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Polycalic Colonies of the Weaver Ant *Polyrhachis dives*

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Abstract In Okinawa, 31 out of 36 examined nests of the weaver ant, *Polyrhachis dives*, (86.1%) contained multiple queens. The number of queens ranged from 0 to 594 with a mean of 44.6. Such polygyny seemed to be attained by retention of new queens in the mother nests, while adoption of new queens in alien nests might be rare or absent. Adjacent nests frequently exchanged colony members with each other, forming a huge polycalic colony which contained a million workers. Further, no aggressive behaviors or only weak ones were observed between workers from different colonies 1.5 and 40 km apart from each other.

Introduction

The weaver ant, *Polyrhachis dives* F. SMITH, widely distributed in Southeast Asia, has been studied by many researchers in regard to its nesting sites and nest constructing methods, foods and natural enemies, applications for control of noxious insects, etc. (MENOZZI, 1932; TAKAHASHI, 1937; HSIAO, 1981; TAKAMINE, 1983). However, these studies have been only minimally concerned with the ant's social organization except for TAKAHASHI (1937), who described polygyny, mating behaviors and multiplication of nests by budding.

In the present research, we studied the social organization of this species, focussing on its polycalic system.

Materials and Methods

Field survey

Field surveys were carried out in the garden of Nagourasou Hotel, Nago, Okinawa, in 1985 and 1986. The area of the study was about 750 m^2. The vegetation consisted of a hedge of *Casuarina equisetifolia* (Casuarinaceae) and a grove of *Erythrina variegata* var. *orientalis* (Leguminosae) on the lawn (Fig. 1 A). In this field were 63 inhabited nests and 17 abandoned ones, mainly in tree canopies, at the beginning of the study.

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Fig. 1. Study field. A: Garden of Nagourasou Hotel, Nago, Okinawa. B: Implantation of a nest (T-A) from Imbu. C: Implantation of a nest (T-B) from Aha.

In addition to general observation, a group-marking technique was used to mark individual workers and queens of some nests in order to recognize their initial nests. A dot of quickdrying ink (Paint Marker) was applied on the gaster of the ants in June and December, 1985. Further, two nests from other localities were implanted in the field and subsequent inter-nest relations were examined by a groupmarking technique applied in December, 1985. A nest made of leaves of *E. variegata* var. *orientalis* (Nest T-A) at Imbu, 1.5 km from the study field, was set near a nest (Nest 3 C; Fig. 1 B) on a tree of the same species in the hotel garden after 200 workers were marked. Next, from a grass nest (Nest T-B) of a colony at Aha, 40 km away, 200 marked workers and 10 marked queens were packed in an empty can with nest materials and set near a nest in a *C. equisetifolia* tree (Nest 9-A; Fig. 1 C) in the hotel garden. After two hours of observation, the can was moved again near a prexisted nest in another empty can in the grassy area of the hotel garden.

A total of 36 nests, including all of the marked nests, were collected in the study field and at Imbu in various seasons and their colony compositions were examined.

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Fig. 2. Thoracic muscle of *P. dives* queen. A: New queen. B: Old queen.

Examination of queens

The degrees of ovarian development, mandibular and thoracic muscle wear, and spermathecal contents of queens and alate females preserved in 70% alcohol were examined under a dissecting microscope.

On the basis of the examinations, queens were classified into three classes: 1) new queens, which had clear thoracic muscle bands (Fig. 2 A), a gaster filled with many fat bodies and undeveloped or slightly developed ovaries, 2) intermediate queens, which had a gaster and ovaries similar to those of a new queen but not clear thoracic muscle bands, and 3) old queens, which had no clear thoracic muscle bands (Fig. 2 B), a gaster with few fat bodies and rather or well-developed ovaries.

Results

Inter-nest relations

On June 24–26, 1985, there were 63 inhabited nests and 17 abandoned ones in the study field, mainly on trees (Fig. 3). Ant routes connecting most of these nests were recognizable (Fig. 3 shows only clear routes on the ground surface). At various places on the routes, some workers were carrying other workers or final instar larvae. Further, on June 25, numerous ants were moving from one nest to five others. The workers were carrying egg clumps, larvae and pupae. Some queens moved by themselves, others by adult transport (Fig. 4 D). In the case of males, only adult transport was observed (Fig. 4 E). When the nest from which the ants moved was examined at the end of the migration, a blind snake, *Typhlops braminus*, was discovered there besides several workers. This snake is known to eat termites and ants. Therefore, the migration was probably due to disturbance of this snake.

