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Competition between ants for coconut palm nesting sites

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About 85 different ant species were found nesting on coconut palms in Malaysia, the Philippines, Sri Lanka, Tanzania and Trinidad. Three occurred in all countries. With the exception of the leaf-nesting *Oecophylla* spp, all nested in leaf axils and spadices mostly between the two sheaths (spathes) and peduncle of the spadix. Up to eight species were found nesting in the same palm and five in the same spadix. In the latter circumstances the nest distribution of different non-dominant species is initially associated with the 'height' of available spaces, the smaller species nesting in the narrower, more distal end and the larger in the proximal end of the spadix. However, the small dominants, *Pheidole* spp and *Wasmannia auropunctata*, initially choose the large spaces in ageing spadices and leaf axils. In the spatially simple leaf axil the most striking association was between the small dominant *Wasmannia auropunctata* and the large ponerine *Odontomachus bauri* with *W. auropunctata* nesting below and between galleries made by *O. bauri* in old and dead leaf axils. Different species with overlapping niche requirements nested very closely in the same part of a spadix. In these circumstances they seemed mutually tolerant, more so than at food sites where one was sometimes observed to displace others. Such observations suggest that apparently simple dominance and displacement concepts can be relatively complex when applied to competition for similar nesting sites, and that this needs to be taken into account in the use of beneficial ants that are important in biological control, and in the suppression of their harmful competitors.

KEYWORDS: Ants, coconuts, diversity, competition, nesting sites.

Introduction

Some 'dominant' ants colonising coconut palms are important natural enemies, especially of some pest Heteroptera, Lepidoptera and Coleoptera. They include *Oecophylla* spp. which are particularly effective against coreid pests in equatorial Africa and the Solomon Islands (Way, 1953; Brown, 1959; Fataye and de Taffin, 1989) and *Dolichoderus thoracicus* in Southeast Asia where its control of cocoa Miridae depends on large populations based on intercropped coconut palms (Way and Khoo, 1991). Other palm inhabiting ants that are useful natural enemies include *Wasmannia auropunctata* against heteropteran pests in Cameroon and the Solomon

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Islands (Bruneau de Miré, 1969; MacFarlane, 1985) and the egg-predatory *Monomorium* spp. (Way *et al.*, 1989; Way and Khoo, 1992).

So-called 'dominant' ant species (Majer, 1972) are characterised by their abundance and mutual hostility such that, in parts of East and West Africa and the Solomon Is., competing dominant ants can prevent control of coconut pests by *Oecophylla* spp. (Way and Khoo, 1992). They include the ground-nesting *Anoplolepis longipes* and *Pheidole* spp. which can also nest in coconut palms (Way, 1953), and the arboreal *Philidris myrmecodiae* (Brown, 1959). Other palm nesting ant species, not recognised as dominants, might also pre-occupy favoured nesting sites of beneficial dominants. Such observations prompted a world-wide study of nesting ant communities in coconut palms. Particular attention was paid to competition for sites in the spadices (Fig.1) which are produced at 3–4 week intervals throughout the year, each remaining on the palm for at least one year during which it provides the nesting site for many ant species.

Methods

The work was done in Zanzibar and the coastal region of mainland Tanzania around Tanga and Dar es Salaam, in southern Malaysia, in southwest and southern Sri Lanka, on the island of Luzon in the Philippines, and in Trinidad. Sampled sites included large commercial monoculture and mixed plantations often with cocoa in S.E. Asia, as well as small farmer systems ranging from monoculture plots of up to about 1 h to mixtures of coconuts with one or more other crops including large trees such as mango but mostly lower story species of which the commonest were cocoa, coffee, cloves (in Zanzibar), citrus and guava.

In all countries a folding ladder was used to examine dwarf palms up to about 5 m high. Longer ladders for examining up to 15 m tall palms were available only in Malaysia and the Philippines. In all countries spadices cut down by coconut climbers from palms of about 20 m were occupied by the same range of ant species as in shorter palms, though relative abundances could not be estimated. Examinations were made

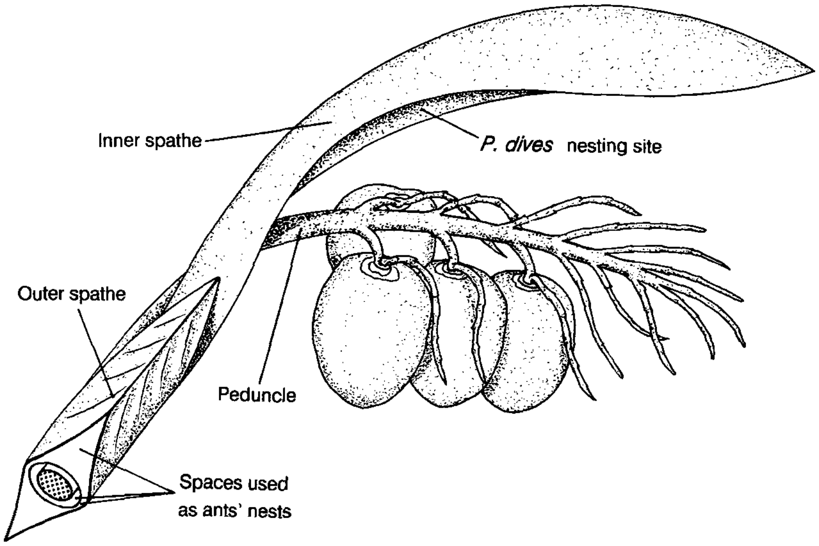

Fig. 1. Diagram of coconut palm spadix showing nesting sites of ant species.

Table 1. Categories used for assessing numbers of a particular ant species foraging and nesting on a single coconut palm.

