Ants (Hymenoptera: Formicidae) of mangrove and other regularly inundated habitats: life in physiological extreme

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Abstract

Ant societies are present in most terrestrial biotopes, and they often show a remarkable ability to adapt to extreme environmental conditions. Many ant species inhabit areas where flooding occasionally occurs. For example, *Lasius flavus* (FABRICIUS, 1782) nests on tidal meadows with unpredictable winter flooding, and they survive the inundation due to their low metabolic activity and to small air bubbles trapped in the soil. Other species, such as *Formica selysi* BONDROIT, 1918, survive flooding by forming swimming rafts of ants and brood and drift to dry environment. The ant communities in regularly inundated habitats of the Brazilian Amazon move their colonies up in the trees during the months of flooding. In tropical mangroves, another regularly inundated habitat, some ant species live under conditions where several environmental factors are extreme all the year round. Ants nesting in the tidal part of the mangrove need to select a nesting behavior which prevents them from drowning. The Australian ant *Polyrhachis sokolova* FOREL, 1902 escapes the flooding in small "air pockets" in their galleries in the mangrove mud, whereas the intrusion of water to the twig nesting Australian ant *Camponotus anderseni* MCARTHUR & SHATTUCK, 2001 is prevented by a soldier blocking the entrance hole during the inundation. The exclusion of water also prevents gas exchange, and in the nests of *C. anderseni*, the CO_2 concentration can reach very high levels of $> 30\%$ and conditions can become anoxic. *Camponotus anderseni* can reduce its metabolism (measured as CO_2 production) to about 1% of normal metabolism when the CO_2 concentration reaches about 25%. Mangrove ants can shift to anaerobic metabolism, which has not been demonstrated for other social insects. The benefits for the ants living under these extreme conditions are mainly lack of competition for nesting sites and food.

Key words: Ants, mangrove, inundation, nest construction, metabolism, oxygen uptake, carbon dioxide production, anaerobic metabolism, review.

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Introduction

Ants show a remarkable ability to adapt to the majority of environmental conditions, and they are present in nearly all biotopes, except the high Arctic and a few islands. Their adaptability and social organization are the main contributory factors to their enormous global success and dominant influence in many ecosystems (HÖLLDOBLER & WILSON 1990).

Like other social insects, ant colonies have nests where the queens reside and the brood is nursed by the workers during their development from egg to imago. Worker ants forage around the nest, and some species (e.g., *Formica* spp.) search for food several hundred meters from the nests (GÖSSWALD 1943). During foraging, the worker ants are exposed to fluctuating temperature and humidity which, when extreme, may periodically restrict their activity. In contrast, the conditions in the nests are moderated and are adequate for the survival of the colony, particularly the vulnerable brood.

The range of environmental temperatures in which ant colonies can survive is remarkable. For example, *Leptothorax acervorum* (FABRICIUS, 1793) nests under stones in arctic Alaska where the soil is frozen for nine months of the

year (NIELSEN 1987); its larval development probably takes more than two years to complete. At the other extreme, desert ants such as *Cataglyphis*, *Ocymyrmex* and *Melophorus* show a very high thermal tolerance. They can forage at soil surface temperatures up to 60 - 70°C (CHRISTIAN & MORTON 1992, RUANO & al. 2000), though the duration of the foraging trips is very limited, because the ants need to go back to the nest to cool down to avoid succumbing to heat stress (GREENAWAY 1981).

Apart from the high temperatures, the desert ants also have to cope with very low humidity and resulting desiccation. In many arid biotopes, ants have to compensate for water losses during foraging by absorption of water vapor during their stay in the more humid nest in the soil (COENENSTASS 1986, LIGHTON & al. 1994).

In contrast to the dry deserts, the ant fauna is quite diverse in many moist areas such as moors and meadows, and even periodically flooded areas can have a rich ant fauna. The flooding can be caused by predictable (e.g., tidal) and seasonal (e.g., monsoon) events, or by unpredictable situations such as heavy rain. Studies of the ant fauna close to rivers have shown that frequent flooding reduces the

Fig. 1: Tidal meadow in Denmark where the plant-covered nests of the ground living ant *Lasius flavus* give the landscape a conspicuous appearance; photograph and copyright: M.G. Nielsen.

number of species (LUDE & al. 1999, MERTL & al. 2009), and the surviving species often show an adaptive behavior to prevent drowning. In Northern Europe the small meadow ant *Lasius flavus* (FABRICIUS, 1782) is one of the species which have adapted to life in tidal meadows, where their conspicuous soil-nest domes are inundated at high tide during winter storms (Fig. 1 and NIELSEN 1981), and their survival is the result of a considerably reduced metabolism at low temperatures.

