

Social Structure and Reproductive Systems of Tramp Versus Endemic Ants (Hymenoptera: Formicidae) of the Ryukyu Islands¹

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ABSTRACT: Currently, 126 ant species have been recorded from the Ryukyu Islands, Japan. Of these, 54 species, many of which are probably new to science, have not yet been identified. A survey on species-habitat relationships made on the island of Okinawa indicated that open lands were occupied predominantly by tramp species, but primary forests contained many endemic species. Colony structure and the reproductive system of the eurychoric species are briefly reviewed and discussed. A secondary polygynous and polydomous system is predominant in these species. This system is characterized by intranidal mating, which may reduce the risk in nuptial flights and ensure the adoption of new queens. A diversity in morphology and behavior, especially in males, seems to develop, provided the workers care for them. Stenochoric forest species are mostly monogynous.

THE RYUKYU ISLANDS form the southern part of the Nansei Islands, situated between 26° and 24° N latitude, comprising the Okinawa Islands and Sakishima Islands. Because they belong to the subtropical zone, the oriental element is dominant in ant species composition (Terayama 1992). In addition, there are many tramp species that have a pan-subtropical or tropical distribution. Such species, as in many parts of the world (e.g., Way 1953, Wilson and Brown 1958, Greenslade 1971; see also Hölldobler and Wilson 1990), are thought to severely impact the native ant fauna in this area. Thus, the preservation of the native component of the biodiversity of an area may depend on the suppression of introduced ant species.

In this study, we investigated species diversity in various subtropical habitats of the Ryukyu Islands, and we discuss the status of

tramp species in terms of their social structure and reproductive system.

MATERIALS AND METHODS

The survey was carried out in the Okinawa Islands and the Sakishima Islands from 1991 to 1993.

The objective of the first sampling method was to determine species-habitat relationships. In several places, time-unit sampling was carried out. As many ant species as possible were collected during a 30-min visual manual search on the surface of the ground, under stones or wood bark, and around the bases of tree trunks, over a ca. 200-m² area. The intensive survey was made in Kunigami-son, the northern part of Okinawa Island, with the help of members of the Myrmecological Society of Japan in August 1991. The study sites in Kunigami-son are shown in Figure 1.

The surveyed forests of this area consist predominantly of *Castanopsis cuspidata* var. *sieboldii* (Makino) and *Persea thunbergii* Sieb. & Zucc. We here tentatively distinguish a "primary" forest from a "secondary" one based on average diameter of trees at ca. 1 m above the ground. The primary forest con-

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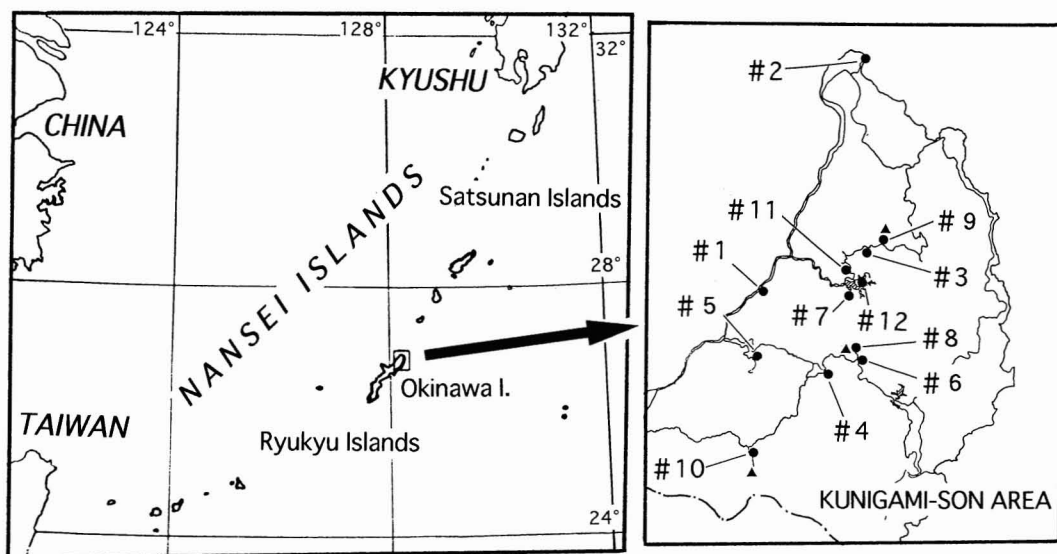


FIGURE 1. Map showing study sites (circles) of time-unit sampling in the Kunigami-son area. 1, Sate (coastal grass land and periphery of village); 2, Cape Hedo (grass land and deforested land); 3, Benoki (a) (deforested land); 4, Ohkuni Forest Road (secondary forest); 5, Yona Experimental Forest (secondary forest); 6, Mt. Terukubi-yama (a) (secondary forest); 7, Benoki (b) (secondary forest); 8, Mt. Terukubi-yama (b) (primary forest); 9, Mt. Nishime-dake (primary forest); 10, Mt. Yonaha-dake (primary forest); 11, Benoki (c) (primary forest); 12, Benoki (d) (primary forest). Triangles indicate tops of mountains.

sists of older trees with a diameter of 60 cm or larger, often having a floor of dead wood (study sites 8–12). The secondary forest consists of younger trees with a diameter of 40 cm or less (sites 4–7). The surveyed open land is represented by a *Zoisia tenuifolia* Wild. community (site 2) or a *Miscanthus sinensis* Anders community (sites 1 and 3). All sites were more or less developed and disturbed by human activities.

