

Review article

Comparison of reproductive strategies and raiding behaviour in facultative and obligatory slave-making ants: the case of *Formica sanguinea* and *Polyergus rufescens*

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Summary. A review of field and laboratory research concerning raiding behaviour, mating strategies and colony founding in *Formica sanguinea* and *Polyergus rufescens* (respectively facultative and obligatory parasites of the *Serviformica* species) is presented. The analysis and comparison of these crucial and peculiar moments in the life cycle of dulotic colonies may be a valid tool to clarify the evolutionary origins of slavery in ants.

Concerning the reproductive behaviour, *F. sanguinea* females mate only in nuptial flights. *P. rufescens* females mate on the ground around their natal nest, or return to a dulotic colony after mating flights and wait for a raid, or mate directly during a raid. Moreover, field observations suggest that *F. sanguinea* adopts a strategy similar to the “male aggregation syndrome”, whereas *P. rufescens* mating strategy can be considered similar to the “female calling syndrome”. In the field, newly-mated queens of both slave-makers participate in raiding swarms: following a slave raid is an advantageous strategy to locate and invade host nests and to establish a new dulotic colony.

For colony formation, *F. sanguinea* presents a great variety of possible strategies (independent foundation and dependent foundation including alliance, adoption, usurpation, and brood sack). This provides evidence of a behavioural plasticity that confirms its nature as a facultative parasite. On the contrary, *P. rufescens* depends only on usurpation, during which the Dufour's gland contents seem to play a crucial role in the appeasement of the residents of the target colony.

Also the raiding behaviour of *F. sanguinea* is less specialized than that shown by *P. rufescens*. In fact, in the obligatory slave-maker the important role of scouts in the organization of slave-raids is confirmed, which are rapid and effective. By contrast, raids of *F. sanguinea* may be regarded as a continuation and expansion of common foraging and predatory activity, as predicted by Darwin's hypothesis for the

origin and evolution of slavery in ants. Nevertheless, the intraspecific raids conducted by *P. rufescens* emphasize also the important role of territorial competition as evolutive cause of dulosis.

Key words: Reproductive strategies, raiding behaviour, slave-making ants, *Formica sanguinea*, *Polyergus rufescens*.

Introduction

It is well known that in ants, slavery (or dulosis) is a form of social parasitism in which the slave-making species exploit the labour of workers derived from colonies of the host species. Typically, the slave-makers regularly conduct group raids against neighbouring colonies of their host or slave species, kill or drive away the adults and pillage their brood. The slaves which eclose from the unconsumed pupal population form a social attachment to the slave-makers (Le Moli and Mori, 1985, 1987a, b; Hare and Alloway, 1987) becoming permanent and full members of the parasitic colony and performing their usual worker-ant functions for the mixed-species colony (Wilson, 1971; Alloway, 1980; Buschinger et al., 1980; Stuart and Alloway, 1983; Stuart, 1984; Mori and Le Moli, 1988).

The slave-making behaviour occurs either intra- or interspecifically and with varying degrees of specialization. In the facultative intraspecific slavery, the parasites attack and raid colonies of their own species. The enslavement of workers of another closely related species can be either facultative or obligatory. The facultative slave-makers appear to be at an early stage in dulotic evolution, since the workers of such species are not extremely specialized and they perform normal tasks of colony life even when slaves are present (Sakagami and Hayashida, 1962; Wilson, 1971; Mori and Le Moli, 1988).

The main difference between the facultative and obligatory dulotic species is simply the ability of the former to maintain the behavioural repertoire typical of the free-living ants. In fact, in the more derived slave-making species the worker caste has become so specialized in raiding that slaves are essential to maintain the colony. Many of the obligatory slave-makers possess both morphological and behavioural adaptations which develop their slave-raiding efficiency but, at the same time, attenuate their ability to perform the normal domestic duties which are left to the slaves (Wilson, 1971; Dobrzanska, 1978; Buschinger et al., 1980; Stuart and Alloway, 1983; Mori and Le Moli, 1988). Moreover, obligatory dulotic species are unable to found colonies independently and must rely on some form of non-independent or parasitic colony foundation. Often this involves usurpation in which newly-mated females penetrate a colony of the host species, kill the resident queen and become accepted by the resident workers which later assist them in rearing the parasitic offspring. In some species, established colonies also reproduce by fission or budding, in which the newly-mated queens depart from the parental nest and penetrate the host colonies accompanied by groups of their own workers (Wilson, 1971; Buschinger et al., 1980; Hölldobler and Wilson, 1990).

