Worker Polyethism Related with Body Size in a Polydomous Red Wood Ant, *Formica* (*Formica*) *yessensis* Forel[1)]

By

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(*With 5 Text-figures and 1 Table*)

Following the previous studies on the population and life cycle of a polydomous red wood ant, *Formica* (*Formica*) *yessensis* Forel, the present paper reports the relation of worker body size to activities for colony maintenance.

Previous studies on the division of labor among workers in various ant species revealed the importance of age and size differences (Buckingham 1911, Ehrhardt 1931, Kiil 1934, Lee 1938, etc.). Partly due to the long life span in workers, the performance change according to aging is not so acute in ants as in the honeybee. On the other hand, many ant species exhibit a marked correlation between task performance and body size.

In the course of the studies on extranidal activities of *F. yessensis*, such correlation is recognized among the workers performing different tasks and is described below in order to facilitate further studies on the complicated polydomous life of this species.

All the specimens used for the study were taken from nest aggregations infesting Ishikari Shore near Sapporo, Hokkaido. The topography of the habitat and the outline of the annual life cycle were described by Ito1971, '73, Imamura 1974, Ito and Imamura 1974.

Methods

1. Measurement of body size

The body size measurement of the workers has been carried out differently by some authors; Buckingham (1911), head width at supraorbital line, and head length from posterior margin of head to apex of clypeus; Lee (1938), body length from front of closed man-

1) Biological and Ecological Studies of *Formica yessensis* Forel. V.

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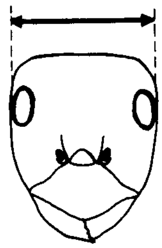

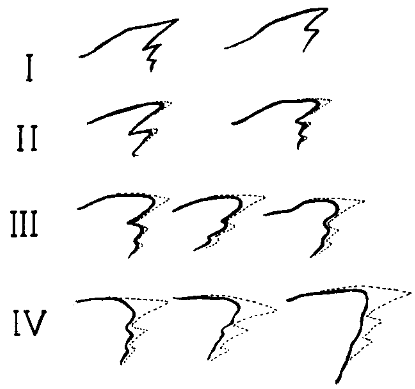

Fig. 1. Fig. 2.
Fig. 1. Outerorbital distance used as body size index.
Fig. 2. Four classes showing degrees of mandibular wear.

dibles to gastric tip; Dobrzanska (1959), head width. Using these measurments as indices for body size, the authors divided the workers into three classes, small, intermediate and large ones.

In the present study, the maximal outerorbital distance was chosen as the index for body size (Fig. 1), for this part is easy to measure correctly and not affected by the deviation due to the slight change in orientation at measurement (mesosoma) or by the physiological condition (gaster). Using this index, the workers were divided into three classes: Small (<1.2 mm), medium (1.2∼1.48 mm), large (1.48 mm<).

2. Estimation of relative age

So far several methods have been adopted in estimating relative age of worker ants. For instance, Otto (1958) and Hohorst (1972) determined the age by the grade of ovarian development. Dobrzanska (1959) traced actual individual history in laboratory by marking. But these methods can not be used for the aged workers in the field because their ovaries are already degenerated and the continuous observation of marked ants are virtually impossible. Therefore degree of mandibular wear was taken as an index for age determination.

The mandibles were distinguished into four classes (Fig. 2) according to the degree of wear: I. Intact or nearly so, that is, completely pointed, II. slightly worn, III. apparently worn and IV. heavily worn. Although the distinction is arbitrary, being not free from subjective judgement, especially at subtle differences, it is sufficient to show a general tendency.

Results

1. Relation between size distribution and task preference

The size distribution in workers performing different tasks is shown in Fig. 3.

