SYNTHESIS & INTEGRATION

Fog and fauna of the Namib Desert: past and future

DUNCAN MITCHELL [iD],[1,2] JOH R. HENSCHEL [iD],[3,4,5] ROBYN S. HETEM [iD],[1,6] THEO D. WASSENAAR,[4,7]
W. MAARTIN STRAUSS [iD],[1,8] SHIRLEY A. HANRAHAN,[6,10] AND MARY K. SEELY[4,6,9,]†

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

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.

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

Fig. 1. The characteristic early-morning fog of the Namib Desert, on the sand dunes of the central Namib sand sea, within a UNESCO World Heritage Site. (Photo: Joh Henschel).

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
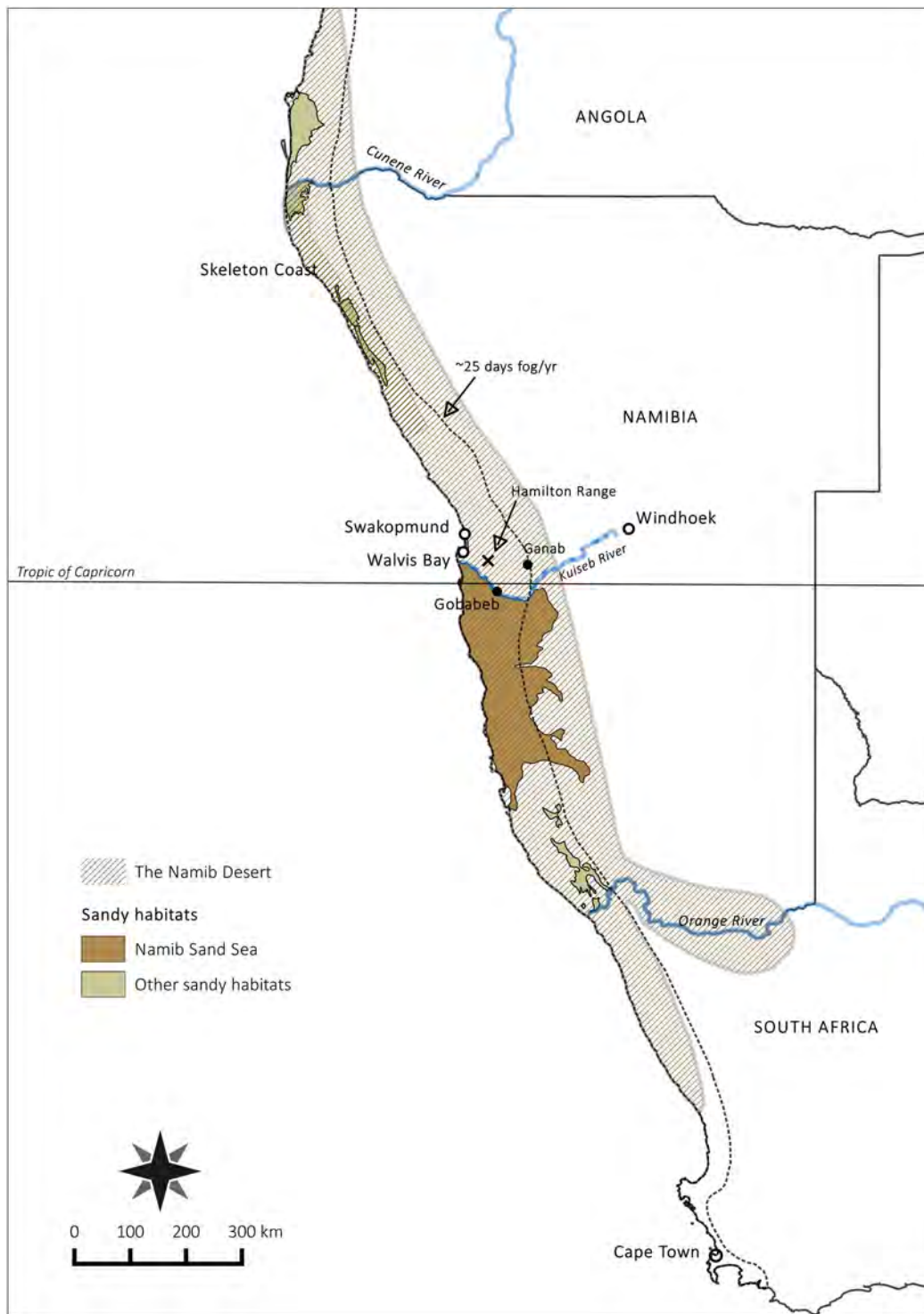
Fig. 2. Geography of the Namib Desert. The extent of the Namib Desert was reproduced from Henschel and Lancaster (2013). In Namibia, the fog line follows the contour delineating the eastern edge of the zone receiving about 25 d of fog per year, based on data from Mendelsohn et al. (2002). Less-frequent fog occurs east of this line.

(Fig. 2. *Continued*)
The shape of this fog line in South Africa and Angola is only approximate; it was estimated there from predictive fog maps in Cermak (2012). "Sandy habitats" refer to areas with sand cover deep enough for dunes to occur frequently. (Drawing: Theo Wassenaar).

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

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

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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 *Eremitalpa 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
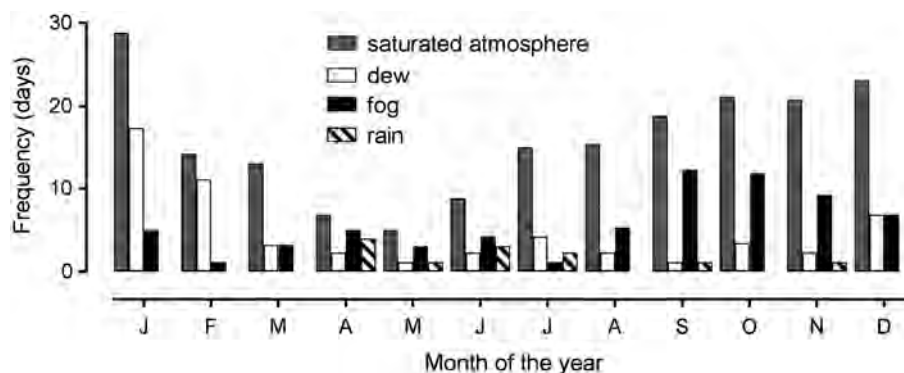

Fig. 3. Number of days per month, in 2001 at Gobabeb Research Institute (Fig. 2), with relative humidity >97% (shaded bars), dew (open bars), fog (black bars), and rain >0.1 mm (hatched bars). (Redrawn from Henschel and Seely 2008).
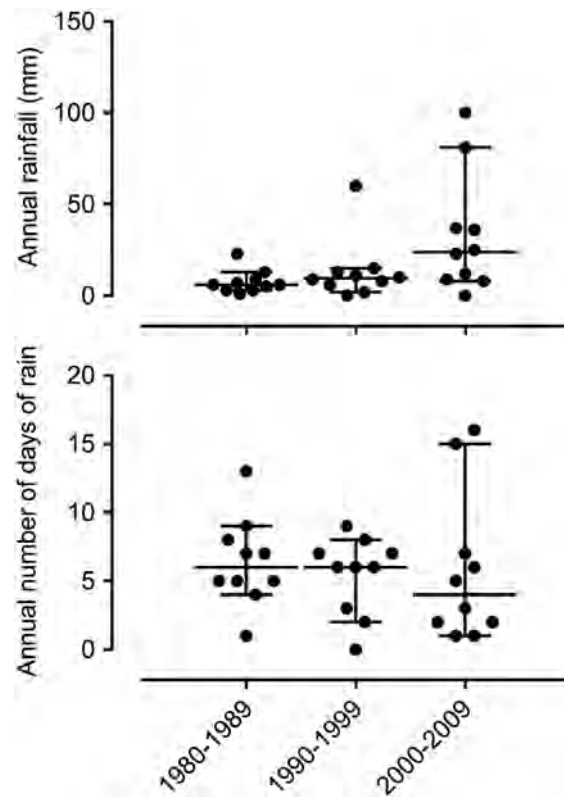
Fig. 4. Annual rainfall (mm) and days of rain per annum (including the median and 95% confidence intervals) at Gobabeb Research Institute for the decades between 1980 and 2010. Decadal rainfall tended to increase but remained <30 mm while days of rain tended to decrease, to below 5 d/yr in 2000–2009. High variability arose mainly from isolated years of unusually heavy rain. Data from Eckardt et al. 2013, replotted.

