Bare areas caused by Hodotermes mossambicus in the northern Namib Desert

Authors: Jürgens, N. & Gunter, F.

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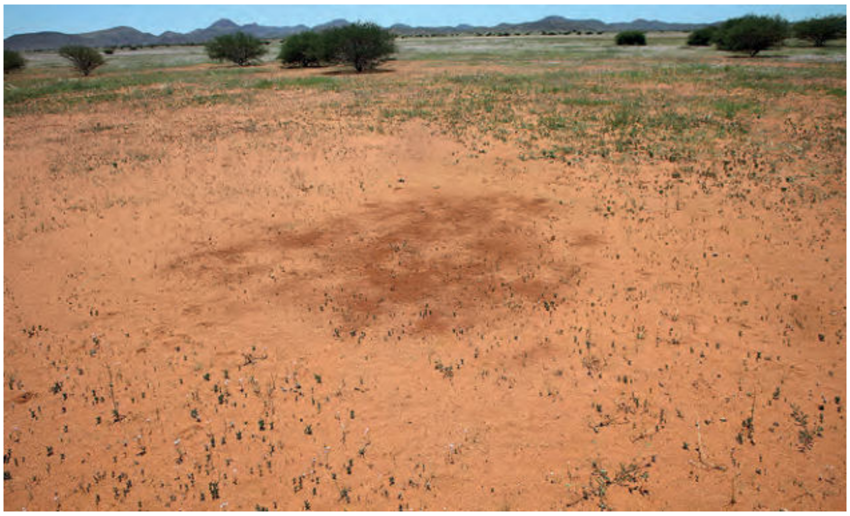

Figure 9.4.4: Circular aggregate of *Ammophila* spec. wasp nests in open savanna (Onjuva Plain NE of Orupembe, Plot 38103, 18.03.2022).

Figure 9.4.5: Ammophila spec. wasps next to a nest.

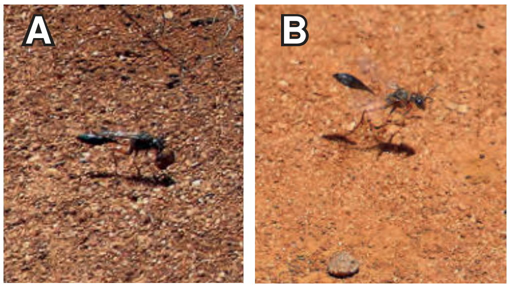

Figure 9.4.6 A and B: Two examples of Ammophila spec. wasps transporting soil material during flight (Onjuva Plain NE of Orupembe, 18.03.2022).

Ammophila sp. wasp nest accumulations

For the sake of completeness a type of circular bare patches shall be mentioned that we occasionally found in sandy plains of the northern Namib, for example in the sparse savanna of the southwestern Onjuva Plain in the Kunene region of Namibia (Fig. 9.4.4). Such circular bare patches are caused by the cumulative activity of hundreds to thousands of *Ammophila* spec. wasps (Sphecidae) which construct hundreds to thousands of their nests in this narrow space.

On 18th March 2022 many wasps were busy with construction works at their tunnels. During this day visit, no in-depth study of the social behaviour was possible nor did we identify the species of *Ammophila*. However, our observations of the behaviour match the description of the behaviour of *Ammophila ferrugieipes* in Gutteridge (2017). The nest consists of a vertical tunnel with a caterpillars provided for the eggs of the wasp. There are no piles of excavated soil but mineral grains were apparently transported away via air. Other wasps brought small stones and clods of earth, again via air transport, apparently to seal their tunnels. The amount of earth movement was sufficient to strongly alter the soil surface in the darker area and to kill almost all plants in a circular area of several meters diameter (Fig. 9.4.4).

9.5 Bare areas caused by *Hodotermes mossambicus* in the northern Namib Desert

Authors: Norbert Jürgens and Felicitas Gunter

Next to *Psammotermes allocerus*, *Hodotermes mossambicus* (Fig. 9.5.1 A) (known as Northern harvester termite) is the most frequent termite in the fairy circle landscapes receiving summer rains. Both species sometimes share the space in the soil at distances of few decimetres. Often the soil dumps of *Hodotermes* are even found within a fairy circle bare patch. The co-existance indicates niche differentiation. In fact, the foraging behaviour of both species is very different. While the small *Psammotermes* colonies forage in the matrix around the bare patch and initially prioritize subterranean biomass, *Hodotermes* is active during the day (Fig. 9.5.1 B), first collects litter and then harvests grass tussocks from the top downwards (Duncan & Hewitt 2009). During the peak vegetation period large numbers of *Hodotermes* workers are rapidly cutting grass culm segments and sometimes also fresh green leaves of dicots and carry them to the foraging port, where too large segments are rejected and finally remain in star-shaped pattern around the foraging port (Fig. 9.5.1 C).