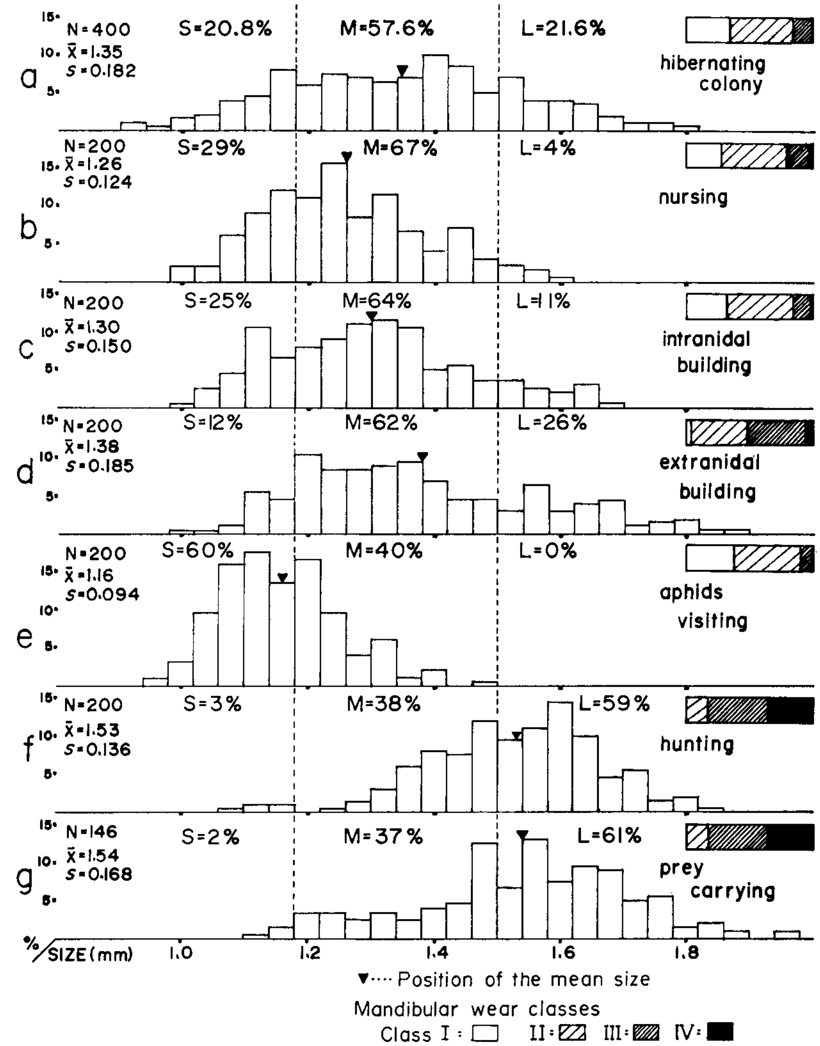

Fig. 3. Size distribution and task performance. N, number of measured individuals. x̄, mean size. *s*, standard deviation. S, small workers. M, medium workers. L, large workers.

Size distribution in a hibernating nest

To know the size distribution in a whole colony, 400 workers were selected at random from a hibernating colony excavated in early March, 1974. The size distribution follows the normal curve, ranging from 0.9 mm to 1.8 mm (mean 1.35 mm) (Fig. 3a). Therefore, *F. yessensis* is apparently monomorphic with ample size variation in workers. Medium-sized workers occupy slightly more than a half, and large and small workers are nearly equal in percentage ratio.

Size distribution and nursing

In early June, 1973, three nests were excavated and the individuals carrying the eggs, regarded as potential nursers, were collected. 200 individuals were chosen by random samplings. The size distribution (Fig. 3b) is approximately normal again, but the percentage of small workers is higher than in Fig. 3a, occupying 29% while large workers only 4%. Medium workers also increased, but in this class the smaller ones were more numerous than in the hibernating colony, resulting in a decrease of the mean to 1.26 mm.

Intranidal building

On the surface of large nests, workers carrying sand particles and other materials from inside to outside of the nest are seen in the season of high colony activity. They are regarded as workers participating in intranidal building activity. In late June and early July, 1973, such workers were collected and 200 individuals were measured (Fig. 3c). The size distribution is similar to that of nursing workers with the percentage ratios of small and medium workers 25% and 64% respectively. The percentage of large workers, however, is higher than in nursing workers, giving a higher mean size 1.30 mm.