Since the first descriptions of the slave-raids of *P. rufescens* (Huber, 1810), the interest of myrmecologists for formicine dulotic species has grown fast and ecological and behavioural knowledge has been derived from pioneering observations at the beginning of this century and more recently from studies conducted both in the laboratory and in the field. Anyway, many aspects of the biology of some formicine slave-makers are still obscure and the lack of information on some processes prevent a secure understanding of the origin and evolution of slavery in ants (Hölldobler and Wilson, 1990).

In this paper, we present a review which summarizes the results of field and laboratory investigations concerning reproductive strategies and raiding behaviour in two species of European slave-making ants. They are the sanguinary ant *Formica sanguinea* Latr. and the Amazon ant *Polyergus rufescens* Latr., respectively facultative and obligatory parasites of the *Serviformica* species.

F. sanguinea is the only Eurasiatic component of the *F. sanguinea* group, which consists of 12 slave-making species, one in Eurasia and 11 in North America (Hölldobler and Wilson, 1990). Because the members of the *sanguinea* group do not have external morphological specializations (in particular sharp mandibles) and some of them often live without slaves, they all have been regarded facultative slave-makers (Hölldobler and Wilson, 1990). Anyway, recent observations suggest that *F. subnuda* and *F. subintegra* represent extreme modes of slave-making behaviour in this group (Savolainen and Deslippe, 1996).

Ants of the formicine genus *Polyergus* are all obligatory parasites. Five species are known: *P. samurai* of Japan and Eastern Siberia, *P. lucidus* and *P. breviceps* respectively of the east and west of North America, *P. nigerrimus* of the ex-Soviet Union, while *P. rufescens* is typically found in Europe (Hölldobler and Wilson, 1990).

Concerning the American amazon ants, most detailed researches were conducted on raid organization, mating behaviour and colony foundation in *P. lucidus* (Tanquary, 1911; Talbot, 1967, 1968; Harman, 1968; Marlin, 1968, 1969, 1971; Kwait and Topoff, 1983, 1984; Goodloe and Sanwald, 1985; Trager and Johnson, 1985; Vargo and Gibbs, 1987) and in *P. breviceps* (Wheeler, 1916; Topoff et al., 1984, 1985a, b, c, 1987, 1988, 1989, 1990; Topoff, 1990, 1997; Topoff and Greenberg, 1988; Topoff and Mendez, 1990). Considerably less is known about *P. samurai* and *P. nigerrimus* since the information about these species is limited respectively to the research by Sakagami and Hayashida (1962), by Marikovsky (1963), Yasuno (1964), and by Hasegawa and Yamaguchi (1994). Finally, notes on the behaviour of the European amazon ant go back to the pioneering studies of Forel (1874) and Emery (1915). Later, information on the biology of this species was given by Dobrzanska and Dobrzanski (1960, 1962, 1989), Köhler (1966), Zaayer (1967), Czechowski (1975a, b, 1977), and Dobrzanski and Dobrzanska (1978).

As regards the raiding behaviour of the obligatory slave-makers of genus *Polyergus*, the question of whether scouts actually exist and, if so, what their real role is, is a crucial and controversial problem. In fact, on the presence and significance of leaderships in the raiding column, there is no agreement among the authors who have studied *Polyergus* slave raids. Dobrzanska and Dobrzanski (1960, 1989) and Köhler (1966) in *P. rufescens*, Talbot (1967) and Marlin (1969) in *P. lucidus* observed that the raiding swarm proceeded with no leader. On the other hand, Kwait and Topoff (1984) and Topoff et al. (1987) showed that scouts lead the raiders to the *Formica* target nest, respectively in *P. lucidus* and *P. breviceps*. Moreover, study of the orientation and homing mechanisms of these slave-makers was neglected until a few years ago.