A particularly astonishing example of ant adaptability is manifested in the mangrove swamp, where, apart from being exposed to high temperatures, the ants are inundated twice a day by the sea (NIELSEN 1997a). They avoid drowning by staying in air-filled cavities in the nest, but because of the temperature, metabolism remains high, and the CO_2 concentration soon reaches very high values (hypocarbic conditions), and O_2 is reduced to low levels (hypoxic conditions) or even exhausted (anoxic conditions).

In this review, I will present information about the extreme environment for ants living in the mangrove and other regularly inundated lands, and attempt to explain how they survive in these conditions.

The mangrove ecosystem

Mangrove is a forest type growing in the tidal zone (Fig. 2), and it is mainly distributed in the tropics. Typically, mean ocean winter temperatures are above 20°C and no frost at all is tolerated (HUTCHINGS & SAENGER 1987). In most coastal mangroves, the landward part will only be inundated at spring tides, whereas the outer part is flooded at each high tide. In the mangrove in Darwin Harbor in northern Australia, where most of my investigations were carried out, the amplitude of the tide is up to 8 meters.

The soils in mangroves are commonly waterlogged, and the high microbial activity often leads to anoxic conditions. Due to evaporation of the seawater, the salt concentration in the higher part of the mangrove can reach quite high values. The dark colored soil or mud surface in the mangrove can frequently exceed 45°C which is near the lethal temperature for most animals (HOGARTH 2007).

Very few tree and scrub species can survive the exceptional soil conditions of this environment, and worldwide, mangrove habitats only support some 55 tree and scrub species (TOMLINSON 1986). The lowest diversities are found in the colder regions or areas far from the centre of the biome. For example, the mangroves of the Red Sea only comprise two species, and those in Florida just three species, whereas the mangrove in the Darwin Harbor contains 30 species (WIGHTMAN 1989).

Mangroves are generally regarded as marine ecosystems due to their significant function as nurseries and foraging areas for many marine fish, crustaceans and mollusks, and they are therefore heavily exploited for food. The valuable mangrove wood is used as timber and for charcoal production. In many areas the degradation of mangroves is due to overexploitation of mangrove trees and to construction of ponds for aquaculture (ALONGI 2002).

Insects are generally present in abundance in mangroves, especially mosquitoes and midges which make their presence felt with serious blood sucking activity. They have been intensively investigated worldwide because of their transmission of diseases, and in many mangroves, e.g., around Darwin, pesticides are used to control their densities. Herbivorous insects play an important role in mangrove ecosystems, and CANNICCI & al. (2008) present a comprehensive review of their impact on vegetation in mangrove forests.

The ant fauna of mangroves

The number of ant species in the mangrove is relatively low, but their population density can be very high, and they are often regarded as the most abundant and influential insect group (SIMBERLOFF & WILSON 1969, HOGARTH 2007). The majority of the ant species are terrestrial from above the

Fig. 2: Mangrove dominated by *Rhizophora stylosa* trees – a typical biotope for the mud-nesting ant *Polyrhachis sokolova*; photograph and copyright: M.G. Nielsen.

tidal level and they have adapted to tidal conditions in the mangrove by nesting arboreally above the level of the highest tide.

Despite this importance of ants in the mangrove, only a few surveys of the ant fauna in the mangrove have been carried out. In an early study, COLE (1983a, b) examined the ant communities in the mangroves of the Key Islands, Florida, in relation to their colonization abilities and the pattern of the communities amongst the islands. A total of 102 species were found in 13 Brazilian mangrove sites (where they were used as indicators of human impact) and all were exclusively arboreal (DELABIE & al. 2006).

In an insect survey in Shankou in China, a total of 13 species of ants were listed, and none of the ant species seemed restricted to the mangrove. The most dominant ant in the survey was *Oecophylla smaragdina* (FABRICIUS, 1775) and it is strictly arboreal like the other species and not influenced by tide at all (GUOFANG 1997). Studies of *O. smaragdina*'s impact on the mangrove fauna have been carried out in a Thai mangrove, where it was found that the ants and their pheromones could deter herbivorous insects and reduce crab herbivory (OFFENBERG & al. 2004a, b, 2006).