Extranidal building

On the nest surface, some workers are seen in carrying nest materials such as pieces of vegetable matter and putting them on the appropriate points. Such workers, regarded as engaging in extranidal building, were collected and 200 individuals were measured (Fig. 3d). The percentage of large individuals is distinctly higher than in case of intranidal building, attaining 26%. The variance (s^2: 0.034) is higher even than that of Fig. 3a (s^2: 0.033). It means the absence of size bias in the workers participating in this task, which is interesting compared with the case of the comparable task, intranidal building.

Aphid visiting

In Ishikari Shore, a windbreak forest of oak, *Quercus dentata*, runs parallel with the shoreline. On the leaves of oak, many workers collect the excreta of aphids in summer and autumn. Such workers were collected in late June and early July, 1973 and 200 workers were measured (Fig. 3e). In collecting the workers special attention was paid to exclude those hunting on the tree. The size distribution is most uniform among those presented in Fig. 3, consisting of only small to small-medium individuals with the very low mean (1.16) and variance (s^2: 0.009).

Hunting and prey carrying

The workers found at a distance of the nest, more than 2 m apart, were collected in late June and early July, 1973 and 200 individuals were measured

(Fig. 3f). Although most of these workers were surmised as practicing the hunting, searching for the food such as live or dead insects, earthworms, etc., the inclusion of some workers engaging in other tasks, for instance, before visiting aphids or after carrying away some waste materials, is likely. To exclude this possibility, 146 workers actually carrying prey were collected through the active season and their body size was measured (Fig. 3g). The accordance of these two results was ascertained by t-test (t: 0.578). Both Fig. 3f and Fig. 3g show that hunting is accomplished by larger workers. Large and medium ones occupy 59–61% and 37–38% respectively, while small ones only 2~3%. The mean is 1.53~1.54 mm and the distribution is sharply contrasting other graphs, especially that of aphid visiting.

Applying t-test to these size distribution, the significant difference was found between any of them, excluding between hunting and prey carrying. Therefore, nursing, intra- and extranidal building, aphid visiting and hunting are carried out by the worker populations of different size distribution, and this is true even between two intranidal tasks, building and nursing.

However, it must be mentioned that the size-linked polyethism is not firmly fixed but plastic. For instance, the size distribution of aphid visiting workers varies according to the season. On October 8, 1973, 200 workers visiting aphids were taken and their body size was measured. As shown in Fig. 4, the medium-sized workers with apparently or even heavily worn mandibles increased and smaller ones decreased in prehibernating aphid visitors compared with summer ones. At this time, the colonies were just before the hibernation and few hunting workers were found out of the nests. Probably some hunting workers participated in aphid visiting in part due to the decrease of sufficient food available in the field.

2. Task performance and relative age estimated by mandibular wear.

Table 1 shows the percentage of mandibular wear classes in workers which were used to show the size distribution given in Section 1.

The age distribution in the whole colony is estimated by the results from the hibernating colony. Most workers in the colony have intact or nearly intact mandibles, while those having apparently worn mandibles (Class III) occupy 15% and those with heavily worn mandibles (Class IV) are found only 1%.

The results in the workers making nursing, intranidal nest building and aphid visiting are similar to that of the hibernating colony except for the higher ratio of intact mandibles in aphid visiting workers. Combined with the smaller mean body size of this group, the result suggests that these ants are rather specialized in the task which does not necessitate the frequent use of mandibles. Therefore, the degree of mandibular wear in these workers might not be an adequate index of aging, merely indicating the infrequent use of mandibles.

In the case of extranidal building the ratio of moderately worn individuals

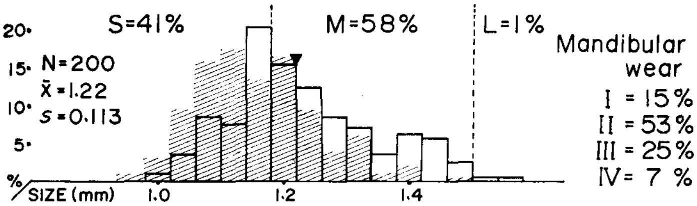

Fig. 4. Size distribution of aphids visiting workers soon before hibernation (Solid line block: Oct. 8, 1973). Hatched block, size distribution in summer (Fig. 3e).

