

Polydomy in ants: what we know, what we think we know, and what remains to be done

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Received 14 March 2005; accepted for publication 1 March 2006

The correct identification of colony boundaries is an essential prerequisite for empirical studies of ant behaviour and evolution. Ant colonies function at various organizational levels, and these boundaries may be difficult to assess. Moreover, new complexity can be generated through the presence of spatially discrete subgroups within a more or less genetically homogeneous colony, a situation called polydomy. A colony is polydomous only if individuals (workers and brood) of its constituent nests function as a social and cooperative unit and are regularly interchanged among nests. This condition was previously called polycalic, and the term polydomy was used in a broader sense for a group of daughter nests of the same mother colony (implying limited female dispersal), without regard to whether these different nests continued to exchange individuals. We think that this distinction between 'polycaly' and 'polydomy' concerns two disparate concepts. We thus prefer the narrower definition of polydomy, which groups individuals that interact socially. Does this new level of organization affect the way in which natural selection acts on social traits? Here, after examining the history of terms, we review all ant species that have been described as expressing polydomous structures. We show that there is no particular syndrome of traits predictably associated with polydomy. We detail the existing theoretical predictions and empirical results on the ecology of polydomy, and the impact of polydomy on social evolution and investment strategies, while carefully distinguishing monogynous from polygynous species. Finally, we propose a methodology for future studies and offer ideas about what remains to be done. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, 90, 319–348.

ADDITIONAL KEYWORDS: ecological constraints – Formicidae – number of queens – social evolution.

INTRODUCTION

In social bees and wasps, each colony has a single nest. However, in ants, one colony may occupy either one nest (i.e. monodomy) or several socially connected but spatially separated nests (i.e. polydomy) (Hölldobler & Wilson, 1977). A colony could then be defined as a group of related workers and associated reproductive; and one or more nests are the structures that house the colony. The occurrence of polydomy in ants (as in termites; Roisin, Pasteels & Braekman, 1986; Adams & Levings, 1987; Bulmer, Adams & Traniello, 2001) is perhaps related to the fact that their workers

are flightless, facilitating connections of colony units (e.g. transport of brood) in discrete nest sites by use of trails.

Unfortunately, much confusion exists concerning exact meanings of the words 'nest', 'polydomy', and 'polycaly', and problems with the terminology provide an unavoidable source of errors. Earlier work, centred mainly on *Formica*, was followed by studies demonstrating that a large number of ant species should be considered as polydomous according to the initial definition by Forel (1874) (i.e. more than one nest, with brood and/or queen absent in at least one nest). Recent advances in our knowledge of ant biology make it necessary to establish a new, clear and unifying definition of polydomy that is more generally valid and better

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differentiates polydomous and monodomous colonies. After reviewing historical meanings of 'polydomy', 'polycaly', and associated descriptive terms, we present a synthetic review of published information, discussing the different hypotheses that have been proposed to explain the existence and pattern of distribution of this complex social trait. We examine correlations between polydomy and other traits, in an attempt to determine whether one or more characteristic syndromes of polydomy can be recognized.

INTEREST OF STUDYING POLYDOMY

The correct identification of colony boundaries is an essential prerequisite for empirical studies of social insect behaviour and evolution. Testing hypotheses about themes such as kin selection, sex allocation, and levels of selection requires identifying colony boundaries. For sex allocation, the colony is the basic unit upon which theory is based. The presence of spatially discrete subgroups within a more or less genetically homogeneous colony is of prime interest because it might permit separation of effects of queen-worker conflict on sex allocation from those of other, potentially confounding factors. However, polydomy generates new complexity because the social community of a colony is dispatched over several places and in several units, exacerbating allocation conflicts that underlie relations within a colony. Does this new level of organization affect the way in which natural selection acts on social traits? Finally, another reason to examine polydomy is the frequent ecological success of polydomous species or societies.

All these reasons reveal a strong need for clear empirical studies and theoretical predictions to understand the causes and consequences of polydomy in ants. Empirical studies should also focus on how variation in other traits (e.g. the number of queens) might modify theoretical predictions. Species in which polydomy is variable within or among populations may be especially promising model systems for exploring selective pressures acting on this and associated traits.

DEFINITIONS OF POLYDOMY

In this review, we introduce a unifying terminology to describe polydomous structures of colonies of ants, although it should be kept in mind that the definition includes several biological phenomena showing more or less continuous variation. We propose here to define 'polydomy' as an arrangement of an ant colony in at least two spatially separated nests. The spatial separation between two nests should be obviously larger than the usual distance between two nest chambers in the core nest structure (see below). Second, we con-

sider as a nest any structure that houses workers and brood (essentially larvae and young pupae because eggs are not usually carried between nests, probably due to being too vulnerable), regardless of the number of reproductive females in the structure (zero, one, or more). The presence of a queen is not a fundamental criterium for the perenniality of a structure because new workers can be recruited to a queenless nest by the rearing of brood from first-instar larvae and pupae transported to it. The presence of brood is fundamental because it induces the expression of behaviour typical of brood care and provisioning, nest site maintenance and defence, and the renewal of generations. The more or less complex network of communication between the different nests, including transport of brood from queenright to queenless nests, argues for a definition of polydomy that does not exclude monogynous species, as did the definition of polycaly by Forel (1874).

Most ant species are multicolonial (i.e. populations consist of entities that function largely independently; Bourke & Franks, 1995), and these include both monodomous and polydomous species. However, in some cases, notably introduced species, some populations are unicolonial (i.e. the constituent nests of an entire population interact frequently, and non-aggressively, with each other). Unicoloniality is associated with very low genetic differentiation between nests: the entire population functions as a single huge polydomous colony (Passera, 1994; Reuter *et al.*, 2001; Tsutsui & Case, 2001; Giraud, Pedersen & Keller, 2002; Elias, Rosengren & Sundström, 2005). Unicolonial societies represent a clear and distinct mode of colony structure (Keller, 1995; Tsutsui *et al.*, 2000), but this strategy is unstable in the long term, surely being linked to a stage of 'establishment' following introduction of the species into a new region (Keller, 1995). By contrast, multicolonial societies include a great range of variation along a continuum between monodomy and polydomy.

Polydomy is sometimes a seasonal phenomenon (Table 1). Generally, in such cases, a colony overwinters in one nest (rarely more than one), which then fractionates into two or more units occupying different nest sites during the active season, coalescing once again the following winter (Higashi, 1979; Alloway *et al.*, 1982; MacKay & MacKay, 1984; Rosengren, Cherix & Pamilo, 1985; Herbers & Grieco, 1994). In some species (e.g. *Formica uralensis*) the ants disperse before winter in numerous hibernation clusters outside the moundnest, probably as a risk-reducing strategy adapted to the high ground water level of the swamp habitat of the species (Rosengren & Pamilo, 1983). Moreover, a polydomous colony can contain one or several queens and, when the colony is polygynous, queens can be present in all nest units or only in some.

Table 1. List of the ant species (Hymenoptera: Formicidae) showing (obligate or facultative) polydomous colonial structure

Tribe	Species	Distribution	Climatic region	Habitat	Nest site	Nest type	Ecological status	Type of polydomy	Seasonal Polydomy	Associated gynes	Colony size	
PONERINAE	<i>Amblyopone pallipes</i>	NEA	TR	RF ¹⁶¹	T ¹⁶¹	C ¹⁶¹	.	F ¹⁶¹	n	P ¹³³ or M ¹⁶¹	1 60,133,87	
	<i>Prionopelta amabilis</i> ^a	NEO (Central America) ¹⁰⁹	TR	RF ¹⁰⁹	T ¹⁰⁹	N ¹⁰⁹	N	F ¹⁰⁹	n ¹⁰⁹	M ^{109,133}	3 85,109,133	
	<i>Prionopelta modesta</i>	NEO (Central America) ¹⁰⁹	TR	RF ¹⁰⁹	T ¹⁰⁹	N ¹⁰⁹	N	F ¹⁰⁹	n ¹⁰⁹	M ¹⁰⁹	4 94,133,87	
	<i>Paraponera clavata</i>	NEO ⁴¹	TR	RF	A ⁴¹	A	D	F ⁴¹	n ¹²⁴	M ^{41,133}	4 24	
	<i>Odontomachus mayi</i>	NEO (South America) ¹²⁴	TR	RF ¹²⁴	A ¹²⁴	C	VS	F ¹²⁴	n ¹²⁴	M ¹²⁴	4 124	
	<i>Hypoponera bondroiti</i>	PAL (Japan)	TE	OA ¹⁷⁴	T ¹⁷⁴	N	VS	F ¹⁷⁴	n ¹³⁴	W ^{42,134}	3 94	
	<i>Pachycondyla berthoudi</i>	ETH (South Africa) ⁴²	TE	MZ	T ⁴²	N	VS	F ¹³⁴	n ¹³⁴	W ^{42,134}	1 42	
	<i>Pachycondyla hantoniata</i>	ETH (South Africa) ⁴²	TE	MZ	T ⁴²	N	VS	F ⁴²	n ¹²⁴	W ⁴²	4 124	
	<i>Pachycondyla goeldii</i>	NEO (South America) ¹²⁴	TR	RF ¹²⁴	A ¹²⁴	A	C	F ¹²⁴	n ¹²⁴	W ⁴²	4 124	
	PSEUDOMYRMECINAE	<i>Pseudomyrmex ejetatus</i>	NEA ¹⁰⁰	ST	OA	A ¹⁰⁰	N	.	O ^{7,100}	n ¹⁰⁰	P ¹⁰⁰	2 100
<i>Pseudomyrmex pallidus</i>		NEA ¹⁰⁰	ST	OA	A ¹⁰⁰	N	.	O ^{7,100}	n ¹⁰⁰	P ¹⁰⁰	2 100	
<i>Pseudomyrmex seminole</i>		NEA ¹⁰⁰	ST	OA	A ¹⁰⁰	N	.	O ^{7,100}	n ¹⁰⁰	M ¹⁰⁰	2 100	
<i>Pseudomyrmex venefica</i>		NEO (Central America) ⁹⁰	TR	RF ¹⁷²	A ⁹⁰	N	D	O ^{7,90}	n ⁹⁰	P ^{90,95}	8 90,94	
<i>Tetraponera</i> sp. PSW-80 near <i>attemuata</i>		ORI (south-east Asia)	ST	RF ¹⁴	A ¹⁴	A	N	F ¹⁴	n ¹⁴	M ¹⁴	5 14	
MYRMICINAE		<i>Catantolacus catalacis</i>	ORI	TR	RF	A	N	N	F	.	M	1
		<i>Catantolacus gaimensis</i>	ETH (West & Central Africa)	TR	RF ¹	T ¹	N ¹	N ⁹	F ¹	n ^{9,1}	P ¹	6 1
		<i>Catantolacus meleyi</i>	ETH (Central Africa)	TR	RF ¹¹⁷	A ¹¹⁷	N ¹¹⁷	N ¹¹⁷	F ⁴⁴	n ^{7,44}	NL ⁴⁴	3 44
		<i>Catantolacus muticus</i>	ORI	TR	RF	A	N	N	F	.	NL	4
		<i>Cephalotes atratus</i>	NEO ²⁸	TR	RF	A ²⁸	N	D	F	n ²⁸	M ²⁸	5 28
	<i>Cephalotes minutus</i>	NEO ¹⁰⁹	TR	RF	A ¹⁰⁹	N	.	F ¹⁰⁹	n ¹⁰⁹	M ¹⁰⁹	2 109	
	<i>Cephalotes umbracellatus</i>	NEO ¹⁰⁹	TR	RF	A ¹⁰⁹	E	.	F ¹⁰⁹	n ¹⁰⁹	M	3 109	
	<i>Crematogaster africana</i>	ETH (Central Africa) ¹¹²	TR	RF	A ¹¹²	C	D	F ¹¹²	n ¹¹²	.	3 112	
	<i>Crematogaster brevispinosa</i>	ETH (South America) ⁴¹	TR	RF	A ⁴¹	C	D	F	n ⁴¹	.	3 41	
	<i>Crematogaster clariventris</i>	ETH (Central Africa) ¹¹²	TR	RF	A ¹¹²	C	D	F ^{99,112}	n ¹¹²	.	3 112	
	<i>Crematogaster depressa</i>	ETH (Central Africa) ¹¹²	TR	RF	A ¹¹²	C	D	F ^{99,112}	n ¹¹²	.	8 51	
	<i>Crematogaster gabonensis</i>	ETH (West Africa) ⁵³	TR	RF	A ⁵³	C	D	F ⁵³	n ⁵³	M ⁵³	.	
	<i>Crematogaster heliophila</i>	ETH (West Africa) ⁵³	TR	OA	A ⁵³	N	D	F ⁵³	n ⁵³	M ⁵³	6 53	
	<i>Crematogaster impressa</i>	ETH (West Africa) ⁵³	TR	OA	A ⁵³	N	D	F ⁵³	n ⁵³	M ⁵³	2 67	
	<i>Crematogaster laevis</i>	NEO (South America) ¹⁰⁷	TR	RF	A ¹⁰⁷	N	.	.	n ¹⁰⁷	M ¹⁰⁷	.	
	<i>Crematogaster lineata parabiatica</i>	NEO (South America) ¹²⁴	TR	RF ¹²⁴	A ⁴¹	C	D	F ⁴¹	n ⁴¹	P ⁴¹	.	
	<i>Crematogaster longispina</i>	NEO (Central America)	TR	RF	.	.	.	F ⁷	n ⁷	.	.	
	<i>Crematogaster scutellaris</i>	PAL + ORI ¹⁰⁷	TE	MZ	.	M ¹¹⁷	E	VS ¹¹⁷	n ¹¹⁷	M ^{97,117}	.	
	<i>Crematogaster striatula</i>	ETH (Central Africa) ¹¹²	TR	RF	A ¹¹²	C	D	F ¹¹²	n ¹¹²	P ¹¹²	3 112	
	<i>Cardiocondyla emeryi</i>	ETH + Antilla ¹³⁰	PAN	AH	T ¹²⁹	N ¹²⁹	U	O (unicol) ¹²⁹	n ¹²⁹	P ¹²⁹	.	
	<i>Cardiocondyla nuda</i>	AAS + Madagascar ^{36,130}	PAN	AH	T ¹²⁹	N ¹²⁹	U	O (unicol) ¹²⁹	n ¹²⁹	P ¹²⁹	2 36	
	<i>Cardiocondyla wroughtoni</i>	HOL + India ¹³⁰	PAN	AH	T ¹²⁹	N ¹²⁹	U	O (unicol) ¹²⁹	n ¹²⁹	P ¹²⁹	.	
	<i>Leptothorax wroughtoni</i>	NEA	TE	TF ⁷⁷	A ⁴²	N ⁷⁷	S	S	y ⁷⁷	NL ⁷⁷	1 156,129	
	<i>Leptothorax ambiguus</i>	NEA	TE	TF ^{5,77}	A ¹⁵⁴	N ⁵⁴	S	S	y ^{5,71,72,78}	P ⁹ 154,155	2 86,94,154,155	
	<i>Leptothorax curvispinosus</i>	NEA	TE	TF ^{5,71}	M ⁷⁸	N ⁷⁸	S	S	y ^{5,71,72,78}	NL ^{77,78}	2 73,78,94	
	<i>Leptothorax longispinosus</i>	NEA	TE	TF ⁶⁸	T ⁶⁸	N ⁶⁸	S	S	y ⁶⁸	M ^{97,95}	.	
<i>Leptothorax nylanderi</i>	PAL (Germany)	TE	TF ⁷⁵	T ⁷⁵	N ⁷⁵	S	S	y ⁷⁵	.	.		
<i>Leptothorax pillagens</i>	NEA (North-eastern USA)	TE	TF ⁷³	T ⁷³	N ⁷³	S	S	y ⁷³	.	.		
<i>Leptothorax tuberculirostris</i>	PAL (Europe) ¹⁰⁵	TE	OA	T ¹²⁸	C	.	F (size-dpdt) ⁹⁹	n ¹²⁸	NL ¹²⁸	2 128		
<i>Protomyrmex americanus</i>	NEA (North-eastern USA)	TE	TF ^{54,60}	T ^{54,60}	N	S	F (size-dpdt) ³⁴	n ^{54,60}	M ^{34,60}	2 54		
<i>Myrmecaria eumenoides</i>	ETH (West & Central Africa) ^{99,105}	TR	OA	T ⁹⁹	C ⁹⁹	N	F (size-dpdt) ⁹⁹	n ⁹⁹	M ⁹⁹	6 94,105		
<i>Myrmecaria opaciventris</i>	ETH (Central & South Africa) ⁹⁹	TR	OA	T ⁹⁹	C	N	F (size-dpdt) ⁹⁹	n ⁹⁹	P ⁹⁹	7 99		
<i>Myrmica punctiventris</i>	NEA	TE	TF ⁶	T ⁶	N	S	F (size-dpdt) ⁹⁹	n ⁶	NL ⁴⁵	2 94		
<i>Myrmica ruginodis (intercrogna form)</i>	PAL (Europe) ¹⁰⁵	TE	TF ⁶⁸	T ⁶⁸	N	S	F ⁶⁸	n ⁶⁸	P ⁹⁵	4 94		
<i>Myrmica sulcinodis</i>	PAL (Europe)	TE	OA	T ¹³²	C	.	F	n ¹³²	P ¹³²	2 94		
<i>Wasmannia atropunctata</i>	HOL + Cameroon (introduced range) ¹³⁰	PAN	AH	T ¹²⁹	N	U	O (unicol) ¹²⁹	n ¹²⁹	P ^{97,129}	4 94		