Marked workers from a given initial nest were rediscovered in other nests, especially among neighboring ones in the same trees, in both June and December trials. The results of a marking applied in December are shown in Table 1. The

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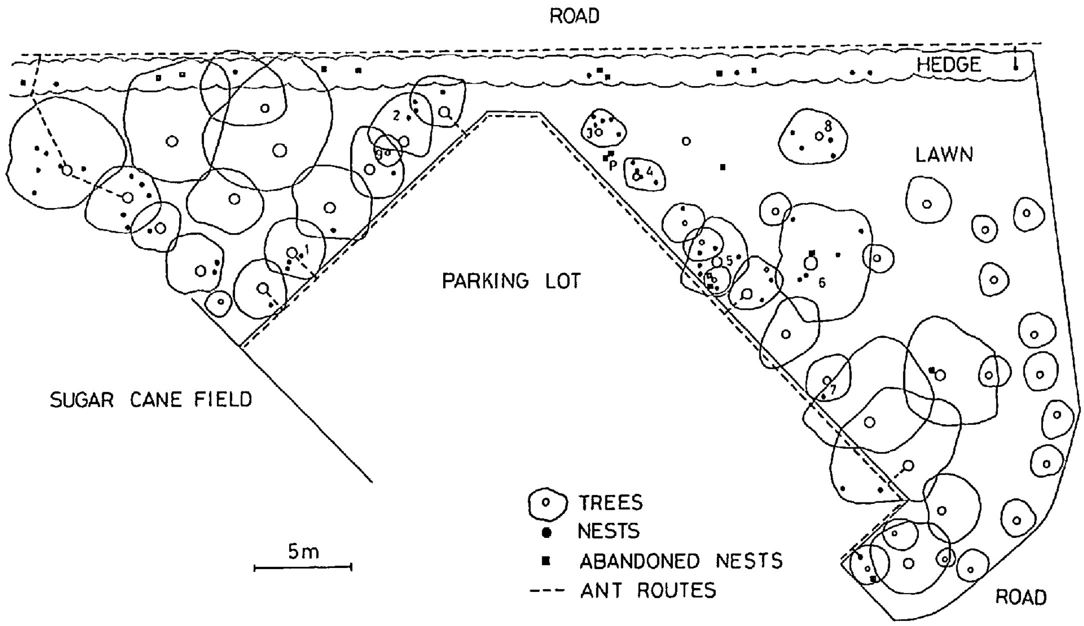

Fig. 3. Distribution of nests of *P. dives* in the study field on June 21, 1985.

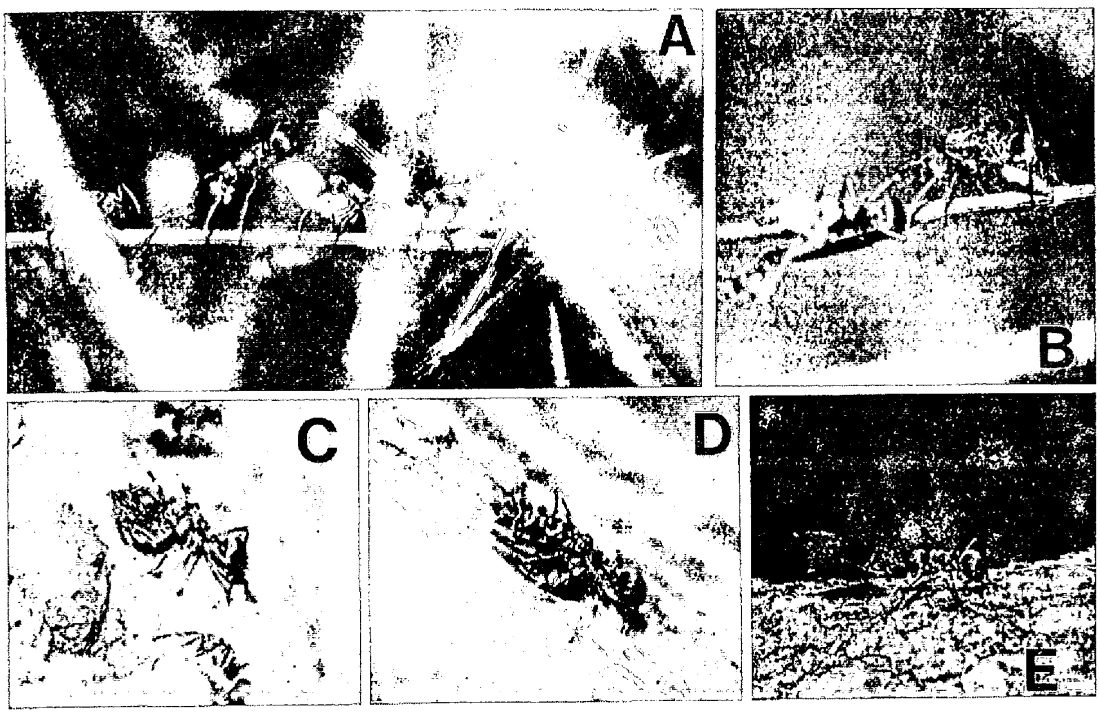

Fig. 4. Inter-nest movement in *P. dives*. A: Transport of immatures. B: A moving queen. C: Transport of a worker. D: Transport of a queen. E: Transport of a male.