The objective of the second sampling method was to determine the colony structure and reproductive system. To accomplish this, the whole colony was excavated and the number of queens was counted for as many species as possible. Among polygynous species, several nests of *Hypoponera bondroiti* (Forel), *Cardiocondyla wroughtonii* (Forel), *Cardiocondyla* sp. 1, *Cardiocondyla* sp. 2, and several nest fragments of *Technomyrmex albipes* (Fr. Smith) were sampled and reared in the laboratory of K.Y. for behavioral and morphological studies.

In addition, findings on social structure,

which were obtained by K.Y. in field studies of the Sakishima Islands in 1985 for *Pheidole megacephala* (F.), *Tetramorium bicarinatum* (Nylander), *Anoplolepis longipes* (Jerdon), and *Paratrechina longicornis* (Latreille) are also given.

All the voucher specimens obtained throughout the study are deposited in the Institute of Tropical Agriculture, Kyushu University, Fukuoka, Japan.

RESULTS

Status of Stenochoric and Endemic Species Versus Eurychoric and Tramp Species

Including this survey, we have counted 126 species from the Ryukyu Islands. This number is about 75% of the total number of species from the Nansei Islands and about half of the total number of Japanese species. A complete list will be presented elsewhere (K.O., unpubl. data). One of the impedi-

TABLE 1

ANTS FOUND IN KUNIGAMI-SON, OKINAWA ISLAND

Ponerinae

1. *Amblyopone silvestrii* (Wheeler)
- *2. *Proceratium japonicum* Santschi
3. *Discothyrea* sp. [medaka]^a
- *4. *Ectomyrmex javanus* Mayr
- *5. *Brachyponera chinensis* Emery
- *6. *Trachymesopus pilosior* (Wheeler)
- *7. *Cryptopone sauteri* (Wheeler)
- *8. *Cryptopone* sp. [hanadaka]^a
- *9. *Ponera* sp. 1 [minami-hime]^a
10. *Ponera* sp. 2 [arehada-hime]^a
11. *Ponera* sp. 3 [hoso-hime]^a
12. *Hypoconerops bondroiti* (Forel)
- *13. *Hypoconerops sauteri* (Forel)
14. *Hypoconerops* sp. [beppin]^a
- *15. *Leptogenys confucii* Forel
- *16. *Odontomachus monticola* Emery

Cerapachyinae

17. *Cerapachys biroi* Forel

Dorylinae

18. *Aenictus lifuia* Terayama

Leptanillinae

19. *Protanilla* sp. [juzufushi]^a

Pseudomyrmecinae

20. *Tetraconerops* sp. [oo-nagfushi]^a

Myrmicinae

- *21. *Aphaenogaster* sp. [ryukyu-ashinaga]^a
- *22. *Pheidole fervens* Fr. Smith
- *23. *Pheidole indica* Mayr
24. *Pheidole megacephala* (F.)
- *25. *Pheidole pili* Santschi
- *26. *Leptothorax* sp. [kiro-muneboso]^a
- *27. *Cardiocondyla nuda* (Mayr)
28. *Cardiocondyla wroughtonii* (Forel)
29. *Cardiocondyla* sp. 1 [hime-hadaka]^a
30. *Cardiocondyla* sp. 2 [usukihiro-hadaka]^a
- *31. *Tetramorium bicarinatum* (Nylander)
- *32. *Tetramorium lanuginosum* Mayr
- *33. *Tetramorium nipponense* Wheeler
- *34. *Tetramorium simillimum* (Fr. Smith)
- *35. *Monomorium chinense* Santschi
36. *Monomorium floricola* (Jerdon)
- *37. *Monomorium fossulatum* Emery
- *38. *Monomorium intrudens* Fr. Smith
39. *Monomorium pharaonis* (L.)
- *40. *Solenopsis* sp. [okinawa-tofushi]^a
- *41. *Oligomyrmex sauteri* Forel
- *42. *Oligomyrmex* sp. [oni-kotsuno]^a
- *43. *Vollenhovia* sp. 1 [yanbaru-umematsu]^a
44. *Vollenhovia* sp. 2 [okinawa-umematsu]^a
45. *Myrmecina* sp. [kogata-kadofushi]^a
- *46. *Pristomyrmex pungens* Mayr
- *47. *Crematogaster laboriosa* Fr. Smith
48. *Crematogaster vagula* Wheeler
49. *Strumigenys lewisi* Cameron

TABLE 1 (continued)

- *50. *Strumigenys* sp. 1 [kakugao]^a
51. *Strumigenys* sp. 2 [hakake]^a
- *52. *Smithistruma leptothrix* (Wheeler)
53. *Smithistruma* sp. [maruge]^a
54. *Pentastruma sauteri* Forel
55. *Epitritus hexamerus* Brown

Dolichoderinae

- *56. *Ochetellus itoi* (Forel)
- *57. *Tapinoma melanocephalum* (F.)
58. *Tapinoma* sp. [konuka]^a
- *59. *Technomyrmex albipes* (Fr. Smith)

Formicinae

- *60. *Anoplolepis longipes* (Jerdon)
- *61. *Paratrechina flavipes* (Fr. Smith)
- *62. *Paratrechina longicornis* (Latreille)
- *63. *Paratrechina* sp. (nr. *bourbonica*)^b
- *64. *Camponotus* sp. 1 [kebuka-ameiro]^a
- *65. *Camponotus* sp. 2 [hoso-umematsu]^a
66. *Camponotus* sp. 3 [aka-hirazu]^a
- *67. *Camponotus* sp. 4^b
68. *Polyrhachis dives* Fr. Smith

NOTE: Asterisks indicate species collected by time-unit sampling.