Table 1. Relation between performance and mandibular wear. 1) Each class was weighted as 1, 2, 3, 4 respectively.

Task		hibernating colony	nursing	intranidal building	extranidal building	aphids visiting	hunting	prey carrying
Number of individuals examined		400	200	200	200	200	200	146
Percentage ratio of classes in mandibular waer	I	35	28	32	3	38	0	0
	II	49	51	52	45	52	13	17
	III	15	18	14	46	9	53	47
	IV	1	3	2	6	1	34	36
Weighted man wear[1)]		1.82	1.96	1.86	2.55	1.73	3.21	3.19

increased compared with those mentioned above; Class II and III occupying 91%. Such increase is more accentuated in hunting (and prey carrying) workers, where individuals with apparently to heavily worn mandibles (Class III, IV) decidedly outnumbers those with more or less intact mandibles. As a whole, the worn mandibles increase in the workers making extranidal functions except aphid visiting, while the intact mandibles prevail in those performing intranidal functions. Finally, the low percentage ratio of the workers with worn mandibles in the hibernating colony might indicate the death of such presumably old workers engaging in hunting or extranidal building before hibernation, because the mortality during hibernation seems low judging from the virtual lack of deaths within hibernating nests (Imamura, unpub.).

Discussions

Since Buckingham (1911) it has been confirmed in many ant species that there is no sharp segregation of tasks according to body size. However, it has also been recognized that there is a general tendency in various species, in which the larger workers engaging more in outdoor activities and smaller ones more in intranidal tasks (Ehrhardt 1931, Goetsch 1934, cf. also Pardi 1950, Sakagami 1953). In the red wood ant, or in the subgenus *Formica*, the same tendency is recognized in *F.* (*F.*) *rufa rufopratensis minor* Gösswald by Otto (1958).

The result obtained by the present study agrees with this general tendency in ants. The unique exception, however, is reported by Dobrzanska (1959). She observed in *F.* (*Raptiformica*) *sanguinea* Latreille the participation of 65% of large workers and only 28.5% of small ones in nursing, whereas the performance of foraging by 6 and 56% of them respectively. Based upon this result she concluded that in the genus *Formica* the smaller workers would be more agressive. But this ascertion contradicts the general trend in ants mentioned above. It is likely that *F. sanguinea* behaves particularly in part due to its peculiar dulotic life depending on the species of the subgenus *Serviformica*, the workers of which are in average smaller.

The degree of mandibular wear shown in the present study is regarded as a combined outcome of aging and tasks preferred. It is reasonable to assume that building and carrying activities give more defacement of mandibles than nursing and aphid visiting. On the other hand, it is also obvious that the mandibular wear proceeds monotonously with aging. For instance, the workers engaging in intranidal building have mandibles apparently less worn than those making extranidal building activity. Nevertheless, the intranidal building is a task made by incessant use of mandibles, the carrying of sand particles and other matters is repeated 7～36 times (mean 12, Higashi unpub.) per 10 min. for many days. This indicates that the difference between workers making intra- and extranidal building is partly conditioned by aging. The scarcity of workers with heavily worn mandibles in a hibernating nest also favors this assumption.

The tendency that the earliest phase of the adult worker life is characterized by the absence of participation in particular tasks, and then young workers nurse the young and some of them gradually change to accomplish the extranidal functions, has been recognized by many authors (Buckingham 1911, Ehrhardt 1931, Wilson *et al.* 1956, Otto 1958, Dobrzanska 1959, Weir 1959 etc.) though not so sharply age-linked as in the honeybee (Rösch 1925 1930, Lindauer 1952, Ribbands 1952, Sakagami 1953, Free 1965, Sekiguchi and Sakagami 1966). This is also recognized in *F. yessensis*, although the absense of participation in particular tasks in the earliest phase is general, especially in large workers because few of them seem to perform nursing.

