

Intercolonial differences in raiding activities in the Japanese slave-making ant *Polyergus samurai*

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Summary

Intercolonial differences in raiding activity were investigated in the field on 9 colonies of the slave-making ant *Polyergus samurai*. Duration of raiding season, the mean start time of the first raiding trip in a day, the mean speed of outbound and inbound trips, and the mean distance to target nests varied significantly among colonies. The variance in start time of raiding was correlated with that in soil temperature and diurnal change pattern in soil temperature at the nest sites. The speed of trips and the first day with trips in the season also correlated with soil temperature at the nest site. Simple environmental factors well explained the observed variances in raiding activity among colonies. Therefore, raiding behaviour of *P. samurai* seemed to be a stereotyped behaviour that is regulated through simple environmental factors.

Introduction

Slave-making (dulosis) in ants is a parasitic way of life in which parasites raid the labor force of other ant species and make them rear the parasites' offspring (Wilson, 1971; Hölldobler and Wilson, 1990). Dulotic species conduct raiding trips to target host nests and rob brood of host species. Because raiding is a conspicuous behaviour, many studies have focused on the details of slave-raids (see Hölldobler and Wilson, 1990).

Slave-making has occurred independently in two phylogenetic branches in the ants, i.e., subfamilies Myrmicinae and Formicinae. Dulotic myrmicine ants are tiny and easy to rear, thus several behavioral studies have been conducted in laboratories (e.g., Alloway, 1979; Alloway and Del Rio Pesado, 1983). On the other hand, because slave-making Formicinae ants are large and nest under the ground, most studies have been based on field observations (but see Kwait and Topoff, 1984).

Among slave-making Formicinae, the genus *Polyergus* consists of 5 obligately dulotic species that parasitize on closely related species of the genus *Formica* and

cannot live without slave workers. Many studies concerning raiding behaviour in *Polyergus* species have been conducted on all 5 species of this genus (for *P. rufescens*, Chechowski, 1975; Mori et al., 1991; for *P. lucidus*, Talbot, 1967, 1968; Marlin, 1968, 1969, 1971; Kwait and Topoff, 1984; for *P. breviceps*, Wheeler (1916), Topoff et al., 1984, 1985a, b, c, 1987, 1988, 1989; Topoff, 1985; for *P. samurai*, Yasuno, 1964; Hasegawa and Yamaguchi, 1994, and for *P. nigerrimus*, Marikovskiy, 1964). In general, several hundred *Polyergus* workers make a raiding column, rush into a target *Formica* nest and remove mainly host pupae. Several studies have shown that raiding trips occur on sunny, hot afternoons in summer and that climatic conditions (sunshine and temperature) affected their raiding behavior (Topoff et al., 1984, 1985a, b, c; Mori et al., 1991; Hasegawa and Yamaguchi, 1994).

Although raids of *Polyergus* are well studied phenomena, there have been few studies in which raiding behaviour of more than one colony was observed simultaneously, because *Polyergus* spp. are rare, and many observers are required to monitor multiple colonies. An exception is the study conducted by Topoff et al. (1985b), in which raiding behaviour of three *P. breviceps* colonies were observed during one season. However, even in that study, little was known about factors that promote intercolonial differences in raiding activity.

We have already reported the general pattern of raiding behaviour of the Japanese species, *P. samurai*, based on an extensive observations on 12 colonies (Hasegawa and Yamaguchi, 1994). In that study, all of the raiding trips of 6 colonies were recorded during the summer in 1992. Thus, comparisons of raiding behaviour among colonies are possible. In this paper, we provide the data on the raiding characteristics of these colonies, and analyzed factors affecting intercolonial differences in raiding activities of *P. samurai*. Differences in colony size, density of host nests around a parasite nest and soil temperature at each nest site are examined to elucidate causes of intercolonial variation in raiding behaviour.

Materials and methods

Study organisms and study site

Polyergus samurai is an obligately parasitic ant distributed in Japan (Yano, 1911). *P. samurai* enslaves a closely related species, *Formica (Serviformica) japonica*, as its labor force. The parasite conducts raiding trips to many *F. japonica* nests from early June to early September in central Japan (Hasegawa and Yamaguchi, 1994). Raiders make a raiding column, rush into the target nest and rob mainly worker pupae of the host. They conduct more than one raid within a day on some occasions. In general, the first raiding column of a day starts to a target nest several hours after the noon, and air and soil temperature in addition to sunshine seem to affect the occurrences of trips (Hasegawa and Yamaguchi, 1994).