Table 1. Continued

Tribes	Species	Distribution	Climatic region	Habitat	Nest site	Nest type	Ecological status	Type of polydomy	Seasonal Polydomy	Associated prey	Colony size
Pheidolini	<i>Aphaenogaster cockerelli</i>	NEA (Southwestern USA) ¹⁴⁶	ST	MZ	T ¹⁴⁶	E ¹⁴⁶	D ¹⁴⁶	F ¹⁴⁶	n ¹⁴⁶	M ¹⁹	.
Pheidolini	<i>Messor barbarus</i>	PAL (Mediterranean zone) ^{2, 19}	ER	MZ	T ^{2, 19}	C(gallerics) ^{2, 19}	D ²	F ² (size-dpdt) ²	n ⁴³	.	.
Pheidolini	<i>Messor capensis</i>	ETH (South Africa) ⁵	TE	OA	T ⁴³	C ⁶⁵	D ⁴³	F ⁴³	n ⁴³	.	4, 66
Pheidolini	<i>Messor wasmanni</i> ^d	PAL (Mediterranean Europe)	ER	OA	T	C ⁶⁵	D ¹⁰⁹	F ⁶⁶	.	.	.
Pheidolini	<i>Pheidole anastasi</i>	NEO (Central America) ¹⁰⁹	TR	RF	A ¹⁰⁹	N ¹⁰⁹	D ¹⁰⁹	F ¹⁰⁹	n ¹⁰⁹	.	.
Pheidolini	<i>Pheidole arizonae</i>	NEO (Central America) ¹⁰⁹	TR	RF	M ¹⁰⁹	N ¹⁰⁹	D ¹⁰⁹	F ¹⁰⁹	n ¹⁰⁹	.	.
Pheidolini	<i>Pheidole desertorum</i>	NEA (south USA)	ER	MZ	T	E	D	F	n ^{79, 129}	P	P ^{79, 129}
Pheidolini	<i>Pheidole megacephala</i>	ETH, NEO, AUS ^{79, 130}	PAN	AH ¹³⁰	T ^{129, 79}	N ¹²⁹	D ^{79, 129}	O (unicol) ^{79, 129}	n ⁵⁷	M ⁵	3, 83
Pheidolini	<i>Pheidole pallidula</i>	PAL (Mediterranean zone) ⁵⁵	ER	MZ ⁵⁵	T ⁵⁵	N ⁵⁵	D ⁵⁵	F ⁵⁵	n ¹⁶⁴	M ⁵	7, 164
Pheidolini	<i>Prisomyrmex pungens</i>	PAL (Japan) ⁶⁴	TE	RF ⁶⁴	T ¹⁶⁴	N ¹⁶⁴	D ¹⁶⁴	F ¹⁶⁴	n ¹⁰⁹	W ¹⁶⁴	1, 109
Pheidolini (?)	<i>Procyptocerus laeviventris</i>	NEO (Central America) ¹⁰⁹	TR	RF	A ¹⁰⁹	N ¹⁰⁹	D ¹⁰⁹	F ^{7, 109}	n ¹⁰⁹	M ¹⁰⁹	1, 109
Pheidolini (?)	<i>Procyptocerus mayri</i>	NEO (Central & South America) ¹⁰⁹	TR	RF	A ¹⁰⁹	N ¹⁰⁹	D ¹⁰⁹	F ^{7, 109}	n ¹⁰⁹	M ¹⁰⁹	1, 109
Solenopsidini	<i>Monomorium destructor</i>	ORI (India [native range])	PAN	AH	T ¹²⁹	N ¹²⁹	D ¹²⁹	O (unicol) ¹²⁹	n ¹²⁹	P ¹²⁹	.
Solenopsidini	<i>Monomorium floridola</i>	ORI (India [native range])	PAN	AH	T ¹²⁹	N ¹²⁹	D ¹²⁹	O (unicol) ¹²⁹	n ¹²⁹	P ¹²⁹	.
Solenopsidini	<i>Monomorium minimum</i>	NEA (North USA) ¹⁶²	TE	OA	T ¹⁶²	E ¹⁶²	D ¹⁶²	F ¹⁶²	n ¹²⁹	P ¹²⁹	.
Solenopsidini	<i>Monomorium pharaonis</i>	WW ^{129, 130}	PAN	AH	T ¹²⁹	N ¹²⁹	D ¹²⁹	O	n ¹²⁹	P ⁹⁷	8
Solenopsidini	<i>Solenopsis geminata</i>	NEW (Central America [native range]) ¹⁸⁶	ER	OA	T ^{9, 136}	E ¹³⁶	D ¹³⁶	F ¹³⁶	n ¹³⁶	P ⁹	7, 136
Solenopsidini	<i>Solenopsis invicta</i>	ETH (introduced range) ⁸⁶	TE	OA	T ⁹	.	D	F	n ⁵⁰	P ^{9, 86, 95, 97}	7, 86
Tetramorini	<i>Tetramorium acauleatum</i> ^e	ETH	TR	RF	A ^{50, 112}	C ^{50, 112}	D ^{49, 50, 112}	F ⁴⁹	n ⁵⁰	M ¹¹²	.
Tetramorini	<i>Tetramorium africanum</i>	ETH	TR	RF	A	C	D	F	n ¹⁴⁸	M	.
Tetramorini	<i>Tetramorium caespitum</i>	PAL (Europe) ^{148, 86}	TE	TF ¹⁴⁸	T ¹⁴⁸	C	D	F ¹⁴⁸	n ¹⁴⁸	M ⁹⁵	6, 94, 86
ANEURETINAE	<i>Aneuretus simoni</i>	ORI (Sri Lanka exclusively)	ST	RF ⁹¹	T ⁹¹	N ⁹¹	D ⁹¹	F ⁹¹	.	NL ⁹¹	2, 91
DOLICHODERINAE	<i>Dolichoderus quadripunctatus</i>	PAL (France) ¹⁵⁹	TE	TF	A ¹⁵⁹	N ¹⁵⁹	D ¹⁵⁹	O ^{159, 160}	n ¹⁰³	M ¹⁵⁹	3, 159
Dolichoderini	<i>Dolichoderus j. bidens</i>	NEO (Brazil) ^{52, 68}	TR	RF	A ^{52, 103}	C ¹⁰³	D ^{7, 103}	F ¹⁰³	n ¹⁰³	NL ¹⁰³	.
Dolichoderini	<i>Liometopum apiculatum</i>	NEA (West USA)	TR	MZ	T	C	D	F	n ¹⁰⁸	M ⁵²	.
Tapinonini	<i>Azeca affert</i>	NEO (Costa Rica) ¹⁰⁸	TR	RF	A ¹⁰⁸	C ¹⁰⁸	D ¹⁰⁸	F ¹⁰⁸	n ¹⁰⁸	M ⁵²	.
Tapinonini	<i>Azeca charifex spiritali</i>	NEO (Costa Rica) ¹⁰⁸	TR	RF	A ¹⁰⁸	C ¹⁰⁸	D ¹⁰⁸	F ¹⁰⁸	n ¹⁰⁸	M ⁵²	.
Tapinonini	<i>Azeca coarctepennis</i>	NEO (Costa Rica) ¹⁰⁸	TR	RF	A ¹⁰⁸	C ¹⁰⁸	D ¹⁰⁸	F ¹⁰⁸	n ¹⁰⁸	M ⁵²	.
Tapinonini	<i>Azeca paraneis bondari</i>	NEO (Costa Rica) ¹⁰⁸	TR	RF	A ¹⁰⁸	C ¹⁰⁸	D ¹⁰⁸	F ¹⁰⁸	n ¹⁰⁸	M ⁵²	.
Tapinonini	<i>Azeca cf. languinosa</i>	NEO (Brazil) ¹²¹	TR	RF	A ¹²¹	C ¹²¹	D ¹²¹	F ¹²¹	n ¹²¹	.	7, 121
Tapinonini	<i>Azeca ovataeops</i>	NEO (Brazil) ¹⁰⁸	TR	RF	A ¹⁰⁸	C ¹⁰⁸	D ¹⁰⁸	F ¹⁰⁸	n ¹⁰⁸	.	.
Tapinonini	<i>Azeca cf. tritici</i>	NEO (Peru) ⁴⁰	TR	RF	A ⁴⁰	C ^{7, 40}	D ³	F ⁴⁰	n ⁴⁰	M ⁴⁰	3, 40
Tapinonini	<i>Azeca trigona</i>	NEO (Panama) ³	TR	RF ³	A ³	C ³	D ³	F ³	n ³	P ³	5, 3
Tapinonini	<i>Dorymyrmex f. insana</i>	NEA	TE	OA	T	E	D	F	n ³	P ³	3
Tapinonini	<i>Iridomyrmex b. nitidiceps</i>	AUS (Australia) ³²	ER	OA	T ³²	E ³²	D ³²	F ³²	n ³²	P ³²	.
Tapinonini	<i>Iridomyrmex purpureus</i>	AUS (Australia) ¹¹⁵	ER	OA	T ¹¹⁵	C ¹¹⁵	D ⁶⁵	F ¹¹⁵	n ¹¹⁵	P ¹¹⁵	7, 94, 86
Tapinonini	<i>Iridomyrmex sanguineus</i>	AUS (Australia) ¹¹⁵	ER	OA	T ¹¹⁵	C ¹¹⁵	D ⁴¹	F ¹¹⁵	n ¹¹⁵	P ¹¹⁵	.
Tapinonini	<i>Iridomyrmex viridicinctus</i>	AUS (Australia) ¹¹⁵	ER	OA	T ¹¹⁵	C ¹¹⁵	D ⁶⁵	F ¹¹⁵	n ¹¹⁵	P ¹¹⁵	.
Tapinonini	<i>Linepithema humile</i>	WW (introduced range) ^{87, 130}	PAN	AH	T ¹²⁹	N ¹²⁹	D ¹²⁹	O (unicol) ¹²⁹	n ⁸⁷	P ^{87, 97, 129}	8
Tapinonini	<i>Tapinoma melanocephalum</i>	WW ^{136, 86}	PAN	AH ¹³⁰	T ^{15, 129}	N ¹²⁹	D ^{15, 129}	O (unicol) ^{15, 129}	n ^{15, 129}	P ^{15, 129}	3, 15
Tapinonini	<i>Tapinoma minutum</i>	AUS (Australia) ^{101, 165, 166}	ER	TF ⁷⁶	T ⁷⁶	N ⁷⁶	D ⁷⁶	F ⁷⁶	n ¹⁶⁵	NL ⁷⁶	3, 76
Tapinonini	<i>Technomyrmex albigipes</i>	PAL (Japan)	TE	TF	A ¹⁶⁵	N ¹⁶⁵	D ⁷⁶	F ¹⁶⁶	n ¹⁶⁵	P ¹⁶⁵	5, 166
FORMICINAE	<i>Camponotus abdominalis floridanus</i>	NEA (Florida) ¹⁰¹	ST	MZ	T ¹⁰¹	E ¹⁰¹	D ¹⁰¹	F ¹⁰¹	n ¹⁰¹	.	5, 101
Camponotini	<i>Camponotus bratus</i>	ETH (Central Africa) ¹²⁰	TR	RF	T ¹²⁰	N ¹²⁰	D ^{120, 49}	F ¹²⁰	n ¹²⁰	.	5, 120
Camponotini	<i>Camponotus cingulatus</i>	NEO ⁵²	TR	RF	A ⁵²	N ⁵²	D ³¹	F ⁵²	n ⁵²	M ⁸²	.
Camponotini	<i>Camponotus detritus</i>	ETH (South-West Africa) ³¹	TR	MZ	T ³¹	C ³¹	D ³¹	F ³¹	n ^{7, 31}	P ³¹	6, 31
Camponotini	<i>Camponotus egeus</i>	ORI (Barneo)	TR	RF ^{137, 138, 139}	T ^{137, 138, 139}	C ^{137, 138, 139}	D ¹³⁹	F ^{137, 138, 139}	n ¹³⁹	M ^{137, 138, 139}	5, 139
Camponotini	<i>Camponotus fenacatus</i>	NEO (A-40, 124)	TR	RF ¹²⁴	A ⁴¹	C ⁴¹	D ⁴¹	F ¹²⁴ (size-dpdt) ¹³⁹	n ⁴¹	P ^{40, 41}	.
Camponotini	<i>Camponotus herculeanus</i>	HOL ^{168, 86}	ER	TF ¹⁶⁸	T ¹⁶⁸	C ¹²⁴	D ¹⁶⁸	F ¹⁶⁸	n ¹⁶⁸	M ⁹⁷	6, 86, 168
Camponotini	<i>Camponotus impressus</i>	NEA (Florida) ¹⁷¹	TE	TF ¹⁷¹	T ¹⁷¹	N ¹⁷¹	D ¹⁷¹	F ¹⁷¹	n ¹⁷¹	M ¹⁷¹	2, 171
Camponotini	<i>Camponotus kawaiiensis</i>	PAL (southern Japan) ⁸⁹	ST	TF	A ⁸⁹	N ⁸⁹	D ⁸⁹	F ⁸⁹	n ⁸⁹	M ⁸⁹	2, 89
Camponotini	<i>Camponotus ligiperdus</i>	PAL (Europe) ⁶²	TE	TF	T ⁶²	E ⁶²	D ⁶²	F ⁶²	n ⁶²	P ⁶²	4, 86, 94
Camponotini	<i>Camponotus madoc</i>	NEA (California) ³⁹	ST	TF	T ³⁹	E ³⁹	D ³⁹	F ³⁹	n ⁶²	P ⁶²	.
Camponotini	<i>Camponotus pennsylvanicus</i>	NEA	TE	OA	T	E	D	F	n	.	4, 94
Camponotini	<i>Camponotus planatus</i>	NEA (Florida [introduced range]) ¹⁶	ST	RF	A ¹⁶	N ¹⁶	D ¹⁶	F ¹⁶	n ¹⁶	P ¹⁶	3, 16
Camponotini	<i>Camponotus</i> ¹ sp. 1	ORI (South-East Asia [Malay Archipelago])	TR	RF	A	N ⁵⁷	D ⁵⁷	F ⁵⁷	n ⁵⁷	M ⁵⁷	5, 57
Camponotini	<i>Colodopsis nipponicus</i>	PAL (Japan) ⁶⁷	TE	TF	A ⁶⁷	N ⁶⁷	D ⁶⁷	F ⁶⁷	n ⁶⁷	M ⁶⁷	.
Gigantopini	<i>Gigantopis destructor</i>	NEO (French Guiana) ²¹	TR	RF	T ²¹	N ²¹	D ²¹	F	n ²¹	M ²¹	2

