

The natural history of *Polyrhachis (Myrmhopla) muelleri* Forel 1893 (Formicidae Formicinae), a weaver ant with mimetic larvae and an unusual nesting behaviour

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To cite this article: W. H.O. Dorow , U. Maschwitz & S. Rapp (1990) The natural history of *Polyrhachis (Myrmhopla) muelleri* Forel 1893 (Formicidae Formicinae), a weaver ant with mimetic larvae and an unusual nesting behaviour, Tropical Zoology, 3:2, 181-190, DOI: [10.1080/03946975.1990.10539460](https://doi.org/10.1080/03946975.1990.10539460)

To link to this article: <https://doi.org/10.1080/03946975.1990.10539460>



Published online: 01 Aug 2012.



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**The natural history
of *Polyrhachis (Myrmhopla) muelleri* Forel 1893
(Formicidae Formicinae), a weaver ant
with mimetic larvae and an unusual nesting behaviour**

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Received 28 December 1989, accepted 30 May 1990

Polyrhachis muelleri has an unusual nesting behaviour: while the other leaf-nesting species of *Polyrhachis* hide their nests by weaving together leaves or by incorporating detritus into the silk web, *P. muelleri* weaves pure silk nests on the lower surfaces of large moderately translucent leaves. Any dark contents of such nests are visible from above through the leaves or from below through the thin silk wall. A special adaptation against visually hunting predators has evolved: the larvae and pupae are green. Habitat selection, plant specificity, competition, nestbuilding, and other aspects of the behavioural ecology of *P. muelleri* are discussed.

KEY WORDS: *Polyrhachis (Myrmhopla) muelleri* Forel 1893 (Formicidae Formicinae), nest, weaver ants, mimesis, habitat selection, ant community, plant specificity, rainforest, South-East Asia.

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INTRODUCTION

One peculiar feature of the large tropical ant genus *Polyrhachis* Smith 1857 is the evolution of the use of larval silk for nestbuilding. That trait certainly played an important role in the extensive radiation of the genus, allowing it to become a

prominent component of the arboreal ant community over a wide geographical range. The ants were **no longer restricted to the limited number of preformed nestsites such as hollow branches or stems or small cavities in epiphytes etc., but were able to colonize the canopy and to establish nests nearly everywhere where leaves or other appropriate substrates for fixing silk threads are available.** These arboreal species show mainly two types of nest building:

1. Nests in folded or rolled leaves or between two or more adjacent leaves. Only small slits have to be closed to regain a closed nesting chamber (pers. obs.).
2. Free large silk nests hanging below leaves or erected on the upper sides of leaves. These nests are normally covered with detritus, which can be very fine and carton-like (most species) or very coarse as in *Polyrhachis arachne* Emery 1896 (DOROW & MASCHWITZ 1990).

MATERIAL AND METHODS

We studied the biology of a large population of *P. muelleri* at Ulu Gombak, 30 km north of Kuala Lumpur, West Malaysia for 2 month-periods during each of the past 5 years. For 1 year we kept one colony in a greenhouse in Frankfurt, Germany to evaluate the nest building behaviour in detail. In the laboratory the ants were kept in a glass terrarium (0.5 × 1 × 0.4 m) at 28 °C and 90% relative humidity.

Abbreviations: m = mean, SD = standard deviation, m* = median.

RESULTS

Taxonomy. *Polyrhachis muelleri* belongs to the *hector*-group of the subgenus *Myrmhopla* (revision in preparation by the senior author). It can be easily recognized by its somewhat flattend hind tibiae (characteristic of the species-group) and by its enormously elongated maxillary palps, which are about 2.5 mm long, nearly as long as the thorax. The holotype worker was described by FOREL (1893), females and males by FOREL (1901) and KARAWAJEW (1906, 1927).