The function of aphid visiting shows an interesting peculiarity both in size and mandibular wear despite of being an extranidal function. Dobrzanska (1959) states that in *F. sanguinea* the foraging excreta from aphids is a passive function similar to nursing, because it demands the minimum of mobility (carrying the excreta to the nest two or three times in 24 hours), following a fixed trail, being relatively stable and less dangerous for repeated use and frequent traffic. In her experiment, an artificial colony composed of only aphid visitors with artificial feeder but isolated from aphids perished without performing functions other than nursing. In case of *F. yessensis* in Ishikari Shore, however, the workers visiting aphids seem not so specialized, for some of them make long trips from the nest without following ant trail as confirmed by individual marking method (Higashi unpub.). For this reason, the unworn mandibles of the workers visiting aphids is interpreted as a combined outcome of task and age. These workers may be older than estimated by mandibles which remain less worn for the task preferred.

Wallis (1965) states that the oldest ants are the principal hunters. In *Myrmica scabrinodis* Nylander, the hunters occupy 10% and the most active ones only 1.3% of all workers (Weir 1958). In *F. yessensis*, too, the principal hunters are old and most of the oldest workers (Class IV) seem to be hunters, because the individuals having heavily worn mandibles occupy as much as 34~36% while only 1% in the whole colony collected during hibernation.

Dobrzanska (1959) states that building (digging) and removal of rubbish can be included among intermediary functions, requiring mobility but less subjected to extranidal hazards. In the present study, nest building is regarded as such intermediary function in both size distribution and mandibular wear. Within this activity, however, the intranidal building is closer to nursing and extranidal building to hunting.

Combining all information enumerated above, the relations among body size, aging and functions executed are schematically presented in Fig. 5. Larger workers may stay in the nest in the early period with less performance of nursing, then may change to intra- and extranidal building, and finally to hunting. Smaller ones may also stay in the nest performing nursing. Some of them may participate in intranidal nesting, then visiting aphids, while others, especially smaller ones, may directly go to aphid visiting. Medium-sized workers may show the pattern intermediate between larger and smaller ones.

But the schema is still premature in many aspects. In contrast to the age-conditioned polyethism in the honeybee, the age-performance relation is not yet correlated with the absolute age due to the worker life span much longer than in honeybee workers, which makes the precise studies difficult and probably obscures the clear transition from one stage to another.

Further, the plasticity in individual workers was stressed by many authors (Ehrhardt 1931, Otto 1958, Weir 1958, Dobrzanska 1959, Wallis 1965 etc.). In *Myrmica rubra laevinodis* Nylander, for instance, if a worker is transferred from one nest to another, she sometimes changes the task but the return to the previous nest makes her release the revival of the previous task once abandoned (Ehrhardt 1931). In *F. polyctena* Foerster, the persistence to a particular task is diurnally conditioned, the highest at afternoon but declining by the evening. Further, the persistence is variable among workers, some ones continue to do one task while others frequently changing tasks (Otto 1958). In *F. sanguinea*, intranidal workers can perform extranidal tasks at the forced emergency (Dobrzanska 1959).

In *F. yessensis*, too, some individually marked workers observed under the

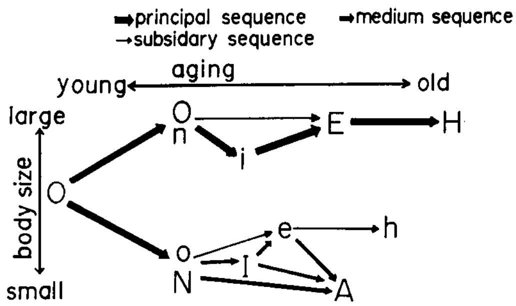

Fig. 5. Size-age-task relation. O, o; no performance. N, n; nursing. I, i; intranidal building. H. h; hunting. A; aphids visiting. Capitals, predominant performance. Smalls, subsidiary performance.

natural condition carried out at least two or three tasks during 16 days in early July, 1973 (Higashi unpubl.). Therefore, under the broad framework determined by size and age, the task performance or division of labor is plastic in *F. yessensis* as in general in most other ants precisely observed.