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. 2012*a*). 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
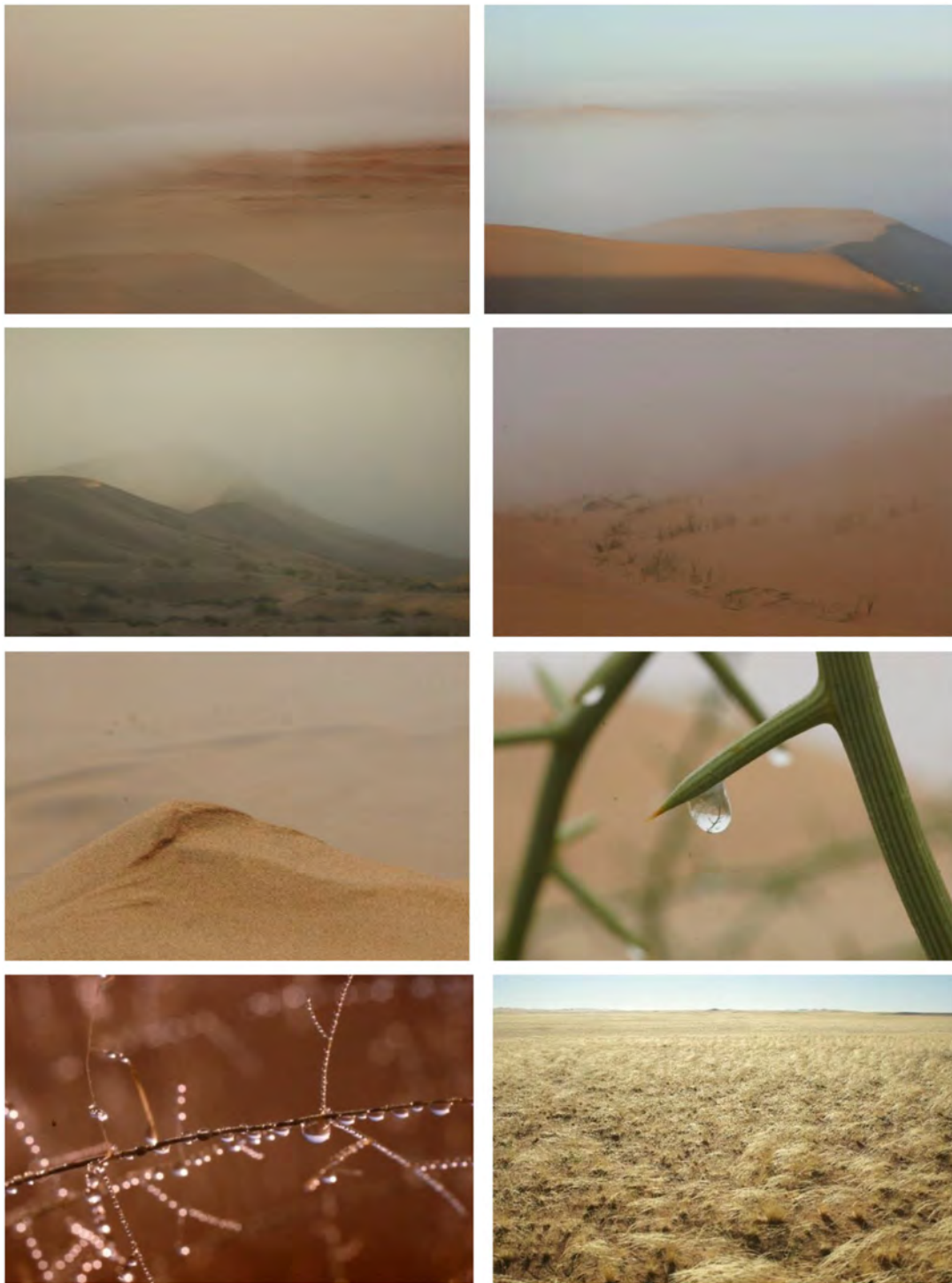
Fig. 5. Fog and dew of the Namib Desert. Left to right top to bottom: fog rolling across the dunes; low fog in valley between dunes; fog lifting off a dune; less dense fog on lower dune slope; dune crest wet after fog; drop of fog water collected on !Nara plant; dew drops collected on grass; grassy interdune plain wet with dew. (Photos: Joh Henschel).
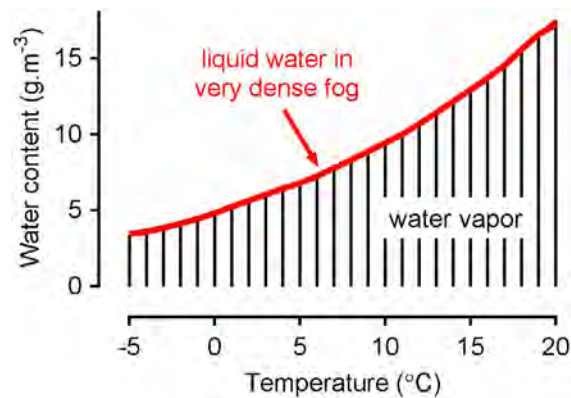
Fig. 6. Vapor and liquid components of dense fog, at different air temperatures. (Redrawn from Eugster 2008).

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
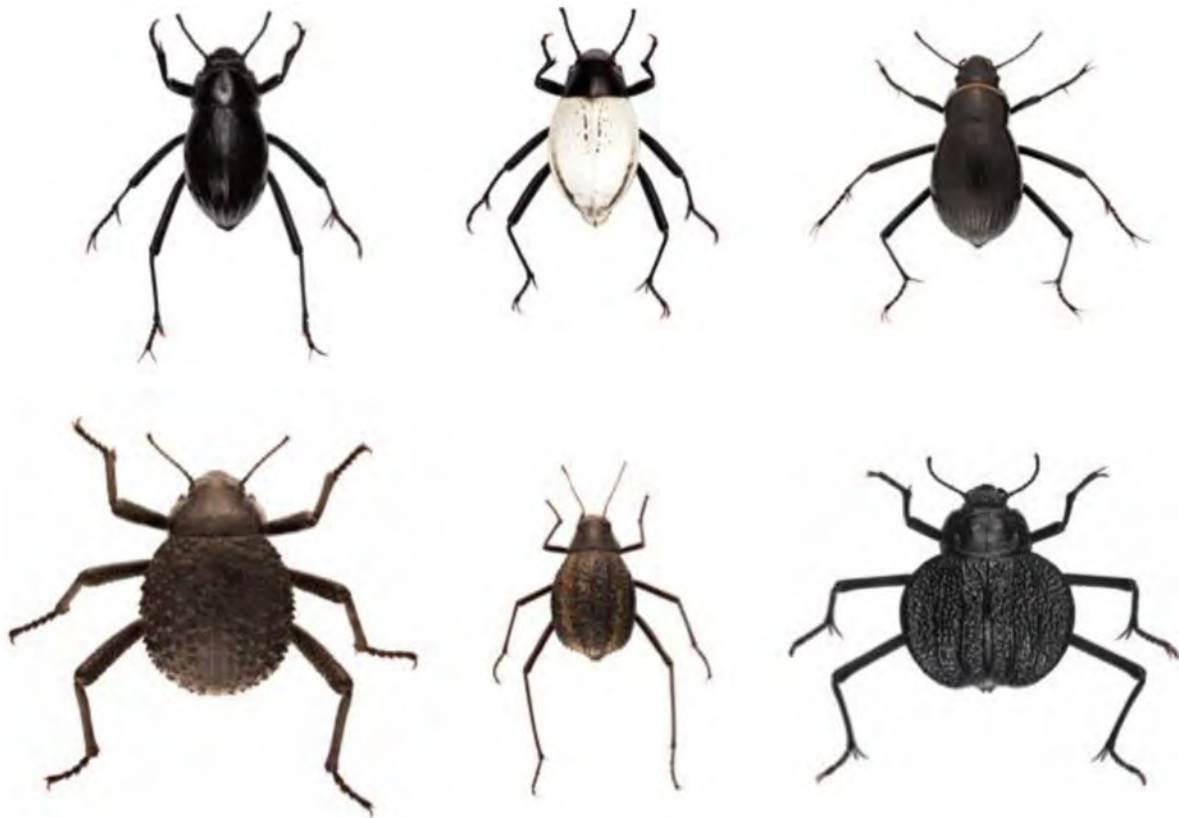
Fig. 7. Some adesmiine tenebrionid beetles of the Namib Desert. Top left to bottom right: *Onymacris unguicularis unguicularis, Onymacris bicolor, Onymacris laeviceps, Physosterna cribipes, Stenocara gracilipes, Onymacris plana*. *O. unguicularis,* and *O. bicolor* are fog-baskers; *O. laeviceps* is an opportunistic fog-harvester and *O. plana* an active fog-harvester. *P. cribipes* was misidentified as *Stenocara* sp. and erroneously described as a fog-basker, in Parker and Lawrence (2001). Indeed, neither *P. cribipes* nor *S. gracilipes* access free water from fog or dew; no "bumpy back" Namib beetles deposit fog or condense dew (see Appendix S4). (Composite photo: Trip Lamb, East Carolina University, USA).