^a Japanese name (in brackets) follows Myrmecological Society of Japan (1989, 1991, 1992).

^b Unidentified species not shown in Myrmecological Society of Japan guides.

ments in studying the fauna of this region is the high ratio of undescribed species (see Ogata 1992): 54 species (42.9%) have not been described. The treatment of such species follows that of the Myrmecological Society of Japan (1989, 1991, 1992).

The results of the Kunigami-son survey are shown in Table 1, in addition to the species already recorded and those collected by general sampling. In total, 68 species are known from this area. The land area of Kunigami-son is 194 km², and this size is about median between that of Miyako-jima Island (148 km²) of the Sakishima Islands and Tokuno-shima Island (248 km²) of the Satsunan Islands. But the species diversity of Kunigami-son is far richer than that of both those islands (43 spp. in Miyako-jima, 45 spp. in Tokuno-shima [Terayama 1992]).

The number of species collected by the time-unit sampling method was 41. They are divided into two types based on the range of distribution: (1) eurychoric species: those having a wide geographic distribution, here

including ones occurring throughout the whole Oriental Region or beyond; in particular, the species expanding by human commerce and living in close association with

humans called tramp species; (2) stenochoric species: those having a narrow geographic distribution, here including species endemic to the Ryukyus and ones occurring ex-

TABLE 2
DISTRIBUTION TYPES, HABITATS, AND COLONY STRUCTURE OF 41 SPECIES COLLECTED BY TIME-UNIT SAMPLING IN KUNIGAMI-SON, OKINAWA

TYPE	DISTRIBUTION ^a	SPECIES	STUDY SITE ^b			COLONY STRUCTURE ^c
			OL	SF	PF	
Eurychoric species		<i>Brachyponera chinensis</i>	3	4,5	8,9,10,12	Polygynous (83.3%)
		<i>Pristomyrmex pungens</i>		7		
	T	<i>Technomyrmex albipes</i>	3	4,5,6	12	
		<i>Pheidole indica</i>	2			
	T	<i>Cardiocondyla nuda</i>	2			
	T	<i>Tetramorium bicarinatum</i>	1,2,3			
	T	<i>Tetramorium lanuginosum</i>	1,2			
	T	<i>Tetramorium simillimum</i>	1,2			
		<i>Monomorium chinense</i>	1,2			
	T	<i>Monomorium fossulatum</i>	2			
		<i>Monomorium intrudens</i>	1			
	T	<i>Tapinoma melanocephalum</i>	1,2			
	T	<i>Anoplolepis longipes</i>	2	6		
	T	<i>Paratrechina longicornis</i>	2			
	T	<i>Pheidole fervens</i>	1	4,5,7	8,10,11,12	
		<i>Paratrechina flavipes</i>	3	5,7	9,10,11	
	<i>Paratrechina</i> sp.	1,3	4			
	<i>Ochetellus itoi</i>	2				
	<i>Pheidole pieli</i>		6	8,9,10		
Stenochoric species		<i>Tetramorium nipponense</i>		6	12	Polygynous (17.4%)
		<i>Vollenhovia</i> sp. 1			8,10	
	E	<i>Cryptopone</i> sp.			10,11,12	Unknown (13.0%)
	E	<i>Solenopsis</i> sp.			11	
		<i>Strumigenys</i> sp. 1			12	
		<i>Odontomachus monticola</i>		4,5	9,10,11,12	
		<i>Ponera</i> sp. 1		5,6,7	10	Monogynous (69.6%)
		<i>Leptogenys confucii</i>			12	
		<i>Lepto thorax</i> sp.		7		
		<i>Camponotus</i> sp. 1		5		
		<i>Camponotus</i> sp. 4		7		
		<i>Smithistruma leptothrix</i>	3		12	
		<i>Oligomyrmex sauteri</i>		6	11	
	E	<i>Oligomyrmex</i> sp.		6	12	
		<i>Proceratium japonicum</i>			9	
		<i>Cryptopone sauteri</i>			9	
		<i>Ectomomyrmex javanus</i>			11	
		<i>Hypoponera sauteri</i>		4	10	
	E	<i>Aphaenogaster</i> sp.		7		
		<i>Crematogaster laboriosa</i>	2			
	<i>Camponotus</i> sp. 2	2				
	<i>Trachymesopus pilosior</i>	2				

^a E, species endemic to the Ryukyus (or believed to be so); T, tramp species.

^b Study sites identified in Figure 1. OL, open land; PF, primary forest; SF, secondary forest.

