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Husbandry and breeding of African Giant Termites (*Macrotermes jeanneli*) at Berne Animal Park

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In memoriam H. Sägesser

With 7 Figures

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Abstract

A termite mound 6 m high with roughly 1 million individuals was reared in the Bern Animal Park vivarium house. The fungus growing species *Macrotermes jeanneli* originates from the Kenyan semi-desert region near Lake Baringo. This paper describes the method of breeding incipient colonies in the laboratory and the first and successful experiment of rearing a live giant termite mound in a zoo. The colony in the vivarium glasshouse is situated in a walled-in compartment with access to natural soil and to an artificial water supply. After a laboratory-reared colony was settled in this place, a chimney shaped mound developed within 2 years to its final height of 6m. The foraging territory of the termites occupied the entire vivarium and in summer even some outdoor areas up to 55 m away from the mound. One year later the first reproductive flighting swarm occured. Three other flighting periods occurred in the following years. All four periods took place in October/November, whereas in the termite's home area it happens in April. The total life span of the colony was 20 years.

After the death of the colony the empty mound was successfully repopulated by introducing a young daughter colony reared in the laboratory. The termites of a full grown nest foraged 30–40 kg of hay per month. Apart from this, they cleared all plant litter from their whole territory. Living plants in the vivarium house were not destroyed, except for a few species. The omnipresent termites provided food for a variety of anurans living in the vivarium house. Any risk of escape into the environment is out of the question in our climatic zone.

The termites in the vivarium house are a great attraction to visitors in the Bern Animal Park. A video touch screen provides supplementary insights into some hidden aspects of the termites' life.

Key words

Termite, *Isoptera*, *Macrotermes*, husbandry, breeding, rearing, reproductive flighting, zoo

Introduction

Macrotermes jeanneli is a fungus growing termite from East Africa. The species characteristically builds spectacular earth mounds with one high, towering chimney. The internal structure of a nest mound is represented in Fig. 1 (after DARLINGTON 1984).

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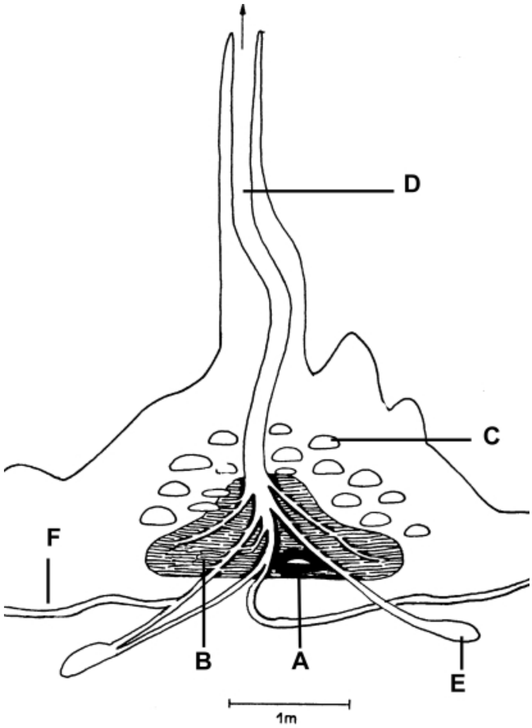

Fig. 1. Vertical section through a mound of *M. jeanneli* (Diagram modified from DARLINGTON 1984).
A.
Royal Cell
B.
Nursery zone
C.
Chamber containing fungus comb
D.
Central air vent
E.
Empty terminal chamber
F.
Underground foraging passage

The colony kept in the Berne Animal Park originates from the population near Marigat in the Lake Baringo area of Kenya, a semi-desert thorn scrub habitat.
Species of the *Macrotermitinae* cultivate a Basidiomycete fungus of the genus *Termitomyces* on the substrate comb they build inside their nest. Forage is chewed up and swallowed by workers, and passes rapidly through their guts (very little of it being digested on the way), then it is used to build the fungus comb. The termites live in direct symbiosis with this fungus, which breaks down cellulose and lignin in the comb (ROULAND 2000) and grows into a dense network of mycelium. After 2 to 5 days (unpublished results) the fungus begins to produce white nodules which are vegetative fruiting bodies full of fungal spores in a protein enriched matrix. Workers eat the nodules and digest the protein, at the same time inoculating spores into the newly built comb. Eventually the comb substrate becomes exhausted, then the termite workers eat it together with fungal mycelium still inside it.
Using a subterranean system of galleries which extends as much as 50 m from the nest, the *Macrotermes* species living in semi-arid regions are able to forage over a broad area and so they process dead vegetable matter in a centrally organised manner. Densities of between 1 and 4 termite nests per hectare are often found in the African savannah, corresponding to a consumption rate of up to 1500 kg dry weight per hectare per year (LEPAGE 1981, for *M. michaelseni*).
Their food consists mainly of vegetable litter which the termite workers collect on the surface and then transport it to the nest through underground passages. Competition with cattle occurs only during droughts if the land is over-grazed. Even in the