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).
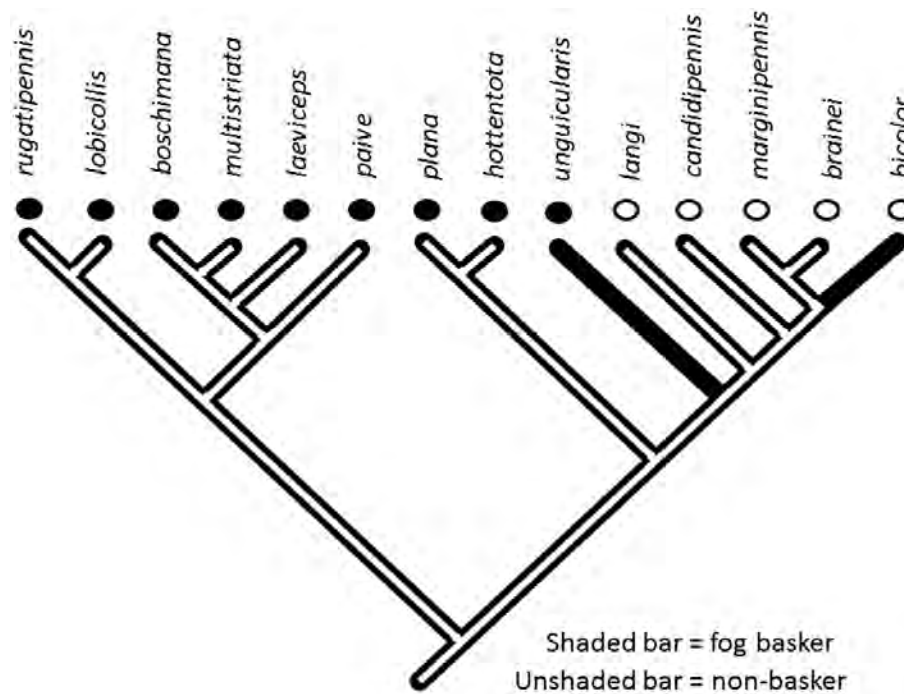
Fig. 9. Phylogeny of fog-basking in *Onymacris* beetles. Open circles denote the "white" tenebrionids (Lamb and Bond 2013). Fog-basking is not a trait of the genus and appears to have evolved independently twice (or has been lost by four "white" species). (Redrawn from Ward and Seely 1996, Lamb and Bond 2013).

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 sabulicola* (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

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

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 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

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).

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

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 water 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. 2012*b*). 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 integuments have a valve subserved 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 tissues are at a temperature lower than that of the surrounding air, because 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 $2.4 \times 1/56 = 0.04$ 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 1979*a*) 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 1979*a*).

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 1982*a*, *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 1979*a*). 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 1979*a*). 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 larvae	Namib tenebrionid	86	Coutchié and Crowe (1979*a*)
O. marginipennis larvae	Namib tenebrionid	83	Coutchié and Crowe (1979*a*)
Arenivaga investigate	Desert cockroach	81	O'Donnell (1982*b*)
Ctenolepisma longicaudata	Ubiquitous zygentoman	60	Heeg (1967)
C. terebrans	Namib zygentoman, previously dehydrated to 80% of normal body mass	45–47.5	Edney (1971)
Thermobia domestica	Ubiquitous zygentoman	45	Noble-Nesbitt (1969, 1975)
Lasioderma serricorne	Cigarette beetle, ubiquitous	43	Knülle and Spadafora (1970)

(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 tenebrionid 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 [$1000 \times 56 \times (100-83)/100$], 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 osmolalities that would be required confirm the experimental observations of Coutchié and Crowe (1979*a*) 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 tenebrionids are alleged to do so, but the research remains unpublished (Appendix S3: Table S1; Coutchié 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, Coutchié and Crowe 1979*b*). 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 *Zophosis* species of tenebrionid 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 *Psocoptera*, 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 hygroscopic 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 *Psocoptera*, *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 hygroscopic 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 hygroscopic 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 $(C_6H_{10}O_5)_n + nO_2 \rightarrow 6nCO_2 + 5nH_2O$. The mass of metabolic water produced, per kJ of energy produced, 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 $O_2 \cdot g^{-1} \cdot h^{-1}$) 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 $O_2 \cdot g^{-1} \cdot h^{-1}$ 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 $H_2O \cdot g^{-1} \cdot h^{-1}$ 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).

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 globose	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 (2001*a*)
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 $L \cdot m^{-2} \cdot d^{-1}$ (equivalent to 1 mm/d)	Sustains plant growth	Robinson and Seely (1980), Pietruszka and Seely (1985), Seely and Griffin (1986), Soderberg (2010)

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 temporally 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

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*		
Lizard *Meroles anchietae*	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 *Pedioplanis husabensis*	Acquires water in excess of its needs from termite diet	Murray et al. (2014)

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 preformed 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 (Hattingh et al. 1984, Henschel et al. 2001, Naidu 2001*b*). 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 (2001*a*)
Onymacris plana	66	13	Nicolson (1980)
Lepidochora discoidalis	-	27	Louw and Hamilton (1972)
Physadesmia globose	-	34	Naidu and Hattingh (1988)

Hyphen: hemolymph volume decreases not reported.

Table 9. Mass gain in a single fog exposure.

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)

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 (Hänsler 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 *Stips 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,

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 osmolytes, 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 osmolytes 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 osmolytes during rehydration in some species (Naidu 1998, 2001*a*, *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 osmolytes, 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.

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 (1979b); Machin (1981)
Onymacris plana (Active fog-harvester)	-	Osmoregulate well during rapid rehydration	Nicolson (1980)
Onymacris rugatipennis (Unlikely to use fog. See Appendix S3)	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 unguicularis (Fog-basker)	Requires food for osmoregulation during rehydration, perhaps for osmolytes. Rapidly re-synthesizes fat during rehydration.	Expected to cope well. In laboratory, did not restore body mass or regulate hemolymph volume or osmolarity during a one-hour drink after 10-d desiccation. Osmoregulation highly unstable for 4 d. In the field, regulation of body water and osmolality much better during rehydration	Naidu (2008), Cooper (1982)
Physadesmia globosa (Opportunistic fog-harvester)	Takes in fog water with sodden detritus	In laboratory (no detritus), efficient on the first day of rehydration but collapsed after that, leaving beetles ataxic	Naidu and Hattingh (1988)
Stenocara gracilipes (Not observed using fog)	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)
Stips stali (Use of fog not studied)	Uses amino acids as osmolytes	-	Naidu (1998)

Hyphen: mechanism unknown.

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 11. Opportunities for research on the relationship between Namib fauna and current fog.