Geographical distribution. Only a few findings of the species are documented in the literature (FOREL 1893, 1901, 1907, 1915; EMERY 1894, 1900; KARAWAJEW 1927). Some more records have been added after our identification of hitherto undetermined museum material and our field trips to Malaysia. *P. muelleri* is now known from Burma (Tenasserim: Mt Mooleyit), Thailand (Nam Buh: N.f. Prae; Pah Meeung Mt), the Philippine Islands (Negros: Dumaguete; Mindanao: Ginoog Misamis Anakan; Talacogon), Malaysia (Sarawak: Rejang delta, Sarikei Distr.; north of Kala-bakan; Selangor: Ulu Gombak, 30 km north east of Kuala Lumpur; Kepong, 30 km west of Kuala Lumpur), Singapore (holotype), and Indonesia (Kalimantan: Pulau Laut; Sumatra: Kepahiang; Pangherang Pisang; Sinabang Simalur; Java: Buitenzorg; Soekaboemie).

Colony structure. Two colonies, both nesting in the same large cluster of *Achasma* Linnaeus 1753 sp. (Zingiberaceae) which was growing in a secondary forest, were subjected to a thorough census. During our intensive search for *Polyrhachis* colonies,

we found more than 40 additional nests of the species at further sites in West Malaysia below *Achasma* leaves. Only one nest was situated below a palm leaf. The two polydomous colonies in the 50 m² large *Achasma* stand were separated from each other by a footpath. One colony had five nests dispersed over an area of 15 m², the other had six nests dispersed over 25 m². Normally only one nest was built in the same plant, on one occasion two nests were found below successive leaves. Nests in general were built at heights of 1-4 m ($m = 2.3$ m, $SD = 0.6$ m, $m^* = 2.2$ m, $n = 19$). A special preference for lower or higher leaves was not observed. The nests contained 1-51 workers ($m = 17.3$, $SD = 13.2$, $m^* = 12$, $n = 19$), 0-17 pupae ($m = 7.2$, $SD = 5.4$, $m^* = 7.5$, $n = 16$), and 3-56 larvae ($m = 21.8$, $SD = 12.2$, $m^* = 20$, $n = 16$). Both colonies were monogynous, with the queen being only slightly larger than the workers.

Nest structure. All nests were oval silk webs, each more or less centred below the rib of one *Achasma* leaf (Fig. 1). The leaves were 70-80 cm long and about 15 cm wide. The nests were 7-20 cm long ($m = 13.6$ cm, $SD = 4.7$ cm, $m^* = 15$ cm, $n = 7$), 4-7 cm wide ($m = 5.3$ cm, $SD = 1.0$ cm, $m^* = 5$ cm, $n = 7$), and hanging down 0.5-3 cm. Leaves whose sides had bent down were preferred as nest sites. The upper nestwall, i.e. the lower side of the leaf, was covered with a silk layer to which larvae and pupae were either attached longitudinally or suspended by a silk thread fastened to their rear