Category	
(1)	Few. < about 10–20 workers seen.
(2)	Moderate numbers. At least 20–50 of a larger ant† or up to about 200 of a smaller species.
(3)	Common. About 50–200 of a larger ant† or 200–1000 of a smaller species. *Oecophylla* sp nests visible on fronds; other ant species nesting in a few spadices/leaf axils.
(4)	Abundant. About 200–1000 of a larger ant† and about 1000–2000 of a smaller species. Some, e.g. *Oecophylla*, *Dolichoderus*, *Tapinoma* spp, with well formed trails on trunks; many nests of *Oecophylla* spp. on fronds, or large nesting populations of other species in spadices/leaf axils.
(5)	Very abundant. > about 1000 of a larger ant† or about 2000–5000 of a smaller ant species. Some, e.g. *Dolichoderus*, *Tapinoma* spp, with strong trails on trunks; a spadix-nesting species in this category would be completely or partly occupying most of the examined spadices/leaf axils.
(6)	Extremely abundant. Sole occupation by > 5000–10 000 of a smaller species. A rare category attained only by *Dolichoderus thoracicus*, *Pheidole* and *Tapinoma* spp.

†These include species of Ponerinae, *Polyrhachis*, *Camponotus* and *Oecophylla*.

of 2–4 sectors of the crown of each palm, where about half of the live and dead spadices, and the axils of dead and dying fronds were examined. Ensheathing spathes of the spadices (Fig. 1) were torn apart and the frond axils pulled open to expose ants nesting in them. Estimates of ant numbers were based primarily on those in the nests, except *Oecophylla* spp. for which overall inspections of foraging ants were made on the crown and trunk. *Oecophylla*, and sometimes *Azteca* and *Dolichoderus* spp, were the only ants seen nesting on the palms away from the spadices and leaf axils. Ant numbers on each palm were categorised semi-quantitatively using a numerical system (Table 1). Some, e.g. *Cardiocondyla wroughtonii*, were rarely found, but others such as *Monomorium* spp occurred on > 25% of palms.

In order to relate ant-sizes to the heights of the spadix cavities in which they nest, dorso-ventral measurements were made of the fore axes of workers of ten different sized species. These were made by determining the straight-line distances between the apex of the forecoxa and the highest point of the promesonotum, in profile, with the coxa fully back against the katepisternum. Such measurements represent the absolute minimum space that an ant could utilise and do not take into account the ant's body carriage and crawling habit that must also determine the size of the crevice that it can enter. No doubt compact workers such as those of *Monomorium* spp can use spaces that similar body-sized species with higher body carriage cannot, for example *Tapinoma melanocephalum*. The queens would also need more space than the largest workers. The heights of crevices in the spadices were measured very crudely, mostly from sawn cross-sections.

Details of other methods are given in the text. Voucher samples of all ant species are deposited in The Natural History Museum, London.

Results

Species diversity

Ants found nesting in coconut palms in the five countries are listed in Table 2.

Tanzania. Twenty-four species were recorded. The most widespread and

Table 2. Ant species recorded nesting in palm trees.

		Nesting sites‡				
Taxa	Country†	L	A	Spo	Spi	
PONERINAE						
Leptogenys falcigera (Roger)	Ta		+			
Platythyrea parallela (Smith)	M			+	+	
Hypoponera sp 1	M			+	+	
Hypoponera sp 2	M		+			
Hypoponera sp	SL		+	+		
Odontomachus bauri Emery	Tr		+			
MYRMICINAE						
Cardiocondyla emeryi Forel	Ta			+	+	
Cardiocondyla wroughtonii (Forel)	M,P				+	
Monomorium floricola (Jerdon)	Ta,M,SL,P,Tr		+	++	++	
Monomorium exiguum Forel	Ta		+	++	++	
Monomorium destructor (Jerdon)	M,SL,P			+	+	
Monomorium dichroum Forel	SL			+	+	
Monomorium latinode Mayr	SL			+	+	
Monomorium talpa Emery	SL			?	?	
Monomorium (sp new)	M			+	+	
Monomorium sp (*scabriceps*-gp)	SL			+	+	
Tetramorium bicarinatum (Nylander)	M,P,Tr		+	++	++	
Tetramorium pacificum Mayr	M,SL			+	+	
Tetramorium simillimum (Smith)	M,SL,P		+	+	+	
Tetramorium lanuginosum Mayr	SL,P				+	
Crematogaster castanea Smith	Ta			+	+	
Crematogaster sp a (nr *opaciceps*)	Ta			+	+	
Crematogaster sp b (nr *opaciceps*)	Ta			+	+	
Crematogaster sp 1	M			+	+	
Crematogaster sp 2	M			+	+	
Crematogaster sp 3	M			+	+	
Crematogaster sp 4	M			+	+	
Crematogaster sp 5	M			+	+	
Crematogaster spp	SL			+	+	Two spp
Crematogaster sp 1	P			+	+	
Crematogaster sp 2	P				+	
Pheidole sp (*megacephala*-complex)	Ta		++	+	+	#Secondary
Pheidole sp (? *ilgi*)	Ta			+	+	#Secondary
Pheidole fervens Smith	M,P		++	+	+	#Secondary
Pheidole oceanica Mayr	M		++	+	+	#Secondary
Pheidole biconstricta Mayr	Tr		+	+	+	#Secondary
Pheidole sp a	Tr		+			#Secondary
Pheidole sp b	Tr		++	+		#Secondary
Pheidole sp	M		+	+	+	#Secondary
Solenopsis geminata (F)	M,SL,P		+	+		#Secondary
Solenopsis saevissima (Smith)	Tr		+			#Secondary
Leptothorax angulatus Mayr	Ta			+		
Wasmannia auropunctata (Roger)	Tr		+	+	+	
Zacryptocerus clypeatus (F.)	Tr			+	+	
DOLICHODERINAE						
Azteca spp	Tr	+	?	?	?	
Dolichoderus thoracicus (Smith)	M,P	+	+	++	++	
Dolichoderus (sp nr *gibbus*)	M	?	+	+	+	
Dolichoderus championi Forel	Tr				+	
Philidris cordatus (Smith)	M		+	+	+	

Table 2. (cont) Ant species recorded nesting in palm trees.