All the 37 species found in a flooded Mexican mangrove were arboreal, but several of these species were normally ground-nesting species which had changed nesting site to hollow branches in the tidal zone (DEJEAN & al. 2003). CLAY & ANDERSEN (1996) investigated the ant fauna around Darwin, Australia, and compared the ants of the mangrove community with the regional savanna and rainforest fauna. *Polyrhachis* was the dominant genus with 6 of the 16 species found, of which the two mud living species, *Polyrhachis sokolova* FOREL, 1902 and *Polyrhachis constricta* EMERY, 1897 were restricted to the mangrove, and the other 4 species to the neighboring habitats. NIELSEN (2000) included the wetter part of the mangrove in his investigation, and as he found additional species, there are now a total of 24 ant species known from the north

Australian mangrove. Two *Camponotus* species – *C. anderseni* MCARTHUR & SHATTUCK, 2001 and *C.* sp. B from the *C. janeti* FOREL, 1895 group (A.N. Andersen, pers. comm.) – are confined to the swamp, being strictly associated with *Sonneratia alba* mangrove trees.

Ants nesting in tidal zones – how to avoid drowning?

Throughout the world, ant colonies can experience flooding due to heavy rain, winter storms and other more or less unpredictable events. In contrast, the mangrove ants are subject to predictable flooding twice per day, and it is to be expected that they will show behavioral and physiological adaptation to the demands of this extreme environment.

There have been few studies of ants' capability to survive total submergence even though many species live in biotopes where flooding can occur. NIELSEN (1981) carried out some submergence experiments on *Lasius flavus* from tidal meadows and showed that all workers could survive 120 hours at 5°C in seawater. Similar and more intensive experiments were carried out by BOOMSMA & ISAAKS (1982) with four ant species from a coastal floodplain. They exposed the workers of *Myrmica rubra* LINNAEUS, 1758, *Myrmica scabrinodis* NYLANDER, 1846, *Lasius niger* (LINNAEUS, 1758) and *Lasius flavus* to treatments completely covering the worker ants in brackish water at 5 - 7°C and they found a mean time of 8.1 - 9.1 days before 25% of the ants had died. Experiments in which the ants were submerged in water with air bubbles resulted, as expected, in much longer survival times.

Submergence experiments with the mud-living mangrove ant *Polyrhachis sokolova* showed that 50% of the workers died after 11 hours at a water temperature of 23°C, and after 3.5 hours at 33°C. Meat ants *Iridomyrmex sanguineus* FOREL, 1910 from a dry area in Darwin showed 50% mortality after 3.6 hours (NIELSEN 1997a; M.G. Nielsen, unpubl.).

The experiments also showed that the survival rate during submergence is strongly dependent on temperature. The

Fig. 3: Swimming *Polyrhachis sokolova* during incoming tide in the mangrove. The front four legs are used as oars and the two hind legs as rudders; photograph and copyright: A. Narendra.

Fig. 4: Soldier ants of *Camponotus anderseni* block the nest entrance to prevent water intrusion during high tide; photograph and copyright: M.G. Nielsen.

Fig. 5: Nest chamber of *Camponotus anderseni* in a twig of the mangrove tree *Sonneratia alba*; photograph and copyright: M.G. Nielsen.

ratio between survival time for 50% of the ants at 33°C and 23°C, respectively, was equivalent to a factor of 3.1, indicating that the time the ants can withstand submergence increased by a factor of 3.1 for each 10°C decrease in temperature. This temperature-dependent survival rate also indicates that survival depends on the metabolic rate of the ants, and that the cause of death is asphyxiation. Thus, the factor 3.1 reflects the influence of temperature on metabolism and the decreasing solubility of O_2 in the water; the value is within the range of the expected respiratory Q_{10} for ants of this size (NIELSEN 1986). Extrapolation of the survival for *P. sokolova* to 3°C using the same Q_{10} at 3.1 gives a survival time of 106 hours, which is similar to the values for temperate ants.

Another important factor for survival under water is air films on the surfaces. These have been shown to extend survival substantially for many arthropods (WIGGLESWORTH 1965), and it could also be important for many ant species submerged for shorter periods.