Taxa	Opportunity	References
Insects		
Lepidochora sp.	How do the trench-diggers extract water from sand? It is not by ingestion of fog-soaked sand.	Seely (1979), Wharton and Richards (1978)
Lepidochora sp., *Physadesmia globosa*	Why do *Lepidochora* shun detritus with 60% water content during fog, but *Physadesmia* eats fog-laden detritus	Seely and Hamilton (1976); Cloudsley-Thompson (1990)
Lepidochora discoidalis	How does this beetle tolerate high hemolymph osmolality during desiccation?	Barton-Browne (1964), Louw and Hamilton (1972), Seely et al. (1983)
Active fog-harvesting tenebrionids	Do buried active fog-harvesters use change in vibrations created by surface wind to predict imminent fog?	Hanrahan and Kirchner (1994)
Nocturnally active invertebrates	Use infrared thermography to investigate whether they cool themselves by radiant heat loss on clear humid nights, so creating a gradient favorable for water vapor absorption	
Tenebrionid larvae and eggs	Water balance of eggs still to be studied. Water balance of larvae still to be studied in the field.	Beament (1961, 1964)
Pachysoma	Scarab dung beetles, all 13 species endemic to the coastal desert along the western coast of southern Africa; fog dependency not studied yet	Holm and Scholtz (1979, 1980), Harrison et al. (2003)
Pachysoma glentoni, *Pachysoma striatum*	Bury food (detritus, dung) that can be saturated with water; does the water come from fog?	Scholtz (1989), Scholtz et al. (2004), Holter et al. (2009)
Zygentoma	Some species can extract water vapor from air with low relative humidity; could they survive in the absence of fog?	Heeg (1967), Edney (1971)
Termites	To what extent are termites fog-dependent? What are the consequences for their predators if termites decline as fog declines?	Bothma et al. (1984), Zeidler et al. (2002), Murray et al. (2014)
Arachnids		
Solifuges	"Namibia probably has the world's greatest diversity of solifuges"; are desert solifuges or their prey fog-dependent?	Griffin (1998)
Mites and ticks	Can Namib ticks and mites access water vapor, as they do elsewhere? Are Namib ticks and mites living in the fog belt fog-dependent?	Beament (1961), Marsh (1987), Coineau and Seely (1983)
Mites	Gather under the leaves of *Welwitschia mirabilis*, but fog does not deposit under those leaves; why are they there?	Marsh (1987), Henschel et al. (2018)
Amphibia		
Bufo vertebralis hoeschi, *Phrynomerus annectens*	Lay eggs in ephemeral pools on inselbergs. Can these pools be filled by fog (as well as rain)?	Channing (1976)
Birds		
Corvus albus, *Corvus capensis*	Common throughout the Namib. Only rarely observed drinking at water holes. Can they survive on metabolic and pre-formed water?	Willoughby and Cade (1967)
Multiple taxa		
	Fog drip is an important source of surface water in wooded fog-dependent biomes, and some coastal fog-dependent deserts. It has been characterized for *Arthraerua* but not trees. Fog drip contains more solutes than does native fog water. How important is fog drip as a source of water and nutrients for Namib animals?	Rundel and Mahu (1976), Gottlieb et al. (2019)

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 offing 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

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Supporting Information

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

Ecosphere

FOG AND FAUNA OF THE NAMIB DESERT: PAST AND FUTURE

Appendix S1

Duncan Mitchell[1,2], Joh R Henschel[3,4,5], Robyn S Hetem[1,6], Theo D Wassenaar[4], W Maartin Strauss[1,7], Shirley A Hanrahan[6,], Mary K Seely[4,6,8†]

[1]Brain Function Research Group, School of Physiology, Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, South Africa

[2]School of Human Sciences, University of Western Australia, Perth, Australia

[3]South African Environmental Observation Network Arid Lands Node, Kimberley, South Africa

[4]Gobabeb Research Institute, Gobabeb, Namibia

[5]Centre for Environmental Management, University of Free State, Bloemfontein, South Africa

[6]School of Animal Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

[7]Nature Conservation Programme, Department of Environmental Sciences, UNISA, Florida, South Africa

[8]Desert Research Foundation of Namibia, Windhoek, Namibia

Email: m.k.seely@gmail.com

Namib Desert fog

The fog of the Namib Desert usually is described as advective fog carried in from the Atlantic Ocean as moisture-laden air is blown over the cold Benguela upwelling, the "the cold dank mist which blows in from the sea" described by Lawrence (1959). The prevailing coastal wind, responsible for characteristic alignment of the sand dunes in the sand sea of the central Namib and for cooling the dunes in the afternoon, is south-westerly (Goudie 1972; Seely and Stuart 1976; Seely 1984). That south-westerly wind conventionally has been identified as the vehicle for the advective fog (Seely and Henschel 1998), and indeed is the source of the low fog so well known in the Namibian coastal towns of Swakopmund and Walvis Bay (Figure 2). However, this low fog currently does not penetrate more than 17 km inland (Seely and Henschel 1998; Andersen and Cermak 2018; Roland Vogt, University of Basle, 2019, *personal communication*), and maximum fog deposition occurs more than 30 km from the coast, declining to near zero on the eastern edge of the Namib (Figure 2; Lancaster *et al.* 1984; Seely 1978; Pietruszka and Seely 1985; Seely and Griffin 1986; Hachfeld 2000; Henschel *et al.* 2001). Where fog deposits depends not just on the origin of the fog and the wind flows, but on land elevation and local topography (Table 1; Seely and Henschel 1998). The summer fogs at Gobabeb, 56 km from the coast, are high stratus cloud fogs, with the clouds originating from turbulence over the Benguela upwelling, and presenting as fog where the cloud intersects the land at altitudes of 200 to 500 m (Seely and Henschel 1998; Eckardt *et al.* 2013). The frequency of formation of stratus clouds varies with latitude, peaking at the Tropic of Capricorn (and Gobabeb has a latitude of 23.56°S), declining with higher and lower latitudes (Olivier 1995), and also declining in the summer months (Cermak 2012). Even after decades of study, the direction from which the moisture in the high stratus cloud fogs enters the Namib remains uncertain, but it is not from the south-west (see Beery 2009; Vogt *et al.* 2016; Spirig et al. 2019).

There is a third type of fog that has been encountered in the Namib, but rarely, and only when winter cold fronts arrive, and that is fog drizzle or frontal fog (Seely and Henschel 1998). A fourth kind of fog, radiative fog, typically arises in cloudless conditions in low-lying areas inland. Whether radiative fog occurs in the inland areas of the Namib has been uncertain (Kimura 2005; Olivier 1995; Seely and Henschel 1998; Walter and Breckle 1986), but recent analysis of the stable isotopes in the fog near Gobabeb indicates that it does occur, and that the immediate source of the fog water is not the Atlantic Ocean (Kaseke *et al.* 2017, Kaseke *et al.* 2018).

Fog water in the Namib has very low osmolality (10-38 mosmol l^{-1}, Louw and Holm 1972; Eckardt and Schemenauer 1998; Shanyengana *et al.* 2002; Eckardt *et al.* 2013). Fog collected over time in gauges may appear to have higher osmolality, especially near the coast (Goudie 1972), but, in the Namib at least, that higher osmolality arises not from solutes in the fog itself, but from contaminants that collect on the fog gauges between fog events (Gottlieb *et al.* 2019).

The origin of the Namib fog is of great interest to meteorologists and climatologists but of less importance to the Namib biota than are fog frequency and predictability, when within the 24h day it occurs, and whether or not the fog deposits. There is no complete record of fog incidence over the nearly 60 years over which the Namib biota have been studied formally, but there have been prolonged intermittent periods for which incidence were recorded. In the 1960s and 1970s there were intervals of up to 63 days between fogs 56 km from the coast (Table 1), but between 1976 and 1981, at Ganab (Figure 2), 44 km further east, there was an interval of 772 days without fog (Lancaster *et al.* 1984). The interval between those fogs that deposit is the crucial interval for fog-harvesters that consume formed water droplets (Appendix S3). For animals that can access dew or acquire water vapor from non-depositing fog, the interval between replenishing events would be much shorter. For 1969, a year for which there were detailed deposition measurements, the interval between events which provided free water (rain, fog,

dew) was two weeks on average (Holm and Scholtz 1980), and in 2001 there was free water on the ground surface at Gobabeb, at least for some hours, on 40% of all the days of the year (Henschel and Seely 2008). At Gobabeb in the 1960s and 1970s, the longest interval without dew or any fog (including non-depositing fog) was 36 days (Seely *et al.* 1983), and, on average over the ten years, there was depositing early-morning fog on at least one day of every month of the year (Seely and Stuart 1976). For the period 1964-1967, there was fog at or near Gobabeb for an average of 102 days per year. It deposited on 60 days per year on average and produced an average of 31 mm of water per year (Goudie 1972). So at Gobabeb at least, events which provided free water were not infrequent but they were unpredictable. The future welfare of fog-dependent biota of the Namib depends on how the fog will respond to climate change (Hänsler *et al.* 2011; Appendix S5).