^c Percentages of polygynous, monogynous, and unknown species are given for eurychoric species and stenochoric species, respectively.

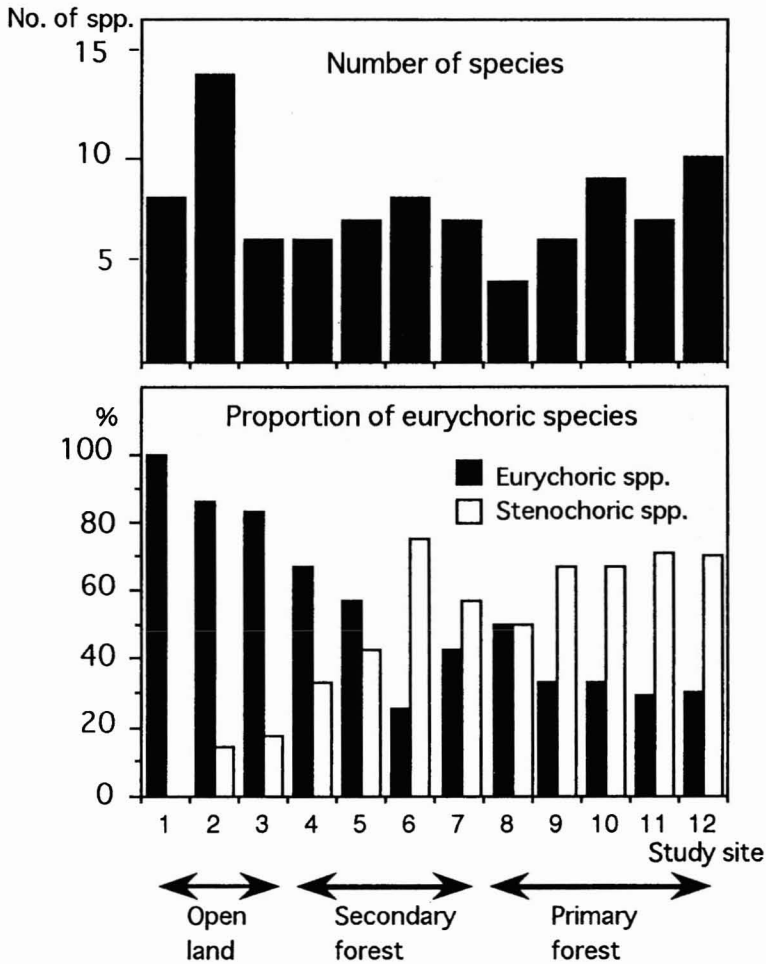


FIGURE 2. The number of species and proportion of eurychoric species in each study site. Study sites identified in Figure 1.

clusively in the Indo-Chinese Subregion, or eastern part of Asia (i.e., Korea, eastern China, Japan, Taiwan). Table 2 shows the types of distribution of the 41 species collected by the time-unit sampling from the Kunigami-son area with their colony structure.

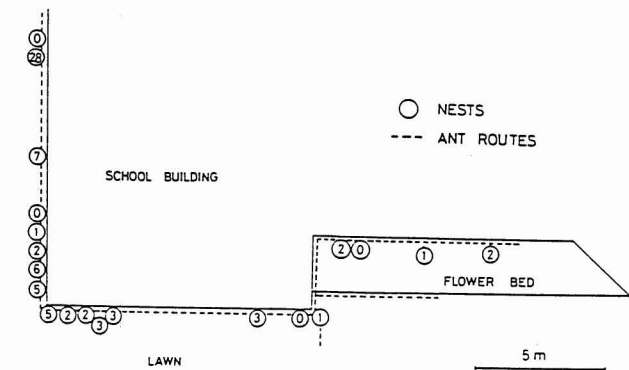
The ratio of these types in each habitat is shown in Figure 2. Most open lands were predominantly occupied by eurychoric species, including distinctive tramp species such as *Cardiocondyla nuda* (Mayr), *Tetramorium bicarinatum*, *Techomyrmex albipes*, and *Anoplolepis longipes*. However, primary forests

have a lower proportion of these species. Instead, that habitat contained many stenochoric species including several undescribed ones such as *Aphaenogaster* sp., *Oligomyrmex* sp., and *Vollenhovia* sp. 1, which seem to be endemic to the Ryukyus.

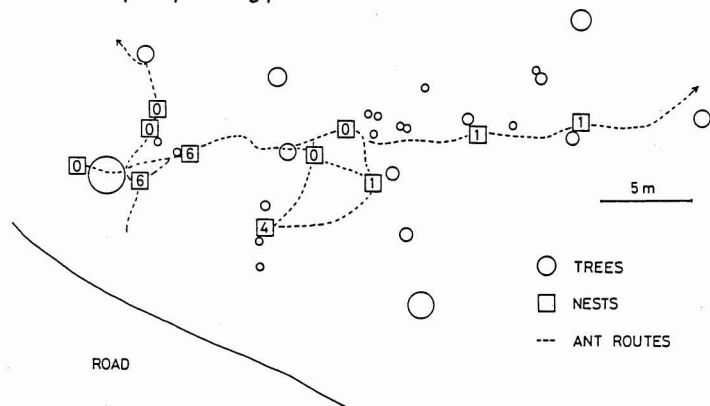
Social Structure and Reproductive Systems in Polygynous Species