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Figure 9.5.1 A: Worker of the Northern harvester termite *Hodotermes mossambicus* (Plot 37115, Dordabis, 20.02.2020).

Figure 9.5.1 C: *Hodotermes mossambicus* workers at the foraging port with the typical star-shaped arrangement of rejected grass culms (Marienfluss Valley, 10.02.2007).

The nesting biology has been described by Coaton (1958) and Coaton & Sheasby (1974). There are no aboveground nest mounds reported for *Hodotermes mossambicus*. Often only the ejection ports are visible at the surface. These are up to 15 cm tall piles of mainly mineral particles with a small amount of organic matter, probably frass (Fig. 9.5.2 A and B). Fresh and still wet dark material is ejected at the top end of tunnels during the early morning hours. Therefore, the cone-shaped pile is topped by one to four chimneys which can have a length of up to 2 cm. In the morning it is often observed that fresh sand is pushed out of the chimney by termites. Therefore, it is not astonishing that often birds (Fig. 8.2.15) and ants (Fig. 8.2.62) search the pile for termites in the morning hours. Due to the dominance of mineral particles, the whole pile can be called soil dump, although these are much larger than the soil dumps of *Psammotermes*.

Figure 9.5.1 B: Workers of *Hodotermes mossambicus* clipping stem and leaf segments during the day (Karasburg, Kalkfontein Ost, Plot 37162, 28.02.2020).

Figure 9.5.2 A and B: Colonies of the Northern harvester termite *Hodotermes mossambicus* cause bare patches of irregular shape within the matrix vegetation. *Hodotermes mossambicus* can remove all aboveground grass biomass over many square kilometres. The activity of *Hodotermes mossambicus* is clearly indicated by the large number of dark brown soil dumps (Marienfluss Valley, Namibia, near Marienfluss Valley Observatory, A: 20.08.2017, B: 12.03.2018).