Studies of the subterranean species *Brachymyrmex depilis* EMERY, 1893, *Forelius pruinosus analis* (ANDRÉ, 1893) and *Forelius* sp. (undescribed), subjected to flooding by spring tides each month, have been made by YENSEN & al. (1980) in the Gulf of California. These authors found that some nests were inundated 149 times per year with flooding durations up to 3.5 hours.

The ant communities in the Brazilian Amazon, where the annual inundation leaves the forest floor flooded for 5 - 6 months, can only survive these conditions by moving their nests up in the trees (ADIS 1982, MAJER &DELABIE 1994). ADIS (1982) reported that leaf-cutting ants of the genus *Acromyrmex* can "walk" on the water surface during foraging in the flooded periods, and when the surface currents were stronger, the ants "now had to swim actively to the adjacent trees." This resembles the swimming behavior observed for *Polyrhachis sokolova*, which walk and jump on the water surface like water striders, and, when swimming, break the surface with the legs, using the four front legs as oars and the two hind legs as rudders (see Fig. 3 and KOHOUT 1988, NIELSEN 1997b). These two types of transport on and below the water surface are clearly shown in the film by ATTENBOROUGH (2005).

Another technique of transport on water is described from the beaches at La Blanquilla Island, Venezuela, by JAFFE (1993). Workers of *Paratrechina*, *Conomyrma*, *Solenopsis* and *Mycetophylax* are foraging in the tidal zone. When they are touched by an incoming wave, they contract the legs and bend the abdomen to the ventral part of the thorax. In this "nymphal" posture, the workers are able to float over the foam of the wave and to surf in front of the rolling wave to the beach. *Formica selysi* BONDROIT, 1918 is known to survive occasional flooding of river beds by forming swimming rafts, consisting of many workers, queens and brood, eventually reaching the bank (LUDE & al. 1999). Adaptations to flooding are known in several other species and may be a widespread and efficient tactic for escape (ANDERSON & al. 2002).

The number of ant species nesting in the tidal zone in the mangroves is extremely modest, and the only published information comes from Australia, where intensive studies have been carried out on a tree living species, *Camponotus anderseni* and a mud nesting species, *Polyrhachis sokolova* (see KOHOUT 1988, NIELSEN 1997a, 2000).

The small ant *Camponotus anderseni* lives exclusively in twigs of the mangrove tree *Sonneratia alba* in a mutualistic relationship with the coccid, *Myzolecanium* sp. 1.

Each colony lives in many small nest cavities, normally the length of one internode and with one entrance hole in each nest situated in the distal part of the cavity. The nests can be very crowded, with the ants and coccids filling up to 50% of the volume (NIELSEN & al. 2006). The nest entrance and the first part of the cavity are excavated by a founding queen when the twig is a soft, young, terminal shoot. Most queens do not survive very long, and the nest cavities, including the new workers, are taken over by the dominant colony in the branch (M.G. Nielsen, unpubl.). During inundation, the entrance hole is blocked with a soldier's head, which effectively prevents intrusion of water into the nest cavity (Figs. 4 and 5). The flat head of the soldier fits exactly to the nest entrance which is very consistent in size with a mean diameter $\pm$ standard deviation of 1.56 ± 0.03 mm (NIELSEN & al. 2006). The nests situated in the lower part of the trees can experience flooding for up to 3 hours (NIELSEN 2000). A similar organization is found in the closely related but less common *Camponotus* sp. B, which also lives exclusively in *Sonneratia alba* twigs (NIELSEN 2000).

A detailed study of the distribution of the ant fauna in the canopy of the mangrove tree *Sonneratia alba* showed that 81% of the nests investigated were occupied by *Camponotus anderseni*. The remaining nests were inhabited by three species of *Tapinoma*, two species of *Crematogaster*, *Monomorium floricola* (JERDON, 1851), and *Tetraponera punctulata* SMITH, 1877, all of them small species living in cavities with entrances so small that surface tension is sufficient to prevent sea water from entering (NIELSEN 2000).

Only the two Australian ant species *Polyrhachis sokolova* and *Polyrhachis constricta* are strictly nesting in the mud in the tidal zone. *Polyrhachis sokolova* has been investigated in detail (NIELSEN 1997a, b, NIELSEN & al. 2003). This black, spiny ant is commonly seen running around on the mud and in the mangrove trees and it is probably the most "marine" ant species recorded because of its nesting sites among crabs and mudskippers. Their nests are found from the dryer *Ceriops tagal* (yellow mangrove) to the wet *Rhizophora stylosa* (red mangrove) zones. In Darwin Harbor, the highest situated nests are immersed for 13% of the tidal cycle and for durations up to 1.25 hours, whereas the lowest nests are covered for 64% of the cycle and the flooding can last up to 3.75 hours, with more than 2 meters of seawater above the nest.