The study site is the Ecology Park of the Natural History Museum and Institute, Chiba, Japan. The Ecology Park is a preserve with ca. 2 ha area in which vegetation of various types are maintained, and several hundred *F. japonica* nests inhabit this area (Yamaguchi, unpubl.).

Data sampling

To find *P. samurai* colonies, a brown tile plate (150×200×5 mm) was settled on each of 160 *F. japonica* nests from April to June in 1992. Most nests made a large chamber under the plate and carried brood (eggs, larvae and pupae) into the chamber. Conditions under the plates were checked once a week. When *Polyergus* workers were found in the chamber, the nest was judged as a *P. samurai* colony. In addition, as the body shape of *Polyergus* larvae are different from that of *Formica* larvae, the type of larvae found in the chamber was also used to distinguish the nests of the two species. In this way, we found 6 *Polyergus* colonies (P1, P2, P3, P4, P5, P8) by early June. The other 6 colonies were found after the first raids (3 June) occurred in the area. Therefore, a total of 12 colonies (P1 ~ P12) were investigated in the study area. We placed an additional 100 plates on other *Formica* nests in April 1993, but we could not find any more *Polyergus* colonies.

Six colonies (P1, P2, P3, P4, P5, P8) were monitored every day from June to late September for raiding activity (see Hasegawa and Yamaguchi, 1994). For most raiding trips, the start time of the first raid of the day, the number in the raiding force, the number of acquired slaves, and the speed of outbound and inbound trips were recorded (Hasegawa and Yamaguchi, 1994). In addition, for a part of trips of the other 4 colonies (P6, P7, P9, P12), we recorded the same raiding characteristics mentioned above. Behavioural data was not obtained from the rest two colonies (P10 and P11).

To determine which factors affect raiding behaviour, colony size, temperatures at nest site and nest density of the host species were analyzed for their correlation with intercolonial variation in raiding characteristics. We found about 400 *F. japonica* nests in the study area and noted their location on a map of the area. Then, nest density of the nest of host species within 10 m from a *Polyergus* colony was calculated. Size of a *Polyergus* colony was estimated by the maximum number of raiders participating in a raid in 1992. These estimates represent the minimum number of workers in a colony. Although the occurrence of raiding trips is correlated with several climate factors in *Polyergus* species (Topoff et al., 1985a; Mori et al., 1991; Hasegawa and Yamaguchi, 1994), the soil temperature was selected as a representative environment conditions. For each 8 *Polyergus* nests (P1, P2, P3, P4, P5, P7, P8, P9), soil temperature at a depth of 3 cm was measured every 30 minutes from 9:30 to 18:00 on 5 September 1993. Four colonies (P2, P3, P7, P9) had relocated their nests in early spring in 1993 (Hasegawa and Yamaguchi, unpubl.); for these colonies, the soil temperature was measured at both old and new nest sites.

Results

Intercolonial variation in raiding characteristics

Table 1 shows raiding characteristics of 9 *Polyergus* colonies. Because only a few trips were observed on P6, and no trip data was obtained for P10 and P11, these 3 colonies were excluded from the analyses. Variation in raiding characteristics among colonies were examined by one-way ANOVA, and results are also shown in

