314.

Rey, B., A. Fuller, D. Mitchell, L. C. Meyer, and R. S. Hetem. 2017. Drought-induced starvation of aardvarks in the Kalahari: an indirect effect of climate change. Biology Letters 13:p.20170301.

Robertson, H. G., S. W. Nicolson, and G. N. Louw. 1982. Osmoregulation and temperature effects on water loss and oxygen consumption in two species of African scorpion. Comparative Biochemistry and Physiology Part A: physiology 71A:605–609.

Robinson, M. D., and D. A. Hughes. 1978. Observations on the natural history of Peringuey’s adder, Bitis peringueyi (Boulenger)(Reptilia: Viperidae). Annals of the Transvaal Museum 31:189–193.

Robinson, M. D., and M. K. Seely. 1980. Physical and biotic environments of the southern Namib dune ecosystem. Journal of Arid Environments 3:183–203.

Roig-Juñent, S., G. Flores, S. Claver, G. Debandi, and A. Marvaldi. 2001. Monte Desert (Argentina): insect biodiversity and natural areas. Journal of Arid Environments 47:77–94.

Roth-Nebelsick, A., M. Ebner, T. Miranda, V. Gottschalk, D. Voigt, S. Gorb, T. Stegmaier, J. Sarsour, M. Linke, and W. Konrad. 2012. Leaf surface structures enable the endemic Namib desert grass Stipagrostis sabulicola to irrigate itself with fog water. Journal of the Royal Society Interface 9:1965–1974.

Rudolph, D., and W. Knülle. 1974. Site and mechanism of water vapor uptake from the atmosphere in xidid ticks. Nature 249:84–85.

Rudolph, D., and W. Knülle. 1982. Novel uptake systems for atmospheric water vapor among insects. Journal of Experimental Zoology 222:321–333.

Rundel, P. W., M. O. Dillon, B. Palma, H. A. Mooney, S. L. Gulmon, and J. Ehleringer. 1991. The phytogeography and ecology of the coastal Atacama and Peruvian deserts. Aliso 16:493–505.

Schmidt-Nielsen, K. 1990. Animal physiology: adaptation and environment. Fourth edition. Cambridge University Press, Cambridge, UK.

Scholtz, C. H. 1989. Unique foraging behaviour in Pachysoma (Scarabaeus) striatum Castelnau (Coleoptera: Scarabaeidae): An adaptation to arid conditions? Journal of Arid Environments 16:305–313.

Scholtz, C. H., J. D. G. Harrison, and V. V. Grebenikov. 2004. Dung beetle (Scarabaeus (Pachysoma)) biology and immature stages: Reversal to ancestral states under desert conditions (Coleoptera: Scarabaeidae)? Biological Journal of the Linnean Society 83:453–460.

Schulze, B. R. 1969. The climate of Gobabeb. Scientific Papers of the Namib Desert Research Station 38:5–12.

Seely, M. K. 1978. The Namib Dune desert: an unusual ecosystem. Journal of Arid Environments 1:117–128.

Seely, M. K. 1979. Irregular fog as a water source for desert dune beetles. Oecologia 42:213–227.

Seely, M. K. 1984. The Namib’s place among deserts of the world. South African Journal of Science 80:155–158.

Seely, M. K. 1985. Predation and environment as selective forces in the Namib Desert. Transvaal Museum Monographs 4:161–165.

Seely, M. K. 1989. Desert invertebrate physiological ecology: Is anything special? South African Journal of Science 85:266–270.
Seely, M. K. 1993. A brief review of the ecology of sandy deserts. Bollettino delle sedute della Accademia gioenla di scienze naturali in Catania 28:51–69.

Seely, M. K., editor. 2012. Namib sand sea world heritage nomination. Namibia National Committee for World Heritage, Windhoek, Namibia.

Seely, M. K., M. P. De Vos, and G. N. Louw. 1977. Fog inhibition, satellite fauna and unusual leaf structure in a Namib Desert dune plant Trianthema hereroensis. South African Journal of Science 73:169–172.

Seely, M. K., and M. Griffin. 1986. Animals of the Namib Desert: interactions with their physical environment. Revue de Zoologie Africaine 100:47–61.

Seely, M. K., and W. J. I. Hamilton. 1976. Fog catchment sand trenches constructed by tenebrionid beetles, Lepidochora, from the Namib Desert. Science 193:484–486.

Seely, M. K., and J. R. Henschel. 1998. The climatology of Namib fog. Pages 353–356 in R. S. Schemenauer and H. Bridgman, editors. Proceedings of the 1st International conference on fog and fog collection. International Development Research Centre, Vancouver, British Columbia, Canada.

Seely, M., J. R. Henschel, and W. I. J. Hamilton. 2005. Long-term data show behavioural fog collection adaptations determine Namib Desert beetle abundance. South African Journal of Science 101:570–572.

Seely, M. K., C. J. Lewis, K. A. O’Brien, and A. E. Suttle. 1983. Fog response of tenebrionid beetles in the Namib Desert. Journal of Arid Environments 6:135–143.

Seely, M. K., and G. N. Louw. 1980. First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. Journal of Arid Environments 3:25–54.

Seely, M. K., and D. Mitchell. 1987. Is the subsurface environment of the Namib Desert dunes a thermal haven for chthonic beetles? South African Journal of Zoology 22:57–61.