Liquid water in surface droplets is available to animals only for a few hours of a day during and after fog or dew forms, both because the cool surfaces necessary for dew formation occur only at night and in the early morning, and because fog usually occurs around midnight, with droplets surviving a few hours after sunrise (Holm and Scholtz 1980; Cermak 2012). The droplets of fog and dew dry up as the day warms (Henschel *et al.* 2001). The fog cloud itself almost always has dissipated completely by early afternoon (Cermak 2012).

Even in dense fog, when water droplets in the air reduce visibility potentially to hazardous levels (Cermak 2012), there is much more water contained in the fog's vapor component than in its droplets (Figure 6, Eugster 2008). On foggy mornings in the Namib, air relative humidity typically is 88% (Soderberg 2010) though it can reach 100% (Schulze 1969). There are many more days per month when air close to the surface reaches a high relative humidity (sometimes more than 97% even in the absence of fog), for at least some period of the day, than there are days per month of fog or other deposition (nearly twice as many at Gobabeb, with more than 120 days recorded in 2001, Figure 3). Periods of the day with high relative humidity tend to be

the same as those at which fog occurs (late at night and into the early hours of the morning, Seely 1989), and so the near-saturated water vapor in the air is unavailable to animals not active then. But during those periods water vapor penetrates into the substrate, leaving water and water vapor available for use later (Kaseke *et al.* 2012).

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Ecosphere

FOG AND FAUNA OF THE NAMIB DESERT: PAST AND FUTURE

Appendix S2

Duncan Mitchell[1,2], Joh R Henschel[3,4,5], Robyn S Hetem[1,6], Theo D Wassenaar[4], W Maartin Strauss[1,7], Shirley A Hanrahan[6], Mary K Seely[4,6,8†]

[1]Brain Function Research Group, School of Physiology, Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, South Africa

[2]School of Human Sciences, University of Western Australia, Perth, Australia

[3]South African Environmental Observation Network Arid Lands Node, Kimberley, South Africa

[4]Gobabeb Research Institute, Gobabeb, Namibia

[5]Centre for Environmental Management, University of Free State, Bloemfontein, South Africa

[6]School of Animal Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

[7]Nature Conservation Programme, Department of Environmental Sciences, UNISA, Florida, South Africa

[8]Desert Research Foundation of Namibia, Windhoek, Namibia

 Email: m.k.seely@gmail.com

Dew and Namib fauna

Dew differs from fog in that the liquid water in dew forms by condensation of vapor on a surface when the temperature of the surface is at or below the dew point temperature, which is the temperature to which the prevailing ambient air would have to be cooled for relative humidity to reach 100%. The most-common cause of surface cooling leading to dew formation is loss of radiant heat to a cold sky, typically at night (Lasiewski and Bartholomew 1969; Beysens 1995). As Agam and Berliner (2006) have pointed out, terms like "dewfall" or "dew deposition" are misrepresentations. Dew neither falls nor deposits, but condenses, and dew droplets may aggregate to form drops of substantial size (Figure 5, lower panels). On the other hand, the liquid water in fog already is in droplets (Figure 5, upper panels). Depositing fog (historically called "precipitating fog", but "precipitating" also is a misnomer) is fog in which the droplets settle under gravity or are blown into objects by wind.

In the Namib, the volume of water formed by dew, as measured by instruments like leaf wetness detectors and polyethylene foil dew collectors (Muselli *et al.* 2006), is more than twice that deposited by fog (Soderberg 2010), but dew will not be available to much of the Namib fauna. First, dew rarely forms on bare sand (Agam and Berliner 2006) such as that which makes up the Namib sand sea. Rather, the water vapor that would have formed dew penetrates into the sand surface, without water droplets condensing on the surface. Dew forms on impermeable surfaces, such as vegetation, detritus, stone or the animals themselves. So animals on vegetationless dunes would not encounter dew in their environment, except on wind-blown detritus. The instruments used to measure dew are impermeable surfaces, so overestimate massively the amount of dew that would form in a sandy desert. Secondly, dew tends to form around sunrise (Kaseke *et al.* 2012a), and so can provide a source of free water only to those taxa that are active on the surface then, or when residual dew droplets persist. That excludes all the diurnally-active tenebrionid beetles and lizards, for example, because they would be

buried below the surface. Some diurnally-active tenebrionid beetles do become active outside their normal activity period to harvest fog actively (see Appendix S3), but no Namib animals have been observed to change activity period to access dew. Unlike most Namib tenebrionid beetles, the majority of Palaearctic desert beetles elsewhere are nocturnally-active (Cloudsley-Thompson 2001), so dew potentially is a more-important water source for beetles in other deserts (Broza 1979). Also elsewhere, there is an ant species (Moffett 1985) and a desert snail (Degen *et al.* 1992; Shachak *et al.* 2002) known to use dew as a source of free water.

For radiant heat loss to cool surfaces to dew point, those surfaces must be exposed to the sky. Long-wave radiant heat like that that leaves the Earth's surface cannot penetrate fog. And the fog is at air temperature, so loss of radiant heat to the fog itself cannot drop surface temperature to below air temperature. So dew cannot form during fog. Because fog arrives late at night, it is possible for dew to have formed earlier when the skies were clear (though dew usually forms around dawn), and for dew droplets still to be available on impermeable surfaces when the fog arrives, because dew droplets can persist until the following morning (Agam and Berliner 2006). It is possible for residual fog and dew droplets to co-exist. They can be distinguished in the Namib by their different profiles of stable isotopes of oxygen (Kaseke *et al.* 2018). So Namib animals that take fog droplets off vegetation opportunistically (Appendix S3) may also take residual dew droplets. But the fog-baskers and trench-diggers ignore vegetation, including detritus, while they are harvesting fog. For them, fog harvesting and dew acquisition are mutually exclusive activities (Seely, 1979).

Dew could be a valuable source of non-rainfall water for animals active on the surface around dawn, which could collect it off vegetation, off themselves, or other impermeable surfaces. Also, the water vapor that penetrates sand when the dew is forming on nearby impermeable surfaces raises the relative humidity in the top layers of the sand (Kaseke *et al.* 2012b), and so may provide the appropriate gradients for vapor absorption by those animals that can absorb

water vapor directly. Water adsorbed on to sand also will provide a source for those animals that can remove water from sand. But even if there is more dew formed in the Namib than deposited fog, it is the fog, rather than the dew, that will likely sustain the Namib fauna.

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FOG AND FAUNA OF THE NAMIB DESERT: PAST AND FUTURE

Appendix S3

Duncan Mitchell[1,2], Joh R Henschel[3,4,5], Robyn S Hetem[1,6], Theo D Wassenaar[4], W Maartin Strauss[1,7], Shirley A Hanrahan[6,*], Mary K Seely[4,6,8†]

[1]Brain Function Research Group, School of Physiology, Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, South Africa

[2]School of Human Sciences, University of Western Australia, Perth, Australia

[3]South African Environmental Observation Network Arid Lands Node, Kimberley, South Africa

[4]Gobabeb Research and Training Centre, Gobabeb, Namibia

[5]Centre for Environmental Management, University of Free State, Bloemfontein, South Africa

[6]School of Animal Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

[7]Nature Conservation Programme, Department of Environmental Sciences, UNISA, Florida, South Africa