dry season, a large *Macrotermes* nest always contains the equivalent of around 200 litres of water (Bodot 1967) which is needed for maintaining humidity inside the nest and is used for construction work and for regulating the temperature by evaporation. These termites are able to extract water from soil against potentials of up to 2 bars (Lys & Leuthold 1994).

The queen and king are the only functional reproductives. The rest of the large nest population are all their offspring, either juveniles or sterile adults belonging to four castes, two worker and two soldier castes. The castes are structurally different from each other, and they divide up the work of the nest between them. The major and minor workers make up the majority of the adult nest population. They are the agents for building, foraging, cultivating the fungus comb and tending the larvae and sexuals. Major workers (genetically male) and minor workers (genetically female) (Noirot 1985) carry out different tasks with some overlap (Noirot 1985). In *M. jeanneli* the foragers are mostly major workers which can be seen outside the nest mound. They are also the ones that build on the mound surface, whereas the minor workers are committed to tasks inside the nest. Major and minor soldiers (both genetically female) make up 7 to 8% of the total sterile nest-population of about one million individuals in a mature colony (Darlington et al. 1992). They defend the colony; the major soldiers guard the entrances to foraging galleries and openings in the nest including the inside of the chimney while the minor soldiers accompany and guard the workers inside and outside the nest.

Food is processed collectively within the colony using the symbiotic fungus *Termitomyces* sp. as a crucial step in organic decomposition. Division of labour between workers of different age was studied in *Macrotermes subhyalinus*, a species closely related to *M. jeanneli* (Badertscher et al. 1983). The older workers (from 25 days until death at about 80 days) are the only ones which leave the nest to forage for food, and to do construction work, whereas younger individuals are consigned to fungus cultivation and brood care within the nest (Traniello & Leuthold 2000).

At certain times of the year winged reproductives (alates) of both sexes are produced alongside the sterile brood. They fly out of the nest in thousands at the beginning during the rainy season, and after dealation they pair up to found new colonies. The pair will remain together enclosed in a fortified capsule (royal cell) for the rest of their lives. This is the ultimate defensive structure against intruding predators, the ants. The egg-laying female (queen) develops an enormously enlarged abdomen (a process called physogastry).

Breeding of *Macrotermes jeanneli* incipient colonies in the laboratory

Our founding reproductives were collected[1] after flighting on 9. IV. 1977 in the field. Incipient colonies were started with dealate pairs set up in round plastic boxes with lid (diameter 57 mm, 20 mm deep). The boxes were prepared by half filling them with sieved moist mineral soil. The cultures were kept in the laboratory in Bern at 26 °C. They were checked every two days for adequate nest humidity. The pair constructed a chamber in which the first batch of eggs was laid soon after. The 1st instar larvae hatched after 30 days. They were fed from mouth to mouth (trophallaxis) by

[1] Collected by J. P. E. C. Darlington, Cambridge, UK

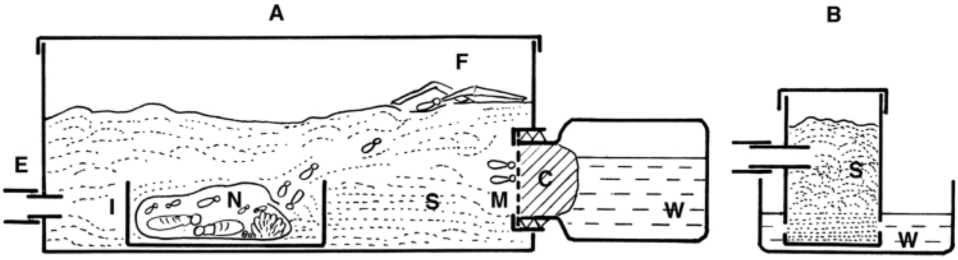

Fig. 2. Equipment for rearing incipient *Macrotermes* colonies in the laboratory.

