Actes Coll. Insectes Sociaux, 7: 111-118 (1991)

RAIDING BEHAVIOUR OF THE OBLIGATORY SLAVE-MAKING ANT, *POLYERGUS RUFESCENS* LATR. (HYMENOPTERA FORMICIDAE)

A. MORI, D.A. GRASSO & F. LE MOLI

Dipartimento di Biologia e Fisiologia generali, Università degli Studi, Via delle Scienze, 43100 Parma, Italy

Summary: The raiding behaviour of the slave-making ant *Polyergus rufescens* Latr. was analysed and quantified in the field during the summer of 1988. The activity of the residents of a colony (with the presence of *Formica cunicularia* ant-workers as slaves) was observed for 10 hours each day from 6 July to 17 August. During this 53-day period of study, 38 raids occurred, among which 27 were followed by the sack of 10 different nests of *F. cunicularia* limited in an area of about 1650 m^2 whereas 11 failed for various causes. Raiding behaviour was always seen late in the afternoon of hot and clear days, and it was formed by the following characteristic phases: *I)* scounting; *II)* pre-raid activity with mass-recruitment; *III)* raid onset with the formation of an outbound column; *IV)* pillage at the target colony of *Formica*; *V)* return of the inbound column to the natal nest with loot transportation. Daylight hour of the beginning and finish of each phase of raiding behaviour was recorded. Moreover, the value of temperature, relative humidity and atmospheric pressure was recorded at the moment of raid onset. During the raiding activity we also noted: the length, the width and the speed of both the outbound and inbound columns; the time spent in the different phases of raid; the number of the raiders and the distance covered by them; the type of booty seized. The behaviour of the "activators" and the scouts was observed as well as their position in the storming swarm. Some activities not well described for this obligatory slave-making species, such as the digging out the soil near the target colony to facilitate the penetration of the raiding column, and the pillage of young or adult slave ants (eudulosis) were also observed in detail and recorded by video-tape.

Key-words: *Ants*, Polyergus rufescens, *social parasitism*, *raiding behaviour*.

Résumé: Comportement lors des raids chez la fourmi esclavagiste obligatoire, *Polyergus rufescens* Latr. (Hymenoptera, Formicidae).

Le comportement de la fourmi esclavagiste *Polyergus rufescens* Latr. lors de raids a été analysé et quantifié sur le terrain pendant l'été 1988. L'activité des ouvrières résidentes d'une colonie (en présence de *Formica cunicularia* en tant qu'ouvrières esclaves) a été observé pendant 10 heures chaque jour du 6 juillet au 17 août. Durant cette périod de 53 jours d'étude, 38 raids ont été observés sur lesquels 27 ont été suivis par le pillage de 10 nids différents de *F. cunicularia* situés dans une aire d'environ 1650 m²; cependant 11 raids n'ont pas abouti pour des raisons diverses. Les raids ont toujours été observés tard dans l'après-midi par journée chaude et serein. Ils étaient constitués par les différentes phases caractéristiques suivantes: *I)* reconnaissance par des éclaireuses: *II)* activité précédant le raid avec recrutement de masse: *III)* départ du raid avec formation d'une colonne "sortante"; *IV)* pillage de la colonie cible de *Formica*; *V)* retour de la colonne "remontante" au nid d'origine avec transport du butin. L'heure du début et de la fin de chaque phase du raid a été enregistrée. De plus, les valeurs correspondat à la température, à l'humidité relative et à la pression atmosphérique ont été notées au moment du départ du raid. Pendant le raid, nous avons également notè: la longueur, la largeur et la vitesse des colonnes sortantes et remontantes; la durée des différentes phases du raid; le nombre d'individus participant au raid et la distance couverte par ces derniers; le type de butin capturé. Le comportement des "activators" et des ouvrières éclaireuses a été observé ainsi que leur position dans la colonne d'assaut. Quelques activités assez peu décrites pour cette espèce esclavagiste obligatoire, telles que le creusement du sol près de la colonie cible pour faciliter la pénétration de la colonne de raid et le pillage de fourmis esclaves jeunes ou adultes (eudulosis), ont également été observées en détail et enregistrées sur magnétoscope.

Mots-clés: *Fourmis*, Polyergus rufescens, *parasitisme social*, *comportement lors de raids*.