Among the American members of the *sanguinea* group, raiding behaviour has been studied in *F. subintegra* (Wheeler, 1910; Talbot and Kennedy, 1940; Savolainen and Deslippe, 1996), *F. wheeleri* (Topoff and Zimmerli, 1991), and *F. subnuda* (Savolainen and Deslippe, 1996). Moreover, the communicative signals that trigger and orient the raids of *F. rubicunda* were identified (Regnier and Wilson, 1971). Finally, the occurrence of long-lasting alarm signals that attract the slave-makers but disperse the defenders ("propaganda substances") discharged by slave-makers belonging to *F. pergandei* and *F. subintegra* was demonstrated (Regnier and Wilson, 1971). The raids of the European blood-red ants *F. sanguinea* have been described by several authors both in the field and in the laboratory (e.g. Huber, 1810; Forel, 1874; Wasmann, 1891; Dobrzanski, 1961, 1965; Czechowski, 1977; Ceusters, 1985).

By contrast, except for some observations concerning the activity of alates and the occurrence of mating flights (Stitz, 1939), the knowledge of mating behaviour of the species belonging to the *sanguinea* complex is poor. Moreover, the mode of colony formation by queens of these species has not been observed in nature, and most information concerning this phenomenon is derived from laboratory studies made at the beginning of this century by Wheeler (1906), Viehmyer

(1908), and Wasmann (1908). On the basis of these pioneering observations, it seems that a variety of possibilities is at the disposal of *F. sanguinea* ants for colony formation (Stitz, 1939). More recently, a study of colony takeover comparing the facultative parasite *F. wheeleri* with the more specialized species *P. breviceps* has been conducted in the laboratory (Topoff et al., 1990). Anyway, as emphasized by Hölldobler and Wilson (1990), the lack of field observations of colony founding by queens of the *F. sanguinea* group in the field 'continues to prevent a secure understanding of the evolutionary origins of dulosis'. Moreover, it is still unknown to what extent the various species of the *sanguinea* complex rely on temporary parasitism to start new colonies, as opposed to conspecific adoption followed by budding.

Reproductive behaviour (particularly colony foundation) and raiding activity are crucial and peculiar moments in the life cycle of the dulotic societies of ants. Therefore, we think that the analysis and comparison of the modalities of these phenomena in the facultative and obligatory slave-makers may be a valid tool to understand the evolutionary origins of slavery in ants. In particular, facultative slave-makers, like those of the *F. sanguinea* complex, represent a crucial link in the evolution of slavery in ants, because they are an intermediate parasitic group between free-living species, on the one hand, and obligatory dulotic species, on the other.

Reproductive strategies

Mating behaviour

Mating is the first step in the complex process of reproduction in ants. In most ant species, males gather in a swarm to call in females for mating (i.e. the "male aggregation syndrome"); in others, especially phylogenetically primitive and parasitic species, single females call males (i.e. the "females calling syndrome") (Hölldobler and Bartz, 1985; Hölldobler and Wilson, 1990; Bourke and Franks, 1995).

Concerning *F. sanguinea*, the mating and post-mating behaviour of reproductives belonging to two sympatric dulotic colonies was analyzed in the field in Northern Italy during the summer of 1996 (Mori and Le Moli, 1998).

The alates were active from the last days of June to the middle of July. One colony produced only females, the other only males. Mass flights, which took place early in the morning on sunny, hot, and clear days, were preceded and followed by many individual departures. Both males and females climbed grass blades or small sticks, where they tested their wings and flew off. The females left their colony about 10 minutes before the males and the two swarms moved away exactly in the same direction. Matings were observed on the trees and the rocks near the area of study. Typical nuptial flights were observed in this species also by Czechowski (pers. comm.). By contrast, intranidal matings were reported by Marikovsky (1967).

Since large numbers of males and winged females met away from parental nests during conspicuous and well-synchronized nuptial swarmings and males gather at specific

mating sites (likely producing sex attractant pheromones simultaneously), the mating behaviour of this facultative slave-maker seems to fall within the "male aggregation syndrome", typical of species that form large colonies and produce hundreds to thousands of reproductives every year (Hölldobler and Bartz, 1985).