A. Breeding box 14 cm × 16 cm × 6 cm
B. Principle of ground-water supply, mainly joined to larger nest boxes (dimensions adapted to the size of the colony)
C. Pressed cotton wool stopper
E. Exit for joining a feeding arena or a water supply with polyehtylene tubing
F. Food supply
I. Initial breeding box
M. Stainless steel screen, mash-width 1 mm
N. Nest cavity in a young colony containing the royal pair, fungus comb and offspring
S. Mineral soil
W. Water

the reproductive pair until 40 days later the first workers appeared. This was the moment to supply forage to the colony and to inoculate *Termitomyces* into the colony. We added small pieces of fungus comb from a *Macrotermes subhyalinus* colony available in our laboratory. The food consisting of small pieces of dry grass was put into the box and changed every two days to prevent mould. The transition from incipient trophallactic feeding by the king and the queen to external foraging by workers, at the same time establishing the fungus comb, is the most critical phase in *Macrotermes* rearing, having a survival chance of less than 50%. Two months later the colonies were transferred into larger boxes of 14 cm by 16 cm and 6 cm deep (Fig. 2 A). The initial small nest boxes were opened and placed at the bottom of the larger container and gently covered with moist soil (Fig. 2 I). A permanent water supply was fixed to the wall of the box, and a feeding arena in a similar box could optionally be connected with a tube (Fig. 2 E). The third step was the transfer into a nest box of 21 by 21 by 9 cm with adding a ground-water supply (Fig. 2 B). One of these colonies was later extended by transfer into a plastic bucket of 55 cm diameter in which it stayed stable for 9 years. At that time the idea was born together with the former director of Berne Animal Park, H. Sägesser, to try the experiment of rearing these termites on free ground in the vivarium house.

Establishing and development of the colony in the vivarium

The vivarium is a glasshouse of approx. 5 300 m^3 air-volume equipped with automatic heating. Minimum temperature during the day must not go below 24 °C and not lower than 20° during night. Cooling is initiated by fresh air ventilation when exeeding 27 °C during sunshine. Humidity is kept between 65 and 85% R. H. by an automatic water spraying device.

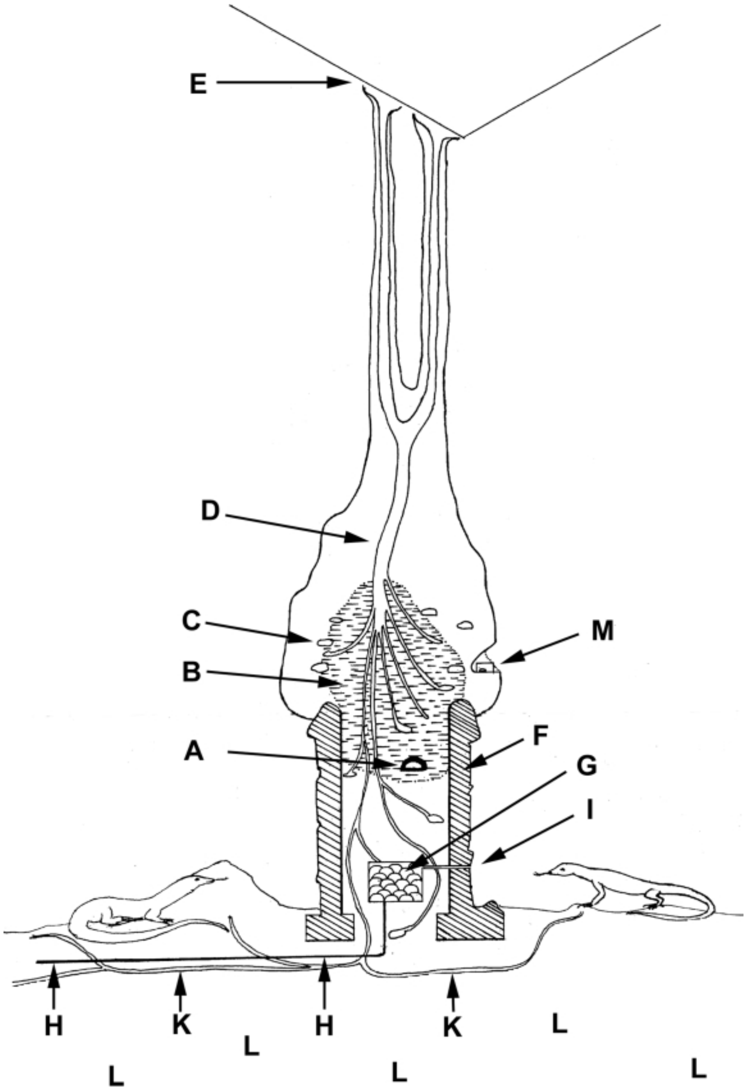

Fig. 3. The nest-mound arrangement in the Vivarium.
A. Royal cell
B. Nursery zone
C. Chamber containing fungus comb
D. Air vent
E. Gap of 2 cm between chimney and the glass-roof
F. Concrete wall
G. Ground-water basin
H. Water inflow
I. Water overflow
K. Underground passage
L. Genuine ground
M. Niche where the young daughter colony was settled for re-colonisation of the dead mound

Fig. 4. The termite mound in the vivarium.