Formicini	<i>Cataglyphis albicans</i>	ER	MZ	T ¹⁵⁰	E ¹⁵⁰	D ¹⁵⁰	F (size-dpbd)	y ¹⁵⁰	M ¹⁵⁰	3
Formicini	<i>Cataglyphis bicolor</i>	ER	MZ	T ¹⁵⁰	E ¹⁵⁰	D ¹⁵⁰	F (size-dpbd)	y ¹⁵⁰	M ¹⁵⁰	5
Formicini	<i>Cataglyphis ibérica</i>	ER	MZ	T ³⁷	N ³⁷	D ³⁷	F (size-dpbd)	37	M ³⁷	4
Formicini	<i>Formica aquilonia</i> (<i>Formica</i> s. str.)	TE	TF	T ⁹⁶	C ⁹⁶	D ^{20,96}	F (size-dpbd)	96	P ^{20,96}	4
Formicini	<i>Formica bruni</i>	TE	TF	T ²⁴	C (mound) ²⁴	D ³⁴	F (size-dpbd)	34	P ³⁴	4
Formicini	<i>Formica chinera</i> (<i>Serviformica</i>)	TE	TF	T ³⁴	C (mound) ³⁴	D ³⁴	F (size-dpbd)	34	P ³⁴	4
Formicini	<i>Formica cunicularia</i>	TE	TF	T ⁹⁶	C	D ³⁴	F	n	.	.
Formicini	<i>Formica exsecta</i> (<i>Coptoformica</i>)	TE	TF	T ¹²	C ⁹⁶	D ⁹⁶	F	n	.	.
Formicini	<i>Formica exsectoides</i>	TE	TF	T ¹²	C ¹²	D ¹²	F	n	P ^{96,125}	3
Formicini	<i>Formica haemorrhoidalis</i>	TE	TF	T ¹⁷⁶	C	D	F	n	P ¹²	7
Formicini	<i>Formica imitans</i>	TE	TF	T ¹⁷⁶	C ¹⁷⁶	D ¹⁷⁶	F	n	P ¹⁷⁶	4
Formicini	<i>Formica ligabris</i> (<i>Formica</i> s. str.)	TE	TF	T ⁹⁶	C ⁹⁶	D ⁹⁶	F	n	P ^{22,23,96}	7
Formicini	<i>Formica nigricans</i> (<i>Formica</i> s. str.)	TE	TF	T ²⁵	C ²⁵	D ²⁵	F	n	P ²⁵	7
Formicini	<i>Formica obscuripes</i>	TE	TF	T ¹¹⁶	E ¹¹⁶	D ¹¹⁶	F	n	.	.
Formicini	<i>Formica opaciventris</i>	TE	TF	T ¹²³	C ¹²³	D ¹²³	F	n	.	.
Formicini	<i>Formica pallidula</i> (<i>nidiventris</i>)	TE	TF	T ¹⁵²	C ¹⁵²	D ¹⁵²	F	n	P ⁹⁵	5
Formicini	<i>Formica parvula</i> (<i>Formica</i> s. str.)	TE	TF	T ¹¹¹	C ¹¹¹	D ¹¹¹	F	n	P ¹¹¹	5
Formicini	<i>Formica perpallens</i>	ST	TF	T ^{63,170}	C ⁶³	D ¹⁶⁹	F	n	P ¹¹¹	5
Formicini	<i>Formica polyctena</i>	TE	OA	T ¹⁴⁹	C	D ¹⁴⁹	F	n	M ¹⁴⁹	4
Formicini	<i>Formica pratensis</i> (<i>Formica</i> s. str.)	TE	TF	T ^{8,96,141}	C ^{8,96,141}	D ^{22,96,141}	F	n	P ^{8,55,96,97,141}	8
Formicini	<i>Formica pressilabris</i> (<i>Coptoformica</i>)	TE	TF	T ^{25,96}	C ^{25,96}	D ^{25,96,140}	F	n	P ^{23,95,96}	8
Formicini	<i>Formica rufa</i> (<i>Formica</i> s. str.)	TE	TF	T ⁹⁶	C ⁹⁶	D ⁹⁶	F	n	P ⁹⁶	8
Formicini	<i>Formica sanguinea</i> (<i>Rapiformica</i>)	TE	TF	T ⁹⁶	C ⁹⁶	D ⁹⁶	F	n	P ^{95,96}	8
Formicini	<i>Formica transkaukasica</i> (<i>Serviformica</i>)	TE	TF	T ⁹⁶	C ⁹⁶	D ⁹⁶	F	n	P ^{96,97}	8
Formicini	<i>Formica truncorum</i> (<i>Formica</i> s. str.)	TE	TF	T ⁹⁶	C ⁹⁶	D ⁹⁶	F	n	P ^{96,97}	8
Formicini	<i>Formica ulkei</i> (<i>Formica</i> s. str.)	TE	TF	T ⁹⁶	C ⁹⁶	D ⁹⁶	F	n	P ^{96,97}	8
Formicini	<i>Formica urolensis</i> (<i>Formica</i> s. str.)	TE	TF	T ⁹⁶	C ⁹⁶	D ⁹⁶	F	n	P ^{96,157}	5
Formicini	<i>Formica yessensis</i> (<i>Formica</i> s. str.)	TE	TF	T ¹²³	C	D ¹²³	F	n	P ^{96,157}	5
Formicini?	<i>Proformica longiset</i>	ER	MZ	T ⁹⁶	C ⁹⁶	D ⁹⁶	F	n	P ⁹⁶	8
Formicini/Camponotini	<i>Polyrhachis arachne</i>	TR	RF	T ⁵⁸	C ⁵⁸	D ⁵⁸	F	n	P ⁵⁸	4
Formicini/Camponotini	<i>Polyrhachis bellicos</i>	TR	RF	A ¹⁰⁷	N ¹⁰⁷	D ¹⁰⁷	F	n	M ¹⁰⁷	4
Formicini/Camponotini	<i>Polyrhachis bicolor</i>	TR	RF	A ¹⁰⁷	C ¹⁰⁷	D ¹⁰⁷	F	n	M ¹⁰⁷	6
Formicini/Camponotini	<i>Polyrhachis dives</i>	TR	RF	A ^{37,107}	C ¹⁰⁷	D ¹⁰⁷	F	n	M ¹⁰⁷	3
Formicini/Camponotini	<i>Polyrhachis doddi</i>	TR	RF	A ⁹²	C ⁹²	D ⁹²	F	n	M ⁹²	7
Formicini/Camponotini	<i>Polyrhachis fuscata</i>	TR	RF	A ¹⁰⁷	C ¹⁰⁷	D ¹⁰⁷	F	n	M ¹⁰⁷	5
Formicini/Camponotini	<i>Polyrhachis illudata</i>	TR	RF	T ^{119,120}	N ¹⁰⁷	D ¹⁰⁷	F	n	M ¹⁰⁷	2
Formicini/Camponotini	<i>Polyrhachis labriosa</i>	TR	RF	T ¹⁴⁷	C ¹⁴⁷	D ¹⁴⁷	F	n	M	4
Formicini/Camponotini	<i>Polyrhachis maesta</i>	TR	RF	A ¹⁰⁷	N ¹⁰⁷	D ¹⁰⁷	F	n	NL	2
Formicini/Camponotini	<i>Polyrhachis muelleri</i>	TR	RF	A ¹⁰⁷	C ¹⁰⁷	D ¹⁰⁷	F	n	NL	2
Formicini/Camponotini	<i>Polyrhachis nigropilosa</i>	TR	RF	A ¹⁰⁷	N ¹⁰⁷	D ¹⁰⁷	F	n	M ¹⁰⁷	1
Formicini/Camponotini	<i>Polyrhachis proxima</i>	TR	RF	A ¹⁰⁷	C ¹⁰⁷	D ¹⁰⁷	F	n	M ¹⁰⁷	4
Formicini/Camponotini	<i>Polyrhachis schelleri</i>	TR	RF	A ¹⁰⁷	N ¹⁰⁷	D ¹⁰⁷	F	n	M ¹⁰⁷	5
Lasini	<i>Lasius alienus</i>	TE	TF	T ⁷³	N ⁷³	D ⁷³	F	n	M ^{95,97}	5
Lasini	<i>Lasius flavus</i>	TE	TF	T ¹⁷²	C ¹⁷²	D ¹⁷²	F	n	M ^{95,97}	5
Lasini	<i>Lasius minimus</i>	TE	OA	T	C	D	F	n	P	3
Lasini	<i>Lasius neglectus</i>	PAN	OH	T ^{10,129}	U ^{10,129}	D ^{10,129}	F	n	P ^{10,129}	3
Lasini	<i>Lasius neoniger</i>	TE	OA	T ⁷³	E ⁷³	D ^{62,163}	F	n	M ¹⁶³	3
Lasini	<i>Lasius sakagami</i>	TE	OA	T ¹⁷⁵	E ¹⁷⁵	D	F	n	P ^{95,175}	2
Lasini	<i>Pseudolasius</i> sp. 1	TR	RF	M	C	N	O	n	P	2
Lasini	<i>Pseudolasius</i> sp. 2	TR	RF	M	C	N	O	n	P	2
Lasini	<i>Pseudolasius</i> sp. 3	TR	RF	M	C	N	O	n	P	2

Table 1. Continued

Tribe	Species	Distribution	Chimatic region	Habitat	Nest site	Nest type	Ecological status	Type of polytomy	Seasonal Polytomy	Associated emy	Colony size
Oecophyllini	<i>Oecophylla longinoda</i>	ETH	TR	RF ^{82,173}	A ^{41,82,173}	C ⁴¹	D ^{41,49}	O ⁴⁹ /F ^{41,154}	n ⁴¹	M ⁴¹	7 ^{86,94}
	<i>Oecophylla smaragdina</i>	AUS (Australia) ^{80,135}	ER	RF	A ^{41,80,135}	C ^{41,80}	D ⁸⁰	O ^{41,135}	n ^{41,80}	M ^{41,80}	6 ¹³⁰
	<i>Anoplolepis longipes</i>	WW ¹³⁰	PAN	AH	T ¹²⁹	N ¹²⁹	U ¹²⁹	O (omical) ¹²⁹	n ¹²⁹	P ¹²⁹	2 ¹³¹
	<i>Phigolepidini</i>	PAL (France) ⁶¹	TE	OA	T ¹³¹	N ¹³¹	VS ¹³¹	F	y ¹³¹	P ¹³¹	2
	<i>Paratrechina bourbonica</i>	WW	PAN	AH	T ¹²⁹	N ¹²⁹	U ¹²⁹	O (omical) ¹²⁹	n ¹²⁹	P ¹²⁹	2
	<i>Paratrechina flavipes</i>	HOL (East Asia [native], USA (introduced)) ⁸⁸	PAN	AH	T ⁸⁸	N ¹²⁹	U ¹²⁹	O (omical) ¹²⁹	n ¹²⁹	M ⁸⁸	4 ¹³⁰
<i>Paratrechina longicornis</i>	WW ¹³⁰	PAN	AH	T ¹²⁹	N ¹²⁹	U ¹²⁹	O (omical) ¹²⁹	n ¹²⁹	P ¹²⁹	4	
TERMITIDAE (Isoptera)											
Nasutitermitinae	<i>Nasutitermes corniger</i>	NEO (Panama) ⁴	TR	RF	A ⁴	C ⁴	D ⁴	F ⁴	n ⁴		
Nasutitermitinae	<i>Nasutitermes nigriceps</i>	NEO (Panama) ⁴	TR	RF	A ⁴	C ⁴	D ⁴	F ⁴	n ⁴		
Nasutitermitinae	<i>Nasutitermes princeps</i>	AUS (New Guinea) ¹⁴²	TR	RF	A ¹⁴²	C ¹⁴²	D ¹⁴²	F ¹⁴²	n ¹⁴²	P ¹⁴²	
Retetitermitinae	<i>Retetitermes flavipes</i>	NEA (USA) ¹³	TR	RF	A ¹³	C ¹⁴²	D ¹³	F ¹³	n ¹³		

^aSynonym of *P. antillana*; ^bsynonym of *Ophthalmopone*; ^csynonym of *Harpagoxenus*; ^dsynonym of *M. semirufus*; ^esynonym of *Macromischoides aculeatus*; ^fsynonym of *Hypoclinea*; ^gsynonym of *Conomyrma*; ^hnow combined as *Anonychomyrma nitidiceps*; ⁱsynonym of *Colobopsis*.