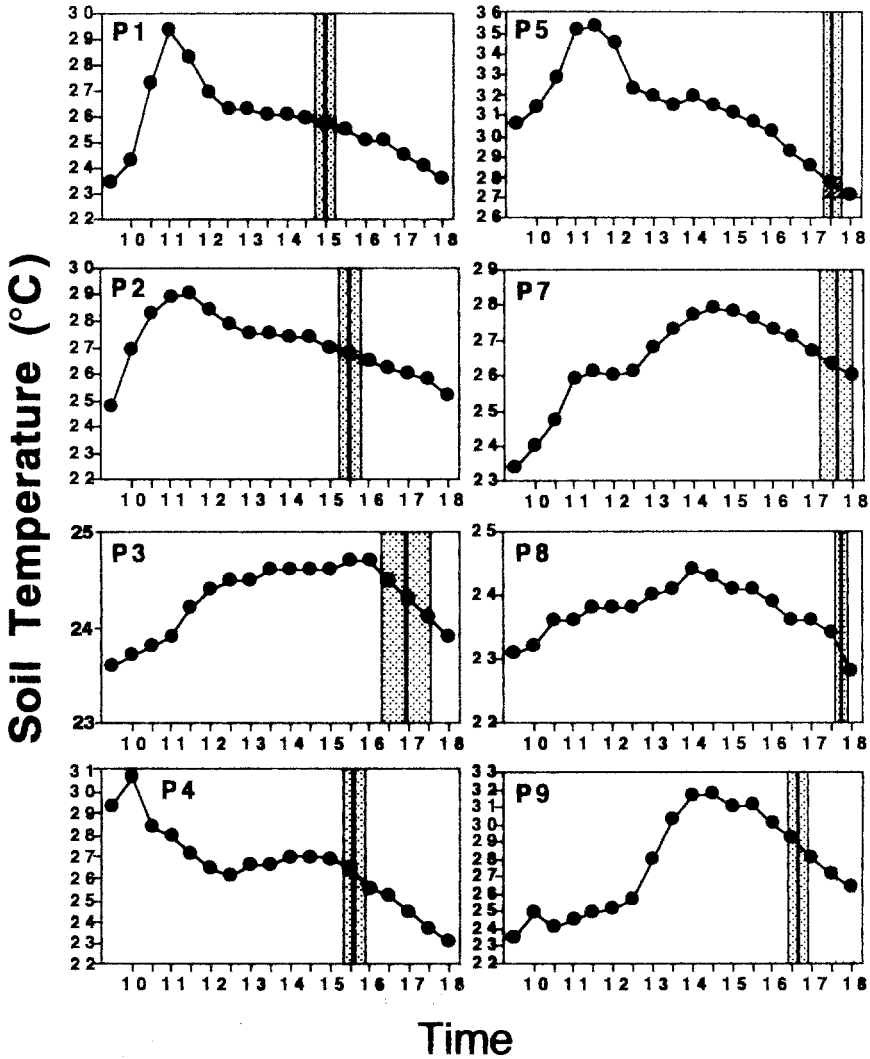


Figure 1. Diurnal change patterns in soil temperature at nest sites of *P. samurai*. The thick vertical lines represent the mean time at which the first raids of the colony occurred in 1992. The thin lines beside shaded area are 95% confidence limits

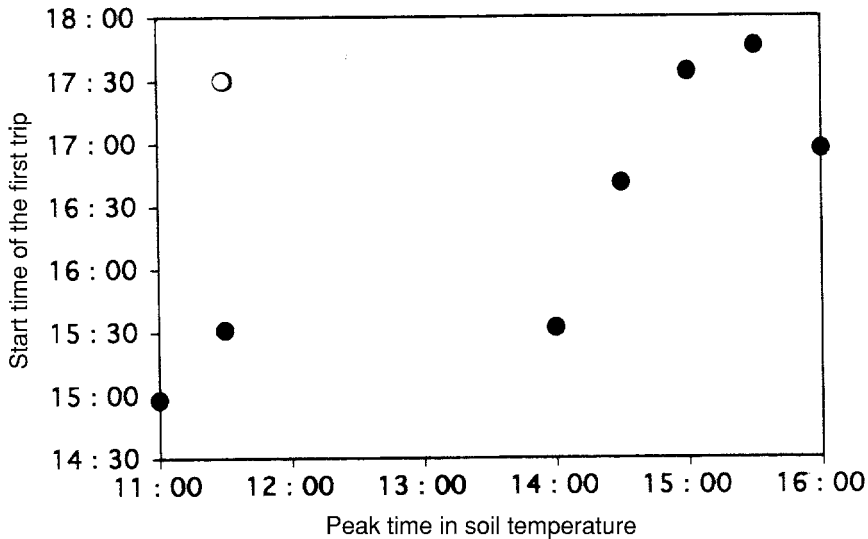


Figure 2. Relation between the last peak of soil temperature in 5 September 1993 and the mean start time of the first trip. The open circle represents the colony P5 that showed slightly different occurrence pattern of raiding trip corresponding to soil temperature at the nest site

Table 1. The ANOVA showed that the mean distance to a target nest, the mean speed of outbound trips, the mean speed of inbound trips, and the mean start time of the first trip in a day varied significantly among colonies.