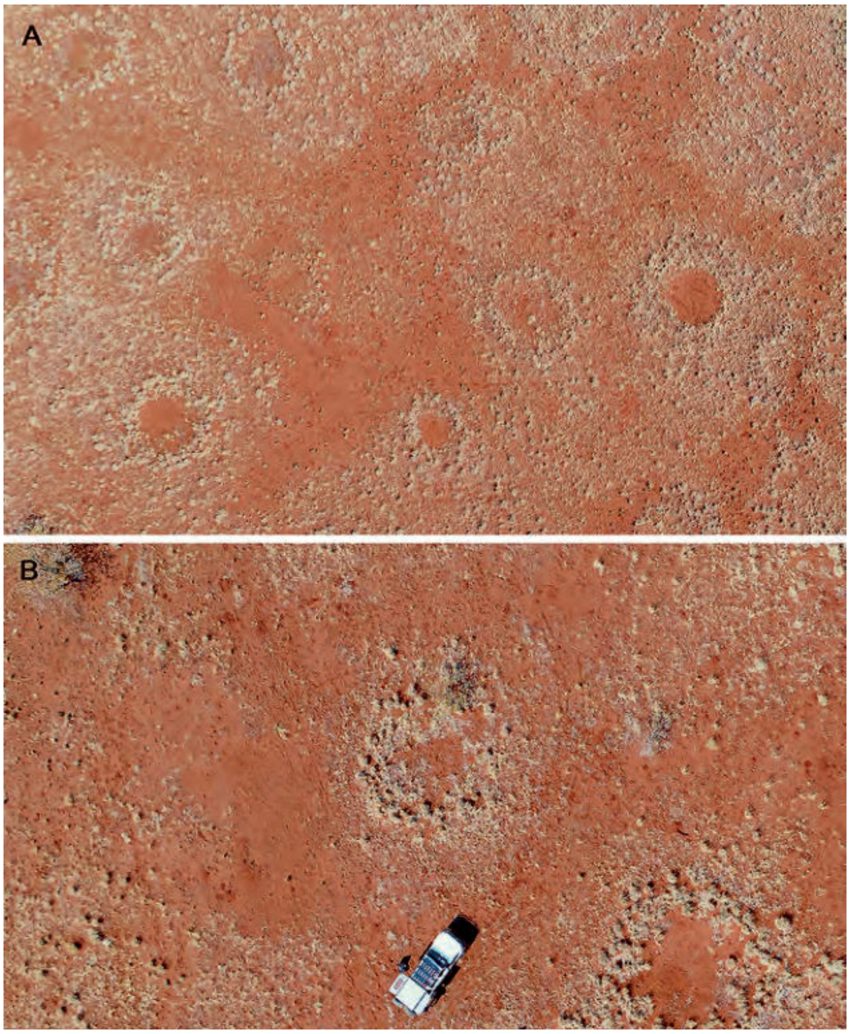

Figure 9.5.3 A and B: The bare patches of *Psammotermes* fairy circles are surrounded by a perennial belt and a halo. Further away, larger barren areas within the matrix vegetation are scattered with many humid soil dumps of *Hodotermes mossambicus* (well visible as darker brown spots (Marienfluss Valley, Featherlion Hill Observatory, 20.08.2017).

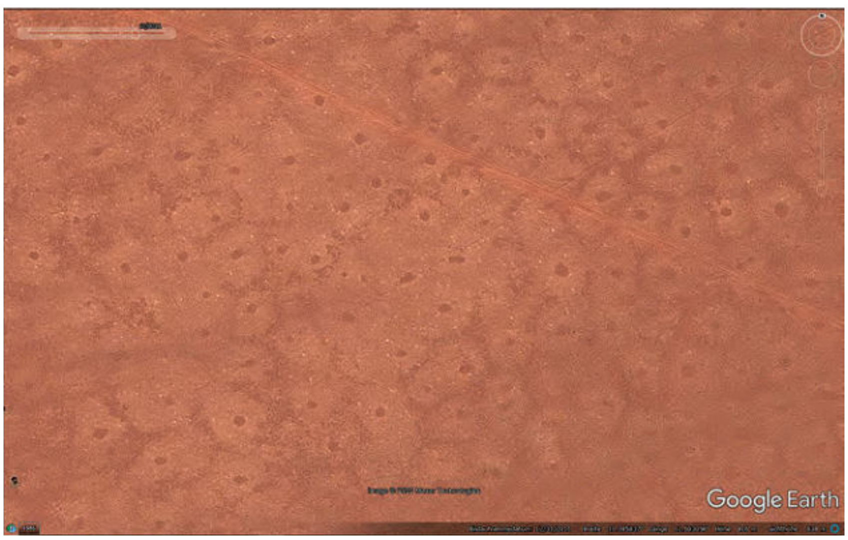

Figure 9.5.4: Tesselated hexagonal pattern with fairy circle bare patches in the centre (dark brown) and bare areas (again dark brown) at the margin of the roughly hexagonal structures (Marienfluss Valley, 17.39 S, 12.50 E) (31.12.2011).

Instead of a single nest, *Hodotermes*, like *Psammotermes*, builds a series of subterranean hives that are linked by massive passages with a diameter from 25 to 75 mm. Due to the many foraging ports and large colony size very large areas (Fig. 9.5.2 A and B) are cleared from grass.

Little is known with regard to the spatial extension of a *Hodotermes* colony. Elder literature rather focused on the harvested biomass of up to 1 to 3 t/ha x yr (Coaton & Sheasby 1974). Becker & Getzin (2000) related *Hodotermes* colonies to the size of fairy circles, without providing measured evidence. This was critized by Grube (2002), but never revoked by Becker and/or Getzin. So far, no robust analysis of the size of the foraging territory of *Hodotermes* colonies has been published.

Ground photographies (Fig. 9.5.2 A and B) give the impression that an unlimited area has been cleared from grass. However, the aerial view reveals complex patterns. In the vegetation zoning of the majority of fairy circles, only the bare patch in the centre is free of vegetation, and the matrix landscape outside the perennial belt is more or less homogeneously covered with vegetation. However, as shown in Fig. 9.5.3, in the Marienfluss Valley the matrix vegetation further away from the fairy circles can also be much sparser or almost completely removed by the foraging of *Hodotermes mossambicus*. In extreme cases, this results in isolated perennial belts bordered by a bare soil surface on either side. This pattern is correlated with a high density of foraging ports and soil dumps of the *Hodotermes mossambicus* (see arrows in Fig. 9.5.3).

Some areas of the Marienfluss Valley (Figs. 3.14 and 3.15, Figs. 6.6.7 to 6.6.9, Fig. 9.5.4) show tesselated hexagonal patterns with fairy circles in the centre. Where these are best developed, nearest neighbour distances of ca. 30 to 40 meter are found. Future studies should investigate whether these patterns are a product of interaction between *Hodotermes* and *Psammotermes*. This would require a detailed mapping of the activity patterns of both, *Hodotermes* and *Psammotermes*.