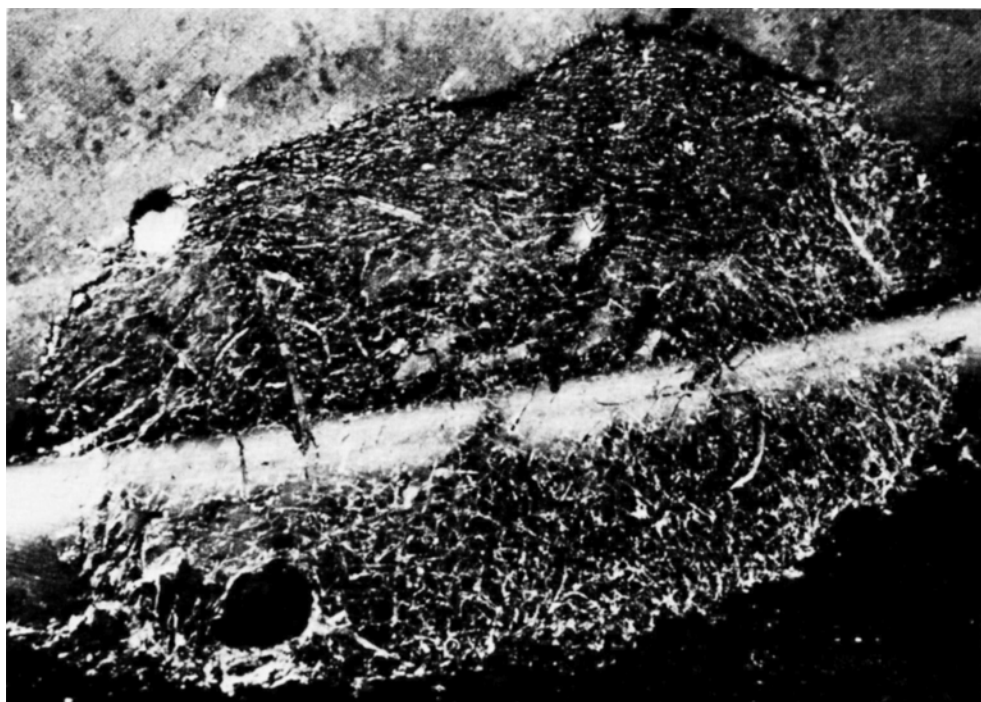


Fig. 1. — Nest of *Polyrbachis (Myrmhopta) muelleri* Forel 1893 on the underside of an *Achasma* leaf.

ends. A few larvae were also attached to the lower nest wall which consisted of pure silk. The silk web was loosely woven and highly translucent. Only occasionally, a few detritus particles such as silk-cocoons, remains of prey, plant debris from leaves, stems or bark, and seeds were incorporated into the nest wall. Even in old nests the detritus particles did not at all hide the contents of the nest (Fig. 1). Each nest had two round to oval entrances ($7 \times 7 - 10 \times 5$ mm), one facing the leaf tip, the other the stalk. The adult ants were black, slender and had long legs, the **first instar larvae were yellowish**, while the **later instars were green**. They pupated in a thin translucent cocoon, where they kept their green colour until sclerotization took place. The pigment responsible for the green colouration is soluble in ethanol.

Nest building and weaving behaviour. The **silk web was constructed of larval silk** in one of four different ways:

1. By a worker ant, which **held a last instar larva** in such a way that the proximal half of the larva was protruding in front of the ant's head. The worker was steadily tapping the front part of the larva with its antennae while touching the rear end of the larva with its forelegs. The larva then began secreting a silk thread which was fixed by the ant to the chosen point of attachment by directing the larva's head to it. The larva itself was nearly immobile during the weaving process: about once a minute (29 times in 30 min) it bent the proximal third of its body sideways. This mode of weaving was the dominant one, occurring in 80% of the observed cases.

2. Two workers cooperated in weaving: one held the larva and was treating it in the manner described above, while the other took the silk from the larva and carried it to the silk web, where it was attached. This mode of weaving occurred in about 10% of the observed cases.

3. Some larvae which had been used before for weaving were fixed to the silk wall of the nest, where they produced silk without any stimulus from a worker. The ants took the silk from the larva's mouth with their mandibles and incorporated it into the silk web. Some of these larvae also attached the newly produced silk to the nest wall by bending their bodies sideways. This method also occurred in about 10% of the observed cases.

4. Silk from destroyed nests was re-used: little pieces were transported to the place where a new web was built and were incorporated there. As long as such material was available, weaving with fresh larval silk was not or only rarely carried out. This behaviour was found very often when a nest was enlarged: former walls were removed in total, so that the nests did not contain any chambers. Silk-like particles were sometimes also incorporated into the nest wall, as were seeds with pappus (field observations) or cotton wool (laboratory observations). Silk from spider webs was not accepted.

Fresh silk threads were self-adhesive, but when old silk material or cotton was used for nest construction, the ants showed a peculiar behaviour to glue it in place: they moistened the contact point between the silk and the nest surface with a droplet from their gaster tip, which was bent down and forward between their legs. We could not identify the site of origin of this secretion. The Dufour gland is not enlarged.