drifting ratio, that is, the ratio of workers marked at a given nest but rediscovered on other nests to all marked workers rediscovered on all inspected nests (HIGASHI, 1978), could not be obtained in this study, because many neighbor nests near the

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marked nests were not examined. However, the minimum values of the drifting ratio could be calculated for each marked nest and for these nests they were more than 0–26.8. The actual values might be two or three times greater if the nests left uncollected had been examined. In conclusion, it is doubtless that all of the 63 nests in the study field belonged to a single colony.

The inter-nest relations between different colonies from other localities were examined three times.

Many marked workers of Nest T-A, implanted from the Imbu colony, were accepted by the workers of Nest 3-C just after setting. There was no aggressive behavior between workers. Three days after implantation, 23 marked workers of Nest T-A were rediscovered in Nests 3-C and P, while 6 marked workers of Nest 3-C were rediscovered in Nest T-A (Table 1). The drifting ratio of Nest T-A was more than 42.6%.

In the case of the implantation of an empty can containing workers, queens and nest materials of Nest T-B at Aha to a place near Nest 9-A, some aggressive behaviors such as biting and pulling were observed, but no worker was killed during two hours of observation. Then the can was moved to a place near another nest in an empty can in a grassy area. In this trial, the workers were immediately accepted with no aggressive behavior. Lastly, 11 marked workers of Nest T-B were rediscovered in Nest 9-A, and 3 marked workers of Nest 9-A in Nest T-B when the nests were examined a day after.

Further, it was ascertained that queens of a given colony were also accepted by an alien colony. When four marked queens of the Imbu colony were released on a nest (Nest 3-C) in the study field on December 16, three queens entered into the nest by themselves and one was carried into the nest by adult transport. Three days later, three of them were rediscovered in the nest and one was in a nest (Nest 8-B) which was about 10 m from the releasing site.

Colony composition

The results of a colony census are shown in Table 2. Most nests contained multiple queens. Only 5 out of 36 nests had no or single queens. The number of queens ranged from 0 to 594. The mean with S.D. was 40.5 ± 64.2 in June, 58.2 ± 126.4 in December and 8.7 ± 10.0 in March. I_δ was 9.4 in June, 5.5 in December and 2.1 in March, all of them, especially that in June, showing very high aggregated distribution patterns.

The number of workers varied from nest to nest, ranging from 56 to 37,560. The mean with S. D. was 1600.9 ± 903.2 in June, 8419.0 ± 8936.5 in December and 1278.7 ± 678.1 in March. There were significant differences between the numbers of workers in December and in June and March ($p<0.01$). The smaller number in June and March might have been caused mainly by the presence of a large number of outdoor workers. On the other hand, outdoor activities were extremely low during the survey time in December when the maximum temperatures were hardly

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Table 1. Movement of marked workers among nests of *P. dives*. Numerals of nest codes correspond to tree codes in Fig. 3. H means hedge. T-A and T-B were implanted nests set near Nest 3-C and Nest 9-A respectively.

Nest code	Color of marking	No. of marked workers	No. of marked workers discovered in nests														
			3-C	3-D	T-A	P	6-B	6-C	8-B	8-C	8-D	8-E	2-B	9-A	T-B	H-A	H-B
3-C	Orange	250	153	11	6	6											2
T-A	Yellow green	200	18		31	5											
6-B	Green	500					132		2								
8-B	Violet	500							205	6		8					
8-C	Blue	500				1			19	90	3	10					
8-D	Pink	200							8	2	80	3					
9-A	Yellow	500											1	251	3	8	
T-B	Luminous pink	200												11	109		
H-A	Red	500														280	
H-B	White	500	1			1											335

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Table 2. Number of colony members in nests of *P. dives*.