The place allocated to the termite nest was a compartment between four concrete walls standing on the natural soil (Parabraunerde) and so the foraging area was unconstrained. A permanent "ground-water" supply was installed at the bottom, and the compartment was filled with soil (Fig. 3) On the 20. X. 1988 the bucket containing the small 11 year old termite colony was buried under the soil surface, while the side walls of the bucket were removed. A PVC tube had been built in previously to initially connect the colony to the water supply. Food (hay) was offered on the soil surface on top of the colony.

Eight months after the settlement a slender tower of 40 cm height was erected on the top of the nest. Four months later this tower had grown to half its final height of about 3 m as an open chimney. Building activity was sporadic and most of it happened within a few days during a warm period when the daytime room temperature was over 30 °C. Two years after the settlement the chimney tower reached the glass

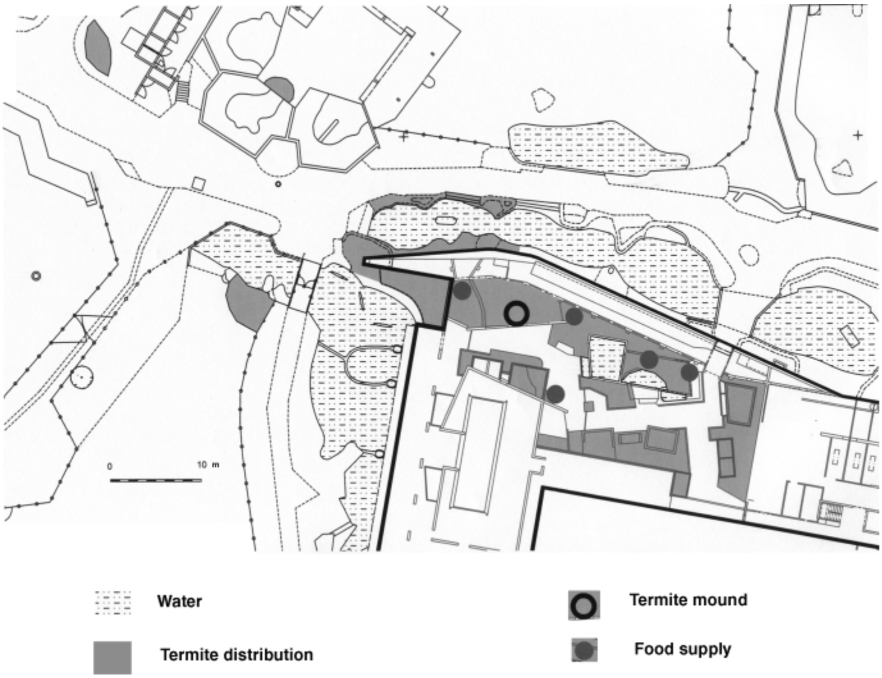

Fig. 5. Ground-plan of the termites foraging area in the vivarium and it's surroundings in summer.
Black circle: Termite mound
Gray field: Foraging area
Gray circle: Permanent feeding places
Water symbol: Water

roof of the building (603 cm from the original nest surface) and another year later, two additional chimneys – atypical for the species – were built up to the top (Fig. 4). The basal part of the mound increased drastically in volume during this period. The chimneys were not always straight. Often newly built tips broke off again. The chimney tips reaching the roof were extended in the shape of a funnel, leaving an air space of 2 cm to the glass (Fig. 3 E).

The termites extended their territory with underground galleries throughout the glasshouse. Earth sheeting and galleries on trees were seen in various places, reaching as far as 55 m outside the building during the summer, when the mean temperature was >15 °C (Fig. 5). To enable these outdoor excursions the termite passages had to pass underneath the seal's pool.