[8]Desert Research Foundation of Namibia, Windhoek, Namibia

Email: m.k.seely@gmail.com

Appendix S3: Table S1. Fog-harvesting fauna of the Namib

Species	Description[1]	Mode	Source of water	Behaviour	Reference
Arachnids					
Carparachne aureoflava	Spiderling *(nymph 1 stage 2 mg; nymph 2 stage to adult 10-1150 mg)*[7]	Active?	Web	On trapdoor external surface amongst fog droplets, high on dune where fog is denser. Normally deep in burrow at this time	Joh Henschel (personal observation). See Fig. 5
Leucorchestris arenicola	Spider *(Adult females 2.6±0.9 g; adult males 2.0±0.5 g)*[8]	Active?	Web	Cling to wet trapdoors on foggy mornings	Henschel 1997
Parabuthus villosus √	Scorpion *(6 g)*[3]	Opportunistic	Vegetation	Takes droplets off grass stems	Polis and Seely 1990; Robertson *et al.* 1982
Seothyra henscheli	Spider *(adults 10-146 mg)*[7]	Active?	Web	Cling to trapdoors on foggy mornings	Henschel 1997
Insects					
Lepidochora discoidalis *(=argentogrisea)* √	Tenebrionid beetle (81 mg) *(80 mg)*[2]	Trench-digger and opportunistic	Sand	Extracts moisture from trench ridges. Residual drops on ventral surface following fog. Water sprayed on dehydrated beetles enters digestive tract. Drinks the water directly; cannot absorb	Louw 1972; Louw and Hamilton 1972; Seely and Hamilton 1976; Seely 1979

				water through the carapace. Loses weight on dry food.	
Lepidochora eberlanzi √	Tenebrionid beetle	?	Sand	?	Seely 1979
Lepidochora kahani √ *(150 mg)*[2]	Tenebrionid beetle	Trench-digger	Sand	Extracts moisture from trench ridges	Seely and Hamilton 1976
Lepidochora pilosa √	Tenebrionid beetle	?	Sand	?	Seely 1979
Lepidochora porti √ *(100 mg)*[2]	Tenebrionid beetle	Trench-digger	Sand	Extracts moisture from trench ridges	Seely and Hamilton 1976
Metriopus depressus *(120 mg)*[2]	Tenebrionid beetle	Active?	?	Activity increases massively in depositing fog; not yet observed to consume droplets	Wharton and Seely 1982
Onymacris bicolor √	Tenebrionid beetle	Fog-basker	Carapace	Head stands in fog, drinks droplets	Hamilton and Seely 1976; Ward and Seely 1996
Onymacris laeviceps √ *(434 mg)*[5] *(530 mg)*[11]	Tenebrionid beetle	Opportunistic	Vegetation	Takes droplets off vegetation only, crepuscular/nocturnal	Seely 1979; Seely *et al.* 2005
Onymacris marginipennis √ *(Larvae: 125-300 mg)*[9]	Tenebrionid beetle	Opportunistic	Larvae: sub-surface air	Water vapor; requires relative humidity more than 83%	Coutchié and Crowe 1979a

Onymacris plana √	Tenebrionid beetle (Adult females 870 mg, males 650 mg) *(Adult 700 mg)*[2] *(Adult 770 mg)*[11] *(Adult 930±250 mg, mean ±SD, n=10)*[14]	Active Opportunistic	Adults: vegetation Larvae: sub-surface air	Takes droplets. Emerges at surface temperatures below 10°C (prefers 20°C – 50°C) following fogs to take droplets Water vapor; requires relative humidity more than 86%	Seely 1979; Nicolson 1980; Seely *et al.* 2005; Bartholomew *et al.* 1985 Coutchié and Crowe 1979a
0nymacris rugatipennis	Tenebrionid beetle *(Adult 500 mg)*[11] *(Adult 720±200 mg, mean ±SD, n=10)*[14]	Opportunistic	Larvae: sub-surface air AdultsX	Water vapor (Research completed but data not published) Riparian, strictly diurnal and thermophilic, unlikely to use fog	Coutchié and Machin 1984 Seely *et al.* 1988
Onymacris unguicularis √	Tenebrionid beetle (600 mg) (600 mg dehydrated, 640 mg rehydrated) *(650 mg)*[2] *(590 mg)*[11]	Fog-basker	Carapace	Head stands in fog, drinks droplets	Hamilton and Seely 1976; Cooper 1982; Ward and Seely 1996; Naidu 2008; Nørgaard and Dacke 2010

	(737 ± 120 mg, mean ± SD)[13]				
Pachysoma glentoni	Dung beetle	Active	Detritus	Buries and eats detritus saturated with water, presumably originating from nocturnal fog; requires evidence for origin of the water	Holter *et al.* 2009
Physadesmia globosa √	Tenebrionid beetle *(Adult 510 mg)*[2] *(Adult 520 mg)*[11] *(Adult 650 mg)*[12] *(Adult 780±310 mg, mean ±SD, n=10)*[14]	Active	Sand	Emerge on foggy mornings and "feed upon sodden detritus". Very lethargic then; normally not active below 15°C air temperature. Naidu and Hattingh (1988) cite Seely (1979) as reporting that *Physadesmia globosa* takes water droplets off vegetation during fogs, but the species is not mentioned in Seely's paper.	Naidu and Hattingh 1988, Seely 1979, Cloudsley-Thompson 1990
		Opportunistic	Larvae: subsurface air	Water vapor (Research completed but data not published)	Coutchié and Machin 1984
Physosterna cribripes	Tenebrionid beetle *(Adult 1.23 g)*[12]	Opportunistic	Larvae: sub-surface air	Water vapor (Research completed but data not published)	Coutchié and Machin 1984
Psammotermes allocerus √	Termite *(workers 1.0-1.2 mg)*[10]	Opportunistic	Sand	Special anatomical devices (hypopharynx) to access capillary water	Grube and Rudolph 1995

				in moist sand; can't drink from droplets or access water vapor	
Stenocara gracilipes X (305±10 mg)	Tenebrionid beetle	Not observed using fog	-	Naidu (2001) surmised that it takes droplets off vegetation or detritus, and so would benefit from efficient osmoregulation during rehydration, but it never has been seen doing so. Its diurnal surface activity period may well prevent it encountering droplets because they will have evaporated by the time that it emerges.	Naidu 2001
Swalepisma mirabilis √	Silverfish	Opportunistic	Sand	Surface active in fog, possibly taking moisture from sand	Watson and Irish 1988
Zophosis amabilis √ $(80 mg)^2$	Tenebrionid beetle	Opportunistic	Gravel on the gravel plains	Nocturnal; weak response to fog	Seely *et al.* 2005; Wharton and Seely 1982
Zophosis carpi √	Tenebrionid beetle	?	Sand	?	Seely 1979
Zophosis (= Anisosis) caudata √	Tenebrionid beetle	?	Sand	?	Seely 1979
Zophosis (=Tarsosis) damarensis √	Tenebrionid beetle	?	Sand	?	Seely 1979
Zophosis eremita √	Tenebrionid beetle	?	Sand	?	Seely 1979
Zophosis fairmairei √	Tenebrionid beetle	Active	Sand	Emerges in fog outside normal activity periods. Extracts moisture from	Seely 1979; Seely *et al.* 2005

	(7 mg)[2] (32 mg)[11]			undisturbed fog-moistened sand, and from ridges of small craters that form as beetles emerge from moist sand	
Zophosis (=Onychosis) gracilipes √	Tenebrionid beetle	?	Sand	?	Seely 1979
Zophosis hamiltoni √	Tenebrionid beetle (4 mg)[2]	Active	Sand	Emerges in fog outside normal activity periods. Extracts moisture from undisturbed fog-moistened sand, and from ridges of small craters that form as beetles emerge from moist sand	Seely 1979; Seely *et al.* 2005
Zophosis (=Cerosis) hereroensis √	Tenebrionid beetle	?	Sand	?	Seely 1979
Zophosis moralesi √	Tenebrionid beetle (70 mg)[2]	Active	Sand, vegetation	Emerges in fog outside normal activity periods. Extracts moisture from undisturbed fog-moistened sand	Seely 1979; Seely *et al.* 2005
Zophosis orbicularis √	Tenebrionid beetle (135 mg)[2] (100 mg)[11]	?	Vegetation	?	Seely 1979
Zophosis triangulifera √	Tenebrionid beetle	?	Sand	?	Seely 1979
Molluscs					
Xerocerastus minutus	Snail	Active?	Vegetation?	Emerges from crevices to feed only during depositing fog events	Hodgson *et al.* 1994

Trigonephrus sp.	Snail (9 g)	Active	?	Normally burrows; becomes active on the surface on foggy mornings	Dallas *et al.* 1991
Amphibia					
Breviceps macrops	Frog	Opportunistic	?	Restricted to habitats with more than 75 fog days per year. Lives in visibly-moist burrows, at least some wet by fog.	Channing and Wahlberg 2011
Bufo vertebralis hoeschi	Toad	Opportunistic	Pools	Nocturnal. Lays eggs in ephemeral pools on granite, filled by rain but possibly also fog.	Channing 1976
Phrynomerus annectens	Frog	Opportunistic	Pools	Lays eggs in ephemeral pools on granite, filled by rain but possibly also fog. Spreads substrate moisture on skin for evaporative cooling; obtains moisture from fog?	Channing 1976
Reptiles					
Bitis caudalis √	Horned adder (males 40-77 g)[6]	Fog-basker	Body	Drinks fog droplets depositing on body. Not normally surface-active at low temperatures.	Murray and Irish 2015
Bitis peringueyi √	Sidewinding adder	Fog-basker	Body	Drinks fog droplets depositing on body. Not normally surface-active at low temperatures.	Robinson and Hughes 1978