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Summary

The relation of task performance to body size and mandibular wear was studied in a polydomous red wood ant, *Formica* (*Formica*) *yessensis* Forel. The main results are:

1) Smaller workers are apt to make intranidal tasks and aphid visiting and larger ones hunting.

2) Nursing is mainly made by younger workers while hunting by older ones.

3) Mandibular wear is used as an index of relative age but not in all cases, for instance, aphid visitors keep relatively unworn mandibles even though they are seemingly older than assumed.

4) Workers participating in building activities are intermediate between nursers and hunters as to size-age relation, those performing intranidal building closer to nursers and extranidal builders to hunters.

Based upon these results, the size-age-task relation was schematically presented. Task performance is regarded as plastic within the framework given by size-age relation.

References

Buckingham, E. N. 1911. Division of labor among ants. Proc. Amer. Acad. Arts and

Sci., XLVI, **18**: 425–507.

Chen, S. C. 1937a. Social modification of the activity of ants in nest-building. Physiol. Zoöl. **10** (4): 420–455.

——— 1937b. The leaders and followers among the ants in nest-building. *Ibid.* **10** (4): 437–455.

Dobrzanska, J. 1958. Partition of foraging grounds and modes of conveying information among ants. Acta Biol. exper. **18**: 55–67.

——— 1959. Studies on the division of labor in ants genus *Formica*. *Ibid.* **19**: 57–81.

Ehrhardt, S. 1931. Über Arbeitsteilung bei *Myrmica*- und *Messor*-Arten. Z. Morph. Okol. Tiere **20**: 755–812.

Free, J. B. 1965. The allocation of duties among worker honeybees. Symposium of the Zoological Society of London **14**: 39–59.

Gösswald, K. and Bier K. 1954a. Untersuchungen zur Kastendetermination in der Gattung *Formica*. 3. Die Kastendetermination von *F. rufa rufo-pratensis minor* Gossw. Insectes Sociaux **1** (3): 229–246.

——— and ——— 1954b. Untersuchungen zur Kastendetermination in der Gattung *Formica*. 4. Physiologische Weisellosigkeit als Voraussetzung der Aufzucht von Geschlechtstieren im polygynen Volk. *Ibid.* **1** (4): 306–318.

——— and ——— 1957. Untersuchungen zur Kastendetermination in der Gattung *Formica*. 5. Der Einfluss der Temperatur auf die Eiablage und Geschlechtsbestimmung. *Ibid.* **4** (4): 335–348.

Hohorst, B. 1972a. Entwicklung und Ausbildung der Ovarien bei Arbeiterinnen von *Formica* (*Serviformica*) *rufibarbis* Fabricius (Hymenoptera: Formididae). *Ibid.* **19** (4): 389–402.

——— 1972b. Jahreszeitliche Veränderungen der Ovariolen bei Arbeiterinnen von *Formica rufinarbis* Fabr. (Hym., Form.). *Ibid.* **19** (4): 403–404.

——— 1972c. Biometrische Untersuchungen an *Formica* (*Serviformica*) *rufibarbis* Fabricius (Hymenoptera: Formicidae). *Ibid.* **19** (4): 405–407.

Horstmann K. 1973. Untersuchungen zur Arbeitsteilung unter den Aussendienstarbeiterinnen der Waldameise *Formica polyctena* Foerster. Z. Tierpsychol. **32**: 532–543.

Imamura, S. 1974. Observations on the Hibernation of a Polydomous Ant, *Formica* (*Formica*) *yessensis* Forel. Jour. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. **19** (2): 438–444.

Ito, M. 1971. Nest distribution of *Formica yessensis* Forel in Ishikari Shore, in reference to plant Zonation. *Ibid.* **18** (1): 144–154.