INTRODUCTION

Slavery in ants is a form of social parasitism in which the slave-making species conduct group raids against nearby colonies of other closely related ants, drive away or kill the

residents, and pillage their brood. Such phenomenon can be either facultative or obligatory, the mean difference between the facultative and obligatory dulotic species being just the ability of the former to maintain the behavioural repertory typical of the free-living ants. In fact, many of the obligatory slave-makers possess both morphological and behavioural adaptations which develop their slave-raiding efficiency but attenuate their ability to perform the normal domestic tasks, so that the slaves are essential to maintain the colony.

The five species of the formicine genus *Polyergus (P. lucidus, P. breviceps, P. nigerrimus, P. samurai, and P. rufescens)* are all obligatory social parasites that conduct spectacular incursions against colonies of the related genus *Formica*, from which they have been phylogenetically derived.

The aim of this paper is to present the results of an eco-ethological field study on raiding behaviour of *P. rufescens* which is found in North America and Europe (Hölldobler and Wilson, 1990).

MATERIAL AND METHODS

The object of our research was a colony located in the province of Mantova (North Italy) and populated by workers of *Formica cunicularia* as slaves. The study was conducted over an unbroken period of 53 days in the summer 1988, during which the colony was monitored (also by video-tape) for 10 hours each day.

During the period of study, at the dulotic colony we observed the activity of both host and parasite. Each day at 5.00 p.m. we recorded the values of air temperature, relative humidity and atmospheric pressure. On the days with slave-raids, the same parameters were recorded at raid onset. We recorded also the distance and compass direction to each target colony during the raids. Moreover, a sample of host ants from each raided nest was collected and identified.

RESULTS AND DISCUSSION

During the period of study a total of 38 raids occurred. In the morning the mixed colony appeared to be a formicary of *F. cunicularia*, since the slave-makers seldom or never peeped out from the nest entrance.

The above-ground activity of *P. rufescens* began when a few workers emerged from the nest at around 2.42 p.m. Probably they are the so-called activators (cf. Dobrzanska and Dobrzanski,

1960; Czechowski, 1977) whose excitation provoked the exit in mass of the other slave-makers. In fact, during the following hour there was the emergence from the dulotic colony of many other *Polyergus* which began to mill around the nest entrance, sometimes moving off to explore in the grass. It was possible to follow 13 scouts whose trips extended at most about 30 m from the natal nest.

Pre-raid activity with mass recruitment began on the average at 4.34 p.m. Several hundred *Polyergus* gathered outside the mother nest and began to mill around the entrance within a radius of about 1 m, contacting and stimulating each other to start a raid. The time devoted to this phase greatly varied in different raids, ranging from a minimum of 2 min to a maximum of 105 min, and lasted on the average about 22 min.

Generally the raid began during the maximum of circling activity, as the ants converged on a dinstinct compass direction and formed a close-packed outbound phalanx. The mean daylight time for raid onset was about 5.00 p.m., but raids began as early as 4.00 p.m. and as late as 6.00 p.m. A rank order correlation test showed a great tendency ($r = -0.582$, $p<0.01$) for raids to begin earlier in the afternoon as the summer progressed (cf. Fig. 1)

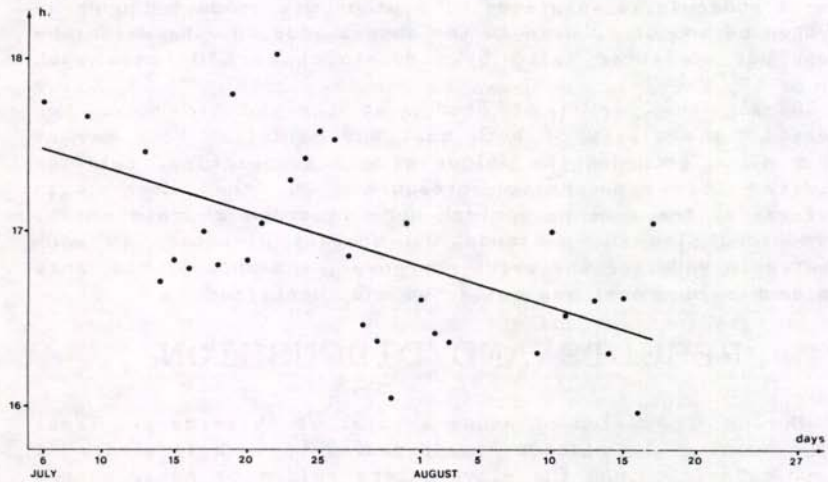

Fig. 1. Hours of raid onset correlated with the days of observation.