			Nesting sites‡			
Taxa	Country†	L	A	Spo	Spi	
Tapinoma melanocephalum (F.)	Ta,M,P,Tr		+	++	++	
Tapinoma sp 1	M			+	+	
Tapinoma sp 2	M			+	+	
Tapinoma sp a	Ta			+	+	
Tapinoma sp b	Ta				+	
Tapinoma sp	P			+	+	
Technomyrmex albipes (Smith)	M,SL,P		+	++	++	
Technomyrmex sp a	Ta			+	+	
Technomyrmex sp b	Ta			+	+	
Technomyrmex sp 1	M			+	+	
Bothriomyrmex wroughtonii Forel	SL			+?	+?	
FORMICINAE						
Oecophylla longinoda (Latreille)	Ta	+				
Oecophylla smaragdina (F.)	M,SL,P	+				
Anoplolepis longipes (Jerdon)	Ta,M,SL,P		++	+	+	#Secondary
Plagiolepis (sp nr *brunni*)	Ta			+	+	
Paratrechina longicornis (Latreille)	Ta,M,SL,P,Tr		++	+	+	#Secondary
Paratrechina fulva (Mayr)	Tr		+			
Paratrechina sp	P		+			
Paratrechina sp 2	M				+	
Paratrechina sp 5	M		+	+		
Paratrechina sp 6	M		+	+	+	
Camponotus abdominalis	Tr			++	+	
Camponotus sexguttatus (F.)	Tr			+		
Camponotus sp	Tr			++	+	
Camponotus sp 1	M		+	++	+	
Camponotus sp 2	M			+		
Camponotus sp	P		+	+		
Camponotus flavomarginatus Mayr	Ta			+	+	
Camponotus sp (*foraminosus* gp)	Ta		+	+	+	
Camponotus sp (*maculatus* gp)	Ta		+	+	+	
Camponotus sp (*maculatus* gp)	SL		+			
Polyrhachis cubaenis Mayr	Ta		+			
Polyrhachis hector Smith	M		+	+		
Polyrhachis tibialis Smith	M,P		+	+	+	
Polyrhachis bicolor Smith	P			+	+	
Polyrhachis dives Smith	P				+	
Lepisiota sp	Ta		+			

†Ta—Tanzania; M—Malaysia; SL—Sri Lanka; P—Philippines; Tr—Trinidad.

‡L—Leaves (fronds); A—Leaf axils including spadix axils; Spo—Between inner and outer spathes; Spi—Between inner spathe and peduncle except *P. dives* in hood of inner spathe.

++—Much preferred nesting site.

#—Species recorded as secondary are primarily ground-nesting.

abundant was *Pheidole* sp., *megacephala* complex. Other dominants included *Oecophylla longinoda* in scattered colonies and *Anoplolepis longipes* which was abundant in parts of Zanzibar Is. (Way, 1953) but absent elsewhere. The other major dominant, *Anoplolepis custodiens*, was locally abundant, sometimes foraging palms in very large numbers but not nesting in them. The commonest non-dominants were three species of *Tapinoma*, *Technomyrmex* sp.1 and two species of *Camponotus*.

Malaysia. Thirty-seven nesting species were recorded. Seventeen could not be

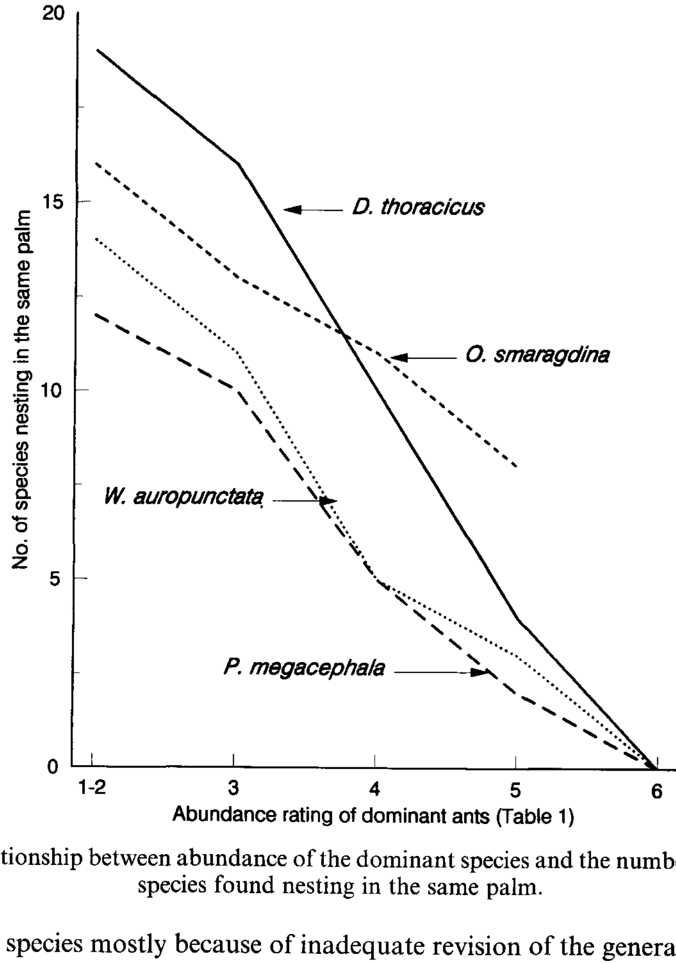

FIG. 2. Relationship between abundance of the dominant species and the number of other ant species found nesting in the same palm.

identified to species mostly because of inadequate revision of the genera that include many undescribed species. One, *Tapinoma* sp., probably comprised at least two. The number of palms occupied and the abundance ratings indicate relative distributions and abundances of each ant species. Some dominant species were locally very abundant, notably *D. thoracicus* and also *Dolichoderus* spp nr *gibbus* and *Philidris cordatus* which were recorded in only two localities. Thriving populations of *Oecophylla smaragdina* comprising colonies each occupying up to about twenty palms (Way and Khoo, 1991) were found scattered throughout the overall sampled region. *Anoplolepis longipes* and *Pheidole* spp, which are recognized as dominants elsewhere, were sparse or localised, the former widely present but usually uncommon and the latter very localised, where it was occasionally abundant on a few palms. The most widely distributed and commonest of the non-dominant ants were *Crematogaster* sp.1, two species of *Monomorium*, and *Tapinoma* spp.

Sri Lanka. Eighteen nesting species were recorded. The only obvious dominant was *Oecophylla smaragdina*. Others, notably *Anoplolepis longipes* were relatively uncommon and rarely nested in palms. *Pheidole spathifera*, the only species of this genus found on coconuts, was also scarce. The commonest non-dominants were undoubtedly *Monomorium floricola* and *Monomorium dichroum*, *Technomyrmex albipes*, *Tapinoma melanocephalum* and *Paratrechina longicornis*.