Food. Predation was neither observed in the field nor in the laboratory, but **remains of bees, flies, grasshoppers, beetles, and ant males were found in the nests**. In the laboratory *P. muelleri* fed on pieces of freshly killed insects (e.g. mealworms and

cockroaches) and honey water solution. Foraging was always carried out by single ants, which patrolled the leaf surface in a zigzag course. It was not restricted to *Achasma* plants but was observed also on bamboo, banana, palm, and low herbaceous vegetation. Recruitment was never observed in the field or in the laboratory. Only in two out of about 50 nests trophobiotic coccids were found (25 and 29, respectively). In the second case an additional nine coccids were present in front of the nest on the leaf. *P. muelleri* was strictly diurnal, being active from 7.00 hr until 19.00 hr local time. Workers stopped their foraging activity during rain.

DISCUSSION

Nesting behaviour. We have found only two records on the habits of *P. muelleri*. One is a note by B.B. Lowery on a label of a specimen in the CSIRO Collection, Canberra: «Mindanao, Talacogon, 8.32N 125.39E, foragers on low shrubs by path, relict rain forest on Agusan River». This is in agreement with our findings that *P. muelleri* is a rain forest species. As it seems possible that the species also lives in banana or ginger plantations which provide similar leaves for nesting, further studies are necessary to investigate its habitat range. The second record is from KARAWAJEW (1906). He received a damaged nest from Java, but could not identify the plant. He described the nest as a 10 cm wide pure-silk nest on a lancet-form soft leaf of about 20 cm length.

The use of larval silk for nest building has evolved convergently several times in the subfamily Formicinae and is known from *Camponotus* (*Myrmobrachys*) Forel 1912 spp. (SCHREMMER 1979a, 1979b) and *Dendromyrmex* Emery 1895 spp. (WILSON 1981) from the New World as well as *Camponotus* (*Karavaievia*) Emery 1925 spp. (MASCHWITZ et al. 1985), *Oecophylla* Smith 1860 spp. (DOFLEIN 1906; HÖLLDOBLER & WILSON 1977, 1983) and *Polyrhachis* spp. (JACOBSON & WASMANN 1905; KARAWAJEW 1914, 1928; FOREL 1921-1923; OFER 1970; HÖLLDOBLER & WILSON 1977) from the Old World. Availability of nest sites appears to be the main limiting factor for most ant species of the rain forest canopy (WILSON 1959, 1987). The ability to weave nests with larval silk circumvents this limitation: the species of *Polyrhachis* (especially in the subgenera *Cyrtomyrma* Forel 1915, *Myrmatopa* Forel 1915, *Myrmhopla* Forel 1915, and *Myrmothrinax* Forel 1915) can establish colonies nearly everywhere in the leaf region (DOROW in prep.). Acquisition of that ability led to an enormous adaptive radiation in *Polyrhachis*, which today comprises several hundred species with a great variety of nesting types. Normally the silk walls of *Polyrhachis* nests are covered with detritus, no matter whether the silk is used for closing small slits or for building whole walls or whether the nest is built between, above or below leaves or in folded leaves (DOROW in prep.) [see Fig. 2 with the nest of *P. (Myrmothrinax) thrinax* Roger 1863]]. The use of pure silk, on the other hand, is a rare phenomenon and, according to our observations, seems to occur regularly only in *P. muelleri* (KARAWAJEW 1906) (Fig. 1) and in *Polyrhachis bicolor* Smith 1858, which builds a nest of the between-leaves-type (Fig. 3) (pers. obs.).