All references listed are incorporated in the bibliography of the article: (1) Acknor (1981, 983); (2) Acosta, Lopez & Serrano (1995); (3) Adams (1990, 994); (4) Adams & Levings (1987); (5) Alloway *et al.* (1982); (6) Banschbach *et al.* (1997); (7) Benzing (1991); (8) Beye *et al.* (1997); (9) Bhatkar & Vinson (1987); (10) Boomsma *et al.* (1990); (11) Braun, Peeters & Hölldobler (1994); (12) Bristow *et al.* (1992); (13) Bulmer *et al.* (2001); (14) Buschinger *et al.* (1994); (15) Bustos & Cherix (1998); (16) Carlin, Reeve & Cover (1993); (17) Cerda & Retana (1987); (18) Cerda *et al.* (1994); (19) Cerdan & Provost (1990); (20) Ceusters (1979); (21) Chagne, Beugnon & Dejean (2000); (22) Cherix (1986); (23) Cherix (1987); (24) Cherix & Maddalena-Feller (1987); (25) Collingwood (1987); (26) Conway (1996); (27) Conway (1997); (28) Corn (1980); (29) Cosens & Toussaint (1985); (30) Crozier, Pamilo & Crozier (1984); (31) Curtis (1985); (32) Cushman, Rashbrook & Beattie (1994); (33) Czechowski (1990); (34) Czechowski (1999); (35) Czechowski & Rotkiewicz (1994); (36) Czechowski & Yamauchi (1997); (37) Dahbi (1997); (38) Dahbi & Lenoir (1998a); (39) David & Wood (1980); (40) Davidson (1988); (41) Davidson (1997); (42) Dean (1989); (43) Dean & Yeaton (1993); (44) Debout *et al.* (2003); (45) DeHeer, Backus & Herbers (2001); (46) Dejean & Féneron (1993); (47) Dejean & Lachaud (1994); (48) Dejean *et al.* (1993); (49) Dejean *et al.* (1994); (50) Dejean, Djeto-Lordon & Durand (1997); (51) Dejean *et al.* (2000); (52) Delabie, Benton & de Medeiros (1991); (53) Delage-Darchen (1974); (54) Del Rio Pesado & Alloway (1983); (55) Detrain (1990); (56) Elmes (1987); (57) Federle, Maschwitz & Fiala (1998); (58) Fernandez-Escudero *et al.* (2001); (59) Fletcher *et al.* (1980); (60) Foitzik & Herbers (2001); (61) Francoeur & Pépin (1978); (62) Gadau *et al.* (1998); (63) Gerst (2001); (64) Gibernau & Dejean (2001); (65) Greenslade & Halliday (1983); (66) Harkness & Isham (1988); (67) Hasegawa (1992); (68) Heinze *et al.* (1996); (69) Helms (1999); (70) Helms *et al.* (2000); (71) Herbers (1986); (72) Herbers (1987); (73) Herbers (1989); (74) pers. observ. cited in Herbers (1989); (75) unpubl. data cited in Herbers (1989); (76) Herbers (1991); (77) Herbers & Grieco (1994); (78) Herbers & Tucker (1986); (79) Hoffmann (1998); (80) Hölldobler (1983); (81) Hölldobler (1984); (82) Hölldobler & Lumsden (1980); (83) Hölldobler & Möglich (1980); (84) Hölldobler & Wilson (1977); (85) Hölldobler & Wilson (1986); (86) Hölldobler & Wilson (1990); (87) Holway & Case (2000); (88) Ichinose (1987); (89) Ito, Higashi & Maeta (1988); (90) Janzen (1973); (91) Jayasuriya & Traniello (1985); (92) Johnson & Crozier (1998); (93) Kannowski (1959); (94) Kaspari & Vargo (1995); (95) Keller (1991); (96) Keller (1993); (97) various references in Keller (1998); (98) Keller & Passera (1990); (99) Kenne (1999); (100) Klein (1987); (101) Klotz *et al.* (1996); (102) Le Masne (1994); (103) Leston (1978); (104) Lévioux & Diomande (1978); (105) Lévioux (1983); (106) Levings & Traniello (1981); (107) Liefke *et al.* (1998); (108) Longino (1991); (109) Longino (2000); (110) Mabelis (1994); (111) Maeder & Cherix (2001); (112) Majer (1976); (113) Maschwitz & Moog (2000); (114) McGlynn (1999); (115) McIver (1991); (116) McIver & Steen (1994); (117) McKey D (1984); (118) Mercier & Dejean (1996); (119) Mercier, Lenoir & Dejean (1994); (120) Mercier *et al.* (1996); (121) Morais (1994); (122) Nickerson *et al.* (1975); (123) O'Neil (1988); (124) Orivel (2000); (125) Pamilo (1991); (126) Pamilo & Rosengren (1983); (127) Pamilo, Crozier & Fraser (1985); (128) Partridge, Partridge & Franks (1997); (129) Passera (1993); (130) Passera (1994); (131) Passera, Gilbert & Aron (2001); (132) Pedersen & Boomsma (1999); (133) Peeters (1993); (134) Peeters & Crewe (1986); (135) Peng, Christian & Gibb (1998); (136) Perfecto (1994); (137) Pfeiffer & Linsenmair (1998); (138) Pfeiffer & Linsenmair (2000); (139) Pfeiffer & Linsenmair (2001); (140) Pirk *et al.* (2001); (141) Pisarski & Czechowski (1990); (142) Roisin *et al.* (1986); (143) Rosengren *et al.* (1985); (144) Rowe & Bristow (1999); (145) Rützel & Heinze (1999); (146) Sanders & Gordon (2000); (147) Sasaki, Satoh & Obara (1996); (148) Savolainen & Vepsäläinen (1988); (149) Savolainen, Vepsäläinen & Deslippe (1996); (150) Schmid-Hempel (1987); (151) Seifert (2000); (152) Smith-Glaser (1994); (153) Snyder & Herbers (1991); (154) Stuart (1985); (155) Stuart (1987); (156) Stuart (1991); (157) Sundström (1989); (158) Sundström (1993a); (159) Torrossian (1960); (160) Torrossian (1974); (161) Traniello (1982); (162) Traniello (1989); (163) Traniello & Levings (1986); (164) Tsuji (1988); (165) Tsuji & Yamauchi (1994); (166) Tsuji *et al.* (1991); (167) Vasconcelos & Davidson (2000); (168) Vepsäläinen *et al.* (2000); (169) Wagner (1997); (170) Wagner (2000); (171) Walker & Stamps (1986); (172) Waloff & Blackith (1962); (173) Way (1954); (174) Yamauchi *et al.* (1996); (175) Yamauchi *et al.* (2001); (176) Zakhvarov (1994).

Thus, a polydomous colony can contain queenless and queenright nests. When colonies are monogynous, only one nest is queenright. Although monogynous and polygynous colonies may at times share common features, it is necessary to clearly distinguish them in discussing polydomy because polygyny and polydomy may both greatly influence social evolution in ants. In the past, because emphasis was especially placed on polygyny, the effects of polydomy have often been underestimated.

Comparison among ant species suggests that the complexification of the nest structure varies continuously, at least among terricolous ants. For a large number of species, generally characterized by small colony size, the nest corresponds to a group of chambers, generally vertically organized and interconnected by galleries (Hölldobler & Wilson, 1990). For most species, the number of chambers and the complexity of the gallery network generally increase as the colony grows. In certain monodomous species, such as *Pachycondyla tarsata* (Dejean, Beugnon & Lachaud, 1993) or *Pachycondyla senaarensis* (Dejean & Lachaud, 1994), the group of chambers of the colony's single nest is connected by several more or less vertically organized galleries. However, in the case of both species, this gallery network is prolonged by several lateral and horizontal galleries, situated several centimetres below the soil surface. Occasionally 10 m long or longer, lateral galleries have several exits, around each of which the workers forage over a small area; the captured prey are transported within these lateral galleries, minimizing the risk associated with external foraging (Dejean *et al.*, 1993; Dejean & Lachaud, 1994). Colonies of another species, *Myrmica opaciventris* (Kenne & Dejean, 1999), also possess a group of nest chambers connected by vertical galleries, as well as lateral and horizontal galleries, but these latter kinds of galleries lead to other groups of nests containing brood, workers and several queens, thereby forming a huge polydomous nest. The high traffic of workers allowed them to transform their superficial trails into trenches, which are steadily transformed over a mean of 90 days into tunnels (or lateral galleries) by adding earth little by little in the upper parts of the trenches (Kenne & Dejean, 1999). As shown by these examples, the progressive passage between monodomy and polydomy might, in certain cases, originate via the exploitation of a foraging area, which is steadily transformed into an additional nest site, certainly enabling reduction of the cost of food transport and of the risk of predation.

Finally, several types of satellite structures do not qualify as nests according to our definition. The presence of such structures containing workers and built away from the nest has also led to confusion about the distinction between mono- and polydomy. Anderson &

McShea (2001) reviewed the various 'adaptive structures that ants build away from the nest'. These include various forms of galleries, outstations, and constructions dedicated to the protection of trophobionts, nectaries or concealed food. Some polydomous species also build certain satellite structures. These structures confer several adaptive benefits to the colony, mainly in terms of defence and food foraging. However, if they contain no brood, they should not be considered as nest sites.

To summarize, polydomy refers to a purely spatial and genetic proximity between several nests, whereas polycaly may be kept, where convenient, to refer to observed non-aggressive behavioural interactions between nests of a polydomous colony. All other functional specializations (Anderson & McShea, 2001), including repeated architectural motifs in the utilization of space for building an ant nest, may be termed as 'modular nesting' (see section at the end of this article). There are connections between the phenomena covered by these two concepts, which may in the future require an all-embracing concept, but this is not the subject of the present review.

REMINDER OF CONFUSING TERMS

Anyone confronting the literature on polydomy is quickly struck by the diversity and confusion of terms, which constitutes an unavoidable source of errors. Early work on *Formica* species illustrates this. Two terms, 'polydomy' and 'polycaly', were frequently employed, either interchangeably in the same text, as synonyms in translation from one language to another, or given different meanings by different authors. Forel (1874) first introduced the term polycaly, which he defined as an arrangement of an ant colony in several nests, each containing a more or less independent population necessarily constituted by brood, workers and one or several reproductive female(s). In the same paper, Forel termed other colonies lacking either brood or queen in one of the nests as polydomous. After the work by Forel (1874), subsequent studies on *Formica* introduced other terms: clan family, column family, pleiad family, polysectional family (or anthill), cluster nest, ephemeral colony, supercolony (con)federation, formicarium, Riesenkolonie, community, complex, maternal and daughter family (or anthill or nest), multidomous colony, society with multiple nests, suprafamily, or conglomeration (Wellenstein, 1929; Majer, 1976; Hölldobler & Wilson, 1977; Lévieux, 1983; Czechowski & Yamauchi, 1994; Zakharov, 1994). The term 'column family' originated with the theory by Zakharov (1994) stating that the intranidal population of a wood ant mound nest is divided into separate sections like an orange. This author even refers to two parallel terminologies to

describe ant social structure as the colony grows: the 'English' terminology, in which there is gradation from colony → polycalic colony → supercolony, and the 'Russian' terminology which builds a series from family → polysectional nest → polycalic colony → true colony → primary federation → secondary federation → confederation. These terms have not been widely adopted.

Moreover, the different units composing a polydomous or a polycalic colony are known by a variety of names: adjacent nests, auxiliary nests (or anthills), breeding nests, bud nests, colonies, colony subunits, feeding nests, intercommunicating nests, nesting units, satellite nests, shelters, secondary nests, sister colonies, subnests, and subsidiary nests (Weber, 1935; Waloff & Blackith, 1962; Majer, 1976; David & Wood, 1980; Lévioux, 1983; Jayasuriya & Traniello, 1985; Traniello, 1989; McIver & Steen, 1994; Morais, 1994; Zakharov, 1994; Klotz, Reid & Klotz, 1996; Banschbach, Levit & Herbers, 1997; Billick, 1999; Dejean *et al.*, 2000; Fernandez-Escudero, Seppä & Pamilo, 2001). These terms generally used to describe nests of polydomous colonies have also been used to refer to various kinds of 'outstations'.

CONFUSING SITUATIONS

A second source of confusion about polydomy is the fact that the degree to which it is expressed often depends on factors such as colony size (Majer, 1976; Tsuji, 1988). Many terms were used by early researchers to describe or distinguish categories in a continuum of social structure. The large range of colony size encountered in some *Formica* species is responsible for the profusion of terms used to describe the different population levels and social structures observed (Zakharov, 1994; see also above). Some species have been described as polydomous only for a small proportion of all colonies (e.g. 2.3–13.7% of all colonies in *Pristomyrmex pungens*; Tsuji, 1988) whereas in other species, such as *Oecophylla longinoda*, polydomy appears to be constant. Several species of *Formica* also exhibit two kinds of colony structure. Some colonies are monodomous and monogynous whereas others are polydomous and polygynous (Pamilo, 1991). However, such a clear relationship between queen number and social structure is far from being a generality among ants and numerous monogynous species are also polydomous (see below).

Two other particular situations, linked to specific biological traits, could be confused with true polydomy. First, mixed colonies could introduce some confusion because they may involve two polydomous species (e.g. *Formica sanguinea* and *Formica cinerea cinerea*; Czechowski & Rotkiewicz, 1997), a monodomous and a polydomous species, or two monodomous species (i.e.

Orivel, Errard & Dejean, 1997). Similar considerations apply to socially parasitic species and their hosts (Del Rio Pesado & Alloway, 1983). Second, some species of the ponerine genus *Centromyrmex*, which are specialized termite predators, inhabit the termitaries they exploit, occupying lodges that may be spatially separated (Delabie, 1995; Dejean & Fénéron, 1999). Such nesting habits, called termitolesty, may thus lead to 'a certain kind of polydomy' (Dejean & Fénéron, 1999), but are not very well known.

POLYDOMY AS A BY-PRODUCT OF POLYGyny?

Polygyny may be the predominant social structure in social insects, especially among ants (Keller, 1993), and interspecific comparisons suggest that polydomy in polygynous species is often a secondary evolutionary step that accompanied or followed evolution of polygyny from a monogynous ancestor. However, although polydomy is often associated with polygyny (Hölldobler & Wilson, 1977; Rosengren & Pamilo, 1983; Ross & Fletcher, 1985; Keller, 1991), many monogynous but polydomous species are known (Way, 1954; Traniello & Levings, 1986; Ichinose, 1987; Snyder & Herbers, 1991; Buschinger, Klein & Maschwitz, 1994; Cerda, Dahbi & de Haro, 1994; for additional examples, see Table 1). As noted by Hölldobler & Wilson (1977), 'the correlation (between polygyny and polydomy) is very weak'. It appears that 'many monogynous ant species are also polydomous, while a few polygynous ones are monodomous' (Hölldobler & Wilson, 1977).

The frequent association of polygyny and polydomy may mean that similar factors favour both traits. The predominant environmental influence determining the degree of polygyny is the cost of dispersal (Keller, 1995). A high cost of dispersal could also promote polydomy. In polygynous populations, polydomy is the consequence of 'budding', a mechanism of local dispersal effected by groups of workers accompanied by one or more queens. The probability of success is usually higher (lower cost of dispersal) than when foundresses disperse alone to attempt to establish independent colonies. In such cases, polydomy is associated with polygyny, either facultative (Higashi, 1979) or obligate (e.g. in *Formica polyctena*; Rosengren & Pamilo, 1983). Here, polydomy reduces conflicts among mature queens of the same polygynous nest. In some cases, budding followed by separation has replaced independent establishment by foundresses as the prevalent process of founding new colonies (a phenomenon called 'fission'). In these cases, a polydomous colony structure may simply be a transient stage (e.g. in *F. polyctena*; Rosengren & Pamilo, 1983).