In this paper, we show just an outline of our results, because the main purpose of the paper is to discuss social and reproductive characteristics of stenochoric and endemic

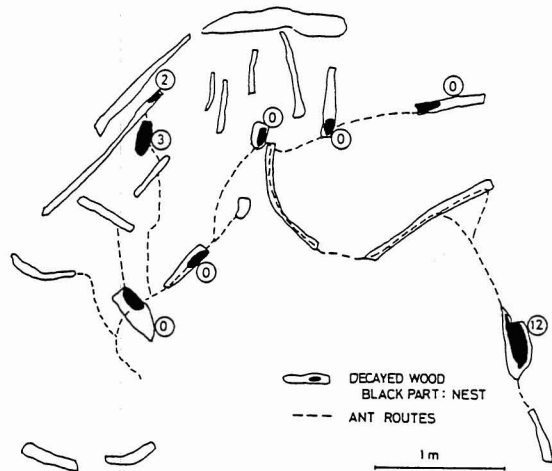
A *Tetramorium bicarinatum*



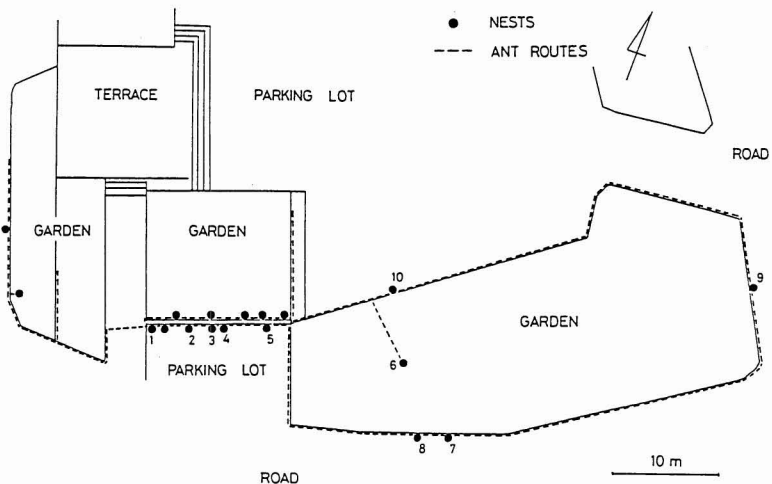
C *Anoplolepis longipes*



B *Pheidole megacephala*



D *Paratrechina longicornis*



versus eurychoric and tramp species. More detailed results will be given in separate papers.

The results of the queen number survey are given in Table 2. Here, *Odontomachus monticola* Emery was monogynous in three colonies in our survey, but three queens were obtained from a single colony (K. Tsuji, pers. comm.). Its status is still unclear.

From the field observations, it was determined that *Pheidole megacephala*, *Tetramorium bicarinatum*, *Anoplolepis longipes*, and *Paratrechina longicornis* form polydomous colonies in the Nansei Islands (Figure 3). In these species, many nests were connected with distinct ant routes. In a colony, several nests contained multiple queens.

The laboratory observations revealed that in *Hypoponera bondroiti*, *Cardiocondyla nuda*, *Cardiocondyla* sp. 1 (sp. 3 of Myrmecological Society of Japan [1992]), and *Cardiocondyla* sp. 2 (sp. 5 of Myrmecological Society of Japan [1992]) there was no hostility among workers from neighboring nests, suggesting that these species are also polydomous (K.Y., B. Corbara, K. Kinomura, and K. Tsuji, unpubl. data, for *H. bondroiti*; W. Czechowski and K.Y., unpubl. data, for *C. nuda*).

Mating behavior was studied mainly in the laboratory, with a few field observations: mating pairs were observed inside the nests of *Pheidole megacephala* and *Tapinoma melanocephalum* (F.).

In *Hypoponera bondroiti*, nests of which often contained multiple wingless queens, all males were wingless, but they showed size dimorphism: major and minor males. Each type of males fought with others of the same type, resulting in either a single male of one size per nest or a pair (major and minor) per nest. No fighting was observed between major and minor males. Both types of males

mated with winged and wingless females inside the nest.

Cardiocondyla sp. 2 has dimorphic males, winged and wingless. The mandibles of the latter are sickle-shaped, as are those of *C. wroughtonii*. Wingless males fought one another until one of the pair was killed. Both winged and wingless males mated with winged queens inside the nest.

In *Technomyrmex albipes*, both males and females show dimorphism: winged and wingless. Wingless males mate with wingless females inside the nest, and winged males mate with winged females outside the nest (Yamauchi et al. 1991a). Morphological studies revealed that the copulatory organs of wingless sexuals were approximately half the size of those of winged sexuals in this species (Figure 4). Crossmating should be impossible between winged and wingless sexuals in this species. However, in *Hypoponera bondroiti*, *Hypoponera* sp. (sp. 4 of Myrmecological Society of Japan [1989]; from Honshu, Japan), and *Cardiocondyla* sp. 1, in which dimorphic males mate with the same kind of females, size differences in male copulatory organs between dimorphic males were much smaller: the mean copulatory organ size of winged males (or major wingless males) was 1.2 times less than that of wingless males (or minor wingless males) in each species (K.O., K. Murai, K. Tsuji, and K. Y., unpubl. data).