Bradypodion pumilus √	Arboreal chameleon (11 g)	Opportunistic	Snout, vegetation	Runs droplets depositing on snout on to tongue, drinks from droplets on vegetation	Burrage 1973
Chamaeleo namaquensis √	Ground-dwelling chameleon (49-77 g)	Opportunistic	Body, sand, rocks, vegetation	Drinks fog water collected in capillary channels on skin, water that drops off body on to sand, and droplets on rocks and vegetation	Burrage 1973
Meroles (= Aporosaura) anchietae √	Dune lizard (2.9 g dehydrated, 3.2 g rehydrated) (males 5.4 g, females 3.1 g)	Opportunistic	Vegetation	Takes droplets, rarely observed drinking but digestive tract distended with clear fluid after condensing fogs. At the coast, consumes kelp flies on which fog has deposited. Caught in traps in heavy fog, outside normal preferred temperature range for surface activity. Freely imbibes free water in the laboratory.	Louw 1971, 1972; Louw and Holm 1972; Cooper and Robinson 1990; Henschel and Seely 2008
Pachydactylus (=Palmatogecko) rangei √	Dune lizard	Fog-basker	Eyes	Licks droplets off eyes	Hughes 1976
Rhoptropus afer √	Rock lizard (1.8-3.3 g, mean 2.6 g)	Obligate fog user	Unknown	Not observed	Murray *et al.* 2014 based on data in Nagy *et al.* 1993
Rhoptropus bradfieldi √	Rock lizard (males 3.6 g Dec/Jan 4.8 g May, females 3.0g Dec/Jan 3.2 g May)	Obligate fog user	Unknown	Not observed	Murray *et al.* 2015

Mammals					
Canis mesomelas √	Black-backed jackal *(males 7.9 kg, females 6.6 kg)[4]*	Opportunistic	Vegetation, rocks	Licks droplets off !Nara, and off rocks in the Skeleton Coast	Goldenberg *et al.* 2010; Louw and Seely 1982 (p.83)
Rhaphicerus campestris √	Steenbok, small antelope (males 9.2 kg)	Opportunistic	Vegetation	Observed once licking droplets off *Tamarix*	Cloete and Kok 1986

√ "Confirmed species", that is those for which there is direct evidence of fog harvesting. Unmarked species are "candidate species" that have good circumstantial evidence for fog harvesting but no direct evidence (yet). X Species studied but unlikely to use fog, or known not to use fog

[1] Masses in regular font are actual values from the papers cited. Masses in italics are derived from other sources including: [2] live masses calculated from the dry masses of Henschel and Seely (1997) assuming a body water content of 54% (Nicolson 1980) except for *O. unguicularis* (64%, Naidu 2008), [3]Lighton *et al.* (2001), [4]Smithers (1983), [5]Louw and Hamilton (1972), [6]DeNardo *et al.* (2002), [7]Henschel J R (personal data), [8]Henschel (1990), [9]Coutchié and Crowe (1979b), [10]Picker M D (personal data), [11]Lighton (1991), [12]Bartholomew *et al.* (1985), [13] Louw *et al.* (1986), [14]Lease *et al.* (2014), .

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Ecosphere

FOG AND FAUNA OF THE NAMIB DESERT: PAST AND FUTURE

Appendix S4

Duncan Mitchell[1,2], Joh R Henschel[3,4,5], Robyn S Hetem[1,6], Theo D Wassenaar[4], W Maartin Strauss[1,7], Shirley A Hanrahan[6], Mary K Seely[4,6,8†]

[1]Brain Function Research Group, School of Physiology, Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, South Africa

[2]School of Human Sciences, University of Western Australia, Perth, Australia

[3]South African Environmental Observation Network Arid Lands Node, Kimberley, South Africa

[4]Gobabeb Research Institute, Gobabeb, Namibia

[5]Centre for Environmental Management, University of Free State, Bloemfontein, South Africa

[6]School of Animal Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

[7]Nature Conservation Programme, Department of Environmental Sciences, UNISA, Florida, South Africa

[8]Desert Research Foundation of Namibia, Windhoek, Namibia

 Email: m.k.seely@gmail.com

Biomimicry, bio-inspiration, and *Stenocara/Physosterna*

The only Namib beetle species observed to fog-bask are the two *Onymacris* species

(Hamilton & Seely 1976; Ward & Seely 1996). In both, the fog-capturing carapace is

grooved and hydrophobic (Henschel & Seely 2008). Twenty five years after the first

observation of fog-basking in Namib beetles, a paper appeared reporting that another Namib

tenebrionid beetle, *Stenocara sp.*, also harvested fog directly, and presented a mechanism for

capturing fog water related to hydrophilic bumps on the carapace (Parker & Lawrence 2001).

Namib beetle experts soon pointed out that not only were the experiments carried out at

temperatures that do not occur in Namib fogs but also that the beetle species depicted in a

photograph in the paper was not any *Stenocara* species but was *Physosterna cribripes*

(Hamilton *et al.* 2003; Figure 7). One of the authors accepted the species correction thirteen

years later, saying the beetle was "renamed", and admitted that the beetle was a "questionable

fog-basker" (Malik *et al.* 2014). The habitat of *Stenocara gracilipes,* a *Stenocara* species that

does occur in the Namib, is dry river beds, and *Physosterna cribripes* lives on the stable

gravel planes. Neither species occurs on the sand dunes where fog-basking occurs, and no

Stenocara or *Physosterna* species ever has been observed in fog (Hamilton *et al.* 2003). A

recent laboratory investigation reported that neither *Stenocara gracilipes* nor *Physosterna*

cribripes could be induced to fog-bask in a fog chamber, and also reported their carapaces to

be entirely hydrophobic (Nørgaard and Dacke 2010). Dead *Stenocara gracilipes* did

accumulate more water per mm^2 from artificial fog than did other dead beetles, but for

reasons related to wind profiles rather than carapace structure. The *Stenocara*/*Physosterna*

paper has launched a biomimicry industry, aimed at constructing fog-capturing devices that

mimic *Stenocara/Physosterna's* carapace (see, for example, Zhai *et al.* 2006; Garrod *et al.*

2007; Dorrer and Rühe 2008; White *et al.* 2013; Uçar and Erbíl 2013; Oyola-Reynoso *et al.*

2016). The beetle biomimicry was commended in a recent review of biomimicry (Weiler and

Goel 2015), and as recently as 17 June 2019, *Stenocara's* supposed fog-basking was heralded in a BBC World Service podcast on biomimicry (https://www.bbc.co.uk/programmes/p07d5k9b). Industry may have delivered creative fog-collecting devices based on hydrophilic bumps on a hydrophobic surface (Lee *et al.* 2012), but those devices are unrelated to how Namib beetles harvest fog. They do not constitute biomimicry.

Parker more-recently seems to have moved on from the idea that *Physosterna cribripes* collects fog. With new co-authors, he has explored the possibility that the carapace surface is suitable for collecting Namib dew at night, by analysing the carapace from a preserved specimen (Guadarrama-Cetina *et al.* 2014). Parker and colleagues concluded that the carapace indeed is suitable, but not on the bumps considered so important in fog collection, nor because of hydrophilic regions (which they now state are absent). Bio-inspired by that conclusion, Harvard researchers designed a dew-collecting artificial surface based partially on the supposed dew-collecting properties of the carapace of *Physosterna cribripes* (Park *et al.* 2016). Attaining a carapace temperature low enough below the dew point to condense dew requires loss of carapace heat by radiation to the cold night sky (see Appendix S2). *Physosterna cribripes* is a strictly-diurnal species (Seely *et al.* 2005). It shelters under rocks or in crevices at night (Wharton and Seely 1982), so is not exposed to the night sky. It is active preferentially on days when the hot and dry east (offshore) wind blows (Wharton and Seely 1982), and when neither dew nor fog form. *Physosterna cribripes* populations crashed in the absence of rain, in spite of fog and dew being abundant (Seely *et al.* 2005). It is not an appropriate species to bio-inspire artificial dew-collecting surfaces. Parker and colleagues also raised the possibility that *Onymacris unguicularis* and *Onymacris bicolor,* rather than, or addition to, fog-basking, collect dew. Those usually-diurnal species indeed do emerge at night, but only in fog, when the night sky is not visible to them. When beetle species are fog-

basking, dew is unavailable to them (Seely 1979; Supplementary material S2). Also, the surface properties optimal for fog collection are quite different to those optimal for dew condensation (Lee *et al.* 2012).