Finally, acquisition of polydomy could be seen as a bet-hedging strategy: if one nest is destroyed, others

remain available to the colony. This advantage applies also to monogynous colonies (if the queen survives destruction of the queenright nest, she could move into one of the other nests), but is likely to be of greatest importance in polygynous colonies. If one queenright nest is destroyed, related queens remain alive in other parts of the colony. However, in *Formica truncorum*, even when they include tens of flourishing nests and hundreds of queens, polydomous and polygynous colonies may succumb within a few years and thus appear unexpectedly vulnerable (R. Rosengren, pers. comm.). In this case, ecological (increased rate of transmission of parasites due to very high density of nests) or genetic factors (selfish behaviours caused by the relatively low relatedness between queens) may be responsible. We are aware of no dataset suggesting that polydomous structure in polygynous species increases the probability of survival of queens and/or colonies.

THE SYNDROME OF POLYDOMY IN ANTS

Features commonly associated with polydomy include the overdensity of same-species neighbours, the exist-

ence of internest distances smaller than those observed in monodomous populations, and the overall pattern of nest aggregation (Stevens, 2000). Are other traits particularly frequent in polydomous ants? We attempted an exhaustive review of the literature to list all ant species which by our criteria can be described as exhibiting facultative or obligatory polydomy. Bibliographic research was facilitated by the ant literature database FORMIS (<http://cmave.usda.ufl.edu/~formis/>), Current Contents, and several personal literature databases kindly made available by individuals (see Acknowledgements). We examined whether various life-history traits were systematically associated with the presence of polydomous structure, and whether they covaried with the type of polydomy, taking into account only the traits for which data were available for more than 50% of all censused species (Table 2). The results of this review are presented in Table 1.

Polydomy has been recorded at least once for a total of 166 ant species belonging to 49 genera. We attempted to determine whether ecological or other biological traits were associated with polydomy, to form some recognizable syndrome. Our objective was

Table 2. List of the traits examined

Trait	Abbreviation	Meaning	Trait	Symbol	Meaning
Distribution	ETH	Ethiopian	Nest type	C	Self-construction
	PAL	Palaearctic		E	Excavation
	HOL	Holarctic		N	Natural cavity
	NEA	Nearctic	Ecological status	D	Dominant
	NEW	New world		U	Unicolonial
	NEO	Neotropical		S	Slave-making species
	AUS	Australian		N	Sub- and nondominant
	ORI	Oriental (= Asian tropics)	VS	Variable status	
	AAS	Australasian	Type of polydomy	F	Facultative (size-dependent)
WW	Cosmopolitan	O		Obligatory (unicolonial)	
Climatic region	TE	Temperate	Seasonal polydomy	N	No
	ER	Temperate + tropical		Y	Yes
	ST	Subtropical	Associated gyny	M	Strict monogyny
	TR	Tropical		P	Strict polygyny
	PAN	Panclimatic		NL	No link between number of queens and nests
Habitat	AH	Associated with humans	Colony size (maximum number of workers)	W	Without queen
	MZ	Mediterranean forest		1	100
	OA	Open areas	2	500	
	RF	Rain forest	3	1000	
	TF	Temperate and boreal forest	4	5000	
Nest-site location	A	Arboricolous	5	10 000	
	T	Terricolous	6	100 000	
	M	Both types	7	1000 000	
			8	> 10 ⁶	

not to draw a comparison between polydomous and monodomous species. Polydomy is an evolutionarily labile trait that has evolved numerous times independently. Polydomy appears not to be linked to any narrow set of ecological or social conditions. Although some traits appeared frequently associated, no syndrome emerged (Fig. 1). Ant species that express polydomous colonial structure do not always present the same set of associated life history traits, whether considering the habitat range, the characteristics of nests, or ecological and social traits. Polydomy is present in all the main subfamilies (Ponerinae, Pseudomyrmecinae, Myrmicinae, Aneuretinae, Dolichoderinae, and Formicidae), and on all continents. The main biomes concerned are forested habitats, both tropical (38.5%) and temperate (28.3%). Open areas are a minority and some habitats (e.g. desert, swamp) were not represented in our sample (they are doubtless also underrepresented among ant studies!). Half of the polydomous species can be characterized as ecologically dominant, but all other positions in competitive hierarchies are also represented (subdominant, subordinate), and it should be kept in mind that competitive hierarchies are relative rather than objective notions (the same species can be dominant or not, depending on ecological conditions). Polydomous species include both terricolous and arbicolous ants, and nest sites can be of various types (natural cavities, self-constructed nests, or excavations). Among species in which polydomy has been recorded, it is a facultative trait in 83.7% of species (among or even within populations). Seasonal polydomy is rare, having been demonstrated only in 10% of polydomous species. Finally, and most importantly, polydomy is not inordinately frequently associated with polygyny, confirming the conclusion of Hölldobler & Wilson (1977). Half of the polydomous species for which gyny status has been described are apparently always monogynous.

To examine whether polydomy is associated with different suites of traits in different lineages, the extent of differentiation among lineages (congeneric species, genera, subfamilies) was assessed by performing principal component analysis (PCA), using the PRINCOMP procedure in SAS, version 8.0 (SAS Institute). The analysis was conducted on a correlation matrix obtained after transformation of the data presented in Table 1, using the optimal scoring method of Fisher (1938) that assigns scores to each class (level) of the variable, character or numeric (SAS Institute Inc., 1999). A pattern of species differentiation level was revealed by PCA. The first three axes explained 82.5% of the total variance and allowed discrimination of three groups on the basis of how polydomy is expressed: species with seasonal polydomy (type I; species with nonseasonal polydomous structure (type II); and unicolonial species (type III) (Fig. 2). None of

the other traits considered, nor the lineages, could explain differentiation. At the generic level, the first three axes explained 77.6% of the total variance (Fig. 3). The first axis allowed the discrimination of genera including unicolonial species (type C) from all other genera. Again, no discrimination between subfamilies was evident. The axis δ (a linear combination of axes 1 and 2) allowed discrimination between groups, mainly in relation to habitat and nest-site location (ground or tree nesting): type A groups together arboreal genera from the New World (these genera are principally composed of monogynous species) and type B groups together terricolous genera, principally from the Palearctic region and tropical Asia. However, it should be noted that estimation of the mean point for each genus may have introduced some bias because this is a narrow way to synthesize all characteristics of species from one genus in only one set of traits.

In summary, similar traits were correlated with polydomy in monogynous and in polygynous species. Whatever the taxonomic level considered, polydomy was always associated with distributional or ecological criteria, but never with subfamily or gyny status. In polygynous species, the potential link between polydomy and foraging strategy or territoriality (when dispersal success of females is low) is always hidden by the overlap of polydomy and polygyny; thus, in these cases polydomy may be parsimoniously considered as a by-product of polygyny. In monogynous species, polydomy may be more clearly linked to foraging strategy, and/or may be a consequence of strong queen-worker conflict. Finally, there are no invariant correlates of polydomy. Transitions between monodomy and polydomy seem to have occurred frequently, apparently in response to various ecological factors. Polydomy is certainly a very labile life history trait, which may vary extremely depending on the ecology of the ant species and on environmental variation. A summary of the different hypotheses explaining the potential evolutionary causes and/or consequences of polydomy is proposed in Table 3, and these hypotheses are discussed thereafter.

ECOLOGY OF POLYDOMY

Polydomy can confer numerous ecological advantages. Yet, without phylogenetic information, it is difficult to determine which of these could be selective advantages that initially favoured polydomy, and which were later consequences of polydomy. The latter can include direct adaptive consequences of polydomy, new adaptive traits whose evolution was favoured by the acquisition of polydomy, or simply by-products of having multiple-nest structure. Polydomous structure allows nests to be dispersed, shortening foraging

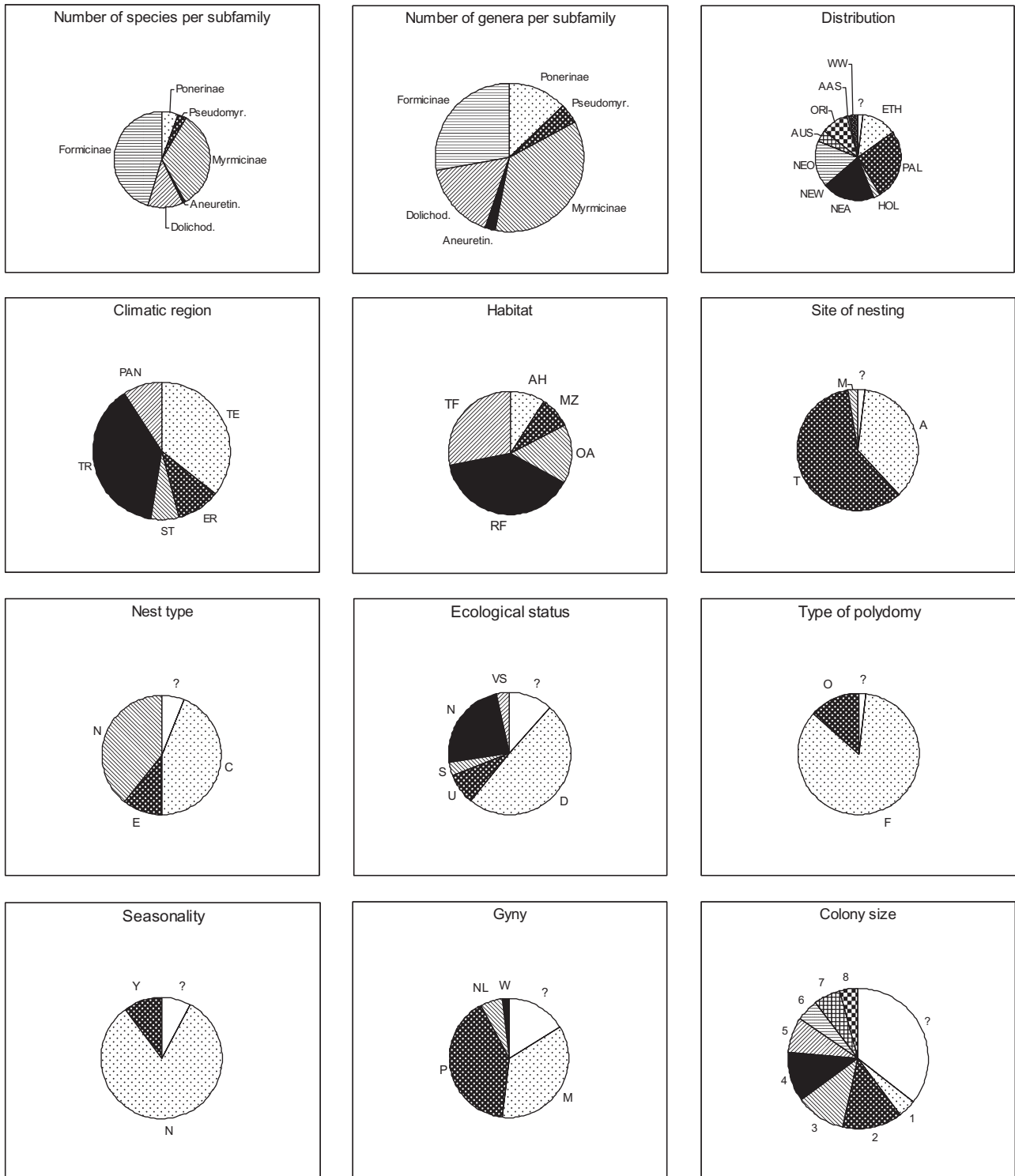


Figure 1. Distribution of each of the traits considered in the 166 ant species for which data were compiled. ? = no information. For definitions of distribution abbreviations, see Table 2.

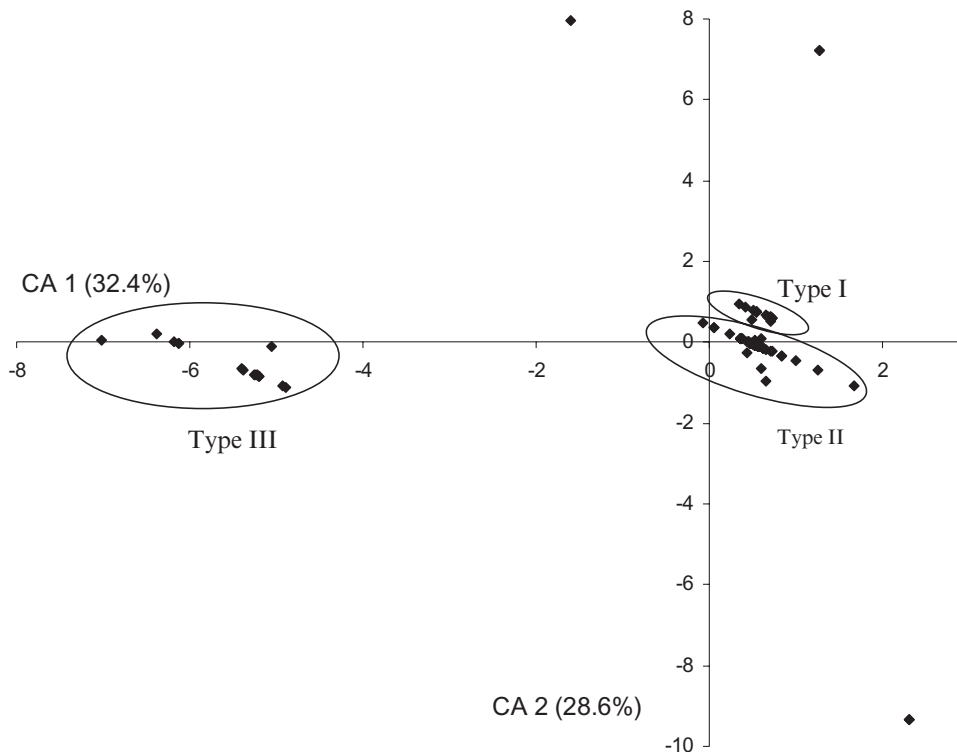


Figure 2. Differentiation among polydomous ant species based on principal component analysis of optimal scores assigned to each considered trait. Species expressing the same type of polydomous structure are encircled: seasonal polydomy (type I), with nonseasonal polydomous structure (type II), and uniconal species (type III).

routes and thereby reducing the costs of central place foraging (McIver, 1991). However, these energetic benefits might be partially countered by strong ecological costs in terms of loss of brood during internest transport, increased risks of predation or desiccation of workers, rapid spread of contagious disease (through trophallaxis), or reduction of population-level genetic variability. All these costs may decrease the efficacy of the worker force, and thereby the productivity of the colony, if they are not counterbalanced by sizeable energetic benefits. In the myrmicine *Cataulacus mckeyi*, such costs of polydomy may explain why polydomous colonies are comprised of relatively older workers than monodomous colonies, and why production of workers appears to be lowered in polydomous colonies (G. Debout & D. McKey, unpubl. data). We present below the ecological implications and potential adaptive significance of polydomy.