Difference in timing of the first trip in the day

Figure 1 shows changes in soil temperature at each nest site for the 8 colonies (P1, P2, P3, P4, P5, P7, P8, P9) on September 1993. The mean start time of the first trip in 1992 (thick vertical lines in Fig. 1) with 95% confidential limits was also shown. The first trip occurred several hours after the last peak of soil temperature at each nest site. Thus, differences in the pattern of change in soil temperature are likely to affect timing of the first trip of the day. However, P5 showed a slightly different pattern in that the interval from the last peak to the first trip(6 hr) was a much longer than that for the other 7 colonies (1–4 hr). The soil temperature at this site was far higher than at the other sites, and, much longer time was required for decreasing the temperature (Fig. 1). Because soil temperature at the first trip was less than 30°C for all colonies, the soil temperature itself was also likely to affect the timing of raiding trips in the day.

If the change in pattern of soil temperature determined the time of the first trip, the last peak of soil temperature at each nest site should correlate with the start of the first trip. Figure 2 shows the relationship between the time of the last peak and the first trip. When all 8 colonies were included, there was no correlation (Kendall’s rank correlation $\tau=0.519$, $P>0.05$). There is, however, a significant correlation ($\tau=0.683$, $P<0.05$) between the two characteristics when P5 data (represented by

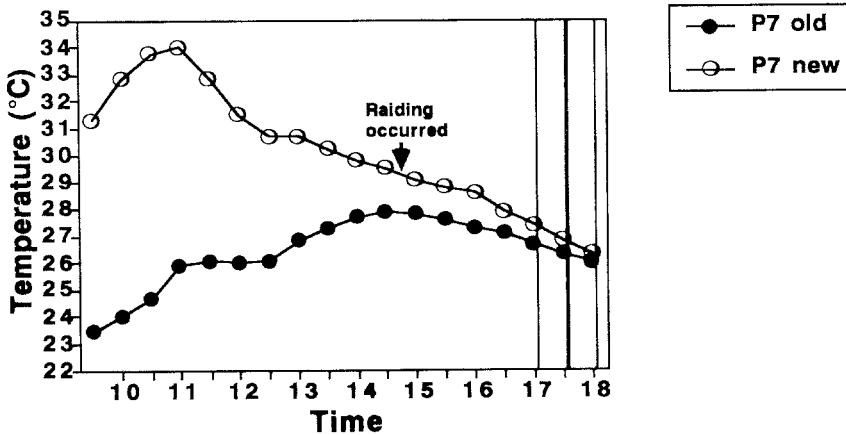


Figure 3. Diurnal change pattern in soil temperature at both old (closed) and new (open) nest sites of the colony P7. The thick and thin vertical lines represents the mean start time of the first raiding trip in 1992 and its 95% confidential limits, respectively. The arrow shows the time at which a raiding trip occurred on 5 September 1993

the open circle in Fig. 2) was excluded. As mentioned above, at the nest site of P5, a much longer time is required to decrease the soil temperature to the usual range for trips. Therefore, the timing of the first trip of the day was likely to be determined primarily by the temperature at the nest site. However, although the soil temperature at nest sites of some colonies, such as P3 and P4, was much less than 30°C, the same relationship was observed. If soil temperature is the only determinant of the start of trips, P3 and P4 should conduct trips more earlier. Thus, change in pattern of soil temperature was seemed to correlate with the timing of the first trip.

Another line of evidence also supported the above conclusions. As mentioned previously, colony P7 had relocated its nest site in early spring of 1993. Figure 3 shows the change in pattern of soil temperature at both the old and the new nest sites of P7. The time of last peak was much earlier at the new site, and, on 5 September 1993, P7 conducted a raiding trip (shown by the arrow in Figure 3) which started much earlier than that observed in the previous year (shown by the vertical line with 95% confidential limits). Because P7 did not conduct such early trips in 1992, this result strongly suggested the importance of change pattern of soil temperature at the nest site as the determinant of timing of the first trips.

Difference in speed of outbound and inbound trips

The speed of raiding column was invariably faster on inbound trips than on outbound one. In addition, there was significant variation in the mean speed of both outbound and inbound trips among colonies (Table 1). Colony size showed no correlation with trip speed (for outbound; $r=0.145$, N.S. for inbound; $r=0.251$, N.S.). Figure 4 shows the relationship between soil temperature at the first trip and trip speed. The speed of inbound trips positively correlated with soil temperature at nest

Table 1. Raiding characteristics of 9 colonies of *P. samurai*. The means and S. E. are shown