A similar tessellated pattern was detected by J. McAuliffe, Desert Botanical Garden, Phoenix, Arizona, in satellite imagery of the Onjuva Plain, which is a large plain filled with aeolian red

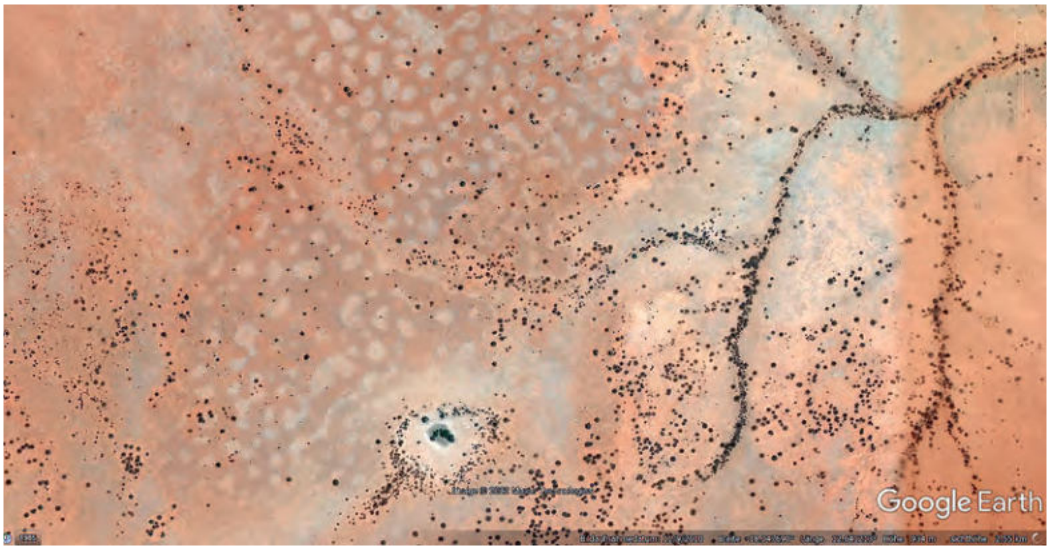

Figure 9.5.5:
Large circular to longish patches with scarce or missing vegetation are well visible in the lowest altitude section of the Onjuva Plain northeast of Orupembe.

sand, located south of the Marienfluss Valley and northeast of Orupembe.

In the southwestern part of the Onjuva plain, near -18.04 S, 12.64 E, large roughly circular or longish white areas are conspicuous which occur at 30 to 40 meter distance within a darker brown matrix (Fig. 9.5.5). The peculiar pattern is limited to that part of the Onjuva Plain that can be interpreted as an endorheic basin which at times may have been the bottom of a lake. The locality was studied on the ground by the fairy circle team from Hamburg University at 23rd March 2016, 22nd November 2021 and 18th March 2022.

We found that the more witish roughly circular areas had scarce or almost missing vegetation, even during the rainy season and during the drought season. The whitish colour was also enhanced by a soil with a higher clay content (Figs. 9.5.6 to 9.5.8 and 9.5.11). The darker matrix was covered by dense grassland (Figs. 9.5.9 and 9.5.10) on more sandy and darker soil. In this grassland fairy circles occur (Figs. 9.5.9 and 9.5.10).

The barer and more whitish areas are regularly covered with the typical foraging ports and soil dumps of *Hodotermes mossambicus*. Collected animals were morphologically and genetically identified as *Hodotermes mossambicus*. Therefore we name these areas "*Hodotermes mossambicus* Disks". As a working hypothesis that needs to be tested, we consider that each of the circular areas may be equivalent to the foraging territory of one colony. This interpretation is supported by the typical foraging patterns of aardvarks that obviously look for termites as food in the disks (Fig. 9.5.8).

Figure 9.5.6:
Drone image of "*Hodotermes mossambicus* Disks" in the southern part of Onjuva Plain (Onjuva Plain, 18.02.2022).

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Figure 9.5.7:
Hodotermes mossambicus soil dumps (dark brown soil mounds in the foreground) and burrowing holes of aardvark (dark hole under the grass island), found regularly within the barer areas (Onjuva Plain, 18.02.2022).