POLYDOMY AS A RESPONSE TO ENVIRONMENTAL HETEROGENEITY

Polydomy has often been considered as a response to various environmental constraints, and several hypotheses have been proposed. Thus, Rosengren & Pamilo (1983) postulated that polydomy may reduce

the risk of colony extinction due to predation or stochastic destruction of nest sites (flooding, falling of the host-tree, destruction of the nests' entrances). Similarly, Pfeiffer & Linsenmair (1998) saw in polydomy a response to variation in patch quality within the territory whereas Levings & Traniello (1981) reported that it simply reflected constraints on nest size and placement.

Polydomy has also been posited to act as a thermoregulatory mechanism. Banschbach *et al.* (1997) postulated that, by choosing the warmest summer nest sites, the seasonally polydomous ant *Myrmica punctiventris* (Myrmicinae) could increase its reproductive output. However, measures of nest temperatures and thermal preferences invalidated this hypothesis. The ants rather chose the coolest nest sites. Thus, if seasonal polydomy is a thermoregulatory mechanism, it functions in this ant in the direction opposite to that originally proposed. Also, whether such regulation has an effect on reproductive output of this species remains unclear. In another myrmicine, *Myrmica sulcinodis*, the thermoregulation hypothesis was partially validated: polydomy is a means to multiply the number of 'solaria'. These special nest chambers are found in small tussocks of bent grass and are required for rearing brood successfully.

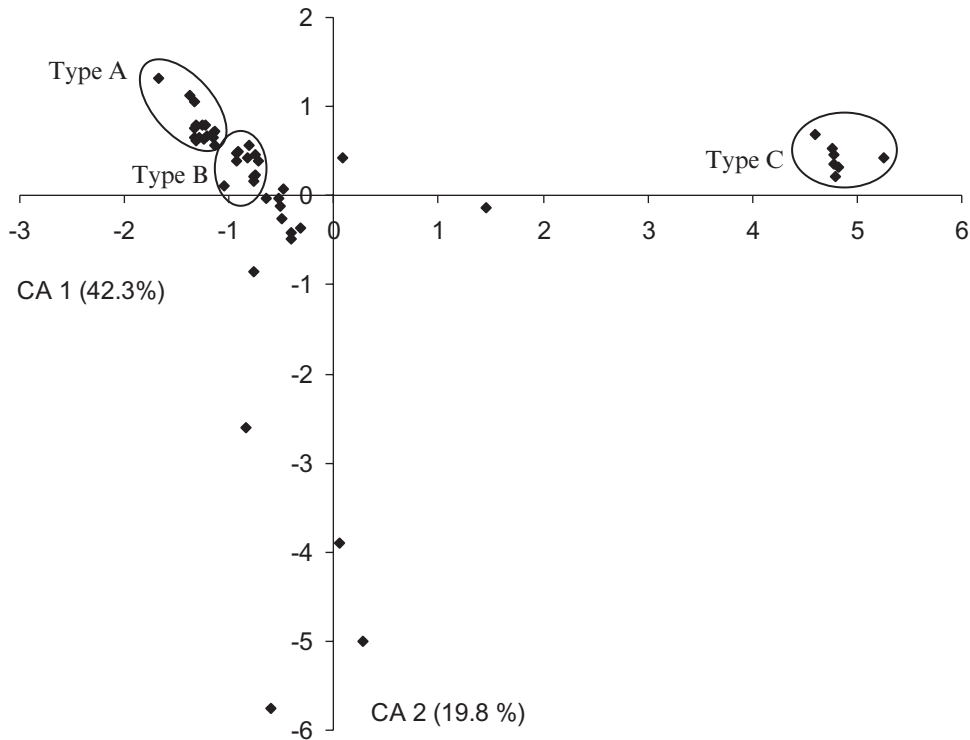


Figure 3. Differentiation among polydomous ant genera based on principal component analysis of optimal scores assigned to each considered trait. Genera expressing the same set of ecological/distributional traits are encircled and the differentiating traits of each group are indicated: arboreal genera from the New World (type A), terricolous genera, principally from the Palearctic zone and Asia (type B), and unicolonial species (type D).

Because these tussocks are scattered within a patch, having multiple nests may increase the rearing capacity and thus the reproductive output of the colony (Pedersen & Boomsma, 1999). This thermoregulatory mechanism was also found in highly polydomous colonies of *F. truncorum* that live on open islands in the Gulf of Finland (R. Rosengren, pers. comm.).

POLYDROMY AND THE EFFICIENCY OF RESOURCE CAPTURE

By acquiring a polydomous structure, a colony may increase its rate of capture of resources (food or nest sites) by the expansion of its foraging area and increased efficiency of foraging. By allowing the colony to forage over a greater area, polydomy also allows the diversification of food resources, and thereby strengthens opportunism in foraging and thereby the stability of the colony's food supply. Social insect colonies have frequently been considered as central-place foragers, similar to some solitary animals (Hölldobler & Lumsden, 1980). However, polydomous ant societies diverge from the classic central-place model because the different nests of a colony are often not aggregated in one central place. They are instead decentralized through-

out much of the colony's territory (i.e. the area that the colony occupies exclusively and defends against intraspecific, and often interspecific, intruders; Hölldobler & Lumsden, 1980). Through this switch from central-place to decentralized or dispersed central-place foraging behaviour, the whole system becomes highly flexible in the distribution of nests and its allocation of workers, brood and resources among nests throughout a colony's foraging area. Such a colony organization should confer advantages when resources are patchily distributed (McIver, 1991; Holway & Case, 2000). In several species from very different subfamilies, such as *Lasius neoniger* (Formicinae) (Traniello & Levings, 1986), *M. punctiventris* (Bansbach & Herbers, 1996a) or *Linepithema humile* (Dolichoderinae) (Holway & Case, 2000), polydomy is proposed to have arisen as an adaptation related primarily to foraging ecology. For *Camponotus gigas* (Formicinae), the link between polydomy and foraging organization has direct morphological and social consequences because a group of specialist transport worker ants carries food from 'source' nests at the periphery to the central queenright 'sink' nest. These transporter ants form a physical subcaste among the minors and behave according to predictions

Table 3. Hypotheses to account for the evolution of polydomy, and their implications for social organization

Hypothesis	Possible implications for social organization
Expansion of the foraging area, increase of the efficiency of foraging (2)	If there is resource heterogeneity in space in time, appearance of 'sink' nests and 'source' nests ? evolution of a special subcaste of transporter ants which carry the food between 'source' and 'sink' nests (6)
Decrease of the risk of colony extinction due to predation or stochastic destruction of nest sites (7)	Poor flow of information between nests (except for ant species with long-distance recruitment behaviour and/or moderate colony size), too small worker groups ? unfavourable defence opportunities
Constraints on nest size and placement (4)	
In polygynous species:	
= by-product of the mode of colony reproduction (budding) and/or of unicoloniality	Allows the formation of new, autonomous colonies by budding or fission of the old polydomous colony (5). As the cost of producing sexuals and the cost of dispersal are decreased, polydomous and polygynous species should show reduced nuptial flight activity, low dispersal, weak territoriality, or colony reproduction by budding (9, 10)
= combination of polygyny with nest site instability (3, 10)	Empirical evidence in <i>Lasius</i> : reduced nuptial flight activity, low dispersal, weak territoriality, polygyny or colony reproduction by budding, cited in (8)
In monogynous species:	
= adaptation related primarily to foraging ecology, especially when prey items are unpredictable in both space and time (8)	In queenless nests, workers may escape queen control over sex allocation, and achieve a sex ratio closer to their own optimum (1)
	Evolution of polygyny?

All references listed are incorporated in the bibliography of the article: (1) Herbers (1984); (2) Hölldöbler & Lumsden 1980; (3) Hölldöbler & Wilson (1977); (4) Levings & Traniello (1981); (5) Pedersen & Boomsma (1999); (6) Pfeiffer & Linsenmair (1998); (7) Rosengren & Pamilo (1983); (8) Traniello & Levings (1986); (9) Wilson (1953); (10) Yamauchi *et al.* (1996).

of central-place foraging theory (Pfeiffer & Linsenmair, 1998).

By this strategy, foraging costs are minimized through a reduction of travel distances and times and thereby also of exposure to natural enemies. The partitioning of the territory may reduce the loss of prey to other competitors (Traniello & Levings, 1986), as well as the costs of prey transport from distant capture points to a single central nest deep within the territory (McIver, 1991). Thus, polydomous ants are thought to achieve energetic savings by decentralization (Hölldöbler & Lumsden, 1980), especially by reducing the overlap in the individual foraging paths (Traniello & Levings, 1986; Davidson, 1997), thereby increasing their foraging efficiency, competitive ability and effectiveness in defending resources (Cherix & Bourne, 1980; Rosengren, 1986).

However, competition for food cannot alone explain some traits frequently associated with polydomy, such as the overdensity of same-species neighbours, the existence of shorter internest distances, and the overall pattern of nest aggregation (Stevens, 2000). Limitation by a resource other than food, such as the availability of nest sites, can better explain these patterns, and polydomy might thus be a response to high or low (depending on the costs of dispersal) density of

suitable nest sites and their size distribution (Herbers, 1989).

Polydomy thus appears to confer advantages in the energetics of foraging and in the exploitation of heterogeneous environments. These advantages can explain the high ecological success of polydomous species or societies. Ecologically dominant ants are often polydomous, and the foraging behaviour of these species suggests that nest relocation and the maintenance of multiple nests both play a role in their competitive prowess. Among well-known polydomous dominant ant species are the tropical *O. longinoda* (Way, 1954) and the temperate *F. truncorum* (Rosengren, 1986; Sundström, 1993a) and other *Formica* species (Cherix, Werner & Catzeffis *et al.*, 1980; Rosengren & Pamilo, 1983; Savolainen & Vepsäläinen, 1989; Punttila, 1996).

POLYDOMY AS A CHARACTERISTIC TRAIT OF TRAMP/INVASIVE ANT SPECIES

Remarkable examples of polydomous, dominant ants are provided by invasive species, such as *Pheidole megacephala* (Myrmicinae) (Hölldöbler & Wilson, 1977), *Wasmannia auropunctata* (Myrmicinae) (Clark *et al.*, 1982), *Lasius neglectus* (Formicinae) (Espadeler

& Rey, 2001), the argentine ant *L. humile* (Dolichoderinae) (Reuter *et al.*, 2001; Tsutsui & Case, 2001; Giraud *et al.*, 2002), and the polygynous form of *Solenopsis invicta* (Myrmicinae) (Passera, 1994); for a review of invasive, unicolonial species, see also Chapman & Bourke (2001). Unicolonial polydomy exhibited by these ant species appears to have facilitated their spread. Holway & Case (2000) propose the following scenario. At introduction, the population size of new invasive species is generally low, leading to a bottleneck and low genetic variation of the introduced populations, as in the Argentine ant *L. humile* introduced in North America (Tsutsui *et al.*, 2000; Tsutsui & Case, 2001). However, Giraud *et al.* (2002) proposed that the spread of the Argentine ant in Europe did not follow a small number of introduction events (bottleneck), and that the lack of aggressiveness could be instead due to a selected decrease of allelic diversity at the recognition loci, a mechanism allowing colonies of the introduced species to rapidly settle in the new area. Because of this low differentiation, lower intraspecific levels of aggression are generally observed, tending to unicoloniality. Here, polydomy is closely tied to the low level of genetic variation (lack of colony closure), and this specific trait generally brings a high ecological advantage in terms of resource capture. Polydomy associated with unicoloniality has probably been the key social trait that led to successful invasion and the replacement of native ants (Holway & Case, 2000).

CONSEQUENCES OF POLYDOMY FOR SOCIAL EVOLUTION

POLYDOMY AND WITHIN-COLONY CONFLICTS

Social insect colonies are not the completely cooperative units depicted by traditional descriptions (Backus, 1993). Instead, there exists a subtle equilibrium between cooperation and competition among all members of an ant colony. Each individual ant might behave to maximize its own inclusive fitness (classical fitness plus kinship components). For example, it has been demonstrated that nepotistic behaviours can arise not only between reproductive females, but also between workers that are able to favour their own close kin when rearing eggs and larvae in colonies headed by several queens (Hannonen & Sundström, 2003). Such selfish or nepotistic behaviour may be favoured up to the point where the resulting decrease in cooperation and social cohesion of the colony leads to reduction of survival and/or reproductive output (Keller, 1995).

In a polydomous colony, due to the greater or lesser independence of each nest, there is a potential to exacerbate conflicts among reproductive

females, among workers themselves or between workers and their mother queen(s), or to generate novel outcomes of conflicts that already exist. Conflicts over traits such as allocation of reproductive effort to males, or who produces males, could be expressed as competition between 'sink' and 'source' nests. These conflicts could arise simply because of the physical barrier between individuals of the different parts of the colony. Distance between nests hinders colony homogenization because it increases predation on workers, sexuals and brood and limits chemical communication between individuals, thereby affecting the control that some colony members may exert on others. Because polydomy provides a novel stage upon which these various conflicts (but essentially queen-worker conflict) are played out, polydomous ant colonies are good models to study the equilibrium between cooperation and competition, by providing opportunities to examine the levels at which selection acts.

However, polydomous ant species have developed particular behaviours, such as exchange of queens or workers, foraging cooperation, or exchange of cuticular compounds between nests, that may function to decrease the conflicts potentially exacerbated by polydomy and thus to create the necessary social environment to harmonize individual and group interests. These behaviours tend to diminish genetic variation among nests, thereby minimizing the potential for genetic conflict. The question remains whether the reduction of conflict is an evolved function of these behaviours, or whether it is a convenient by-product of behaviours whose adaptive significance lies elsewhere.

A NEW LEVEL OF SELECTION: THE NEST-LEVEL

Any study of how insect societies are structured presents a levels-of-selection problem. Natural selection ultimately acts on genes, whatever the level of organization considered, and selection at the level of individuals is usually congruent with selection acting at the level of genes because an individual is a society of cooperating genes. Selection can be said to occur at a supra-individual level if the gain in fitness for the genes at this level is great enough to counterbalance a loss in fitness at the individual level. In consequence, some authors have proposed that an ant colony could be likened to a 'superorganism' with its own colony-level fitness. When we consider a polydomous structure, a new level of organization, the nest-level, may emerge. Whether selection occurs at this new level is a pertinent question when studying polydomous societies. Indeed, in some polydomous ants, it has been suggested that 'nest-level' allocation is subjected to stronger selection than is allocation at the colony level

(Herbers, 1984; Snyder & Herbers, 1991). Banschbach & Herbers (1996b) demonstrated that resource allocation to maintenance (proportion of resources allocated to workers rather than reproduction) and sex allocation (allocation of reproductive effort between the sexes) were both strongly dependent on the number of workers in the nest, and less strongly dependent on queen presence/absence in the nest. They suggest that only nest-level traits are important in determining variation in fitness.