Nest code	Locality	Date	Worker	Queen	Alate female	Male	Pupa (A & A)	Larva	Egg
1-A			1,654	13	0	143	1,080	+	+
2-A			444	15	0	0	472	+	+
3-A			1,091	8	0	111	280	+	+
3-B	Nago	25-VI-'85	1,130	19	0	0	651	+	+
5-A			3,300	198	0	4	421	+	+
6-A			1,630	37	0	0	25	+	+
7-A			1,095	19	0	0	1,920	+	+
8-A			2,463	15	0	1,126	1,418	+	+
I-A			3,897	4	121	157	509	+	?
I-B			260	0	9	7	18	+	?
I-C			37,560	64	264	3,280	7,600	+	?
I-D	Imbu	15-XII-'85	11,240	20	0	80	7,240	+	?
I-E			5,020	5	129	200	635	+	?
I-F			484	1	0	293	0	+	?
I-G			395	3	2	5	0	—	?
2-B			7,556	594	1,037	8,018	533	+	+
3-C			4,143	58	4	4,901	135	+	+
3-D			5,511	54	0	10,133	53	+	+
6-B			14,848	23	0	704	2,592	+	+
6-C			2,695	24	0	10,375	943	+	+
8-B			16,448	60	1	3,424	10,560	+	+
8-C	Nago	18, 19-XII-'85	7,292	17	14	7,747	185	+	+
8-D			704	0	0	2,520	0	—	—
8-E			8,053	47	0	11,608	231	+	+
9-A			8,576	49	2	2,368	9,920	+	+
H-A			13,184	100	4	15,072	12,480	+	+
H-B			22,784	85	167	18,944	10,880	+	+
P			2,380	2	1	490	1,500	—	—
T			3,768	12	0	480	480	+	+
I-H			1,930	0	15	335	0	+	—
I-I	Imbu	8-III-'86	56	0	0	33	0	—	—
I-J			820	2	0	42	0	+	—
I-K			1,200	22	0	0	0	+	—
N-A			1,560	10	0	2,520	0	—	—
N-B	Nago	8-III-'86	2,010	23	0	2,380	0	—	—
N-C			1,375	4	0	77	0	+	—

above 17°C under the influence of the cold Siberian air mass.

Males were observed in nests at all survey times, though the ratio of nests with males was high in December. The mean number with S. D. of males was 173.0±389.4 in June, 4800.3±5617.4 in December and 769.6±1154.0 in March. The maximum number was 18,944 in December. On the other hand, the ratio of nests with alate females and the number of alate females in each nest was much smaller.

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The mean with S. D. was 0 in June, and 83.6±230.0 in December and 2.1±5.7 in March. The maximum was 1,037 in December. The production of males may be conducted all the year round, with a peak in autumn, while that of alate females may be done over a rather short time, perhaps from late summer to early winter. In this connection, TAKAHASHI (1937) reported that alate females were observed in nests from late October to early February in Taiwan, though KONDOH (1975) observed them in mid-August. Larvae were observed all the year round, while eggs and pupae were absent in March, suggesting low activities in egg production

Table 3. Number of new to old queens in each nest in *P. dives*.
* indicates a nest with alate females.

Nest code	Date	Number of queens			
		Total examined	Old	Intermediate	New
1-A	25-VI-'85	10	10	0	0
2-A		15	15	0	0
3-A		8	8	0	0
3-B		10	10	0	0
5-A		10	10	0	0
6-A		10	10	0	0
7-A		10	10	0	0
8-A		10	10	0	0
I-A*	15-XII-'85	4	1	0	3
I-C*		10	3	3	4
I-D		10	10	0	0
I-E*		5	2	2	1
I-F		1	1	0	0
I-G*		3	1	0	2
2-B*	18, 19-XII-'85	20	11	1	8
3-C*		10	7	0	3
3-D		10	10	0	0
6-B		10	10	0	0
6-C		10	10	0	0
8-B*		10	10	0	0
8-C*		10	5	0	5
8-E		10	10	0	0
9-A*		20	17	0	3
H-A*		10	10	0	0
H-B*		10	7	0	3
P*		2	1	0	1
T-A		10	10	0	0
I-J	8-III-'86	2	2	0	0
I-K		10	9	1	0
N-A		10	6	4	0
N-B		12	0	11	1
N-C		4	3	1	0

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and larval growth in winter.

Eight of 63 inhabited nests were collected on June 25 for examination of the colony structure. However, 104 active nests besides 18 abandoned ones were noted on December 15, showing that inhabited nests had multiplied 1.9 times over 6 months. In December, the worker population in nests was estimated as more than 876,096 (ca. 1,200/m^2).

Examination of queens

From the examination of thoracic muscle, fat bodies in the gaster and ovarian development, queens were classified into three classes: new, intermediate and old. The ratios of nests containing new queens were 0% (n=8) in June, 47.6% (n=21) in December and 14.3% (n=7) in March. As shown in Table 3, new queens were obtained from 71.4% of 14 nests which had alate females, but not from nests without alate females except Nest N-B, in which there were several intermediate queens. However, this does not exclude the possibility that Nest N-B might have produced alate females and these new and intermediate queens might have been ones which had remained in the nest after mating, because it seemed that most of the alate females had already either departed from or remained in the nest by that time.