The termites collect vegetable litter wherever they have access. In addition to the forage they find themselves they consume 30 to 40 kg of hay per month as their main source provided at a feeding place 10 m from the mound (Fig. 5). Living plants in the vivarium house are generally not much attacked, except for some species such as tree-ferns, palm trees (*Rhapis exelca, Licula grandis*), and *Grevillea robusta*. The latter was periodically defoliated, after which it recovered to splendid sprouting. All the plants which were attacked little or not at all showed more vigorous growth

Fig. 6. Reproductive flight.
An alate emerging from a flight hole, another one flying off. Many workers and soldiers are gathered around the emerging place.

when they were on soil that had been disturbed by termite activity. The omnipresent termites turned out to be an ideal and sufficient food resource for the many nocturnal frogs and toads living in the vivarium house.

The first flighting of the colony took place three years after settlement in the vivarium house (21. X. 1991 after 17.00 h). We estimated that 50 000 alates swarmed out. On the preceding days many horseshoe-shaped slits and small take-off platforms were built on the mound, which afterwards served as flight holes. Shortly before and during the flight an army of hundreds of minor soldiers and major workers and some major soldiers and minor workers spread out around the take-off places (Fig. 6). Two days later, at the same time of day, another flight of some hundreds of alates took place. The following day there was a third flight of some thousands of individuals. One week after the principal flight a very minor flighting occurred, and another week later a final one.

The following year around the 10. XI. 1992, flighting occurred again. In 1995 on the 14. XI. one single alate flew out, and on the 20. XI. 1996 a moderate and last flighting occurred of this colony.

During the flying hours the winged reproductives spread all over the vivarium house. A spectacular hunting activity for this precious prey could be observed by all type of lizards and fishes. Hunting by the archer fish *Toxotes jaculator* was an especially exciting attraction for visitors.

From the major flighting in 1991 we reared a stock of second generation incipient colonies in the laboratory by the method described above. In 1997 the vivarium-colony died 20 years after it was founded. Two years later we started the experiment of

Fig. 7. Minor and larger Soldier of *Macrotermes jeanelli.*

re-populating the large deserted mound with a daughter-colony in a box of 21 cm by 21 cm by 9 cm. The box was inserted in a niche prepared in the wall of the mound (Fig. 3 M). Initially the young colony was periodically fed and watered in the niche until it expanded the nest and found access to external food sources. Two years later the first new building structures appeared on the old mound. Three years after installation (summer 2002) the colony had reached mature status, when the workers and soldiers had their maximum size. New earth humps were built on and around the mound (Fig. 4 left at the bottom). Foraging activity expanded to the extent of the former colony.

Public presentation and feedback

The termite mound gives the vivarium house an unique and dominant architectural feature. It is a landmark of high attraction for most visitors as inquiries have shown. But it is more than a monument. As soon as visitors realize that the colony is alive, they show great astonishment and enthusiastic interest. They will touch the mound structure and will find traces of termites all over the vivarium house such as earth galleries and gnawing patterns on the bark of trees. They will eventually uncover a feeding place and detect hundreds of individuals, workers and soldiers, and hear the alarm signal of soldier's heads banging, or even experience the bite of a major soldier which is painful and can draw blood, but is not poisonous (Fig. 7). The sensitive visitor will also get the feeling of an unpredictable, ecological self-dynamic within the vivarium house and possibly detect the termite's traces outdoors. Beside the mound a touch screen provides video information about hidden structures and behaviour inside the nest, presented under 6 selective themes of choice: foraging and proceeding of food, building behaviour, communication, defence, dispersal flight, queen and king. The subject "Termites" has become a very popular topic, and is frequently chosen for individual school homework.

Discussion

It is of special interest that *Macrotermes* incipient colonies are able to survive for many years under subdued conditions in small containers in the laboratory and still have the potential to grow quickly and to become a giant mound population as soon as the necessary space is offered. In the field we have observed that when large numbers of termite nests had been killed by predators, they were replaced within one or two years by new, growing mounds (*M. subhyalinus, M. bellicosus*). We think that they had all been waiting in a cryptic immature stage, and started growing as soon as they were freed from territorial pressure of competition (Darlington et al. 1992; Jmhasly & Leuthold 1999).

Earlier observation was confirmed that the symbiosis between termites and the fungus *Termitomyces* is not specific to a particular species since the specimen of the fungus inoculated from Kenyan *M. subhyalinus* laboratory cultures was accepted by the *M. jeanneli* incipient colony.