During the first week following the mass flights, about 30 dealate queens were seen returning to their mother colony, approaching the nest, and trying to enter it. Dealate queens were observed participating in raiding swarms moving from this colony against several nests of *Serviformica* species. Once at the host colony, the slave-making females participated in digging the entrance of the target nest, entered it, and were never seen returning to the original dulotic colony. This observation supports the hypothesis that *F. sanguinea* relies on temporary parasitism to start new colonies, as opposed to conspecific adoption followed by budding.

Since *Polyergus* newly-mated queens are not capable of rearing even their first brood, they penetrate a colony of *Formica*, kill the resident queen(s), and become accepted by the resident workers (Topoff et al., 1988; Topoff, 1990). In this connection, the mating and post-mating behaviour of *Polyergus* queens includes several adaptations for reaching host colonies of *Formica*. In fact, after the mating flights, dealate females of *P. lucidus* often return to a dulotic colony, wait for a raid, and follow the raiding swarm to the target colony (Talbot, 1968; Marlin, 1971; Kwait and Topoff, 1984). By contrast, *P. breviceps* females copulate directly during a raid of their homocolonial workers (Topoff and Greenberg, 1988).

Flights of winged forms of the European amazon ant were observed in the field by Emery (1908, 1909, 1911), Czechowski (1975a) and Mori et al. (1991). To corroborate these data, the behaviour of the alates belonging to three sympatric colonies of *P. rufescens* located in the Apennines near Parma, were recorded during the summer of 1992 (Le Moli et al., 1994; Mori et al., 1994a).

The alates were active within the nests between the first days of July and the end of August. An interesting feature of the reproductive biology of this species is the variation of relative abundance of sexual forms from colony to colony. In fact, a total of 42 mass flights were observed, 6 (14%) of males, 19 (45%) of females, and 17 (41%) of males and females together. These data are consistent with those on the American species *P. lucidus*, for which colonies bearing only males were also described (Marlin, 1971). The strategy of producing mostly males or females is likely to occur in some species of the genus *Formica*, whose colonies tend to have a strongly biased sex-ratio or, if a nest produces both sexes, they often emerge at different times of the season. In both cases, inbreeding is effectively prevented (cf. Pamilo et al., 1978; Pamilo and Rosengren, 1983). These observations show that, in colonies of *P. rufescens* producing both sexes, the males emerge and fly off some days before females. Moreover, when nuptial flights involving males and females occur, although the timing of the take-off overlaps between sexes, the males fly from the nest first. Hence, the mating flight activities are not well synchronized within the colony.

It was also recorded that reproductives were active within colonies in different periods of the season, and differences in the timing of the reproductives' activity were also recorded among colonies.

All flights took place on sunny, hot and clear days and lasted about 50 min. Alate females appeared later than males. A considerable portion of alate females emerged during the period of mating flights but did not fly off. They remained in the surroundings of the dulotic nest and copulated on the ground. Probably winged females attracted males by releasing a sexual pheromone produced by the mandibular glands, as is the case of *P. breviceps* (Topoff and Greenberg, 1988). In fact, we observed that after a female began opening and closing her mandibles, a male arrived making erratic movements until he succeeded in copulating. This field observations has been recently confirmed by laboratory experiments that showed the crucial role of mandibular glands in eliciting the attraction of males (Visicchio, 2000). Sometimes, more than one male could approach simultaneously the same female and generally the male which copulated was the first one to arrive, though he could be disturbed by unsuccessful suitors. As a rule, multiple mating did not occur. After mating, females shed their wings in a short time (average time of 6 min) and then hid in the vegetation surrounding the nest. Many alate females did not come out of the nest at the time of mating flights, but emerged later, with *Polyergus* workers which were engaged in the raiding activity, and participated in the raid. Several of these females were seen copulating during slave-raids, as also recorded for *P. breviceps* (Topoff and Greenberg, 1988). Alate females would either enter the target colonies or return to the dulotic nest before the inbound column. Some alate females participated in the pillage of the host brood during a multiple raid, since in the inbound column they were seen carrying a *Formica* cocoon.