All of the 295 queens examined were inseminated. On the other hand, only eight of the 121 alate females examined (6.6%) had inseminated spermathecae. The ratio of nests with inseminated alate females was 42.9% (n=14).

Table 4. Frequency distribution of number of mature and semimature eggs in the queen gaster in Nest 5-A.

Number of eggs observed in queen gaster	0	1	2	3	4	5	6	7	8	9
Number of queens	15	17	17	16	13	11	4	3	2	2

The number of eggs in the gasters of the queens of Nest 5-A are given in Table 4. The frequency distribution of the number of mature and semimature eggs in the gasters fitted a negative binomial distribution pattern (k=4.15). Here, it is noteworthy that each queen had well-developed ovaries, even if she had no mature or semimature eggs. In other nests too, queens were similar to each other in ovarian development.

Discussion

A colony is defined as a group of individuals which constructs a nest and rears offspring in a cooperative manner, and a nest as the structure which they inhabit and where they rear the offspring. In most ant species, a colony occupies a single nest, generally consisting of dense, mutually connected chambers (monocalic). But in certain species a colony occupies several nests which are connected by ant routes

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or by exchange of colony members (polycalic).

The polycalic system is considered a highly differentiated social organization of ants, though recently such a system has been found among some termites (HOLT & EASBY, 1985). From the existence of polycalic species in taxonomically diverse groups, WILSON (1971) speculated that pairs or sets of three or more polycalic and monocalic sibling species might be widespread among the ants. For further understanding of polycalic systems, comparative studies are required of more diverse groups than have so far studied.

In this study, we report on a polycalic system of *Polyrhachis dives* which is widely distributed in Southeast Asia, with special attention to the inter-nest relations and the secondary polygyny of this species.

Inter-nest relations

Although the values indicate only the minimums, the drifting ratio in *P. dives* ranged from 0 to 42.6% in 10 trials including two of implanted nests. Actually, the values may be two or three times larger, judging from the ratio of examined nests to total surrounding nests. These values are similar to those obtained in *Formica yessensis*: 13% (ITO & IMAMURA, 1974) and 21.2–70.4% (HIGASHI, 1978). It is obvious that workers frequently change their nests, especially among neighboring ones, forming a huge polycalic colony. However, further studies are required to clarify whether or not they tend to stay in a specified nest during a certain period.

The relations among ants of different colonies seemed to be rather complicated. Workers of the Imbu colony were accepted by those of the Nago colony with no aggressive behavior between them. On the other hand, workers of the Aha colony were attacked but finally accepted by workers of a nest made in a *C. equisetifolia* tree, while they were accepted immediately by a nest made in an empty can in a grassy area. In general, it is known that ants recognize colony mates by means of a colony odor determined genetically or environmentally (CROZIER, 1979). In the case of *P. dives*, different colony odors produced environmentally seem to cause aggressive behaviors between workers. Although direct evidence has never been obtained, it is possible that colonies founded independently may fuse into a single colony.

By such a polycalic system, this species can rapidly reproduce its population and occupy a local habitat in high densities. HSIAO (1983) recorded in China that 50 implanted nests of *P. dives* increased to 300 over 10 years and also that an area of 1.33 ha inhabited by this ant spread to more than 13.33 ha over 8 years. In this study, 55 nests increased to 104 nests over six months.

Secondary polygyny

In the present study, *P. dives* had 86.1% polygynic nests. On the basis of queen anatomy, it is obvious that the polygyny was attained by adoption of new queens (secondary polygyny). However, it was not directly clarified where these new queens came from, since we did not observe mating behaviors except one case

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in which a male copulated with a dealated female near a nest on December 15. In this connection, TAKAHASHI (1937) suggested that nuptial flights might be abandoned in this species and that mating might occur also in nests. In the present study, too, it is strongly suggested that new queens remained in their mother nests after mating near or in the nests and that they did not enter alien nests, at least just after mating, given the facts that new queens were discovered in most of the nests with alate females but not in those without alate females except in one case.

Thus a high degree of relatedness may be maintained among colony members. For instance, the coefficient of relationship between a foundress queen and her granddaughter is 3/4 and that between a worker and her niece is 5/8, if a foundress copulates once and her daughter queen copulates with a brother. On the basis of such a genetic structure, secondary polygyny might be established more easily, resulting in its frequent occurrence among the ants.

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