The 20-year life span of our first colony makes an important contribution to knowledge in a field where there is more speculation than hard data available (Lepage & Darlington 2000 p. 351). The controlled conditions and continuous observation make it almost certain that the founding reproductives were alive and active for the whole of the 20 year period (although is known that *Macrotermes* nests can sometimes replace their reproductives).

Our successful re-colonisation of the mound after the death of the original colony is the first experimental proof that an existing vacant mound can be re-occupied (see e. g. Lepage & Darlington 2000 p. 351).

An interesting observation is the building of three chimneys. We explain the impulse for this atypical behaviour by the inhibition of air ventilation when the first chimney touched the roof. It may, however, also be influenced by the lack of wind-powered ventilation in the glasshouse. The final ingenious adaptation to the situation was the extension of the radius of the chimney rims, leaving a slit open to the roof for allowing sufficient air draft.

It was the first time that mound-building termites of the subfamily *Macrotermitinae* have swarmed in captivity. The dates of the four flighting periods in November/December in our vivarium, compared to the observed flightings in the field in April, indicate that the circa-annual reproduction cycle is not endogenously inherited. It is interesting, though, that the four flighting periods always took place in the same season of the year, although the climatic and photoperiodic cycles are so different from the termites' equatorial home country. The factors determining the development of reproductive brood in termites are still very little understood. In the field the flighting event is triggered by the onset of the rainy period. How is it in the glasshouse where there is never a distinct rain?

The development of a *Macrotermes* colony in a glasshouse to quasi natural dimensions by expanding its feeding area to the outdoor environment in summer (even passing underneath a water pond) is an astonishing result of our experiment.

Many species of lower termites can multiply by colony splitting and can live in timber in heated buildings in our latitude. In contrast, with a mount building higher termite such as *Macrotermes*, there is no risk of escape into the enviroment because the only thinkable way of dispersal is establishing new colonies in the terrain by winged reproductives, which, of course, is impossible in our climate zone.

Zusammenfassung

Im Berner Tierpark steht ein lebender 6 m hoher Termitenbau mit rund einer Million Einwohnern. Es handelt sich um eine pilzzüchtende Termitenart *Macrotermes jeanneli* aus der Herkunftsgegend Lake Baringo in Kenia. Es wird die Aufzucht junger Laborkolonien beschrieben und das geglückte Experiment, eine solche Kleinkolonie erstmals in einem Zoo zu einem naturgroßen ausgewachsenen Nesthügel zu entfalten. Die Kolonie steht im Vivarium, einem Glashaus, in einer mit Mauer umfassten Gehegenische auf natürlichem Grund. Dort haben die Termiten Zugang zu einer künstlichen Grundwasseranlage und gleichzeitig unbeschränkten unterirdischen Auslauf in die Umgebung. Nach Einsetzen der Jungkolonie entwickelte sich der kaminartige Nesthügel innerhalb von 2 Jahren zu seiner endgültigen Höhe von 6 Metern. Das Auslaufterritorium erfaßte bald das ganze Vivarium und erstreckte sich im Sommer ins Freiland an Orte bis zu 55 m vom Nest entfernt. Im Jahr darauf fand der erste Schwarmflug von Geschlechtstieren statt. In den folgenden Jahren erfolgten drei weitere Schwarmperioden. Alle vier Schwarmperioden fanden im Oktober/November statt, im Gegensatz zur Flugzeit im April im Ursprungsland. Die Kolonie starb 20 Jahre nach Zuchtansatz. Dies ist ein bedeutungsvoller Befund zur Lebensdauer einer Königin. Der ausgestorbene Nesthügel konnte erfolgreich wieder besiedelt werden nach Einsetzen einer vorgängig im Labor angezüchteten Tochterkolonie.

Die Termiten werden mit 30–40 kg Heu pro Monat gefüttert. Zusätzlich räumen sie in ihrem Aktionsbereich sämtliches abgestorbene Planzenmaterial weg. Es können aber lebende Pflanzen – mit Ausnahmen einiger Arten – im Vivarium gehalten werden. Die alldurchsetzte Gegenwart der Termiten im Vivarium deckt den Futterbedarf für manche andere Mitbewohner, vor allem verschiedene Krötenarten. Die Gefahr einer unerwünschten Vermehrung dieser Termitenart ist in unserer Klimazone ausgeschlossen.

Die Termiten verleihen dem Vivarium den Charakter eines eigenen Ökosystems. Sie werden von den Besuchern vielfältig wahrgenommen und lösen auch reges Interesse aus. Ein Video „touch screen“ vermittelt zusätzliche Einblicke in die verborgenen Bereiche der Termitenkolonie.

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