However, not all investigators agree about the pertinence of the 'nest-level' in analysing selection on social traits. Sex allocation, for example, appears to remain subject to selection at the colony level, despite the polydomous structure of the colony. For example, in *Technomyrmex albipes* (Dolichoderinae), whose mature colonies are highly polygynous and polydomous, a colony functions as a whole entity. Between-colony variances of allocation levels are always larger than the within-colony-internest variances. The homogeneity of life-history traits between nests is probably due to the frequent movements of workers between the nests of a colony (Tsuji & Yamauchi, 1994; Dahbi *et al.*, 1996). Nevertheless, polydomous ant colonies represent unique opportunities to explore how selection might operate hierarchically.

MODIFICATIONS IN REPRODUCTIVE AND SEX ALLOCATIONS

Whatever the colony structure, reproductive strategy may vary in time depending on conditions of competition, availability of nest sites (space saturation) and access to resources. However, a multinest structure will intrinsically lead to modifications in resource allocation and of the reproductive strategies adopted by the colony. Whereas precise theoretical models treat the effects on resource allocation of traits such as polygyny, multiple mating or worker reproduction (Crozier & Pamilo, 1996; Frank, 1998), the lack of theory specifically treating polydomy hampers progress in this domain. Looking at polydomous colonies as metapopulations could help, at least for polygynous societies. Indeed, the polydomous colony can be seen as the intermediate level in a metapopulation hierarchy, in which the highest level is constituted by the set of conspecific colonies within an area and the lowest level is represented by the population of reproductive queens within a single nest. However, metapopulation theory has yet to be applied to allocation strategies in polydomous colonies. We list below all the theoretical predictions of which we are aware that have been made about reproductive resource allocation or sex allocation in polydomous ant species.

Theoretical predictions on the allocation of resources to reproduction

Although most work on queen-worker conflict has focused on sex allocation patterns, other allocation decisions may also be subject to conflict. Pamilo (1991) predicted that queen-worker conflict over the division of resources between reproduction and growth (reproductive allocation) may occur in social insects but, until recently, this conflict over allocation to workers vs. sexuals (growth vs. reproduction) had not been well studied nor further developed by theoreticians (Backus, 1995). Contrary to the predictions of Pamilo (1991), Bourke & Chan (1999) demonstrated that a conflict over relative resource allocation to sexuals vs. workers is not expected to occur under the conditions of monogyny, monoandry, and worker sterility because, under these circumstances, queen and workers can only invest in sexuals (new queens and males) derived from the colony queen. At population sex ratio equilibrium, potential conflict over reproductive resource allocation is absent because both parties maximize fitness by maximizing the colony's total output of these sexuals. This does not prevent potential conflicts over sex allocation from occurring. Resolving the apparent contradiction between the results of Pamilo (1991) and Bourke & Chan (1999), Herbers, DeHeer & Foitzik (2001) developed a model that shows the dependence of reproductive-allocation conflict on sex-allocation conflict. The queen-worker conflict over reproductive allocation depends not only on the existence of a conflict over sex allocation, but also on the existence of variation in sex ratios across different colonies in a population.

On the other hand, because the interests of queens and workers differ over when queens should be replaced in the case of polygyny, workers could bias allocation in favour of rapid reproduction and readopting of daughter queens. Indeed, in the case of recurring queen turnover, workers always favour queen replacement sooner than the queen, since they trade siblings ($r = 0.5$) for offspring of a full sister ($r = 0.375$), whereas the queen trades offspring ($r = 0.5$) for grand-offspring ($r = 0.25$) (Crozier & Pamilo, 1996; Bourke & Chan, 1999). In other words, exacerbated differences in the relative allocation of resources to new queens and new workers should be observed between queenless and queenright nests in polygynous colonies, if the queen controls the investment in sexuals in queenright nests. These differences can also occur under worker control because variations of sex ratio are expected between queenless and queenright nests (see below) and a male-biased sex ratio can accelerate queen replacement by workers (Crozier & Pamilo, 1996). Reuter & Keller (2001) proposed a model on potential conflicts over resource allocation in the production of workers, males and gynes that considered

the power that queens and workers have to manipulate resource allocation. Taking into account the selection pressures acting on queens, workers and larvae, they showed that queen–worker conflict occurs over sex allocation but that the investment in workers is below both parties' optima. The strongest conflict is between queens and workers on the one hand, and female larvae on the other, over the developmental fate of the latter.

The effects of polydomy on the conflict over resource allocation between production of workers and of sexuals have never been considered, despite the fact that this allocation is certainly a fundamental decision in the life history of a colony. Indeed, workers are assumed to be associated with colony survivorship and they represent the interface between the colony and the environment. Conflicts may arise when queens and workers have options other than ones for which their fitness optima coincide. For example, when some of the nests of a colony are queenless, workers may have greater opportunity to alter significantly the allocation pattern because, in these nests, one of the two parties is absent. Only one empirical study has detected queen–worker conflict over allocation to growth vs. reproduction, in *Leptothorax longispinosus* (Backus, 1993). Banschbach & Herbers (1996b) showed strong differences between populations in worker allocation for *M. punctiventris*, but they were unable to link these variations to any social (queen number, colonial structure) or ecological parameters. Herbers *et al.* (2001) performed new analyses of the data sets for both species, based on the predictions of their new model. Variation in reproductive allocation as a function of sex allocation did not show clear patterns, but the approach underlines the need for further tests of conflict theory that take into account the effects of sex allocation and of colony size on reproductive allocation.

Theoretical predictions on sex allocation

Although inclusive fitness theory predicts that partial or complete worker control of sex allocation leads to overall female-biased sex ratios, authors generally agree that male-biased investment at the colony-level is expected under polydomy. Three hypotheses have been advanced.

1. In polygynous societies, polydomy is often associated with nest-founding by budding (a queen leaves the nest accompanied by a few workers) or colony fission (a mature nest 'explodes' to form several groups of workers, each with one or more queens). The latter phenomenon is so far known exclusively from driver ants (Dorylinae). In both cases, dispersal range of females is much smaller than that of males. Even if these phenomena should mitigate sib-competition in

the natal nest, they could also lead to sib-competition between nest-founding females (a form of local resource competition) if the local habitat patch is saturated with nests, or if the resource level in the habitat patch is low. Under these conditions, colonies are expected to produce a small number of new queens and a large number of males (Clark, 1978; Craig, 1980; Bulmer, 1983).

2. In species that reproduce only through swarming (budding or colony fission), the investment in workers associated with the nest-founding gynes should be counted as an investment in the female function when calculating the sex investment ratios (Macevicz, 1979). Because colonies require only one or a few queens, this has led to the prediction of highly male-biased numerical sex ratios amongst the alates themselves. Because the workers that participate in budding cannot be entirely included in investment in production of females (these workers will have invested some portion of their lives before budding in raising males), estimating a true investment ratio becomes rather problematic. Thus, sex ratio amongst alates remains the easiest, although biased, sex allocation estimator (Nonacs, 1993).

3. In the same way, diploid males, although generally sterile, are still in practice recorded as males when the sex ratio is assessed because they often cannot be distinguished from other males. In the case of queen control of the sex ratio, these diploid males could even be counted as females, because they are 'intended' females, in the sense that they originated from eggs fertilized by the queen. In ants, heterozygosity at one specific locus determines females, haplozygosity determines males, and homozygosity determines diploid males (Bourke & Franks, 1995). In polygynous, polydomous colonies, inbreeding might be substantial in each of the subnests, leading to higher frequencies of diploid males than in monodomous colonies. For example, in some polydomous island populations of *F. truncorum*, up to 10% of males were diploid (Pamilo *et al.*, 1994).

Two other considerations, although not necessarily leading to predictions of a male-biased sex ratio, lead to the related prediction that sex ratios in polydomous colonies should not be as female-biased as expected from relatedness asymmetry (Trivers & Hare, 1976).

4. Polydomous societies are often polygynous. As the queen–worker conflict is diminished, then even in the case of total worker control, we should expect a sex ratio closer to 1 : 1 than 3 : 1 (Trivers & Hare, 1976; Bourke & Franks, 1995).

5. Polydomy leads to increased nest densities. In polygynous colonies, polydomy reduces local mate

competition (LMC) (i.e. brother-brother competition for mating) by increasing the number of females which will succeed in nest establishment locally (Pamilo & Rosengren, 1984), thus reducing the bias towards females. However, LMC has been only rarely shown to occur in ants.

Despite these predictions, empirical evidence for male-biased sex ratios in polydomous colonies is weak and inconsistent, the few existing studies giving strongly contrasted results. In two species, sex ratios were found to be even at the colony level (*M. punctiventris*, Snyder & Herbers, 1991; *Tetraponera* sp. PSW 80, Buschinger *et al.*, 1994). Male-biased sex ratios were found in polydomous colonies of *Myrmica rubra* (Walsh, Seppä & Sundström, 2001), as well as in several *Formica* species (Rosengren, Cherix & Pamilo, 1986; Sundström, 1995), although female-biased sex ratios were found in populations of *Formica aquilonia* (Pamilo & Rosengren, 1983) and *F. polyctena* (R. Rosengren & M. Elias, unpubl. data). However, all five hypotheses described above consider the colony level, and are based directly or indirectly upon the supposition that polydomous ant species are polygynous. Predictions under monogyny are more vague. If workers win the conflict in queenless nests, female-biased sex ratios may be expected under monogyny. However, if worker reproduction occurs, male-biased sex ratios may arise in queenless nests. Thus the question remains, what are the effects of the number of queens on sex allocation in polydomous colonies? This question will be addressed in the following two sections, which compare patterns expected under polygyny and monogyny.

Among-nest variation in polygynous species

If several nests of a colony contain at least one queen, then within-colony-between-nest variation in sex ratios, and in particular sex ratio specialization at the nest level, must be taken into account in explanations of among-colony variation in sex ratios. We present here these mechanisms, as partially reviewed by Sundström (1994), and discuss how each may be affected by polydomy.

1. Variations in resource levels may shift the nest sex ratio towards a male or female bias.
2. Colony- or nest-level sex allocation may vary because of varying relative effects of competition between males for females (LMC; Hamilton, 1967) and competition between females for resources, nests and/or food (local resource competition; Clark, 1978; Craig, 1980), due to differential dispersal of the sexes (inferred from various sex ratio patterns). However, LMC has remained controversial in ants, mainly because (1) manipulation of sex allocation by workers

in response to relatedness asymmetries (Trivers & Hare, 1976) is an additional powerful mechanism of female bias and (2) the predominant mating system in social insects is thought to make LMC unlikely (sexuals of most species mate randomly in nuptial flights; Hölldobler & Wilson, 1990). Nevertheless, several species have evolved alternative mating tactics (limited male dispersal, intranest copulation), and LMC has been shown to occur in some ants (Cremer & Heinze, 2002).

3. The smaller a nest, the more it allocates to the sex that does not experience resource competition, because productivity is more or less correlated with nest size. Thus, large nests specialize in the other sex. This may cause a highly biased colony/population sex ratio.
4. Nests with a high relatedness asymmetry between workers are predicted to specialize in the production of the sex (generally females) to which they are relatively more related than is the average nest in the colony. Those with a lower relatedness asymmetry are selected to compensate any bias induced by the former ones, and generally may specialize in males (Boomsma & Grafen, 1991).

Thus, peripheral nests of a colony are expected to be selected to produce long-distance dispersive females, whereas central nests should produce just a small number of short-distance dispersive females and numerous males dispersing both inside and outside the colony (Trivers & Hare, 1976; Nonacs, 1986; Bourke & Franks, 1995). A likely consequence is that central nests recruit more females. As proposed in some previous studies, polygyny indirectly selects for lower queen longevity (Keller & Genoud, 1997; Keller, 1998). Queen turnover might thus be higher in central than in peripheral nests. Relatedness asymmetry would be greater in central than in peripheral nests, such that central nests would produce more males than peripheral nests. The runaway selection thus predicted could be reduced if peripheral nests have greater access to resources or if queens are actively exchanged between nests, leading to homogenization of relatedness or of colony odour. The balance between dispersal strategy and relatedness asymmetry would then affect the degree to which sex ratio is biased differentially between nests.

If high population density, leading to a significant increase in the total amount of resources usable in the inhabited patch, leads also to food sharing between nests, then the colony could bias its sex ratio. Indeed, in a polydomous colony, some nests can be dependent on ants of other nests of the same colony for foraging. This has been termed local resource enhancement (LRE; Schwarz, 1988). This increase of the total amount of food available can be achieved by

either active protection of the food sources (e.g. aggregations of aphids) from arthropod competitors, predators, and parasitoids (through protection behaviours and/or active exclusion from the local habitat of most competitors of ants), or by more efficient use of the resources. For example, many aphid species used by ants for honeydew can only survive if they are regularly 'milked' by attending ants, and ants can enhance the productivity of this food resource simply by consuming it. The colony thereby creates an 'artificial resource patch' (Rosengren & Pamilo, 1983). However, resource enhancement by this mechanism is outpaced by nest multiplication within a limited patch. There should hence be a threshold point where saturation of the habitat (with ants and nests) exceeds LRE. This threshold point should depend on the size and productivity of the patch, and it may never be reached in practice if the patch size is 'infinitely large'. This may be the case, for example, with some *Formica* species inhabiting vast forest areas. A female bias can be predicted below this threshold point and a male bias above it for two reasons. First, queens are more expensive to produce than males. The Trivers–Willard hypothesis would thus predict that a surplus of females is produced as long as the patch saturation remains under the threshold point (Trivers & Willard, 1973). Second, males are not only cheaper to produce, but are also, in polygynous-polydomous colonies, a better vehicle for genes to escape from the misery of a degenerating resource patch because females in these cases often stay in the natal nest or disperse through budding. However, other authors have argued that LRE would enhance the production of sexuals overall, rather than bias sex allocation (Herbers, 1990).

In brief, in polydomous and polygynous colonies, sex allocation in different nests appears most likely to be determined by a combination of relatedness patterns and LRC. However, a colony- and a population-level bias towards males is expected because of unavoidable competition for resources between proximate nests and between queens for new nest sites near the natal nest. LRC may be the main factor that determines sex ratio in polydomous colonies of polygynous ant species.

Among-nest variation in monogynous species

The main potential consequence of polydomy for allocation in monogynous ant species is a unique opportunity for workers in queenless nests to evade queen control and thereby to sexualize brood. Thus, significant differences in sex allocation could be predicted between queenless and queenright nests. Furthermore, the fact that nests tend to rear single-sex broods should generally reflect the intensity of the queen–worker conflict, although this could be partially an

arithmetical consequence of very small nest size in many of the cases studied.

Few studies have considered variation of allocation in polydomous but monogynous ant species, and only one has clearly demonstrated that workers are striving to evade queen control. This study considered *M. punctiventris* (Myrmicinae), in which queenless nests allocate more resources to reproductive females than do queenright nests, although all workers descend from only one singly mated queen. Here, 'split sex ratios' reflect chance expectations exacerbated by a biological cause, polydomy, which could be considered to be the outcome of worker behaviours aimed at taking control over sex allocation (i.e. as a consequence of a strong queen–worker conflict over investment in producing males; Snyder & Herbers, 1991; Banschbach & Herbers, 1996b).