——— 1973. Seasonal population trends and nest structure in a polydomous ant, *Formica* (*Formica*) *yessensis* Forel. *Ibid.* **19** (1): 270–293.

——— and S. Imamura 1974. Observations on the nuptial flight and internidal relationship in a polydomous ant, *Formica* (*Formica*) *yessensis* Forel. *Ibid.* **19** (3):

Kiil, V. 1934. Untersuchungen über Arbeitsteilung bei Ameisen (*Formica rufa* L., *Camponotus herculeanus* L. und *C. ligniperda* Latr.). Biol. Centralblatt **54**: 114–146.

Lee, J. 1938. Division of labor among the workers of the Asiatic carpenter ants (*Camponotus japonicus* var. *aterrimus*). Peking nat. Hist. Bull. **13**: 137–145.

Lindauer, M. 1952. Ein Beitrag zur Frage der Arbeitsteilung im Bienenstaat. Zeitschr. vergl. Physiol. **34**: 299–345.

Morley, B. D. W. 1946. Division of labor in ants. Nature **158**: 913–914.

Ökland, Fr. 1931. Studien über die Arbeitsteilung und die Teilung der Arbeitsgebietes der roten Waldameise (*F. rufa* L.). Zeitschr. Morph. Ökol. Tiere **20**: 63–131.

Otto, D. 1958. Über die Arbeitsteilung im Staate von *Formica rufa rufo-pratensis minor*

Gössw. und ihre verhaltensphysiologischen Grundlagen. Wiss. Abh. Deuts. Akad. Landwirtsch. Berlin **30**: 1–169.

Pardi, L. 1950. Recenti ricerche sulla divisione di lavoro negli Imenotteri sociali. Boll. di Zool. **17**: 17–66.

Ribbands, C. R. 1952. Division of labour in the honeybee community. Proc. Roy. Soc. (B) **140**: 32–43.

Rösch, G. A. 1925. Untersuchungen über die Arbeitsteilung im Bienenstaat. 1. Teil. Die Tätinkeiten im normalen Bienenstaate und ihre Beziehungen zum Alter der Arbeitsbienen. Zeitschr. vergl. Physiol. **2** (6): 571–631.

———— 1930. Untersuchungen über die Arbeitsteilung im Bienenstaat. 2. Teil: Die Tätigkeiten der Arbietsbienen unter experimentell veränderten Bedingungen. *Ibid.* **12** (1): 1–71.

Sakagami, S. F. 1953. Untersuchungen über die Arbeitsteilung in einem Zwergvolk der Honigbiene. Beiträge zur Biologie des Bienenvolkes, *Apis mellifera* L. I. Jap. Jour. Zool. **11** (2): 117–185.

———— 1959. Arbeitsteilung in einen weisellosen Bienenvölkchen. Zeitschr. Bienenforsch. **4**: 186–193.

Sekiguchi, K. and S. F. Sakagami 1966. Structure of foraging population and related problems in the honeybee, with considerations on the division of labour in bee colonies. Hokkaido Nat. Agr. Exp. Sta., Rep. No. **69**: 1–65.

Wallis, D. I. 1964. The foraging behaviour of the ant, *Formica fusca*. Behaviour **23**: 149–175.

———— 1965. Division of labor in ant colonies. Symp. Zool. Soc. London **14**: 97–112.

Weir, J. S. 1958. Polyethism in workers of the ant *Myrmica*. Insectes Sociaux **5** (1): 97–128 (3): 315–339.

———— 1959. The influence of worker age on trophogenic larval dormancy in the ant *Myrmica*. *Ibid.* **6** (3): 272–290.

Wilson, E. O. 1955. Division of labor in a nest of the slave making ant *Formica wheeleri* Creighton. Psyche **62** (3): 130–133.

————, Eisner, T., Wheeler G. C. and J. Wheeler 1956. *Aneuretus simoni* Emery, a major link in ant evolution. Bull. Mus. comp. Zool. Harv. **115**: 81–99.

———— 1971. The insect societies. Belknap Press. Harvard. 548 pp.