After mating flights, some dealate females were observed following the route of previous raids (probably relying on the chemical trail laid down by raiders) and reaching a *Polyergus* colony, not necessarily their own, as described also for *P. lucidus* (Marlin, 1971; Kwait and Topoff, 1984). There they wandered around with females that copulated near the dulotic colony. Dealate females were seen approaching the nest cautiously and trying to enter it. They were always treated with hostility by all the slaves and the slave-makers they met and were driven away in a short time. Probably they were waiting for a raid, since they would remain in the nest surroundings up to six days.

Dealate females were seen participating in slave-raids. Once at the target nest, some of these dealate females penetrated the attacked colony, whereas another portion returned to the surroundings of the dulotic colony with the inbound column. Therefore, it was likely that more than one dealate female could enter simultaneously the same target colony.

The behaviour of *P. rufescens* alate females appears to be more variable than that of the American congeneric species. In fact, *P. lucidus* females copulate mostly after mating flights (Talbot, 1968; Marlin, 1971), while *P. breviceps* females typically copulate almost always only during slave-raids (Topoff and Greenberg, 1988). By contrast, *P. rufescens*

females adopt a more diverse strategy, since they *a*) copulate after mating flights, *b*) during slave raids and, in addition, *c*) on the ground close to their nest. Field observations suggest that, whatever mating strategy is adopted by *P. rufescens* females, they may take part in slave-raids. In fact, because of their parasitic mode of colony founding, *Polyergus* females must locate and invade a *Formica* nest. Following a slave-raid swarm by newly-mated young queens is an advantageous strategy to penetrate host nests and to establish a new colony. The invasion and subsequent usurpation of the host colony may be facilitated by the panic and disorganization produced by raiding swarms (Talbot, 1968; Topoff and Greenberg, 1988). Since more than one fertilized female participates in slave-raids and penetrates simultaneously the same target colony, pleometrosis could occur. In this case, an interesting question regards how initial pleometrosis results in the monogyny typical of the slave-making ant species (see the paragraphs on "colony founding").

On the basis of these observations on mating behaviour of *P. rufescens*, we can conclude that *a*) nuptial flights are inconspicuous and not well synchronized between sexes; *b*) the females do not disperse widely, but tend to remain near their natal nest or to return to a dulotic colony after the mating; *c*) the females likely release sex pheromones to attract the males. Therefore, the mating behaviour of this obligatory slave-maker seems to fall within the "female calling syndrome", as is the case of other socially parasitic and myrmecophylous myrmicine genera (Buschinger, 1968, 1971, 1975; Buschinger and Alloway, 1979) and of *P. breviceps* (Topoff and Greenberg, 1988).

Colony founding

For the newly mated females, colony founding is the second phase of reproduction. Though the mode of colony founding varies greatly in ants, two main strategies are generally displayed by young queens to form new colonies: the independent mode, in which, after insemination, the females withdraw into a brood chamber and start new colonies without the help of workers; and the dependent mode, in which young queens are supported from the beginning of colony formation by their nestmates or by workers from another colony (Hölldobler and Wilson, 1990; Keller, 1991; Bourke and Franks, 1995).

The dependent mode of colony foundation typically occurs in parasitic ants, in which newly mated females can exploit even a heterospecific worker force. At one extreme, queens of inquiline gain acceptance into mature host colonies, coexisting with the resident queen(s) and producing only sexual offspring, which are reared by the host workers (Buschinger and Klump, 1988). In contrast, the elimination and replacement of host queen(s) during foundation are the rule for temporarily parasitic and slave-making ants. Young queens of temporary parasites are assisted by the host workers only during the initial stage of colony establishment. In slave-making species, the host workers rear the offspring of the parasites until its worker population is sufficiently

large to supplement the slave force by slave raids. During the raid, the dulotic workers attack other nests of the host species and pillage the brood from which the slaves emerge (Buschinger, 1986; Buschinger and Klump, 1988; Hölldobler and Wilson, 1990; Topoff, 1990). Anyway, before entering the host colony, newly-mated females of parasites must find it. *F. sanguinea* and *P. rufescens* use a common behavioural adaptation for locating and penetrating a colony of the host species. In fact, in the field, newly-mated queens of both slave-makers participate in the raiding swarms.