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Ecosphere

FOG AND FAUNA OF THE NAMIB DESERT: PAST AND FUTURE

Appendix S5

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[1]Brain Function Research Group, School of Physiology, Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, South Africa

[2]School of Human Sciences, University of Western Australia, Perth, Australia

[3]South African Environmental Observation Network Arid Lands Node, Kimberley, South Africa

[4]Gobabeb Research Institute, Gobabeb, Namibia

[5]Centre for Environmental Management, University of Free State, Bloemfontein, South Africa

[6]School of Animal Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

[7]Nature Conservation Programme, Department of Environmental Sciences, UNISA, Florida, South Africa

[8]Desert Research Foundation of Namibia, Windhoek, Namibia

Email: m.k.seely@gmail.com

The future of Namib fog

There has been just one attempt at modelling the future of fog over the Namib (Appendix S5: Figure S1; Hänsler *et al.* 2011). The model projects a small increase in the number of fog days at the coast (typically from about 100 to about 120 per year) and a proportionally-similar spatially-variable decrease further inland (typically from about 50 to about 40 days), over the rest of the century (Appendix S5: Figure 1). A circulation system similar to that which generates Namib fogs prevails on the coast of California, USA (Sydeman *et al.* 2014), and there fog precipitation already has declined massively (Johnstone and Dawson 2010). In the Central Valley of California, the number of days with dense fogs decreased by 50% between 1980 and 2010 (Herckes *et al.* 2015). Studies of cloud forests, where the mechanism of water delivery essentially is the same as with fog, have indicated that the cloud base is expected to rise with increasing atmospheric temperatures (Still *et al.* 1999, Foster 2001). If the fog base rises in the Namib, fewer fogs will deposit or even reach ground level (Soderberg 2010).

It will not be the future volume or the rate of fog deposition that determines the fate of the fog-dependent fauna of the Namib, though, but the future fog regularity (Louw and Holm 1972). It is the reliability of fog events that has shaped the Namib's current fauna (Pietruszka and Seely 1985). What we need to be able to predict is the interval between future fog events, and the variability in that interval, for sites between the coast and the eastern boundary of the Namib. It is notoriously difficult to model the atmosphere/ocean/land coupling that is necessary to predict the extent, the location and the timing of fog in the future (Koračin *et al.* 2014; Torregrosa *et al.* 2014). So when we contemplate the future of fog-dependent fauna under climate change, it currently has to be without secure knowledge of the nature of fog on which they will have to depend, if, indeed, any fog remains.

In parallel to modelling the future of fog, we need to monitor fog and dew deposition over the fog belt, and some instrumentation to do so in real time already has been installed (Kaspar *et al.* 2015; Spirig *et al.* 2019), with an array of stations in the Namib measuring fog and dew, and other microclimate variables, mainly in the gravel plains inland from Walvis Bay (http://www.gobabebtrc.org/index.php/component/content/article/49-monitoring/269-fognet-weather-stations). Fixed instruments can provide measurements of the fog at only a limited number of sites, and can capture only partially the spatial variability of the fog. Satellite imaging, ideal for measuring spatial distributions, has difficulty separating fog from higher stratus clouds (Olivier 1995, but see Cermak 2012), and is unable to distinguish between depositing and low-level non-depositing fog (Seely and Henschel 1998 but see Schultz 2006, who used remote sensing to map the occurrence of fog-wetted lichen). Although the low population density of Namibia will limit resolution, a citizen-science fog survey, like that of the Scottish snow survey (Spencer *et al.* 2014), could report local fog events, and identify those that are depositing events.

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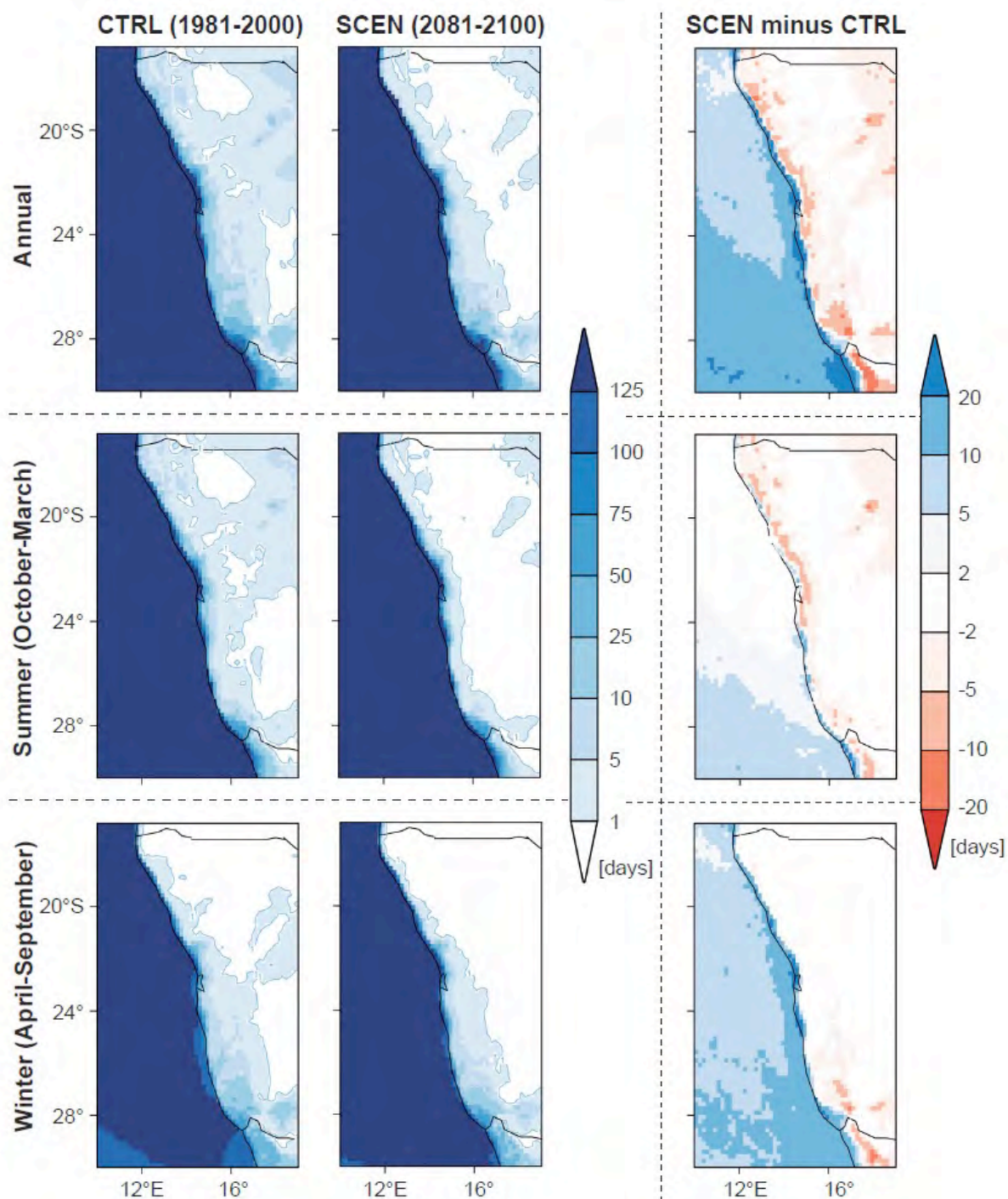
Appendix S5: Figure S1. Mean number of fog days per year (top row), in summer (middle row) and winter (bottom row) simulated for 1981-2000 (left column, "CTRL") and 2081-2100 (middle column, "SCEN"). The right column shows the difference between 2081-2100 and 1981-2000. From Hänsler *et al.* (2011), by kind permission of the University of Bonn, Germany.