Colonies	P1	P2	P3	P4	P5	P7	P8	P9	P12	ANOVA
No. of trips	63	46	32	34	48	12*	33	16*	5*	–
No. of raiders	1837	781	1597	1044	1260	665	392	837	115	–
Density of host nests (nest/m ²)	0.242	0.064	0.115	0.115	0.153	–	0.280	0.025	0.064	–
Distance to target nest (m)	15.6±1.1	15.7±1.3	11.9±1.1	7.2±0.5	15.2±0.9	5.5±0.1	7.2±0.7	17.2±1.8	7.1±0.3	P<0.01
Speed of going trip (cm/min)	88.2±3.2	105.8±8.1	90.6±13.4	73.8±5.1	106.0±4.6	–	76.7±7.6	164.8±35.0	–	P<0.01
Speed of returning trip (cm/min)	189.4±1.0	215.1±11.1	210.7±20.3	173.6±8.6	228.9±11.4	–	108.4±3.8	286.2±40.3	–	P<0.01
Start time of the first trip	14:58±7.7	15:31±7.7	16:57±18.9	15:32±6.4	17:50±5.6	17:34±13.9	17:46±3.0	16:41±7.9	17:28±11.5	P<0.01

*: a part of raiding trips was observed.

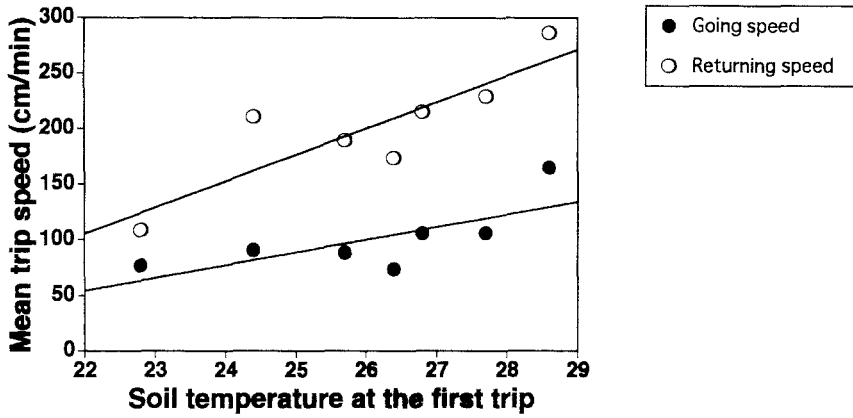


Figure 4. The relation between soil temperature at the first trip and the mean speed of outbound (closed) and inbound (open) trips of *P. samurai*

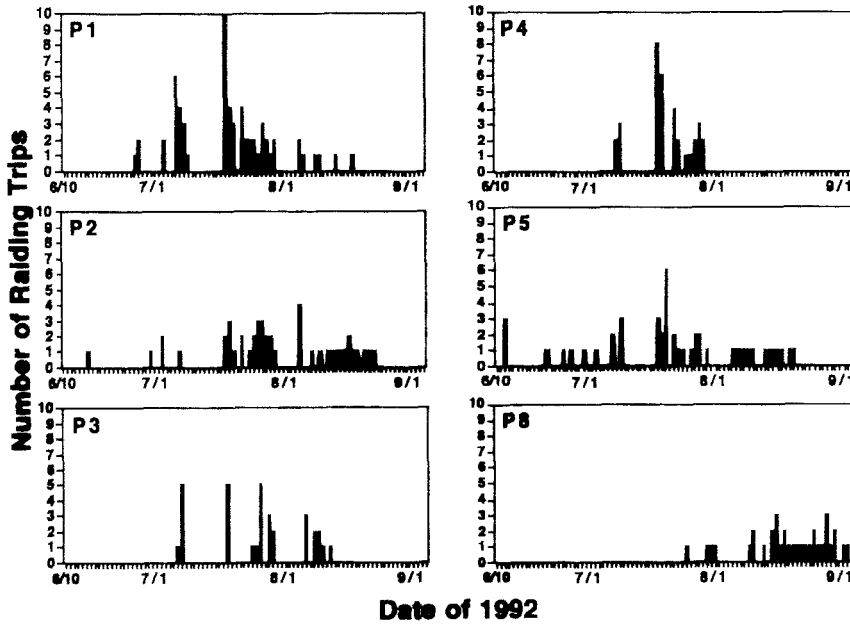


Figure 5. Occurrences of raiding trips for 6 colonies of *P. samurai* in the summer of 1992

site ($r=0.859$, $P<0.05$). In addition, the correlation of soil temperature on the out-bound speed was marginally insignificant ($r=0.727$, $P=0.06$). Therefore, the temperature at the nest site, or at least other factors correlated with soil temperature, affected to speed of trips.