DISCUSSION

Status of Stenochoric and Endemic Species Versus Eurychoric and Tramp Species in the Ryukyus

The tendency of the stenochoric species to be found in forests and the eurychoric species

◀ FIGURE 3. Distribution of nests, ant routes, and number of queens in each nest. A, *Tetramorium bicarinatum* nested under ground on grass lawn of Kohama-jima Island (Sakishima Islands) (August 1985). B, *Pheidole megacephala* nested in and under decayed wood at a herbaceous beach of Kohama-jima Island (August 1985). C, *Anoplolepis longipes* nested under decayed wood, empty cans, empty bags, and other materials in a secondary forest of Iriomote Island (Sakishima Islands) (August 1985). D, *Paratrechina longicornis* nested in spaces between slates, stones, and bark and stem of trees at City Hall of Ishigaki-jima Island (Sakishima Islands) (August 1985). Numerals in A, B, and C show queen number. Numerals in D show nest code: nests 1–7, 9, and 10 had 35, 8, 21, 69, 273, 4, 1, 35, and 4 dealated queens, respectively.



FIGURE 4. Copulatory organs of *Technomyrmex albipes* (dorsal view). A, winged male; B, wingless male. Scale, 100 μm .

to be observed in open land can be seen in many islands of the Ryukyus. For example, the well-known tramp species *Pheidole megacephala*, *Monomorium pharaonis* (L.), and *Cardiocondyla wroughtonii* are also common in open land throughout the Ryukyus. *Pheidole megacephala* is predominant along the seashore. *Polyrhachis dives* Fr. Smith is still expanding its distribution in Okinawa (Takamine 1987). These tramp species have invaded some secondary forests, but only rarely primary forests. In contrast, all four of the recently described endemic species (*Amblyopone fulvide* Terayama, *Probolomyrmex okinawaensis* Terayama & Ogata, *P. longinodus* Terayama & Ogata, and *Pheidole ryukyuensis* Ogata) were obtained from dense forests (Ogata 1982, Terayama 1987, Terayama and Ogata 1988). These results suggest that it is especially important to preserve the primary forests for protection of native ant species in the Ryukyus. Without primary forests, there will be a diversity of tramp ant species, but fewer endemic species.

The same tendency was shown by Wilson (1959) in New Guinean ant fauna. He discussed this trait in terms of dispersal history, and later (Wilson 1961) proposed the taxon cycle hypothesis. Although we cannot identify the evolutionary stage of each species because of poor phylogenetic information, Wilson's species of "stage I," or "the species apparently in the process of expansion," corresponds to our eurychoric species. In the following discussion we focus on the social structure and reproductive system of the eurychoric species.

Secondary Polygyny—An Important Characteristic of the Majority of Tramp Ant Species

Polygyny is not a rare phenomenon in ant societies. The ratio of the species that have polygynous colonies is about 50% in Europe (Bourke 1988), 52.4% in Okinawa, and 53.1% in Honshu, Japan (K.Y., Y. Itō, and K. Kinomura, unpubl. data). The ratio in

eurychoric species, especially in the tramp species, is conspicuously high, whereas the endemic or stenochoric species are mostly monogynous. The proportion of polygynous species (including ones that have multiple reproductive intercastes or workers) exceeds 80% in the eurychoric species in the study area (Table 2). Among these polygynous species, it is known that new queens (or reproductive intercastes or workers) are regularly adopted by the mother colony (secondary polygyny) in *Pristomyrmex pungens* Mayr (Tsuji 1988), *Cardiocondyla nuda* (Yamauchi and Kinomura 1993), *Technomyrmex albipes* (Yamauchi et al. 1991a), for example. Secondary polygyny may also be found in the other species.

The adaptive significance of secondary polygyny may be characterized by the following: (1) high risk of colony fragmentation because of frequent nest destruction or frequent nest relocation (i.e., most fragmented colonies can multiply if there is at least some survival among queens or reproductive intercastes); (2) no ceiling on egg production (i.e., the egg production of a colony increases). Therefore, the size of the colony grows. Thus, secondary polygynous species, usually associated with polydomy, can live successfully in frequently disturbed environments and/or in habitats that are long-lasting, patchily distributed, and large enough to support large populations (Hölldobler and Wilson 1977; see also Nonacs 1988). They often occupy an area in high density, which makes for a higher probability of victory in competition with other ant species (Higashi and Yamauchi 1979, Yamauchi et al. 1981, 1982).

Among eurychoric species of the study area, only *Paratrechina* spp. and *Ochetellus itoi* (Forel) are monogynous. *Paratrechina* sp. (near *bourbonica* [Forel]) is an excellent pioneer species. It first appears in bare cultivated land and in river terraces after flooding, for example.