Philippines. Twenty-three nesting species were recorded. The commonest were

Table 3. Number categories (ref. table 1) of dominant* ant species above which the other listed commonly occurring ant species were not found nesting in the same plam tree.

Categories 1–2 (10–200	Category 3 (200–1000)	Category 4 (1000–2000)	Category 5 (2000–5000)
Wasmannia auropunctata (Trinidad)			
Paratrechina longicornis *Azteca* sp. *Pheidole* spp.	*Monomorium floricola*	*Tapinoma melanocephalum* *Camponotus sexguttata*	*Camponotus abdominalis* *Camponotus* sp. *Odontomachus bauri*
Dolichoderus thoracicus (Philippines)			
Polyrhachis tibialis *Polyrhachis bicolor*	*Paratrechina* sp.1 *Oecophylla smaragdina* *Camponotus* sp.1 *Crematogaster* sp.1	*Paratrechina longicornis* *Tapinoma melanocephalum* *Technomyrmex albipes*	*Monomorium floricola*
Dolichoderus thoracicus (Malaysia)			
Paratrechina spp. *Polyrhachis tibialis* *Platythyrea parellela*	*Paratrechina longicornis* *Oecophylla smaragdina* *Camponotus* sp.1 + 2 *Cardiocondyla wroughtonii* *Tetramorium pacificum* *Pheidole oceanica* *Paratrechina* sp.6	*Hypoponera* sp.1 *Polyrhachis hector* *Technomyrmex albipes* *Crematogaster* sp.1	*Monomorium floricola* *Monomorium* sp (new) *Tapinoma* spp *Technomyrmex* sp.1
Pheidole megacephala (Tanzania)			
Crematogaster sp. nr *opiceps* *Crematogaster castanea*	*Oecophylla longinoda* *Monomorium floricola* *Monomorium* spp.	*Tapinoma* sp.a *Monomorium exiguum* *Leptothorax angulatus* *Technomyrmex* sp. a	*Camponotus maculatus* *Camponotus forminosus* gp

Table 3: continued

Categories 1–2 (0–50)	Category 3 (50–200)	Category 4 (200–1000)	Category 5 (> 1000)
Monomorium floricola† (Sri Lanka + Malaysia)			
	Tapinoma melanocephalum	*Camponotus* spp.	*Oecophylla smaragdina*
		Paratrechina longicornis	*Crematogaster* sp.
		Crematogaster spp.	*Technomyrmex* sp.
		Technomyrmex albipes	
Oecophylla smaragdina (Sri Lanka + Malaysia)			
Paratrechina longicornis	*Dolichoderus thoracicus*	*Technomyrmex albipes*	*Monomorium floricola*
Camponotus spp.		*Crematogaster* sp.	
		Tapinoma melanocephalum	

†The egg predator *Monomorium floricola* although often abundant is not regarded as a 'dominant'.

Monomorium floricola, *Dolichoderus thoracicus*, *Tapinoma melanocephalum*, *Technomyrmex albipes* and *Paratrechina longicornis*. *Oecophylla smaragdina*, *Anoplolepis longipes* and *Pheidole fervens* were common in very localised sites.

Trinidad. Sixteen nesting species were recorded during a less intensive search than in the other countries. The dominant *Wasmannia auropunctata* was widely abundant. *Azteca* spp. must also be classed as a dominant, and a few nests were collected but most were on palms that were too tall to examine. Other common ants included *Odontomachus bauri*, *Tapinoma melanocephalum*, *Paratrechina longicornis* and *Camponotus* spp.

Overall distribution and abundance. About 85 different species were found nesting in coconut palms in the five countries. *Tapinoma melanocephalum*, *Paratrechina longicornis* and *Monomorium floricola* were recorded in all of them; other *Monomorium* spp were widely present, and beneficial species also included *Oecophylla* spp—locally common in Africa and Asia, and *Dolichoderus thoracicus* in parts of Malaysia and the Philippines. *Wasmannia auropunctata* was widespread and abundant in Trinidad. *Pheidole* spp were widely abundant, and *Anoplolepis longipes* locally abundant in Zanzibar (Tanzania). Both compete harmfully with the beneficial *Oecophylla* spp (Way and Khoo, 1992).

Species nesting in the same palm

Dominant ants had a notable impact on numbers of co-existing species (Fig. 2) but, except when a species reached numbers in categories 5 and 6, at least two and up to eight other species were often found nesting with it in the same palm (Table 3). In Tanzania, for example, one combination included the foliar nesting *Oecophylla longinoda* (category 3–4) with spadix and leaf-axil nesting *Tapinoma* sp a(4), *Camponotus foraminosus* (3), *Monomorium exiguum* (3), *Technomyrmex* sp a(2), *Leptothorax angulatus* (2) and *Lepisiota* sp(3). *Pheidole megacephala* was absent or relatively scarce (categories 0–2) in the common presence of *O. longinoda* (3–4) and *vice versa*, as might be expected from competing dominants, despite their different nesting sites (Table 2). As a primarily ground nesting species, *P. megacephala* numbering up to about category 4 occurred with several other species which mostly nested in younger spadices, with *P. megacephala* predominating in old and dead leaf axils and spadices (Table 3).

The dominant *Dolichoderus thoracicus* was much less overtly aggressive than *Oecophylla* and *Pheidole* spp, and often occurred in the same palm with many other minor species (Table 3, Fig. 2). In Malaysia, for example, *D. thoracicus* (category 2) was nesting in one palm with *Tapinoma* sp (2), *Technomyrmex* sp 1 (3), *Camponotus* sp 1(2) and sp 2(2), *Polyrhachis hector* (2), *Crematogaster* sp 1(2), *Pheidole oceanica* (2) and *Paratrechina* sp 6; also in Trinidad *Wasmannia auropunctata* (4) was nesting in one palm with *Odontomachus bauri* (3), *Camponotus abdominalis* (4), *Camponotus sexguttatus* (3), *Camponotus* sp a (3), *Tapinoma melanocephalum* (4) and *Zacryptocerus clypeatus* (2). Although not a recognised dominant, *Monomorium floricola* coexisted abundantly in Sri Lanka with large populations of other species; for example, *M. floricola* (category 5) occurred with either *Crematogaster* sp. (category 4) or *Technomyrmex* sp (4) and with *Oecophylla longinoda* (3) also nesting in the same palm (Table 3). *Monomorium* spp were unique in remaining abundant (up to category 5) in palms occupied by category 5 numbers of *Oecophylla smaragdina* and *Dolichoderus thoracicus* (Table 3) but not with *Wasmannia auropunctata* and *Pheidole megacephala*. Yet, in Trinidad some *Camponotus* spp and *Odontomachus bauri* nested in the presence of the abundant dominant *W. auropunctata* (5). *Camponotus* spp. in Tanzania similarly nested in the present of category 5 populations of *P. megacephala* in Tanzania (Table 3).