The colonies of *Polyrhachis sokolova* are often polydomous, and the underground galleries can cover an area of more than 50×100 cm. Normally, the nests are slightly elevated from the mud flat with small volcano-like nest entrances. The galleries are most abundant in the upper 20 cm of the mud, but can reach down to 45 cm. The numerous small chambers and galleries are situated around the complex mangrove root systems, which prevents the air filled chambers from collapsing under the high pressure at high tide (Fig. 6). The galleries are always excavated in materials which are quite air- and water-tight, so air caught in the convoluted gallery system will remain in small pockets, where the ants and brood can cluster to survive the flooding. The flooding of the nests and the way in which the ants and brood retreat to the air pockets were wonderfully captured in the film "Life in the Undergrowth" (ATTENBOROUGH 2005).

Fig. 6: Polyurethane-foam cast of a *Polyrhachis sokolova* nest from mangrove. Cross section 40 cm from the centre of the nest with an intact root system; the measuring tape indicates the mud surface; photograph and copyright: M.G. Nielsen.

Air bubbles in the soil nests or closed cavities are without doubt the most important factor in allowing the survival of the ants in warmer climate where metabolic rates are higher. In contrast, ants in colder climates can survive totally immersed for days, and, if there is any air trapped, they can survive for weeks.

Low oxygen content in nests during inundation

As the ants survive drowning by retreating to small, closed air pockets in the mud or nest chambers in wood, the oxygen supply is limited. Therefore, the ants could be facing hypercarbic and anoxic conditions.

Intensive studies have been carried out on *Polyrhachis sokolova*, where the CO_2 concentration in the galleries in the mud nest has been measured in three nests through the tidal cycle (NIELSEN & al. 2003). The CO_2 concentration peaked during and just after inundation when the ants were gathered in the air pockets in the nest, and it increased by up to 11% in one of the nests. When the tidal water retreated and the ground water in the mangrove sank, fresh air was sucked into the galleries through the entrance. At the next high tide, most of the air in the nest was replaced with seawater (except in the air pockets), and when the water retreated, the seawater was replaced with fresh air, so the nest was very efficiently ventilated with each tidal cycle.

The metabolic activity of microbes in the mud was measured (NIELSEN & al. 2003), and it accounted for more than 85% of the CO_2 production in *Polyrhachis sokolova* nests. Therefore, without the frequent replacement of the air in the galleries, microbial activity would result in perpetual hypercarbic conditions under which the ants could not survive for long.

The oxygen concentration in *Polyrhachis sokolova* nests has not been monitored closely due to technical difficulties with oxygen sensors in the mud. The ground water in the mangrove is anoxic; saturated seawater at 30°C can at most contain 4.5 ml O_2 / liter, and the tidal water in the smaller galleries will probably contain much less. The oxygen concentration in the air pockets with ants will decrease much faster than CO_2 increases because very little oxygen can diffuse from the water to the galleries, whereas

Fig. 7: Oxygen measurement in a sealed natural nest of *Camponotus anderseni;* photograph and copyright: M.G. Nielsen.

CO_2 easily can be absorbed in the water. Therefore, when we measure 11% CO_2 in the air pockets during flooding, the oxygen concentration must be much lower than 10%.

Compared to other terrestrial social insects, the CO_2 concentrations in the mud nests of *Polyrhachis sokolova* are quite high. MATSUMOTO (1977) found carbon dioxide concentrations of up to 5.2% in termite nests with fungus combs, but nests without fungus gardens had less than half that concentration. KLEINEIDAM & ROCES (2000) investigated the carbon dioxide concentration in the gigantic nest of the leaf-cutting ant *Atta vollenweideri* FOREL, 1893 and they found a passive, but efficient ventilation of the nest by movement of the air above the nest, and by the shape of the nest. They found that the carbon dioxide concentration never exceeded 2.8% in the refuse area below the fungus garden, and the highest concentration in the nesting area was 1.5% in the seven nests investigated.