Intranidal Mating and Wingless Males Widespread in Secondary Polygynous Species

Because deleterious genes are more likely to be expressed in haploids than in diploids, a population of haploid males acts as an efficient

remover of deleterious genes through natural selection, and females enjoy a lower probability of the expression of the deleterious genes in haplodiploid organisms (Matsuda 1987). Haplodiploidy seems to be a genetic basis for frequent intranidal mating (probably most of them are inbreeding, but see Kaufmann et al. [1992]), which might be widespread in the mating systems of ants, especially of secondary polygynous ones (e.g., *Hypoponera* spp. [Le Masne 1956, Hamilton 1979; K.Y., B. Corbara, K. Kinomura, and K. Tsuji, unpubl. data], *Cardiocondyla* spp. [Stuart et al. 1987, Heinze et al. 1993, Yamauchi and Kinomura 1993], *Epimyrma* spp. [Buschinger 1989], *Technomyrmex* spp. [Terron 1972, Yamauchi et al. 1991a], *Lasius* spp. [Yamauchi et al. 1981, Loon et al. 1990], etc.).

Intranidal mating reduces the risk involved in nuptial flight and ensures the adoption of new queens for the mother nests. It has also been suggested that secondary polygyny is correlated with independent foundation of queens (Keller 1991). The species with this type of mating may multiply in new places if a queen or a colony fragment settle there. Moreover, wingless males are advantageous if they do not perform extranidal mating, because the colony can reduce the investment cost for males. For example, the weight of the wingless male is approximately half that of the winged male in *Cardiocondyla* sp. 1 (Yamauchi and Kinomura 1993). Moreover, sex ratios are highly female-biased in *Cardiocondyla* spp. (Kinomura and Yamauchi 1987, Yamauchi and Kinomura 1993) and *Technomyrmex albipes* (Yamauchi et al. 1991a). Therefore, it is not surprising that wingless males have evolved where intranidal mating was established. In fact, wingless males occur in phylogenetically diverse genera such as *Hypoconerinae* (Ponerinae), *Anergates*, *Cardiocondyla*, *Formicoxenus* (Myrmicinae), *Technomyrmex* (Dolichoderinae), and *Plagiolepis* (Formicinae). Inside the nest, males are taken care of by the workers. Therefore, males are relatively free from natural selection such as predatory pressure. In such a condition, diverse sexual behavior might have evolved. For example, wingless males of *Hypoconerina punctatissima*

(Roger) (Hamilton 1979), *H. bondroiti* (K.Y., B. Corbara, K. Kinomura, and K. Tsuji, unpubl. data), and *Cardiocondyla* spp. (Stuart et al. 1987, Heinze et al. 1993, Yamauchi and Kinomura 1993) fight one another to monopolize the nest in which new queens emerge and mate. In *C. wroughtonii*, wingless males kill the rival males by manipulating the nestmate workers with "bite-inducing pheromone" (Yamauchi and Kawase 1992). In *Hypoconera eduardi* (Forel) (Le Masne 1956) and *Hypoconera* sp. (sp. 4 of Myrmecological Society of Japan [1989]; K.Y., pers. obs.), wingless males mate with callow females even inside the cocoon.

Differentiation in Colony Structure and Reproductive System among Secondary Polygynous Species

Figure 5 is a schematic illustration of typical reproductive systems in polygynous and polydomous species (excluding parasitic ones), showing morphological differentiation in sexuals.

Type I is the most basic type among polygynous and polydomous species: the sexuals are winged, and they have alternative mating tactics: if both sexuals are produced in the same nest during the same period, they mate inside the nest (or very near the nest entrance), whereas they fly away to mating places in the absence of counter sexuals. *Lasius sakagamii* Yamauchi & Hayashida (Yamauchi et al. 1991b) and *Formica lugubris* Zetterstedt (temporary social parasite) (Cherix et al. 1991) are representative examples.

Type II may be a modification of type I: nuptial flight is reduced here. *Lasius neglectus* Loon, Boomsma & Andrasfalvy probably belongs to this type (Loon et al. 1990). Many of the best-known tramp species, including *Monomorium pharaonis*, *Pheidole megacephala*, *Linepithema humile* (Mayr) (formerly *Iridomyrmex humilis* [Mayr]), and *Wasmania auropunctata* (Roger) (see Hölldobler and Wilson 1977) belong to type I or II.

Type III is seen in *Hypoconera* sp. (sp. 4 of Myrmecological Society of Japan [1989]) and

Technomyrmex albipes. In these species, intra- and extranidal routes are taken by wingless and winged sexuals, respectively. In the former species, crossmating between winged and wingless sexuals is still possible in the laboratory, but it seems to be rare because of the difference in their emergence period (K.Y., pers. obs.). In the latter species, however, behavior and morphology are so differentiated between winged and wingless sexuals that crossmating should be impossible, despite the overlap in their emergence period (Yamauchi et al. 1991a; K.O., K. Murai, K. Tsuji, and K. Yamauchi, unpubl. data).

Type IV is seen in *Hypoconera bondroiti*, in which all males are completely wingless but show size dimorphism. They fight one another inside the nest, and the winner can mate with both winged and wingless queens there. Winged queens generally disperse and wingless queens remain in the mother nest (K.Y., B. Corbara, K. Kinomura, and K. Tsuji, unpubl. data). *Hypoconera punctatissima* (tramp species [Taylor 1967]) belongs to this type, although male dimorphism is not known.

Type V is represented by *Cardiocondyla wroughtonii* and *Cardiocondyla* spp. (spp. 3–5 of Myrmecological Society of Japan [1992]; Yamauchi and Kinomura 1993). In these species, nuptial flight is reduced. Winged and wingless males engage in intranidal mating, although the former leave the nest if there are few or no winged queens. Some of the mated queens remain in the nest, but the majority undertake dispersal flights only after intranidal mating.