As a relatively unaggressive dominant, *Dolichoderus thoracicus* tolerated smaller species such as *Monomorium floricola* and *Tapinoma* spp both of which sometimes reached category 5 in the presence of similarly abundant *D. thoracicus*, yet *Camponotus* spp were apparently much less tolerated or were deterred, in contrast to their co-existence with the more aggressive *Wasmannia auropunctata* and *Pheidole megacephala* (Table 3). All the larger, relatively fast-moving minor species were negatively associated with similarly large and active dominants, for example, *Camponotus* sp and *Paratrechina* spp which were not found nesting where numbers of the dominant *Oecophylla smaragdina* rose above categories 1—2 (Table 3).

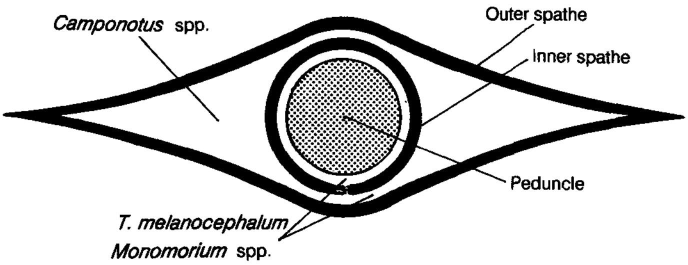

FIG. 3. Diagrammatic cross-section of spadix showing chosen nesting sites of *C. flavomarginatus*, *C. sexguttatus* and *Camponotus* sp that commonly occur with those of *T. melanocephalum* and *Monomorium* spp.

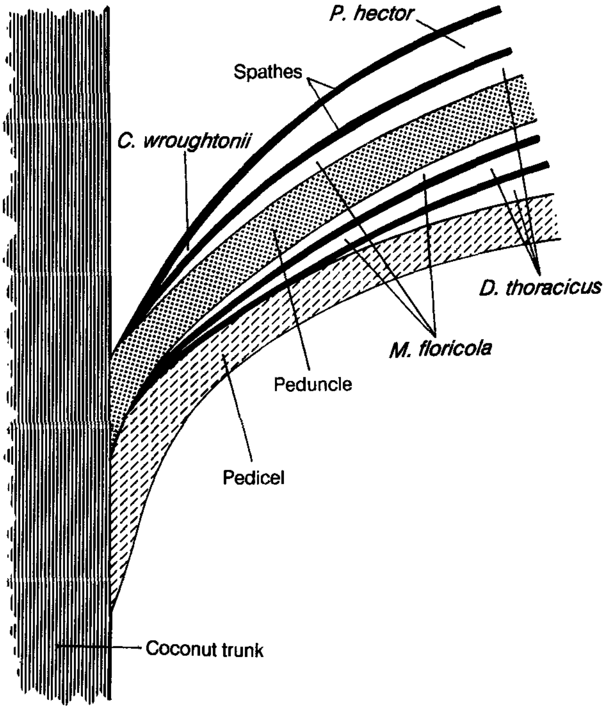

FIG. 4. Diagrammatic longitudinal section of leaf and spadix bases showing nesting sites of four cohabiting species.

Paratrechina longicornis was scarce in the presence of *Pheidole megacephala* and *Wasmannia auropunctata* which, like *P. longicornis*, nest and must compete with it at ground level as well as in the palm trees. *P. longicornis*, however, nested more successfully in trees dominated by the unaggressive, primarily tree nesting *D. thoracicus* (Table 3).

Nesting sites

Leaflets. The nests of the weaver ants *Oecophylla* sp. are confined to the leaflets which are woven together and their inverted V-shaped under-sides woven across to

Table 4. Body heights of worker ant species in relation to approximate heights of initially chosen nesting cavities in the coconut palm spadix.

Species	†Range of body hts (mm)	†Approximate minimum hts (mm) of nesting spaces
Monomorium floricola	0·23–0·26	> 1
Cardiocondyla wroughtonii	0·26–0·32	< 1
Tapinoma melanocephalum	0·30–0·34	> 2
Wasmannia auropunctata	0·34–0·38	> 5
Pheidole megacephala—minor	0·42–0·49	> 5
Pheidole megacephala—major	0·74–0·80	> 5
Hypoponera sp	0·52–0·66	> 3
Dolichoderus thoracicus	0·60–0·82	> 3
Camponotus sexguttatus	0·84–1·22	> 5
Camponotus flavomarginatus	1·10–1·50	
Polyrhachis hector	1·80–2·52	

†See Methods Section for details.

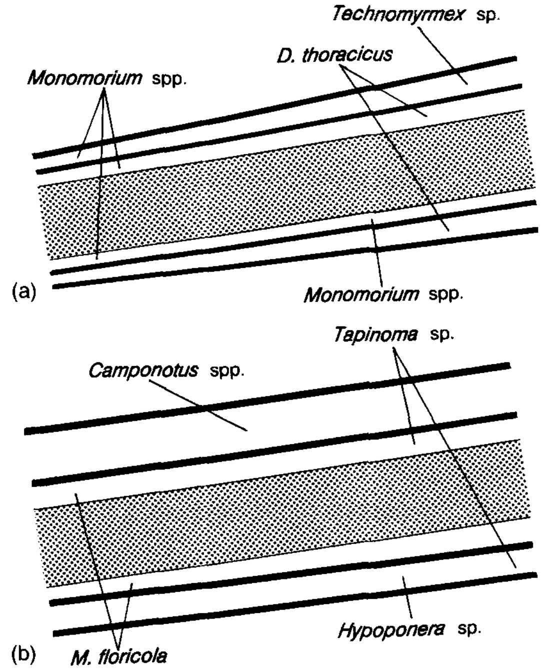

FIG. 5a,b. Diagrammatic longitudinal sections of spadices indicating different sized spaces occupied by cohabiting ant species.