The respiration of the tree-nesting ant *Camponotus anderseni* has been intensively investigated in relation to changing concentrations of CO_2 and O_2 in the nest chambers during the tidal cycle (NIELSEN & al. 2006, NIELSEN & CHRISTIAN 2007, NIELSEN & al. 2009). When the soldier ant blocks the entrance during inundation, the water is effectively prevented from intrusion, and at the same time gas exchange with the atmosphere is effectively blocked, as diffusion through the wood and the ant's head is negligible. The small nests are occasionally quite crowded (Fig. 5) and up to 50% of the volume can be filled with ants and coccids, so with a normal respiration, all the O_2 would be consumed within 20 - 30 minutes (NIELSEN 2000).

The respiration of *Camponotus anderseni* – measured as CO_2 production – has been investigated in the laboratory in natural nests sealed to simulate inundation (Fig. 7). Figure 8 shows the CO_2 production expressed as percentage of the rate in normal atmospheric conditions in relation to the CO_2 concentration in the nests. The experiments showed that the ants reduced their respiratory rates to 1% of normal respiration when the CO_2 concentration reached about 30%, which is a remarkable adaptation to these extremely high CO_2 concentrations (NIELSEN & al. 2006).

The oxygen supply in natural nests of *Camponotus anderseni* was also studied in some detail in order to establish the conditions inside the nest during the tidal cycle compared with normal terrestrial conditions. When the nests are open at low tide, oxygen depletion is substantial in the part of the nest furthest from the opening, and in a 120 mm
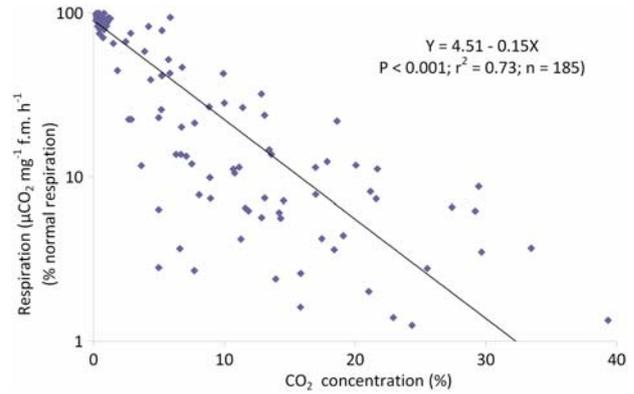
Fig. 8: Respiratory rate (μl CO_2 mg^{-1} fresh mass h^{-1}) of *Camponotus anderseni* as a function of CO_2 concentration in sealed nests. Respiratory rate is expressed as % of the (normoxic) control rates metabolism under atmospheric conditions; data from NIELSEN & al. (2006).
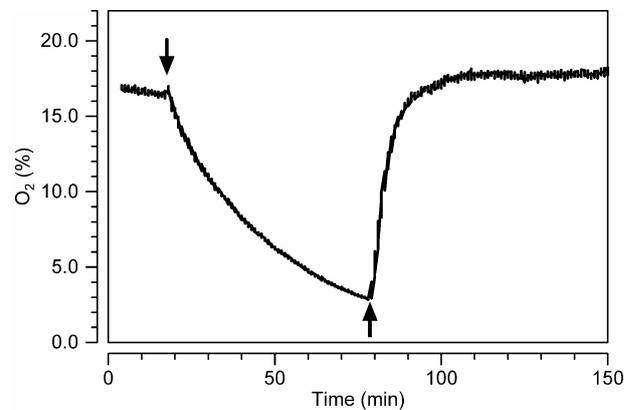
Fig. 9: Oxygen concentrations in a natural nest of *Camponotus anderseni* during simulated inundation. The arrows indicate closing and opening of nest entrance. Reproduced by permission (NIELSEN & al. 2009).
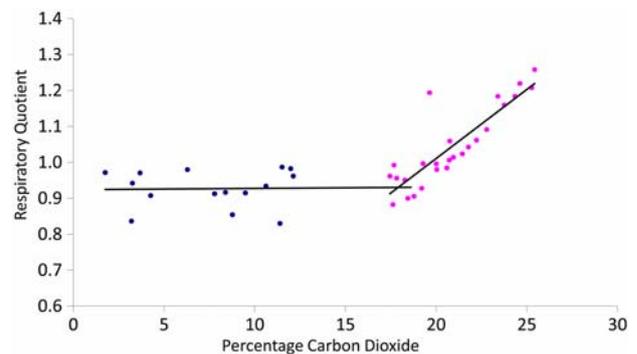
Fig. 10: Respiratory Quotient (RQ) for workers of *Camponotus anderseni* in closed respiration chambers at different CO_2 concentrations at the end of the experiment. The horizontal line represents the CO_2 concentrations with constant RQ; the ascending line shows the CO_2 concentrations associated with increasing RQ, representing increasing anaerobic respiration. Reproduced by permission (NIELSEN & CHRISTIAN 2007).