Type VI is seen in *Cardiocondyla nuda* and probably many other *Cardiocondyla* species (Heinze et al. 1993, Yamauchi and Kinomura 1993). In this type, all males are completely wingless, and mating is conducted inside the nest. Most mated winged queens were observed to fly away for independent colony foundation only after intranidal mating.

In addition to this kind of sexual reproduction, asexual reproduction is known in the eurychoric *Pristomyrmex pungens* and *Cerapachys biroi* Forel. These two species have no queen caste, and the workers pro-

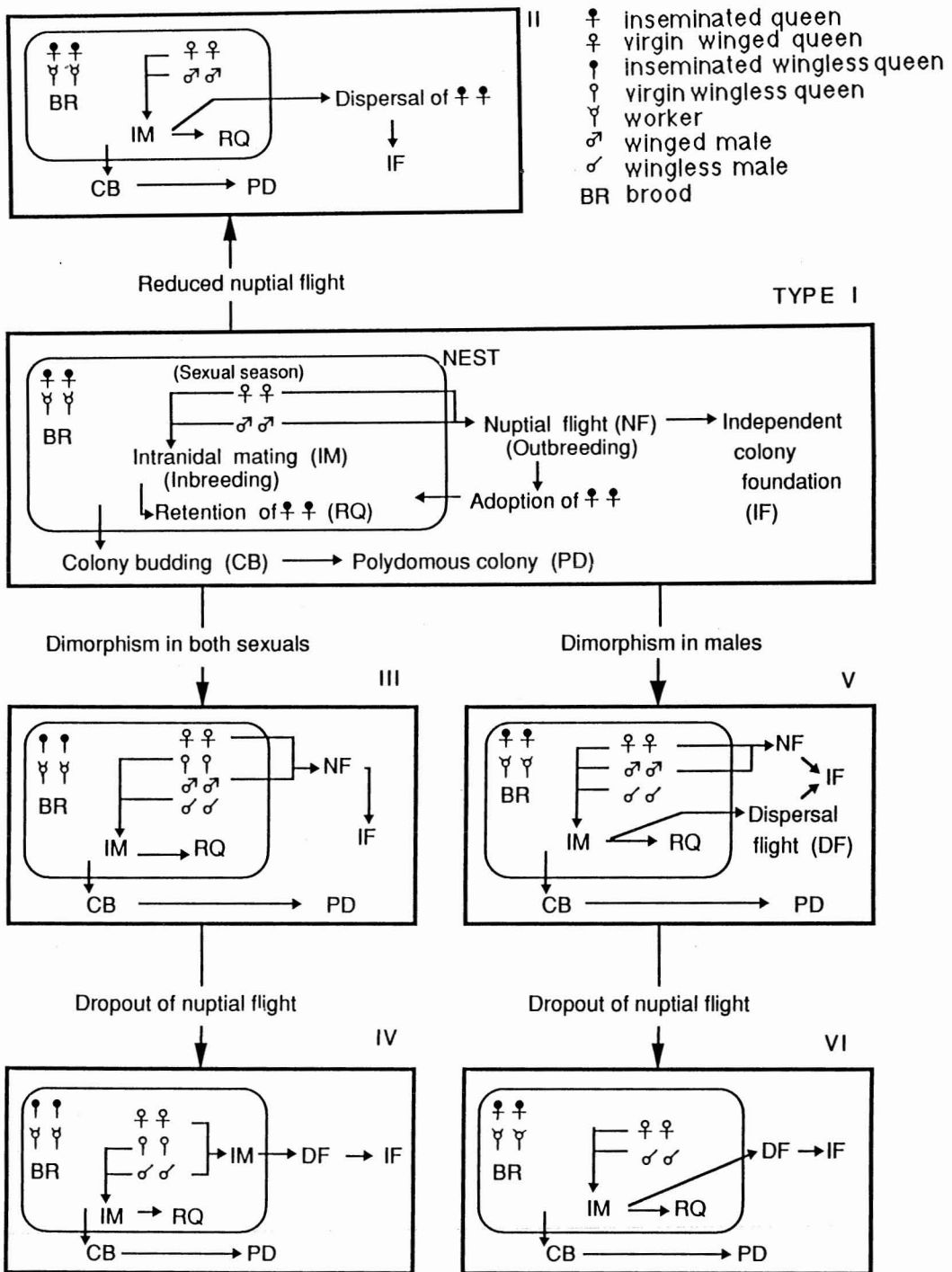


FIGURE 5. Various types of colony structures and reproductive systems in secondary polygynous species.

duce diploid eggs that develop into workers by thelytokous parthenogenesis (Tsuji 1988, Tsuji and Yamauchi 1990).

Thus, the majority of the tramp ant species seemed well adapted for rapid territory expansion by virtue of their specific colony structure (secondary polygyny) and reproductive system (using intranidal mating, colony budding together with nuptial or dispersal flight, independent colony foundation), as mentioned above. In addition, another factor is also important in migration to other places: most tramp species live in open lands where they may have many more opportunities to come in contact with human activities.

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