The brown detritus-covered nests of most *Polyrhachis* species are located below smaller leaves of trees [e.g., *Polyrhachis (Myrmatopa) schang* Forel 1879] and themselves resemble dead brown leaves, while those on the bark of trees [e.g., *Polyrhachis (Myrmhopla) tubifex* Karawajew 1927] are similar to pieces of bark. But such detritus

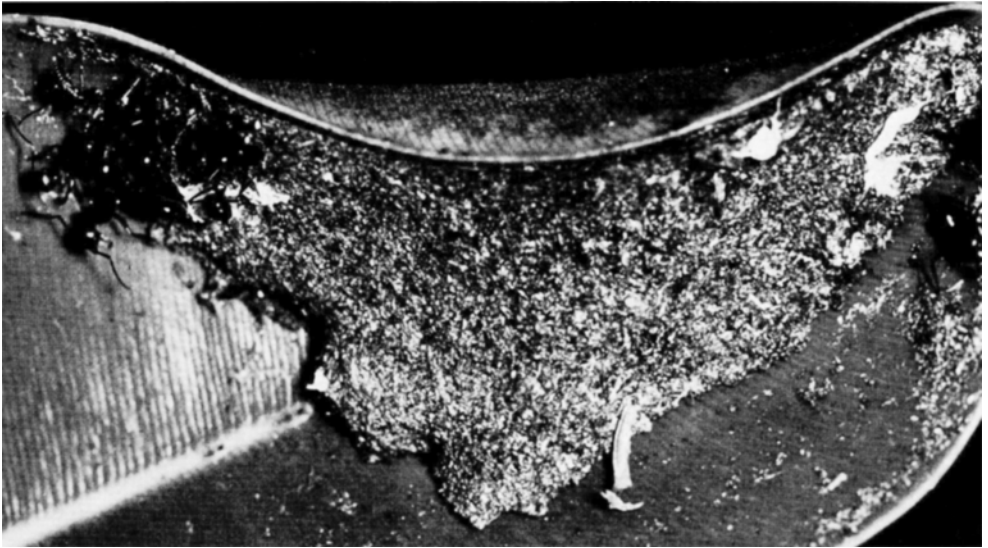


Fig. 2. — The typical silk nest with a thick detritus cover of *P. (Myrmothrinax) thrinax* Roger 1863 as an example of the most common type of nest in the genus *Polyrbachis*.

covered nests would not be hidden below a large leaf of a palm or ginger plant. Instead they would be conspicuous from above as a dark area shining through the leaves. Also from below such a nest would be also clearly visible. *P. muelleri* with its ample silk nests, however, has developed strategies against those problems, enabling it to colonize large moderately translucent leaves. No shaded area can be detected



Fig. 3. — Silk wall of the nest of *Polyrbachis (Myrmhopta) bicolor* Smith 1858 between two leaves of a citrus tree.

through the leaf and also, from below, the nest is difficult to see and may be taken for a spider's web. But the building of a translucent nest raises a new problem: the contents of the nest are clearly visible. Two special features may have evolved to reduce the conspicuousness of the contents of the nest: larvae and pupae possess a mimetic green colouration and the pupae are enclosed in only a very finely spun translucent cocoon, through which the green pupae can be seen.

In addition, two further features, which are common in *Polyrhachis* and also occur in some other ant genera, are protective against enemies: when being attacked, the adult ants rush out of the nest, disperse on the lower surface of the leaf and wait there for a long time in the typical defense posture of *Polyrhachis*, with the gaster bent forward between the legs, distracting a potential predator from the contents of the nest (FOREL 1909). If attacked again, they drop to the ground. Foragers on the upper leaf surface quickly flee to the underside of the leaf and then behave like their colony members at the nest.

The slender body and the long legs of the worker ants may have the effect of disrupting the body outline.

The green cryptic colouration of the brood is unique among the ants. A similar camouflaging effect is probably gained by the green colour of the workers of the Australian population of *Oecophylla smaragdina* (Fabricius 1775) (SAVILLE-KENT 1897) and by the colour of *Oecophylla* queens in general, which have green gasters during colony foundation. As we have observed in Malaysia, the queen of *Oecophylla smaragdina* does not use any shelter during colony foundation but nests freely on the leaf surface during that time (pers. obs.).