long nest, the oxygen concentration can be as low as 15.7%. During simulated flooding, in which the nest entrances

Fig.11: *Polyrhachis sokolova* workers having a "seafood party" on a dead crab washed up by the tide; photograph and copyright: M.G. Nielsen.

were closed, the oxygen concentrations dropped further to very low levels after one hour. After opening the nest entrance, the oxygen concentration increased again; it took almost 20 minutes before the concentration was back to the level that prevailed previous to the closing of the nest (Fig. 9) (NIELSEN & al. 2009).

The oxygen uptake of *Camponotus anderseni* workers was investigated using small Warburg chambers (1.5 - 2.1 ml) (NIELSEN & CHRISTIAN 2007). In the experiments where CO_2 was absorbed, the oxygen concentration showed a linear decrease to about 4%, whereas the O_2 uptake in chambers without absorbent showed a decrease with a different pattern, consisting of three parts. The first component of this decrease is a linear decrease to about 18%, which is the normal O_2 concentration in open natural nests. The second phase is an exponential decrease continuing to about 4% O_2, showing that the CO_2 concentrations influenced the O_2 uptake. The final component is also exponential, but with a much smaller slope (NIELSEN & CHRISTIAN 2007). The linearly decreasing pattern indicates a constant respiratory rate independent of the O_2 concentration between 21% and about 4%, which is the lower critical limit for the survival of colonies of *C. anderseni* in a CO_2-free atmosphere (M.G. Nielsen, unpubl.). Therefore, the significantly lower O_2 uptake in the experiments without CO_2 absorbent demonstrated that it is the CO_2 concentration that depresses the respiratory rates and not the decreased O_2 concentrations as long as the O_2 concentrations were > 4%.

The respiratory quotient (RQ = liberated CO_2 / consumed O_2) of *Camponotus anderseni* has been calculated for a series of experiments (NIELSEN & CHRISTIAN 2007), and Figure 10 shows the RQ as function of the final CO_2 concentration in the artificial nest. Figure 10 shows a constant RQ of about 0.92 in CO_2 concentrations up to 15

- 18%, and NIELSEN & al. (2006) found an RQ of 0.94 under natural conditions in the mangroves at low tide. This indicates that there was no anaerobic respiration in this range of CO_2 concentrations. As CO_2 concentration in the respiration chamber increased, also the RQ rose. This line indicates that anaerobic respiration is initiated at concentrations around the intersection of lines of the two parts of the regression, which is at about 18% CO_2.

Further evidence of anaerobic metabolism is the change in production of metabolites in *Polyrhachis sokolova*, *Camponotus anderseni*, and *Oecophylla smaragdina*. By using nuclear magnetic resonance spectroscopy on ants which have experienced anoxic conditions and on control ants, substantial changes in the concentrations of glucose, maltose, coenzyme A, trehalose, and alanine were demonstrated (M.G. Nielsen, A. Malmendal, P.G. Henriksen unpubl.). Anaerobic metabolism in social insects has not been demonstrated before, which may be due to the fact that lactate, which was assumed to be an indicator of anaerobiosis, is not produced in the species we investigated and probably not in the species earlier (*Lasius niger*, investigated by BOOMSMA & ISAAKS 1982).

High temperatures can also be a problem for the ants. The above mentioned laboratory experiments (NIELSEN & al. 2006) with *Camponotus anderseni* were mostly carried out at 25°C, i.e., a temperature markedly lower than the measured nest temperature which is about 6°C higher than the air temperature at the same height during the daytime. Therefore, on hot days, when the air temperature exceeds 40°C, the temperature in the small nests can be close to the lethal temperature for ants. Further, the oxygen demand of the ants increases at least 4 times at air temperatures around 40°C as compared to the laboratory experiments (RQ = 2.2; NIELSEN & al. 2006).

Finally, the lack of freshwater is another challenge for the ants in the mangrove. Consumption of honeydew or extraction of plant sap is often the only freshwater source in dry periods, when no dew is available.

What is the benefit of living in these extreme conditions?

