Trophobiotic interactions of giant ants *Camponotus gigas* (Hym. Form.) and wax cicada *Bythopsyrna circulata* (Hom. Flatidae) on a *Syzygium*-tree (Myrtaceae) in a tropical rainforest on Borneo

Martin Pfeiffer [1] and K. Eduard Linsenmair [2]

[1] University of Ulm, Department of Experimental Ecology (Bio III), Albert-Einstein Allee 11, 89069 Ulm, Germany

[2] University of Würzburg, Department of Animal Ecology and Tropical Biology, Am Hubland, 97074 Würzburg, Germany

Introduction

Recent studies based on nitrogen isotope ratios have shown that particularly canopy ants are cryptic herbivores that mainly feed on extrafloral nectar and liquid exudates of their trophobionts (Davidson et al. 2003). This liquid, the "honeydew", produced in ample quantities by Homoptera and Heteroptera is the ecological foundation for most dominant ants in the canopy (Tobin 1994).

However, only few researchers examined single ant-Homoptera interactions in detail to study behavioral interactions and to quantify nutritional benefits to the ants. Here we investigate the trophobiotic interaction of giant ants *Camponotus gigas* with Flatidae *Bythopsyrna circulata*. Specifically we (1) measured honeydew output of the Flatidae, (2) observed task sharing of ants during honeydew gathering, and (3) examined exchange of honeydew among ants during its transport to the nest.

1

B. circulata produces large quantities of honeydew

The weight of the drops produced by larvae (mean = 0.62 mg, S.D. = 0.01, n = 113) and adults (mean = 1.95 mg, S.D. = 0.05, n = 47) differed significantly (U-test: U = 0.0, Z = -3.46, p < 0.001).

Tending by ants stimulated honeydew production

Time intervals of honeydew secretion of the Flatidae were significantly shorter when Homoptera were tended by ants (see Fig. 1): time intervals between single drops differed between tended and untended adults on average by about 340 seconds (U-test: U = 82.5, Z = -5.56, p <0.001), in larvae by 54 seconds (U-test: U = 3525.5, Z = -318, p < 0.01).

Honeydew output of larvae was 24 mg/h, of adults 42 mg/h.

Calculated at body weight (mean for larvae of all stages: 96.4 mg, S.D. = 4.2, n = 18, for adults: 102.8 mg, S.D. = 40, n = 9) we found for larvae an hourly production of 24.6% of their body weight, for adults of 40.6%.

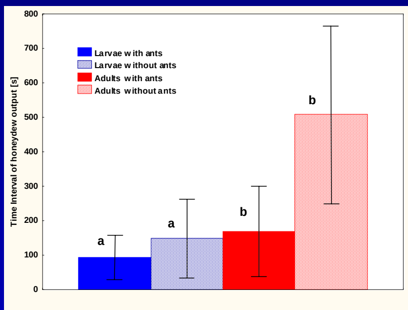

Fig. 1 Acceleration of honeydew production by ants' tending of the Homoptera larvae and adults (a: p < 0.01, b: p < 0.001).

Total input of honeydew of one ant colony was 7.1 g per night

Mean input of honeydew per ant was 27.3 mg (S.D. = 36.2, n = 74). In one night a mean of 260 transport ants returned to the nests, so we calculated a common input of at least 7.1 g honeydew during one night.

2

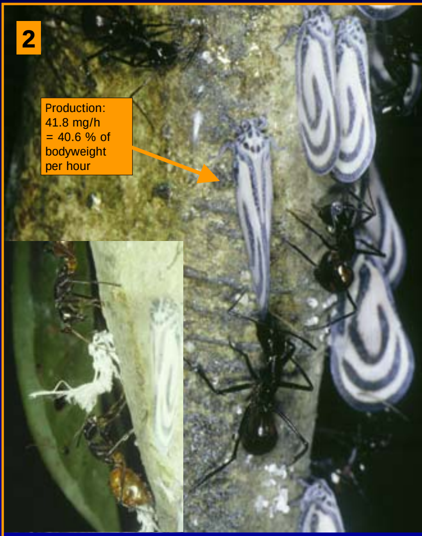

Fig. 2 (large): Workers of *C. gigas* are tending Flatidae *B. circulata* adults. (small): A collector (below) and a second ant that is „antennating from ahead" (above) are tending a larva of *B. circulata*. In both pictures collectors try to catch the falling drop of honeydew.