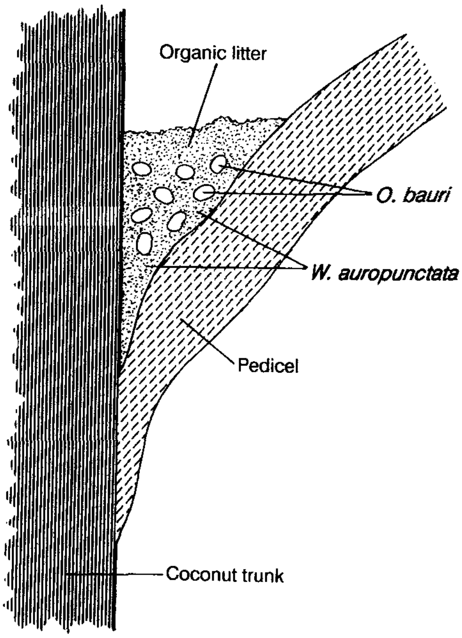

FIG. 6. Diagrammatic longitudinal section of the axil of an old leaf where *O. bauri* and *W. auropunctata* commonly nest together in accumulated organic litter.

form nesting chambers. Sometimes the still-flexible leaflets of freshly emerged leaves are bent and rolled together to form a ball-like nest of the kind characteristic of nests on trees with simpler leaves. *Dolichoderus thoracicus* was also found tending brood in the in-curving lamellae of leaflets of dying and dead leaves. Such nesting sites were most commonly used when very large populations (category 5–6) were fully occupying nesting sites in spadices and leaf axils. Otherwise no other ants were found nesting in the leaf fronds, except *Azteca* sp. observed from the ground on a tall palm.

Leaf axils. About 14–16 leaves develop per year and each lives for about 3–4 years (Ohler, 1984). Leaf stumps from leaves cut when nuts are harvested may remain attached to the palm trunk for more than a year after they have died. Many ant species were found nesting in the basal part of the axils of mature, dying and dead leaves, including leaf stumps (Table 2). Such nests were mostly made amongst rotting organic matter that accumulates as the leaves age (Fig. 6).

Spadices. One spadix (inflorescence) develops in almost every leaf axil, and at harvesting after about one year, each is cut off leaving the stump. The spadix comprises the flower- and nut-carrying peduncle which is ensheathed by two spathes, the inner with a large hood which opens to expose the inflorescence, and the unhooded outer spathe (Fig.1).

Exposed carton nests of *Azteca* spp. were seen in leaf axils at the bases of spathes, and carton nests of *Polyrhachis dives* were built on exposed parts of the spadix, particularly within the incurved underside of the inner spathe hood (Fig.1). All other species, totalling about 68, were nesting in the narrow cavities between the two spathes and/or between the inner spathe and the peduncle (Table 2; Fig.1), though *Tapinoma melanocephalum*, when very abundant (category 6), also tended brood among the fibrous network in the palm crown and even on the exposed underside of the spadix hood.

Relationships between species nesting in spadices and leaf axils Spadices. A diagrammatic cross-section of the spadix (Fig.3) shows relatively narrow spaces between the inner spathe and the peduncle but larger spaces especially within the 'wings' of the outer spathe. The spaces narrow towards the distal end and become particularly small where the spathes join the peduncle (Fig. 4). The sizes of spaces vary, even between spadices of similar age, and they become much larger as the ageing spathes begin to gape apart, particularly after the spadix has died. The significance of available space is evident from nesting places of different species in circumstances where colonies of several species were nesting in the same tree, and particularly when two or more were nesting in the same spadix. Figs 4, 5 exemplify the preferred nesting sites of some common ants although, when a species was virtually the sole occupant of a particular tree (category 6), it used all nesting spaces large enough for its size. Where two or more species occurred in the same spadix, it was evident that chosen nest areas mostly approximated to the heights of the available spaces (Table 4; Figs 4, 5). For example, the small species occupied the narrower cracks, especially between the inner spathe and the peduncle. Amongst the small species, the relatively fast moving *Tapinoma melanocephalum* carries its body higher than the others, especially *Cardiocondyla wroughtonii*, so it seems to need more space (Fig. 5b) than its thoracic measurements suggest (Table 4). The larger ants occupied the much larger spaces in the wings, e.g. some *Camponotus* spp (Fig. 3), or the gaping spaces in old or dead spadices, e.g. *Polyrhachis hector* (Fig. 4) as well as *Camponotus* spp. *Cardiocondyla wroughtonii* was found only in the very narrowest spaces close to where the inner spathe joins the peduncle (Fig. 4). The utilisation of nesting sites was particularly well defined during early growth of the spadix. *Monomorium* spp were usually the first to occupy newly opened spadices, but the situation becomes relatively confused as the parts of the spathe begin to separate as it matures and dies. Dying and dead spadices remained attractive to species such as *Monomorium floricola* but were selectively chosen by larger species, notably some *Camponotus* and *Polyrhachis* spp., and by the primarily ground nesting species *Paratretchina longicornis*, *Anoplolepis longipes* and *Pheidole* spp.

Up to five species were found nesting in the same spathe, and groups of workers and brood of different species were sometimes separated by only about two millimetres, suggesting remarkable co-evolution of tolerance in these circumstances. *Monomorium* spp. were the most common co-habitees with other species (Table 3, Figs 4, 5). The 'dominant' fiercely stinging small ant *Wasmannia auropunctata* was also frequently recorded nesting in the same spadices especially with other larger ants (Table 3).