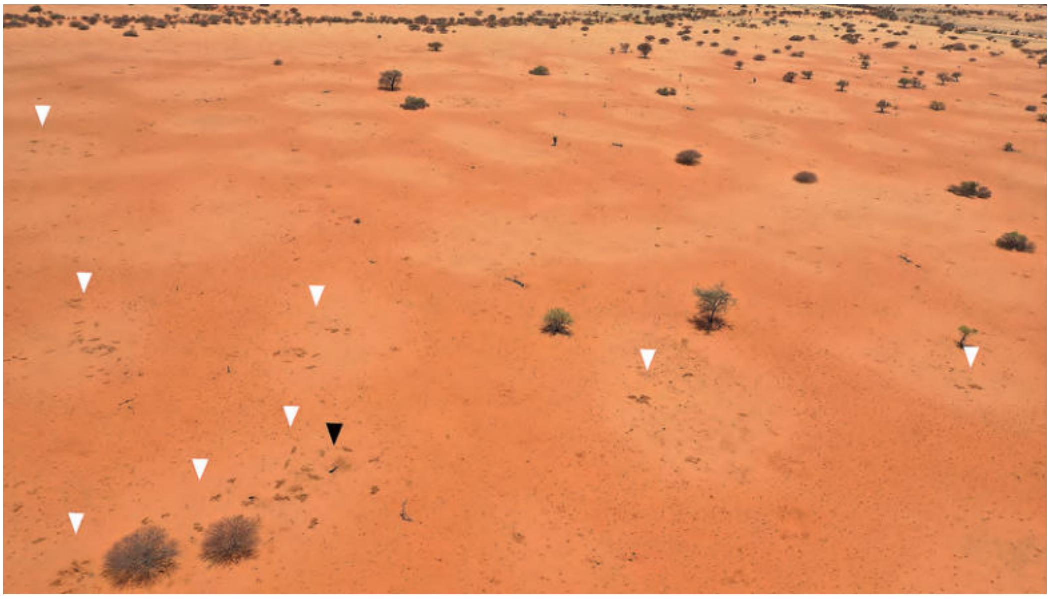

Figure 9.5.8:
Burrow (black arrow) and foraging holes (white arrows) of aardvark only in the more whitish circles (Onjuva Plain, 22.11.2021).

Figure 9.5.9:
Matrix area between three "*Hodotermes mossambicus* Disks", including about eight fairy circles in different development states (Onjuva Plain, 22.11.2021).

Figure 9.5.10:
Fairy circle found in the matrix (Fig. 9.5.9) of the *"Hodotermes mossambicus* Disks". Only within the bare patches of the fairy circle, soil dumps of *Psammotermes* are found, visible as slighty darker ochre spots of several centimeter diameter (Onjuva Plain, 22.11.2021).

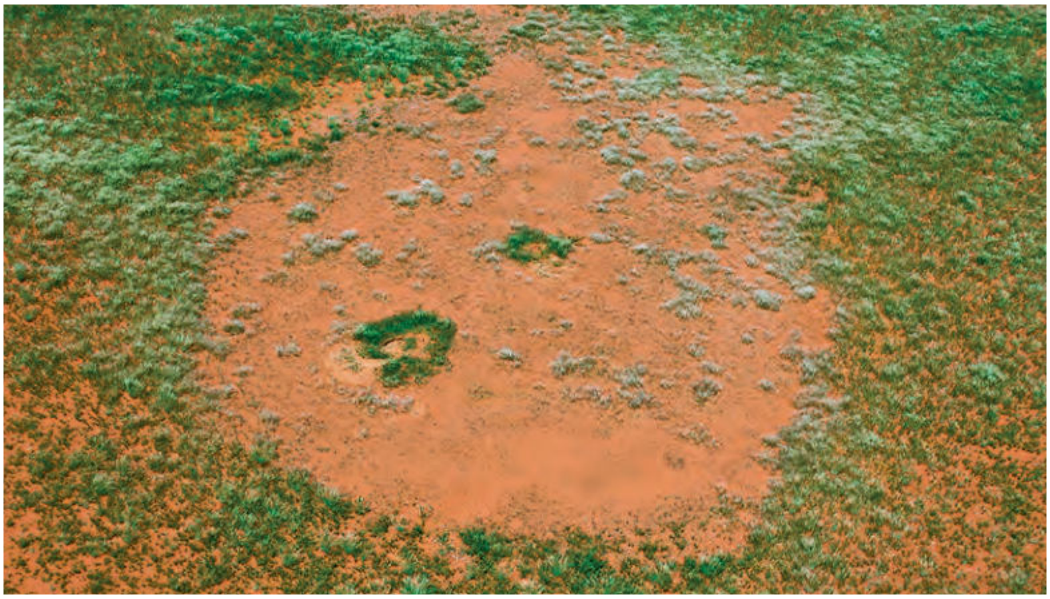

Figure 9.5.11 A an B:
Aardvark burrow in a bare circle caused by *Hodotermes mossambicus* (Onjuva Plain northeast of Orupembe, 18.03.2022).