Difference in the mean distance to a target nest

The mean distance to a target nest also significantly varied among colonies (Table 1). The soil temperature at nest sites showed no correlation with this characteristic ($r=0.545$, N.S.). The mean distance also did not correlate with the nest density of the host species or colony size (for nest density, $r=-0.234$, N.S.; for colony size, $r=0.521$, N.S.). A partial correlation analysis, however, showed an interesting result. When nest density was controlled, the partial correlation coefficient between the mean distance to target nest and colony size was raised to 0.616. On the other hand, the partial correlation coefficient between the mean distance and the nest density decreased to -0.441 when colony size was controlled. However, both partial correlation coefficients were still not statistically significant, probably due to the small sample size ($n=8$, $df=5$).

Difference in start of raiding season

The occurrences of raiding trips for the 6 *P. samurai* colonies (P1, P2, P3, P4, P5, P8) are shown in Figure 5. Because only a few raids were observed on P7, P9 and P12, these colonies were excluded from the analyses in this section. There are considerable differences in duration of raiding season among colonies. For example, the raiding duration of P4 and P8 almost did not overlap. In fact, above ground activity of P8 was not observed until late July although P8 was monitored every day.

There was no significant correlation between start days and colony sizes ($\tau=-0.222$, N.S.), or nest density of the host species ($\tau=0$, N.S.). To determine what factors affect the start of raiding season, the relationship between date of the first trip in the season and the maximum soil temperature at each nest site was examined. Because *P. samurai* never conducted raiding trips during the morning, when the change in pattern of soil temperature had more than one peak, the maximum temperature during the afternoon was used, e.g., for P4. Figure 6 shows the relationship between the maximum soil temperature and the day of the first trip in 1992. There is a negative correlation between the two factors ($\tau=-0.733$, $P<0.05$), and thus, the difference in temperature at each nest site seemed to cause the variability in the start of raiding season.

Discussion

The present study demonstrated that there are significant intercolonial differences in several raiding characteristics in *P. samurai*. Although many researchers have studied raiding behaviour of *Polyergus* spp. (Wheeler, 1916; Talbot, 1967, 1968;

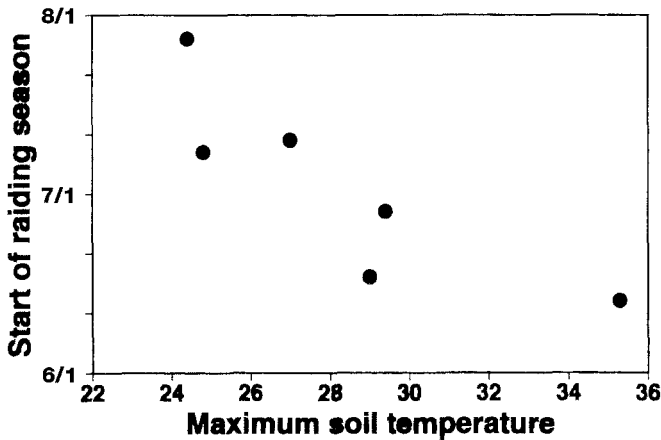


Figure 6. Relation between the start day of the first trip in 1992 and the maximum soil temperature in 5 September 1993

Marlin, 1968, 1969, 1971; Kwait and Topoff, 1983, 1984; Topoff et al., 1984, 1985 a, b, c, 1987, 1988, 1989; Trager and Johnson, 1985; Topoff, 1985; Vargo and Gibbs, 1987; Topoff and Greenberg, 1988; Mori et al., 1991; Hasegawa and Yamaguchi, 1994), little is known about intercolonial difference in raiding activity. In this study, the start time of the first trip in the day, the mean distance to a target nest, the speed of trips and the start day of raiding season significantly varied among colonies. However, the analyses also suggested that difference in several characteristics are explained by simple factors. In particular, temperature (measured as soil temperature) at nest sites seemed to affect on the raiding behaviour of *P. samurai*.