The four other studies of which we are aware considered species in which workers seem not to escape queen control. The first treated *Tetraponera* sp. PSW-80 near *attenuata*. The colonies of this bamboo-nesting south-east Asian pseudomyrmecine ant are monogynous and highly polydomous (up to nine bamboo stems inhabited). Gyne development is suppressed in the queen's internode and, to a lesser extent, in the internodes of the same stem. Despite the fact that gynes develop in queenless nests, workers do not appear to escape queen control, because the numerical and the investment sex ratios are 1 : 1 and 3 : 1, respectively (Buschinger *et al.*, 1994), as predicted by Trivers & Hare (1976). The same pattern was found in multinest colonies of the monogynous ant species *Cataglyphis iberica*: relatively more worker brood are present in the queenright nest than in queenless nests, and sexual brood is only found in queenless nests (Cerdeña, Dahbi & Retana, 2002). The third study concerns *Protomognathus americanus* (Myrmicinae), whose polydomous colonies each contain a single queen that is singly inseminated. Worker reproduction has been observed in queenless and queenright nests, and accounts for more than 70% of all males. Despite this fact, there is no evidence for a queen–worker conflict. Male-biased allocation ratios in this species are due instead to the effects of independent polydomous nest units and LRC among queens (Foitzik & Herbers, 2001). Finally, in the facultatively polydomous but monogynous species *C. mckeyi*, split sex ratios were found whatever the colony structure (Debout *et al.*, 2003), and workers do not appear to derive any benefit from polydomous structure in term of escape from queen control.

VARIABILITY IN COLONY CLOSURE

Colony closure preserves the colony's social integrity and prevents intrusion by heterocolonial workers. Col-

ony closure depends on the capacities to recognize and discriminate between familiar individuals and unfamiliar intruders, which are usually attacked (Dahbi *et al.*, 1996). The claims made in several previous studies that in polydomous ant species low intracolony relatedness should result in inefficient nest-mate recognition are based on the assumption of polygyny, not on polydomy *per se* (Keller & Passera, 1989; Provost & Cerdan, 1990; Banschbach & Herbers, 1996a).

The only studies on colony closure in polydomous ants have been conducted on monogynous species, *Cataglyphis iberica* (Formicinae) and *Cataulacus mckeyi* (Myrmicinae). In the terricolous species *Cataglyphis iberica*, polydomy is not seasonal, but all exchange of workers among nests is stopped in winter. However, colony closure remains very high and nest-mate recognition is unchanged after regrouping (Dahbi *et al.*, 1996). For this species, colony integrity may be maintained through transport of young adult workers (Dahbi *et al.*, 1997) and exchange of cuticular compounds (Dahbi & Lenoir, 1998a). All workers share the same cuticular hydrocarbon profile, irrespective of their provenance (queenright or queenless nest). Colony odour in this polydomous and monogynous ant thus derives from worker cues, and not only from the queen (Dahbi & Lenoir, 1998b). Similar conclusions were reached concerning *C. mckeyi*, a tropical plant-ant (Debout *et al.*, 2003). Both studies demonstrate that polydomy does not necessarily lead to a relaxation of colony closure, even if rates of exchange of workers between nests are very low.

SPATIAL DISTRIBUTION OF NESTS WITHIN A POPULATION AND ITS CONSEQUENCES FOR GENETIC STRUCTURE

Spatial aggregation of nests is the expected pattern under polydomy (Herbers, 1985, 1989), and it should lead to specific patterns of spatial genetic structure. One empirical study showed effectively that *Leptothorax ambiguus* (Myrmicinae) nests with similar genotypes tended to cluster in space, generally reflecting polydomous colonies (Herbers & Grieco, 1994). Differentiation among subpopulations of polygynous, polydomous populations of *F. truncorum* has also been detected, contrasting with the lack of differentiation among subpopulations of monogynous, monodomous populations of the same species (Sundström, 1993b). Recent studies on the polygynous, polydomous ant *F. polyctena* (Beye, Neumann & Moritz, 1997) also support the idea of strong local genetic structure, as a result of the budding process associated with polydomy (Elias *et al.*, 2002). In polydomous populations of *Formica pratensis*, spatial and genetic distances were correlated, again

Table 4. Theoretical consequences of a polydomous structure

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- (A) An aggregated spatial distribution of nests
 - (B) Between-nest exchanges of individuals, mainly workers, but also brood, females and queens
 - (C) Uniformity of workers' chemical profiles: all workers of all the nests of a colony share one 'gestalt' odour
 - (D) Strong colony closure vs. low nest closure: direct consequence of points (B) and (C)
 - (E) Colony male-biased sex-ratio: a parsimonious explanation is LRC (over nest sites) plus the constant-female hypothesis
 - (F) A strong genetic relationship between individuals of a same colony (regardless of nest provenance)
 - (G) Special patterns of abandonment/colonization of nests, depending on resource availability (seasonal polydomy)
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indicating budding as the predominant dispersal mechanism (Beye *et al.*, 1998; Pirk *et al.*, 2001). How the genetic structure is related to the pattern of nest distribution in such populations of polydomous colonies, and how it affects competition and selection on sex ratios at the local scale, are interesting and open questions.

A METHODOLOGY TO DESCRIBE POLYDOMY AND TO EXPLORE ITS EFFECTS

The boundaries of separate polydomous colonies in a population are often unknown. There is a need for appropriate methods to permit the mapping of nests in populations of polydomous colonies following a standardized methodology. Colony boundaries can be determined according to spatial, behavioural, and genetic criteria, and preferably all of these in combination. Here, we propose a step-by-step methodology aimed at facilitating the distinction of new cases of polydomy, so that the effects of polydomy on population structure and ecology can be more thoroughly explored. The traits examined, with the hypotheses justifying their examination, are compiled in Table 4.

DESCRIPTION OF PARTICULAR SPATIAL PATTERNS

Nests can be mapped and analysed using the very efficient nearest-neighbour method (Clark & Evans, 1954; Simberloff, 1979), as in some cornerstone studies, such as those on *Leptothorax* spp. (Herbers, 1986) or on *L. neoniger* (Traniello & Levings, 1986). Nest clustering is detected by calculating the distance to the nearest neighbouring nest, and comparing that to theoretical values calculated by simulation over all the mapped nests.

FOLLOWING MOVEMENTS OF INDIVIDUALS

Information on movements of workers, or of dispersal of sexuals, could be provided by direct observations and/or mass or individual marking of workers and/or pupae followed by recapture (Rosengren & Pamilo, 1983). However, care must be taken in interpreting the apparently cooperative nature of many of the nest–nest interactions. Reciprocal movements of young workers and brood between nests, often interpreted as ‘cooperative exchanges between nests’, may also be signs of competition or parasitism between nests, or attempts to alleviate overcrowding in the own nest while simultaneously flooding adjacent nests with progeny genetically related to the carrier ants and their mothers. Similarly, workers visiting neighbouring nests may be stealing or begging food, or could even be ‘spies’ scouting a neighbouring nest before a take-over. Likewise, observations of trophallaxis between workers from different nests must be considered with caution. Studies using isotope-marked food showed actually that food exchange by trophallaxis between *Formica aquilonia* workers from distant nests occurs with the same high frequency as between nestmate workers (Rosengren, 1979), or, more surprisingly, that such food exchange even takes place between ants of different species (Bhatkar & Kloft, 1977). Observation of ‘cooperation’ is thus not alone sufficient to establish the borders of polydomous colonies, probably because trophallaxis is also an appeasement signal correlated with at least mild aggression (R. Rosengren, pers. comm.).

DEGREE OF COLONY CLOSURE

Aggression tests conducted using pairwise reciprocal comparisons of mature nests, and/or investigation of variability in the composition of the major cuticular hydrocarbons, allow determination of the degree of colony/nest closure (i.e. Dahbi *et al.*, 1996; Debout *et al.*, 2003). Results of aggression experiments must also be interpreted with caution, since the level of aggression between workers from different nests (of the same or different colonies) may vary in space and time, and may depend on factors such as diet composition or food availability (e.g. in *L. humile*, see Liang & Silverman, 2000; Silverman & Liang, 2001; Suarez *et al.*, 2002). In *F. polyctena*, R. Rosengren also observed very rare cannibalistic ‘wars’ within nests of the same colony. Occurring in spring when activity resumes, such battles among previously interconnected and genetically related nests do not lead to rupture of their relations later on in the season. Worker exchange and reciprocal carrying of workers and brood continue as before the incident. These spring battles may be due to severe starvation conditions (R. Rosengren, pers. comm.).

GENETIC ANALYSIS

Because of the limits of behavioural methods noted above, they must be complemented by genetic analyses to confirm the relatedness between individuals of a putative polydomous colony. Whether occupants of different nests belong to a single polydomous colony can be assessed by comparing the relatedness of nestmate workers (R_{same}) with (1) their relatedness to workers of the nearest neighbour nest ($R_{\text{nearest neighbour}}$), deduced from aggression experiments to be concolonial or heterocolonial and (2) their relatedness to workers of all other studied nests. The overall frequency of polydromy among nearest-neighbour nests in a population can be estimated by dividing $R_{\text{nearest neighbour}}$ by R_{same} (Pedersen & Boomsma, 1999). Methods of spatial correlation, hierarchical *F*-statistics, matrix correlation or regression of genetic and spatial distance, could also give clues to detect similar worker genotypes among neighbouring nests. It should be noted that, if nests containing only one queen contain more than one matriline of workers, three explanations are possible: (1) these monogynous nests are fractions of larger polygynous and polydomous colonies; (2) these nests have recently lost a second queen, whose worker offspring remain in the nest; and (3) there is considerable mixing of workers among colonies (lack of colony closure).

DETERMINATION OF SOCIAL STRUCTURE

Finally, census of each caste for entire colonies (at the nest and entire colony levels) yields insights about how conflicts over resource and sex allocation are resolved within the colony and among its constituent nests. The effects of polydromy will be most easily examined when there is variation in this trait within a single species, because this situation provides the opportunity to relate this life-history trait to ecological factors.

WHAT REMAINS TO BE DISCOVERED ABOUT POLYDROMY IN ANTS?

Much remains to be done on polydromy in ants! We lack both complete empirical studies and theoretical models. Here, we present some suggestions for research priorities, aimed at understanding in depth the phenomenon of polydromy and all its implications, and at placing this biological trait within the evolutionary history of ants. The main message in this review is to point out the great need for adequate description of the life history traits of the studied species. Generally, the biologies of particular ant species are known by only a few individuals and it is very difficult to gain satisfactory data on even simple traits such as the number of queens or the mean colony size. One priority is comparative study of different populations of

species polymorphic for this trait, or of closely related polydomous and monodomous species. Such studies would enable distinction between those life-history traits related to polydomy that are (proximate or ultimate) causal factors of polydomy, and those that are adaptive traits related to polydomy or by-products of it.

Plant-ants or 'phytoecious' ants (Quek *et al.*, 2004), namely ants that nests only in myrmecophytes (plants with various, usually specialized, hollow stem- or leaf-cavities called domatia; Davidson & McKey, 1993), may be particularly convenient models for studying polydomy for two reasons. First, boundaries of nests (and colonies) are clearly identifiable, making experimentation easier than in many terricolous ants. Second, their polydomy may exist at several spatial scales (e.g. between and within trees). Indeed, for all plant-ant species that we know, in mature colonies, all ants on a single tree originate from a single colony. Can each domatium be considered a nest of a highly subdivided colony? Comparative studies of various ant-plant systems whose domatia differ in their architecture could allow the study of polydomous structures at a smaller spatial scale. Among myrmecophytes, the individual plant's population of domatia can be (1) spatially highly subdivided, with each internode (e.g. *Leonardoxa*; McKey, 1984), stipule-pair (e.g. *Acacia*; Janzen, 1966), or leaf-pouch pair (e.g. *Maieta*; Vasconcelos, 1991) being a separate domatium; (2) a system intermediate in its degree of subdivision (e.g. *Barteria fistulosa*, in which each long plagiotropic branch is a separate domatium; Janzen, 1972); or (3) a single interconnected, branching cavity extending throughout the plant's stem system (e.g. *Vitex* lianas; Djiéto-Lordon *et al.*, 2005).

Some scientists have noted the parallels between the foraging strategies and modular growth of polydomous ant colonies and clonal plants (Harper, 1977; Harper & Bell, 1979). Workers of polydomous colonies 'forage' for new nest sites, and subnests enable expansion of the area over which a colony collects food resources, such as ramets of a clonally growing plant (López, Serrano & Acosta, 1994). The application of modular demography theory (with its morphological and functional analysis of resource capture) to ant ecology must consider that an ant colony, unlike clonal plants, is never a single clone. Conflicts between ants in a colony, due to ever-present (even low) relatedness asymmetry, will prevent total cooperation between subunits of a colony (Stevens, 2000).

The existence of polydomy could aid in our understanding of some within-colony social conflicts. For example, seasonal polydomy in a monogynous society may provide opportunities to understand how queen-worker conflicts are resolved. However, as we have already noted, empirical data are lacking, even for

'well-known' species. For example, here, we only retained traits for which data were available for more than 50% of species. Other interesting traits related to polydomy could not be examined due to the fragmentary nature of data. Even the mean number of nests per colony cannot be compared among polydomous species. No study has yet examined the relationships between worker polymorphism and polydomy. Are different worker morphs differentially distributed among nests? Worker monomorphism is assumed to be linked to polygyny and colonies of taxa with polymorphic workers are assumed to be less prone to be dispatched over several nest sites (Frumhoff & Ward, 1992). However, in *C. gigas*, polydomy is associated with the existence of a specialized 'transporter' subcaste (Pfeiffer & Linsenmair, 1998). Data are also lacking on the difference in queen longevity between mono- and polydomous colonies within a species, the existence of effective reproduction through budding, and the relatedness between nests.

Finally, we need to place polydomy into the context of a global ant molecular phylogeny (for the most recently published ant molecular phylogeny, see Moreau *et al.*, 2006). This is necessary to explore the origin of polydomy, to determine how many times it appeared independently, and to examine associations between the evolution of polydomy and that of polygyny.

ACKNOWLEDGEMENTS

We thank A. Dalecky, M. Dufaÿ, P. Pamilo, and P. S. Ward for interesting discussions and valuable comments on various drafts of the manuscript, and especially the late R. Rosengren, who thoroughly criticised, commented on and annotated an almost final version of this review. We are greatly indebted to the following individuals for having kindly put their own literature databases and personal knowledge at our disposition: C. Djiéto-Lordon, M. Kenne, A. Maeder, J. Orivel, R. Rosengren, and P. Stevens. Our work on ants has been supported by a thesis grant from the French Ministry of Education and Research (G.D.), and by grants from the Institut Français de la Biodiversité and from the National Geographic Society's Committee for Research and Exploration (D.M. and G.D.). M.E. acknowledges the financial support provided through the European Community Improving Human Potential Programme under contract HPRN-CT-2000-00052 (INSECTS network), and under contract HPMF-CT-2002-01781 (Marie Curie individual fellowship). The literature survey pertaining to this study was concluded in January 2004 and was submitted in March 2005. This paper is dedicated to the late R. Rosengren, who shared his irreplaceable knowledge of *Formica* societies and who greatly improved this manuscript.

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