GENERAL INTRODUCTION

As animals move through their environment they encounter an enormous range of stimuli. Their senses provide them with the ability to perceive information about these stimuli. Depending on the stimulus situation and the behavioral context, each stimulus plays a different role. Animals must decide what set of stimuli to attend to and have to integrate the information obtained in order to respond in a way that ultimately advances reproductive success (Dukas 1998).

The sensory capacities of a species are tailored to fulfill its specific ecological needs (Wehner 1990). Thus, animal senses are biological features that have been shaped by natural selection to promote adaptive behavior. On the other hand, sensory systems have limitations, e.g. phylogenetic constraints, that in turn can restrict animal behavior (Chittka *et al.* 1999).

The many differences among species in the design of sensory systems reflect the effects of evolution (Waterman 1975; Endler 1992). Hence, a knowledge of the natural history of a species can help identify key problems confronting a species and thereby provide cues as to what special proximate mechanisms the members of that species are likely to possess. Knowledge of the limitations of a sensory system can provide valuable information about behavioral constraints (Dukas 1998).

Consequently, a synthesis of sensory physiology and behavioral ecology is necessary for a thorough understanding of animal behavior. Questions about the sensory capacities of an animal need to be asked from the perspective of the animal’s behavioral ecology. Such an approach to animal behavior is termed sensory ecology (Ali 1978; Dusenberry 1992).

The subject of this thesis is the sensory ecology of carbon dioxide perception in leaf-cutting ants. Carbon dioxide (CO_2) is the major end product of the metabolism of all heterotropic organisms. Thus, CO_2 is ubiquitous and its concentration differs considerably in space and time in almost all habitats. Perception of CO_2 is common in insects whereas it is absent in vertebrates. For social insects living in closed dwellings CO_2 concentrations provide information about the availability of oxygen since oxygen and CO_2 concentrations are coupled through respiration and insects are unable to perceive oxygen. Thus, to assure optimal colony growth in their nest, the assessment and control of CO_2 concentrations is probably crucial.

The first part of the thesis deals with the ecological relevance CO_2 for leaf-cutting ants. In chapter one, microclimatic conditions in field nests of the leaf-cutting ant *Atta vollenweideri* are examined. The influence of nest ventilation on CO_2 concentrations inside the nest chambers is assessed. In order to quantify the impact of nest ventilation on colony respiration, reduced nest ventilation is simulated in a laboratory experiment. Nests of *Atta vollenweideri* are built by the ants in a way that promotes passive nest ventilation. The mechanisms underlying nest ventilation are studied in the second chapter.

The focus of the thesis then moves to the role of CO_2 in a different behavioral context: orientation behavior. In the third chapter the orientation of leaf-cutting ants (*Atta sexdens*) in a CO_2 gradient is described and a possible function of CO_2 orientation in colony organization is proposed.

The second part of the thesis deals with the sensory systems providing the ants with information about CO_2. Chapter four describes how the sensilla responsible for CO_2 perception in *Atta vollenweideri* were identified and gives a detailed description of their morphology and ultrastructure. The characters of the sensilla are compared with those of other chemosensory sensilla. Finally, in chapter five the neural activity of the CO_2 receptor cell is examined providing information about how the CO_2 stimulus is actually perceived by the ants.

Thus, the thesis spans from the sensory basis of CO_2 perception in leaf-cutting ants to the importance of this perception ability in the ants natural environment.

The animals

Fifteen species of *Atta* are known, all limited to the New World. Together with ants of the genus *Acromyrmex* the species of *Atta* show the unique ability to cultivate fungi on fresh plant material inside their nests. All members of the colony subsist entirely on these fungus gardens (Hölldobler and Wilson 1990).

The size of mature leafcutter colonies is enormous. Colonies of both *Atta vollenweideri* (Forel, 1893) and *Atta sexdens* (Forel, 1908), the two species studied in this thesis, can house up to five million individuals. *Atta sexdens* is the best known and economically most important species of the tribe. Its foragers climb trees and bushes to cut leaf fragments for fungus cultivation. The species has a wide distribution, reaching from the Caribbean to the North of Argentina where it overlaps with the distribution of *Atta vollenweideri* (Weber 1972).

Colonies of *Atta vollenweideri* live south of the tropic of Capricorn in the basin of the Río Parana and westwards in the area of Grand Chaco, in Paraguay and Argentina (Daguerre 1945). They have the southernmost distribution within the higher Attines and are better adapted to dry conditions and cold winters than the other species of the tribe (Brener and Ruggiero 1994). The main habitat of the species is the flat palm savanna with the two dominant grass species *Elyonurus muticus* and *Paspalum spec.* which the foragers collect for fungus cultivation.

The nests of Atta vollenweideri

Huge mounds emboss the flat palm savannas of the Neotropics. Starting with a small single hole in the ground colonies of *Atta vollenweideri* have built these mounds, excavating more than 15 m^3 of soil to build their subterranean nests (Weber 1966).

The nests show a specific architecture. Mounds of mature colonies are up to 1 m high and 9 m in diameter and have more than 100 openings. From the openings long channels lead to several thousand chambers that are frequently interconnected. The main channels run downward, directed centrally from the openings to the area with fungus chambers. From this central part of the nest the channels bend towards the periphery and connect directly with dump chambers, found at a depth of 6 m below the surface. In mature nests the volume of the channel system and the chambers often exceeds 10 m^3. Of this, only about 2 m^3 carry fungus garden in chambers of about 1.5 l in size (Jonkman 1980).