The mangrove ants experience such extreme and testing conditions that it is to be wondered, why they have colonized these environments. The mud of the mangrove swamp is the most unlikely environment for terrestrial ants, but for the mud-nesting *Polyrhachis sokolova*, an abundance of "sea food" is served on the mud at each low tide, which compensates for the time the ants are confined to their nests when the tide is in (Fig. 11). So by virtue of its remarkable adaptation to regular immersion, this species avoids competition with other ants and invertebrates.

For the tree-nesting *Camponotus anderseni*, the benefit is a different one: Cavities and holes in trees and branches are usually a site of considerable competition between many different kinds of organisms. Such competition is largely reduced by the regular immersion of the mangrove trees, and so *C. anderseni*, thanks to its remarkable adaptations to regular flooding, obtains an advantage over potential competitors. In essence, these two ant species, by virtue of their remarkable adaptations, are able to exploit a fertile niche free from other competitors.

Prospects

The ant fauna in the mangrove is generally very sparsely investigated and therefore a lot of exciting biological adaptation is waiting to be elucidated. Some of the most obvious questions are: How many true mangrove ant species exist worldwide? How are they adapted to the influence of tide? How are the queens founding new nests? DE-JEAN & al. (2003) report that all the ant species they found in the Mexican mangrove were nesting arboreally, but outside the mangrove, most of these species were ground nesting – is it a widespread phenomenon that ants change their nesting behavior, when they inhabit the mangrove? Also, it is commonly phrased that ants are "very important" or even "the most important insect or arthropod" in the mangrove, but there seem not to be experiments where the significance of ants has been quantified in relation to other components in the ecosystem.

There are so many possibilities for new exciting investigations in the mangrove. I hope that entomologists will defeat the bloodsucking insects and uncomfortable conditions and carry out their research in this fascinating and threatened biotope.

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Zusammenfassung

Ameisen kommen in den meisten terrestrischen Lebensräumen vor und oft weisen sie eine bemerkenswerte Fähigkeit auf, sich an extreme Umweltbedingungen anzupassen. Viele Ameisenarten besiedeln Bereiche, die gelegentlich überflutet werden. Beispielsweise hat *Lasius flavus* (FABRICIUS, 1782) Nester in Gezeitenwiesen mit nicht vorhersagbaren Flutungen im Winter und er überlebt die Überschwemmungen dank seiner geringen metabolischen Aktivität und kleinen, in der Erde eingeschlossenen Luftblasen. Andere Arten, wie *Formica selysi* BONDROIT, 1918, überleben Hochwässer, indem sie schwimmende Flöße von Ameisen und Brut bilden und an trockene Stellen driften. Die Ameisengemeinschaften in regelmäßig überfluteten Lebensräumen des brasilianischen Amazonasgebiets verfrachten ihre Kolonien für die Monate der Überflutung in die Bäume hinauf. In tropischen Mangroven, einem anderen regelmäßig überschwemmten Habitat, leben einige Ameisenarten unter Bedingungen mit ganzjährig extremen Umweltfaktoren. Arten, die in der Gezeitenzone der Mangroven ihre Nester haben, benötigen ein Nestbauverhalten, das sie vor dem Ertrinken bewahrt. Die australische Ameise *Polyrhachis sokolova* FOREL, 1902 überlebt Überflutungen in kleinen "Lufttaschen" in ihren Gallerien im Mangrovenschlamm, wohingegen das Eindringen von Wasser bei der in Zweigen nistenden, australischen Art *Camponotus anderseni* MCARTHUR & SHATTUCK, 2001 durch das Blockieren des Nesteingangslochs durch einen Soldaten verhindert wird. Der Ausschluss von Wasser verhindert auch den Gasaustausch und in Nestern von *C. anderseni* kann die CO_2-Konzentration auf sehr hohe Werte von > 30 % steigen und die Bedingungen können anoxisch werden. *Camponotus anderseni* kann seinen Metabolismus (gemessen als CO_2-Produktion) auf etwa 1 % des normalen Metabolismus reduzieren, wenn die CO_2-Konzentration etwa 25 % erreicht. Mangrovenameisen können auf anaeroben Metabolismus umschalten, was für andere soziale Insekten nicht nachgewiesen wurde. Die Vorteile ihres Lebens unter diesen extremen Bedingungen ist für die Ameisen vor allem das Fehlen von Konkurrenz um Futter und Stellen für die Nestanlage.

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