Temperature seemed to affect both speed of trips and start of raiding season. There are significant correlations between soil temperature at nest sites and trip speed (Fig. 3). Mori et al. (1991) reported that air temperature at nest site was significantly higher in days with trips than in days without trips. A similar relationship between temperature and raids have been shown in *P. samurai* (Hasegawa and Yamaguchi, 1994). *Polyergus* spp. may require high temperature for raiding activity. It is also likely that when temperature is high, *Polyergus* workers can move more quickly than under low temperature. In fact, when we checked under the nest plate in days with low temperature (days in which the maximum soil temperature was less than 23 °C), movement of *Polyergus* workers was very sluggish compared with that at raiding trips (pers. obs.). Thus, low temperature may be a physiological constraint on the raiding behaviour of *P. samurai*.

If the above speculation is correct, the correlation of soil temperature with start of raiding season is seemed to be reasonable. The maximum soil temperature at each site would correlate with amount of sunshine at the site. Accordingly, when the nest site is a relatively sunny place, soil temperature would attain the threshold for raiding trip earlier than at a less sunny site. As a result, the first trip in the season would occur earlier at sites with high soil temperature. Thus, the start time of raidings may be regulated by a simple environmental factor, i.e., soil temperature at

the nest site. However, in case of trip sepped, this characteristic may be affected directly by the other temperature factors because the ants are small and polikilothermic. Thus, experimental manipulations on several thermal environments are required to elucidate explicitly effects of temperature on raiding behaviour.

The first trip in the day occurred shortly after the last peak of the soil temperature at the nest site (Fig. 1). This result is consistent with the diurnal activity pattern of *P. breviceps* (Topoff et al., 1985a). *P. breviceps* showed a similar peak of activity in relation to the change in pattern of air temperature (Topoff et al., 1985a). Moreover, P7 changed the time of the first trip according to the last peak of soil temperature at the nest site (Fig. 3). If only soil temperature is the determinant of start of raiding trips, P7 should delay trips to the same temperature range observed in 1992. Thus, change pattern itself, or at least some other factors strongly correlated with soil temperature, would be a determinant of occurrence of raids. However, temperature itself is also likely to affect the start time of trips because all colonies conducted trips within a narrow range of soil temperatures (23.8~29.2 °C), and P5 delayed trips until the time at which soil temperature decreased below 30 °C. Thus, very high temperature may prevent *Polyergus* workers from above ground activity. Therefore, microclimatic difference at each nest site seemed to affect variability in occurrence of raiding trip among colonies.

It is interesting to speculate on the observed relationship among three characteristics, i.e., the mean distance to a target nest, colony size and nest density of the host species. The result of the partial correlation analysis on these three characteristics seemed to suggest that colony size and nest density of the host species have a reverse effect on the mean distance to a target nest, although the correlation was not statistically significant. Yasuno (1964) reported that nests of *Formica japonica* disappeared from the surrounding area of a *P. samurai* nest during the raiding season and intruded again in the area during the other season. Yasuno's result suggested that a *P. samurai* colony raids target nests from the near to the distant. If so, nest density of the host species should negatively correlate with the mean distance of trips to a target nest, because a *Polyergus* colony that nests at a low host-density site would trip to more distant target nests to obtain an enough amount of slaves. On the other hand, because a large *Polyergus* colony would require more slaves than a small colony, the large colony would raid to more distant *Formica* nests. The observed relationship may result from this scenario. The observed insignificance of the partial correlation coefficients may be result from the small sample size. More data are needed to elucidate this possible relationship.

In the other *Polyergus* species, a raiding column travels a much longer distance to a target nest than *P. samurai* did. For example, trip distances were 7 to 85 m in *P. breviceps* (Topoff et al., 1985b), 15 to 286 feet (4.6 to 87.2 m; Talbot, 1967) or over 100 m (Vergo and Gibbs, 1987) in *P. lucidus* and 70.36 ± 6.53 m (mean \pm SE) in *P. rufescens* (Mori et al., 1991). As mentioned above, nest density of the host species negatively correlated with the mean distance to a target nest. Differences in nest density of the host species may explain the difference in raid distance among species.

Finally, this study showed that many differences in raiding characteristics among colonies were explained by simple environmental factors (soil temperature at the nest site, change pattern in soil temperature and nest density of the host species).

Whereas, colony size had a little effect on the difference in raiding activities. Accordingly, the raiding behaviour of *P. samurai* seemed to be a stereotyped behaviour that is regulated by simple environmental factors. Thus, experimental manipulation of environmental factors in the laboratory and in the field would be useful to elucidate its effects of raiding behavior of *Polyergus* species.

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