FOREL (1909) stated that all species of *Polyrhachis* and *Camponotus* Mayr 1861 build cocoons. WHEELER (1915) reported the loss of cocoon weaving in species of the *Polyrhachis* subgenus *Cyrtomyrma* and noted that 20 other species of different subgenera all weave cocoons. Despite our intensive search we did not find any *Polyrhachis* species from the other subgenera that had naked pupae. HÖLLDOBLER & WILSON (1983) reported the loss of cocoon weaving from an Australian species of the subgenus *Cyrtomyrma* and drew the conclusion that the larvae contribute all their silk to the nest and therefore cannot build cocoons. The thin cocoon of *Polyrhachis* (*Myrmhopta*) *muelleri*, however, does not seem to be the result of the extensive use of silk for nestbuilding, but a cryptic adaptation to let the green colour of the pupae shine through. As a side effect, energetically costly silk protein can be saved in this way, but this means less protection against environmental effects and greater susceptibility to injury by enemies or the ants themselves. The reasons why cocoons are reduced in many different species of ants is not well understood at this time. Comparing the amounts of larval silk incorporated in *Polyrhachis* (*Cyrtomyrma*) nests with those of other *Polyrhachis* species, it has to be doubted that naked pupae could be the result of intense use of larval silk for nest weaving. Even *Polyrhachis dives* Smith 1857 with its huge silk nests builds cocoons (DOROW in prep.). Moreover, according to KARAWAJEW (1906, 1929) who studied the larval glands of several ant species, the glands of *P. muelleri* larvae are not smaller than those of other species of *Polyrhachis* which weave nests and normal cocoons.

Nestbuilding behaviour in *Polyrhachis* cannot generally be considered to be less highly evolved than in *Oecophylla smaragdina*, as stated by HÖLLDOBLER & WILSON (1983). On the contrary, *P. muelleri* also uses the most highly evolved weaving type in ants, where a worker ant holds the larva and makes the weaving movements itself.

Also the use of a pure silk nest in *P. muelleri* cannot be considered more primitive than the use of a silk nest covered by detritus, but is a highly specialized adaptation. The additional use of a fluid for glueing old silk threads to the nest is not known even in *Oecophylla*. Another very remarkable feature of *P. muelleri* is that it uses a set of weaving methods ranging from primitive to highly evolved ones. Only in the coordination of work is *Oecophylla smaragdina* more highly evolved than *Polyrbachis*: the workers cooperate in a sophisticated manner and even form chains of workers for active manipulation of leaves (HÖLLDOBLER & WILSON 1983). Such a behaviour has not been observed in *Polyrbachis* so far.

P. muelleri as well as many other arboreal species of *Polyrbachis* and the dominant *Oecophylla smaragdina* use their nest weaving ability to establish several subunits of their colonies sometimes over a large area. This principle of scattered bases serves three advantages:

1. A large area can be controlled without the need for long distance patrols.
2. The distances to food sources are reduced. This is especially important for non-aggressive trophobiotic, individually foraging species or species with small colonies: *P. muelleri* and many other species of *Polyrbachis* cannot defend a food source against aggressive single foragers such as *Diacamma* Mayr 1862 sp. or against, e.g., myrmicine ants with very fast recruitment systems.
3. It is very unlikely that an enemy or a catastrophe will destroy all nests of a colony at once, so the ants from destroyed or raided nests may find shelter in one of the remaining nests.

Ant community. *P. muelleri* is a rare species with an evasive behaviour when it encounters other ants. Other species of ants were tolerated by *P. muelleri* in the *Achasma* cluster. *Technomyrmex* Mayr 1872 sp., for example, had pavilions with Hormaphididae close to a *P. muelleri* nest, and a species of the *Polyrbachis* (*Myrmhopta*) *mucronata*-group was also nesting in a small carton nest with an inner silk lining below the rib of an *Achasma* leaf. *Polyrbachis* (*Cyrtomyrma*) *rastellata* (Latreille 1802) nested in a dead folded *Achasma* leaf, *Hypoclinea* Mayr 1855 sp. in a rolled tip of an *Achasma* leaf. *Polyrbachis* (*Myrmhopta*) *calypso* Forel 1911 and *Camponotus* sp. were visiting homopterans at tips of *Achasma* leaves. *Echinopla* Smith 1857 sp. and *Crematogaster* Lund 1831 sp. were foraging on the leaves. Only one fight with another ant species was observed: it occurred between a forager of *Polyrbachis hector* Smith 1857 and one of *P. muelleri* on ca 50 cm high herbaceous vegetation. An *Aenictus* Shuckard 1840 sp. raid through the *Achasma* cluster did not detect the *P. muelleri* colonies.