Leaf axils. Many of the spadix-nesting species also nested in leaf axils which, however, were first selected by species such as *Odontomachus bauri* and by the primarily ground-nesting species. The relative simplicity of this nesting space in the leaf axil perhaps explains the infrequency with which it was shared by different ant species. A notable exception was the frequent coincidence of *O. bauri* and *Wasmannia auropunctata* (Fig. 6). The relatively large ponerine makes galleries in organic matter lodged in the leaf axil, with *W. auropunctata* nesting below in the narrower base of the axil but also sometimes amongst the organic matter that forms the walls of the *O. bauri* galleries (Fig. 6).

Significance of nesting habits

Nest sites of species associated with coconut palms are as follows:

(a) solely ground nesting, e.g. *Anoplolepis custodiens*. In Tanzania this is an aggressive predatory dominant that was not found nesting in palm trees but locally foraged them in numbers reaching categories 5–6. The numbers of *A. custodiens* were strongly negatively related to those of other dominants which did not nest in palms when *A. custodiens* reached number categories > 1–2 (*Pheidole megacephala*) or 3 (*Oecophylla longinoda*). Yet in Tanzania *A. custodiens* was seen to tolerate ten other palm nesting species including category 4 populations of *Tapinoma* sp b and *Technomyrmex* sp a in the presence of category 6 *A. custodiens*, and category 5 *Tapinoma melanocephala*, *Plagiolepis* sp nr *brunnii*, *Technomyrmex* sp b, and category 3–4 *Crematogaster* sp nr *opaciceps* and *Camponotus* sp *maculatus* gp in the presence of categories 4–5 *A. custodiens*. *A. custodiens* workers were never seen entering the nesting sites of these ants, which foraged successfully, despite day and night activity of *A. custodiens*;

(b) primarily ground nesting and secondarily palm nesting dominants which seemingly cannot live independently in the trees, e.g. *Pheidole megacephala* and *Anoplolepis longipes*. *P. megacephala* is a widely abundant ground nesting species in the coastal region of Tanzania but it nested especially in old and dead leaf axils and spadices, notably during the wet season when it moves brood from seemingly waterlogged soil (Z. Seguni, personal communication). In these circumstances foraging *P. megacephala* attacked and destroyed nesting *Oecophylla longinoda* colonies (Way, 1953) and also suppressed or impaired other tree nesting ants such as *Crematogaster* and *Monomorium* spp despite different preferred nesting sites (Tables 2, 3). This suggests intolerance in foraging areas. Yet, other species such as some *Camponotus* spp with similar nesting sites succeeded even in the presence of category 5 populations of *P. megacephala* (Table 3);

(c) species that can nest successfully in both ground and sites, e.g. *Wasmannia auropunctata* and *Tapinoma melanocephalum*. In Trinidad, the dominant *W. auropunctata* was always found in association with tree or bush vegetation, for example in monoculture cocoa where it nested predominantly in the ground. Yet, in coconut palm plantations it was nesting abundantly in the trees sometimes with no evidence of contact with, or dependence on, ground conditions. It seems mutually incompatible with dominant *Azteca* spp, which have carton nests, and also with another dominant, *Pheidole* sp (Table 3), which uses nesting sites similar to those of *W. auropunctata* (Table 2). Yet *Camponotus* spp and *Odontomachus bauri* were commonly present even when populations of *W. auropunctata* reached category 5 (Table 3). The coincidence of *O. bauri* and *W. auropunctata* nesting in the same leaf axils is particularly striking (Fig. 6);

(d) primarily palm nesting and secondarily ground nesting species that depend to varying degrees on nesting sites in trees. Such species probably include some *Monomorium*, *Technomyrmex* and *Tetramorium* spp all of which compete for similar nesting sites in the spadices. *Dolichoderus thoracicus* was always associated with palms and other trees that provide suitable nesting sites, and, although it makes nests or bivouacs in leaf litter on the ground, it is, for example, dependent on palm trees for the nesting sites that enable it to reach populations capable of protecting interplanted cocoa from some heteropteran pests (Way and Khoo, 1991, 1992);

(e) species nesting solely in trees or shrubs. These included the leaf nesting *Oecophylla* spp and the carton nesting *Azteca* spp and *Polyrhachis dives*.

The *Crematogaster* spp were also found nesting solely in trees including coconut palms where they favoured the spaces around and inside the spathes that were also favoured by many other species (Table 2).

Discussion

Most species that nest in coconut palm spadices initially chose nesting spaces which are appropriate for their sizes though the smaller common ones expand into larger spaces when their populations rise above about category 3. However, the important small-sized 'dominants', such as *Pheidole* spp and *Wasmannia auropunctata*, initially colonised much larger spaces in old and dead leaf axils and spadices from which they spread to smaller spaces in the spadices. *Monomorium* spp were the first to colonise newly opened spadices where they chose the smaller spaces that are also preferred by later colonists such as *Tapinoma*, *Tetramorium* and *Technomyrmex* species. In these circumstances it is likely that colonising *Dolichoderus thoracicus* can be precluded by already established populations of the above smaller non-dominant species as well as by other dominant species expanding from their preferred nesting sites in older leaf axils and spadices. This is supported by evidence that *Anoplolepis longipes* (Khoo and Chung, 1989) and *Pheidole fervens* (M. J. Way, personal observations) can prevent artificial establishment of *D. thoracicus* for use as a beneficial natural enemy. The negative relationships between abundance of dominant species (Fig. 2) and the species diversity of other ants that commonly nest in the same palm also signifies competition. In this context, the beneficial, leaf nesting *Oecophylla smaragdina*, which does not use spadices and leaf axils as nesting sites, tolerated small spadix- and leaf axil-nesting species, but not medium to large ones such as some *Camponotus* spp and *Paratrechina longicornis* (Table 3) with which its competition is only for foraging space. Relationships between species that nest in spadices and leaf axils are more complex. For example, the dominant *Pheidole* spp and *Wasmannia auropunctata* were less tolerant of other small ants than of some relatively large *Camponotus* spp (Table 3). The common co-existence of *Wasmannia auropunctata* with *Odontomachus bauri* in leaf axils is remarkable, suggesting that the former benefits, perhaps as a predator on *O. bauri* eggs.