The column was sometimes longer than 10 m, wider than 40 cm at its head, and 20 cm at the middle. A salient particular of its organization was the presence of 1 or 2 scouts which seemed to lead the swarm. The conclusion that the raiding column proceeded with leaders contrasts with previous observations of Dobrzanska and Dobrzanski (1960) and Köhler (1966) in this species, whereas it perfectly agrees with the results of studies conducted in the American species of *Polyergus* by Kwait and Topoff (1984) and Topoff *et al.*(1987).

The mean number of workers participating in the raid was 1061. They advanced steadily at a mean speed of about 1.5 m/min along most of the outbound route, without disturbing other ants nests they passed, but sometimes stopping to search a *Formica* nest entrance.

As the raiding phalanx advanced across the terrain, many raiders moved from side to side. Moreover, many of them moved up and down the column, so that the composition of the swarm varied constantly.

Some alate and dealate queens were seen in the middle of the outbound column during 4 raids. None of them returned to the mixed natal nest with the raiding ants, one entered a colony of *Formica* and was not observed leaving it. This behaviour, described in this *Polyergus* species also by Forel (1874, cited by Emery, 1908) and by Emery (1908), is probably an excellent strategy to find and to invade a target colony of the host species, as suggested by Talbot (1968).

When a target colony of *Formica* was located, the penetration was almost immediate. Several raiders gathered in front of the entrance and began to move the little stones that blocked it and to dig the soil. This behavioural pattern of excavation, which allowed an easier mass-entrance, is peculiar to the raiding context, since in the mixed colonies the slave-makers left such labour to their slaves, as demonstrated by Sakagami and Hayashida in *P. samurai* (1962).

The raiding action of *P. rufescens* inside the target nest was so rapid that generally it took only few minutes to see the first raiders again above ground carrying the host loot. The low mean time spent on pillage seems to confirm that *Polyergus* workers, as other slave-makers (Regnier and Wilson, 1971), probably use pheromones that prevent the organization of defence by the residents and disperse the few defenders.

Worker pupae were captured preferentially, but big larvae and about a dozen of callow workers were carried away as well. In 3 raids, the raiders emerged from the target colony carrying mature adults of the host species. They were carried in pupal position into the parasite nest, but it was not possible to determine if they were killed by the residents or accepted and incorporated into the labour force of the dulotic colony. In

the latter case, this would be the first example of eudulosis (*sensu* Kutter, 1957) observed in the field.

Coming back home, the raiding column was more loosely organised and advanced at a mean speed of about 2 m/min, following exactly the same trail as the outbound trip. The differences between the speeds recorded during the trip to the target nest and the return to the mother nest are statistically significant ($p < 0.001$, 2-tailed Mann-Whitney 'U' test). This is probably due to the following of a chemical trail deposited during the outbound trip in addition to the use of optical cues, as demonstrated by Topoff *et al.* (1984) in *P. breviceps*. However, also a strong motivation to return home with the captured brood can be suggested.

On the average, *Polyergus* workers covered a distance of about 70 m per raid and the raid lasted about 50 min. At the dulotic nest, the raiders either dropped their booty at the nest entrance where it was picked up by the slaves, or carried it into the nest.

The above-ground activity of *P. rufescens* stopped immediately after they reached the mother nest, on the average at about 6.30 p.m.

Eleven (29%) raids ended in failure. Generally, a big puddle of water due to artificial or natural rain stopped the raiding column. The raiders fanned out and began circling as in their pre-raid activity at the dulotic nest. They dug around stones, in grass and leaves. If a *Formica* colony was not found, these searching movements lasted 5 to 10 min, then the raid was aborted and the ants returned to the mother nest.

During the remaining 27 (71%) raids, 10 colonies were attacked and sacked. According to Emery's rule (Emery, 1909), the raided colonies belonged to a species phylogenetically close to *P. rufescens*, namely *F. cunicularia*. On the contrary, the nests never attacked by the slave-makers, belonged to species less phylogenetically close to the raiders, as *Myrmica sabuleti*, *Lasius alienus*, *Lasius niger*, and *Tetramorium caespitum*.