The nestweaving ability in conjunction with the highly specialized cryptic adaptations enables *P. muelleri* to colonize one of the few habitats in the rainforest with shortlived monocultural stands: gaps with large clusters of Zingiberaceae. According to our observations these areas contain much less prey objects for ants than diverse habitats. Such areas are probably not favourite foraging sites for dominant species like *Oecophylla smaragdina*, which need a large amount of food for their large colonies and tolerate only very few species in their territory (HÖLLDOBLER & LUMSDEN 1980). So it seems likely that *P. muelleri* occupies a niche with low competition pressure from dominant ants. In this case, other enemies are probably more important and adaptations have mainly been developed against them: the unique green larvae and pupae and the thin translucent silk webs of cocoons and nests of *P. muelleri* may work

against visually hunting vertebrate predators, especially birds. It is known, that ants form an important part of the diet of many bird species and that even spiny species are eaten by many birds (DAHL 1899, BEQUAERT 1922, GREENSLADE 1979).

After abundant occurrence of *P. muelleri* at our study site over a period of 5 years, fast growing tree species, especially *Piper* Linnaeus 1753 sp., interspersed the monoculture of *Achasma*. Parallel to this succession, the nest numbers of *P. muelleri* decreased markedly. At the end of our study time *Oecophylla smaragdina* entered the *Achasma* cluster, but did not reach the area with the nests of *P. muelleri*.

Dominant species set up distributional patterns which determine the distribution of subdominant species (GREENSLADE 1979). The genus *Polyrhachis* evolved a broad spectrum of adaptations including the construction of silk nests and non-aggressive behaviour for filling the niches left unoccupied by dominant and subdominant species. The genus seems to be an ideal subject for the study of highly specialized niches and for understanding the complex interactions between species in the rain-forest.

ACKNOWLEDGEMENTS

We thank Prof. Yong Hoi Sen and Prof. Kiew Bong Heang (University of Malaya, Kuala Lumpur, Malaysia), Dr Tho Yow Pong, Wulf Killmann and his gtz-research team (Forest Research Institute, Kepong, Malaysia) for their kind help during all our studies in Malaysia, including the provision of laboratory and field station facilities. Dr Claude Besuchet (Muséum d'Histoire Naturelle, Genève), Barry Bolton (British Museum, Natural History, London), Dr Janine Casevitz-Weullersse (Muséum National d'Histoire Naturelle, Paris), Dr Gary F. Hevel (National Museum of Natural History, Smithsonian Institution, Washington), Rudolf J. Kohout (Queensland Museum, Brisbane), Dr Borge Petersen (Zoologisk Museum, Kobenhavn), Dr Valter Raineri (Museo Civico di Storia Naturale, Genova), Prof. Robert W. Taylor (Australian National Insect Collection, Canberra), and Prof. Edward O. Wilson (Museum of Comparative Zoology at Harvard University, Boston) have kindly loaned specimens of *Polyrhachis*. Many thanks also to Konrad Fiedler and Rüdiger W. Klein (University of Frankfurt) for helpful comments on the manuscript. The senior author wishes to thank the Hermann-Willkomm-Stiftung and the «Vereinigung der Freunde und Förderer der Johann Wolfgang Goethe-Universität Frankfurt am Main» for their kind financial support of research trips to Australia and the United States. Field work in Malaysia was supported by the Deutsche Forschungsgemeinschaft.

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