Seely, M. K., D. Mitchell, and G. N. Louw. 1985. A field technique using iridium-192 for measuring subsurface depths in free-ranging Namib Desert beetles. South African Journal of Science 81:668–688.

Seely, M. K., and J. Pallett. 2008. Namib: secrets of a desert uncovered. Venture Publications, Windhoek, Namibia.

Sherbrooke, W. C. 1990. Rain-harvesting in the lizard, Phrynosoma cornutum: behavior and integumental morphology. Journal of Herpetology 24:302–308.

Skinner, J. D., and G. N. Louw. 1996. The springbok Antidorcas marsupialis (Zimmerman 1780). Transvaal Museum Monographs 10:1–50.

Slobodchikoff, C. N., and K. Wismann. 1981. A function of the subelytral chamber of Tenebrionid beetles. Journal of Experimental Biology 90:109–114.

Soderberg, K. S. 2010. The role of fog in the ecohydrology and biogeochemistry of the Namib Desert. Dissertation. University of Virginia, Charlottesville, Virginia, USA.

Southgate, R. I., P. Masters, and M. K. Seely. 1996. Precipitation and biomass changes in the Namib Desert dune ecosystem. Journal of Arid Environments 33:267–280.

Spirig, R., et al. 2019. Probing the fog life-cycles in the Namib desert. Bulletin of the American Meteorological Society 2019:2491–2507.

Thuiller, W., G. F. Midgley, G. O. Hughes, B. Bomhard, G. Drew, M. C. Rutherford, and F. I. Woodward. 2006. Endemic species and ecosystem sensitivity to climate change in Namibia. Global Change Biology 12:759–776.

Torregrosa, A., T. A. O’Brien, and I. C. Faloona. 2014. Coastal fog, climate change, and the environment. EOS, Transactions American Geophysical Union 95:473–474.

Tracy, C. R., N. Laurence, and K. A. Christian. 2011. Condensation onto the skin as a means for water gain by tree frogs in tropical Australia. American Naturalist 178:553–558.

Tschoinkel, W. R. 1973. The sorption of water vapor by windborne plant debris in the Namib Desert. Madoqua Series II 2:21–24.

Tschoinkel, W. R. 2010. The foraging tunnel system of the Namibian desert termite, Baucaliotermes hainesi. Journal of Insect Science 10:1–17.

Vale, C. G., and J. C. Brito. 2015. Desert-adapted species are vulnerable to climate change: insights from the warmest region on Earth. Global Ecology and Conservation 4:369–379.

Van Schalkwyk, L. 2011. Fog forecasting at Cape Town International Airport: a climatological approach. Thesis. University of Pretoria, Pretoria, South Africa. https://repository.up.ac.za/handle/2263/28956

Walter, H.-H. 1936. Die ökologischen Verhältnisse in der Namib-Nebelwüste (Südwestafrika) unter Auswertung der Aufzeichnung des Dr. G. Boss (Swakopmund). Jahrbücher für Wissenschaftliche Botanik. Berlin 84:58–222.

Wang, L., K. F. Kaseke, and M. K. Seely. 2017. Effects of non-rainfall water inputs on ecosystem functions. Wiley Interdisciplinary Reviews: Water 4: e1179.

Ward, D., and M. K. Seely. 1996. Adaptation and constraint in the evolution of the physiology and behavior of the Namib Desert tenebrionid beetle genus Onymacris. Evolution 50:1231–1240.
Watson, R. T. 1989. Niche separation in Namib Desert dune Lepismatidae (Thysanura: Insecta): detriti-vores in an allochthonous detritus ecosystem. Journal of Arid Environments 17:37–48.

Watson, R. T., and J. Irish. 1988. An introduction to the Lepismatidae (Thysanura: Insecta) of the Namib Desert sand dunes. Madoqua 15:285–293.

Wharton, R. A. 1983. Dispersal, diel periodicity, and longevity of *Stips stali* (Haag) (Coleoptera: Tenebrionidae). Coleopterists Bulletin 37:27–33.

Wharton, G. W., and A. G. Richards. 1978. Water vapor exchange kinetics in insects and acarines. Annual Review of Entomology 23:309–328.

Wharton, R. A., and M. Seely. 1982. Species composition of and biological notes on Tenebrionidae of the lower Kuiseb River and adjacent gravel plain. Madoqua 13:5–25.

Williams, J. B. 1999. Heat production and evaporative water loss of dune larks from the Namib Desert. Condor 101:432–438.

Willoughby, E. J. 1971. Biology of larks (Aves: Alaudidae) in the central Namib Desert. Zoologica Africana 6:133–176.

Willoughby, E. J., and T. J. Cade. 1967. Drinking habits of birds in the central Namib Desert of South West Africa. Scientific Papers of the Namib Desert Research Station 31:1–35.

Winston, P. W., and D. H. Bates. 1960. Saturated solutions for the control of humidity in biological research. Ecology 41:232–237.

Withers, P. C., G. N. Louw, and J. Henschel. 1980. Energetics and water relations of Namib Desert rodents. South African Journal of Zoology 15:131–137.

Zeidler, J., S. Hanrahan, and M. Scholes. 2002. Termite species richness, composition and diversity on five farms in southern Kunene region, Namibia. African Zoology 37:7–11.

Zheng, Y., H. Bai, Z. Huang, X. Tian, F.-Q. Nie, Y. Zhao, J. Zhai, and L. Jiang. 2010. Directional water collection on wetted spider silk. Nature 463:640–643.

**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2996/full