Simple, compound and multiple raids were observed. Simple raids, with only 1 attack on a given day, were the most frequent. Compound raids, during which there were 2 attacks against the same host nest on the same day, occurred 4 times. In this case, after returning, many raiders continued to mill around and formed a second column that in a short time left the mixed colony again. Finally, a multiple raid occurred, during which 2 different host colonies were raided immediately one after the other.

At raid onset the sky was completely clear on 30 (94%) of the 32 days with raids, and only slightly cloudy on the other 2 (6%) days. Only on 2 (9%) of the 21 raid-free days was the sky

cloudless. This datum seems to support the hypothesis that also *P. rufescens* workers, like those of *P. breviceps* studied by Topoff *et al.* (1984), use the position of the sun and the polarized light, in addition to chemical cues, for scouting and orienting during raiding activity.

Unlike the values of relative humidity and atmospheric pressure, there was a statistically difference ($p < 0.001$, 2-tailed Mann-Whitney 'U' test) in the values of temperature recorded on days with (mean value 32.5 °C) and without (mean value 29.7 °C) raids.

Therefore, the absence of clouds and the temperature seem to be the most important weather conditions to influence raiding activity.

Certainly some aspects of the raiding behaviour of *P. rufescens* are not completely clear. Therefore, we intend to investigate some behavioural traits, and in particular the fate of the queens, the role of the scouts, the cues of orientation and the phenomenon of eudulosis.

ACKNOWLEDGMENTS

We wish to give our sincere thanks to Mr. A. Bellini and Mr. D. Bellini for the kind hospitality in the area of study. Thanks are also due to Miss E. Balestrini for designing the figure included in the text. This research was supported by grants from M.U.R.S.T. (40% and 60%) and C.N.R.

REFERENCES

CZECHOWSKI W., 1977. - Recruitment signals and raids in slave-maker ants. *Ann. Zool.*, 34, 1-26.

DOBRZANSKA J., DOBRZANSKI J., 1960. - Quelques nouvelles remarques sur l'éthologie de *Polyergus rufescens* Latr. (Hymenoptére, Formicidae). *Insectes Soc., 7,* 1-8.

EMERY C., 1908. - Osservazioni ed esperimenti sulla formica amazzone. *Rend. sessioni R. Acad. Sci. Ist. Bologna, 12,* 49-62.

EMERY C., 1909. - Über den Ursprung der dulotischen, parasitischen und myrmekophilen Ameisen. *Biol. Zbl., 29,* 352-362.

HÖLLDOBLER B., WILSON E.O., 1990. - *The Ants.* Springer-Verlag, Berlin Heidelberg.

KÖHLER F., 1966. - Untersuchungen zur Orientierung der Raubzüge der Amazonameise *Polyergus rufescens* Latr. *Insectes Soc., 13,* 305-310.

KUTTER H., 1957. - Ein neue Form der Sklavengewinnung bei Ameisen. *Umschau:* 327-329.

KWAIT E.C., TOPOFF H., 1984. - Raid organization and

behavioural development in the slave-making ant *Polyergus lucidus* Mayr. *Insectes Soc., 31,* 361-374.

REGNIER F.E., WILSON E.O., 1971. - Chemical communication and "propaganda" in slave-maker ants. *Science, 172,* 267-269.

SAKAGAMI S.F., HAYASHIDA K., 1962. - Work efficiency in heterospecific ant groups composed of hosts and their labour parasites. *Anim. Behav., 10,* 96-104.

TALBOT M., 1968. - Flights of the ant *Polyergus lucidus* Mayr. *Psyche, 75,* 46-52.

TOPOFF H., BODONI D., SHERMAN P., GOODLOE L., 1987. - The role of scouting in slave raids by *Polyergus breviceps* (Hymenoptera: Formicidae). *Psyche, 94,* 261-270.

TOPOFF H., LA MON B., GOODLOE L., GOLDSTEIN M., 1984. - Social and orientation behavior of *Polyergus breviceps* during slave-making raids. *Behav. Ecol. Sociobiol., 15,* 273-279.