Dolichoderus thoracicus, although seemingly unaggressive, is recognised as a dominant which, as the sole species, can exist locally as extremely abundant populations (category 6) in Malaysian coconut/cocoa plantations. Yet, many other ant species, occupying similar nesting sites, occur commonly in the presence of abundant to very abundant *D. thoracicus* populations (category 4–5) (Table 3). Groups of sexuales, worker ants and brood of several species, including *D. thoracicus*, *Technomyrmex* and *Monomorium* spp, sometimes occurred within about 2 mm of each other inside the spadices. Small populations of the dominant *Pheidole* spp and *Wasmannia auropunctata* were also nesting close to non-dominants without evident hostility. In such circumstances the ants must share common exits to foraging areas where, however, less tolerance was sometimes observed. For example, *Pheidole fervens* was seen aggressively displacing other ants from a food find, and *Monomorium floricola* workers, arriving later at a bait, were frequently observed insinuating themselves at one end, with recruits slowly covering its surface and supplanting *D. thoracicus* and *Camponotus* spp. On the ground, *Monomorium* sp was often seen similarly displacing the aggressive dominant *Solenopsis geminata* (M.J.W. personal observations).

Competition has been studied between co-existing species with different kinds of nesting sites, e.g. Pontin (1961, 1963) and in relation to micro-climatic conditions Brian (1952a,b; 1956a,b). In these circumstances there are distinctly different critical dimensions of the nesting site niche that permit co-existence (Wilson, 1971). In the coconut palm spadix different sized spaces are preferred but sometimes such differences seem insignificant and there are large overlaps. Pre-occupation is probably of key importance and yet it is noteworthy that so many species are adapted to co-exist as groups of sexuales, workers and brood so closely in structurally similar spaces. This was even observed with species that are normally considered as aggressive dominants. Such evidence suggests that mechanisms have evolved within some circumscribed tropical ant communities such that nesting species can co-exist in similar sites including some normally recognised as extirpators (Wilson, 1971). Nest defence is fundamental to survival but has been poorly studied relative to defence of food finds and of territory (Wilson, 1971; Vepsäläinen and Pisarski, 1982; Levings and Traniella, 1988; Savolainen and Vepsäläinen, 1988). It is evident that mechanisms for safe co-existence in nesting sites can be notably more subtle than in foraging areas. The nature of such competition needs to be taken into account in work aimed at enhancing the role of ant species that are important in biological control (Way and Khoo, 1991, 1992).

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References

Brian, M. V., 1952a, Interaction between ant colonies at an artificial nest-site, *Entomologists Monthly Magazine*, **88,** 84–88.

Brian, M. V., 1952b, The structure of a dense natural ant population, *Journal of Animal Ecology*, **21,** 12–24.

Brian, M. V., 1956a, Segregation of species of the ant genus *Myrmica*, *Journal of Animal Ecology*, **25,** 319–337.

Brian, M. V., 1956b, The natural density of *Myrmica rubra* and associated ants in West Scotland, *Insectes Socieux*, **3,** 437–487.

Brown, E. S., 1959, Immature nutfall of coconuts in the Solomon Islands. I. Distribution of nutfall in relation to that of *Amblypelta* and of certain species of ants, *Bulletin of Entomological Research*, **50,** 523–558.

Bruneau De Miré, P., 1969, Une fourmie utilisée au Cameroun dans la lutte contra des mirides du cacaoyer *Wasmannia auropunctata* Roger, *Café, Cacao, Thé*, **13,** 209–212.

Fataye, A. and Taffin, G., De, 1989, Lutte integrée contre *Pseudotheraptus devastans* et espèces voisines, *Oleagineux*, **44,** 525–530.

Khoo, K. C. and Chung, G. F., 1989, Use of the black cocoa ant to control mirid damage in cocoa, *The Planter, Kuala Lumpur*, **65,** 370–383.

Levings, S. C. and Traniella, J. F., 1988, Territoriality, nest dispersion and community structure in ants, *Psyche*, **88,** 266–319.

MacFarlane, R., 1985, *Annual Report 1984 Honiara*: Research Department, Agricultural Division, Solomon Islands Ministry of Agriculture and Lands, 27 pp.

MAJER, J. D., 1972, The ant mosaic in Ghana cocoa farms, *Bulletin of Entomological Research*, **62,** 151–160.

OHLER, J. G., 1984, *Coconut, tree of life* (FAO Plant Production and Protection paper no. 57, Food and Agriculture Organisation, Rome), 446 pp.

PONTIN, A. J., 1961, Population stabilisation and competition between the ants *Lasius flavus* (F.) and *L. niger* (L.), *Journal of Animal Ecology*, **30,** 47–54.

PONTIN, A. J., 1963, Further considerations of competition and the ecology of the ants *Lasius flavus* (F.) and *L. niger* (L.), *Journal of Animal Ecology*, **32,** 567–574.

SAVOLAINEN, R. and VEPSÄLÄINEN, K., 1988, A competition hierarchy among boreal ants: impact on resource partitioning and community structure, *Oikos*, **51,** 135–155.

VESPSÄLÄINEN, K. and PISARSKI, B., 1982, The taxonomy of the *Formica rufa* group: chaos before order, in P. E. House and J. L. Clément (eds) *Biosystematics of social insects*, Systematics Association special volume 19 (New York: Academic Press), pp. 27–35.

WAY, M. J., 1953, The relationship between certain ant species with particular reference to biological control of the coreid, *Theraptus* sp., *Bulletin of Entomological Research*. **44,** 669–691.

WAY, M. J., CAMMELL, M. E., BOLTON, B. and KANAGARATNAM, P., 1989, Ants (Hymenoptera: Formicidae) as egg predators of coconut pests, especially in relation to biological control of the coconut caterpillar, *Opisina arenosella* Walker (Lepidoptera: Xyloryctidae) in Sri Lanka, *Bulletin of Entomological Research*, **79,** 219–233.

WAY, M. J. and KHOO, K. C., 1991, Colony dispersion and nesting habits of the ants *Dolichoderus thoracicus* and *Oecophylla smaragdina* (Hymenoptera: Formicidae) in relation to their success as biological control agents on cocoa, *Bulletin of Entomological Research*, **81,** 341–350.

WAY, M. J. and KHOO, K. C., 1992, Role of ants in pest management, *Annual Review of Entomology*, **37,** 479–503.

WILSON, E. O., 1971, *The Insect Societies* (Cambridge, MA: Belknap Press of Harvard University Press), 548 pp.