Behavioral patterns of *C. gigas* during flatids' tending

B. circulata has none of the morphological adaptations for direct transfer of the honey-dew to the ants. Cicadas were tended by minors of *C. gigas* that showed 3 behavioral patterns to deal with that fact (see Fig. 2):

"**Collecting**" (**C**) The ants sat directly below the Homoptera with the flatids' abdomina between their antennae, which rhythmically swung up and down. When flatids flicked the honeydew drops away, the tending ant tried to catch the falling drop with its mandibles or front legs. Then it sucked the drops from its body surface.

"**Antennating from ahead**" (**AA**) The ant sat above or lateral to the cicada and antennated its front part.

"**Helping**" (**HP**) The ants gathered the droplets that had hit the collectors in such a way that they were not able to remove them by themselves. Often they begged collectors to perform trophallaxis; each attended 4 to 6 collectors to gather honeydew (Fig.4). When they had filled their gasters they returned directly to the nest. "Helpers" frequently detached ants that performed tasks C or AA.

Methods

The night active *Camponotus gigas* Latreille 1802 is one of the largest ant species of the World, with a mean head width of minors of 3.56 mm (Pfeiffer & Linsenmair, 2000). Our focus colony had about 7000 foragers and a territory of 0.8 ha. Colonies were polydomous with between 8 and 14 nests (Pfeiffer & Linsenmair, 1998).

We recorded data during night time in a primary mixed dipterocarp lowland forest **in Kinabalu National Park on Borneo, Malaysia.**

Honeydew production. From larvae and adults of the Homoptera we measured time intervals of honeydew output during tending by ants and without it. We weighed 47 honeydew droplets of adults and 113 droplets from larvae.

Ants' interaction during honeydew gathering. 137 individually marked ants were observed during honeydew collecting: a) "general behavior" (1 month, 91 records), b) "focused on interactions" (10 nights, each with 4 hours of observation).

Honeydew input of the ants. To measure ants' mean transport capacity we weighed 421 marked ants when they left or entered the trophobiotic association. We counted activity at the *Syzygium*-tree.

Literature

Davidson, D. W., S. C. Cook, Snelling R.R. and Chua T.H. (2003). "Explaining the ab-undance of ants in lowland tropical rainforest canopies." Science **300** (5621): 969-972.

Pfeiffer, M. and K. E. Linsenmair (1998). "Polydomy and the organization of foraging in a colony of the Malaysian giant ant *Camponotus gigas* (Hym./Form.)." Oecologia **117**: 579-590.

Pfeiffer, M. and K. E. Linsenmair (2000). "Contributions to the life history of the Malaysian giant ant *Camponotus gigas* (Hymenoptera / Formicidae)." Insectes Sociaux **47**(2): 123-132.

Tobin, J. E. (1994). Ants as primary consumers: diet and abundance in the Formicidae. Nourishment and evolution in insect societies. J. H. Hunt and C. A. Nalepa. Boulder CO, Westview Press: 279-308.

3

Fig. 3 Liquid food exchange (oral trophallaxis) between two workers of *C. gigas.*

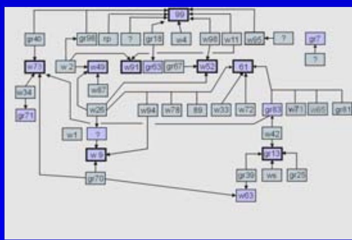

Fig. 4 Flow chart of honeydew exchange by trophallaxis between „helpers" and „collectors". „Helpers" (thick lines) gathered honeydew from collecting ants and transported it to the nest.

Trophallaxis is a "key invention" that permits optimal utilization of transport capacities

Using trophallaxis (Fig. 3) all workers that returned to the nest from the trophobiotic association transported honeydew in their gasters, even if they did not perform the "collecting" task (Fig. 4). While ants at the trophobiosis had all the same size, honeydew transport between nests was done by larger specialist transport ants, that carried a load five times larger than average workers (Pfeiffer and Linsenmair, 1998). Both cases illustrate that trophallaxis is the precondition for optimal foraging in nectar feeding ants.

Upshot: *C. gigas* uses complex behavioral patterns to optimize its energetic profit from trophobionts.

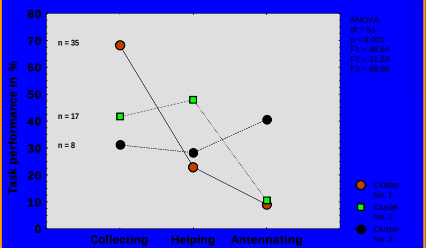

Fig. 5 Task sharing of 56 workers during a 1-month-period of observation. Each group of ants preferred one of the three different tasks.

Contact: martin.pfeiffer@biologie.uni-ulm.de