As previously described, field observations on mating behaviour of *F. sanguinea* support the hypothesis that this species relies also on parasitism to start new colonies. Because it was impossible to make detailed observations of every aspect of colony founding process in nature, we carried out laboratory experiments under controlled conditions. These studies enable us to explore the parasitic potentialities of this species and provide insight into the kinds of behavioural patterns which are likely to occur in nature (Mori and Le Moli, 1998).

The following patterns of colony formation were studied in the laboratory: independent (by one or more females kept together) and dependent foundation including *a*) adoption by a conspecific, a mixed or a host colony; *b*) alliance with a female of host species; *c*) usurpation in a host colony; *d*) appropriation of host brood.

The different developmental stage of ovarioles of the females kept together, but in the absence of workers, suggests that, in the first stage of colony life, only one queen lays eggs, whereas the others (i.e., auxiliary females) act as workers. It has been suggested that young *F. sanguinea* nests are monogynous and old ones polygynous (Pamilo and Varvio-Aho, 1979), even if Dlussky (1967) states that *F. sanguinea* is exclusively monogynous. Because of the lack of aggressive interactions among the queens, a functional monogyny obtained through pheromone-based chemical reproductive competition seems probable (Bourke and Franks, 1995). The likely formation of a reproductive hierarchy may explain the higher success of these *F. sanguinea* females than that shown by the isolated females. It is worth noting that when Czechowski (1996) kept several queens of *F. sanguinea* together with slave pupae, each time only one female survived.

Adoption by a conspecific queenright colony suggests the possibility that, in the field, newly-mated females of this species may be not only readopted into their parental nests but also accepted into alien nests. This phenomenon could be followed by budding, but we have seen no evidence of such a process. The tolerance of residents toward the alien gynes is in accordance with the high degree of polygyny observed in the mature colonies of this species (Pamilo and Seppä, 1994). The presence of a resident queen made the integration of the young females in the mixed colonies more difficult compared with the integration into queenless colonies. During successful usurpations, the intruding female drove away the resident queen from the nest, appropriated her brood and was almost immediately adopted by most of the resident workers. Moreover, both adoption and usurpation were more success-

ful in incipient than in mature host nests. Smaller colonies clearly offer less resistance to the parasite queen's attempt to penetrate the target colony. This observation supports the hypothesis that adoption and usurpation in incipient colonies of the host species are adaptive strategies for *F. sanguinea* queens and agrees with the discovery by Ito and Higashi (1990) of two natural incipient colonies of this species, probably founded through the usurpation of *Serviformica* colonies.

In the first stage of colony formation, the newly-inseminated *F. sanguinea* females may also place themselves in a brood chamber together with *Serviformica* queens, leading to an interspecific reproductive alliance and allowing their own brood to be reared by host females.

Finally, colonies may result when inseminated females invade a host nest, most likely during a slave-raid, carry off brood, and allow it to hatch in a hiding place. The high reproductive success obtained by these queens after the sack of the host brood may likely be explained by the absence of heterocolonial or heterospecific adult workers. These individuals, which were always present in the experiments of adoption and usurpation and which often attacked the alien queens, would offer resistance to the *F. sanguinea* females' social integration. Moreover, the hatching of the slave workers, which began to tend and feed the parasitic queen and to act as helper ants in the founding of a new colony, likely made reproduction easier for these females than for those kept alone.

In conclusion, laboratory experiments and field observations show that queens of *F. sanguinea* have a whole range of possible strategies open to them to start a new colony. Even though independent colony founding by a single female is improbable, after the nuptial flight the young queens may be helped by auxiliaries, may be adopted into a conspecific colony, or may rely on temporary parasitism.

The variety of possible strategies of *F. sanguinea* newly mated females for colony formation provides evidence of a behavioural plasticity in this species and confirms its nature as a facultative parasite.

Also the socially parasitic mode of founding new colonies by queens of *P. rufescens* was analysed in the laboratory (Mori et al., 1995). Newly-mated females of this species were individually introduced into artificially established colonies of two *Serviformica* species, i.e. *F. cunicularia* (the slave present in the natal dulotic nest) and *F. rufibarbis* (another potential slave present in the study area).

The data obtained show that the females of this obligatory slave-maker, before laying eggs, must penetrate the host colony, kill the resident queen, become accepted by the adult workers and appropriate the host brood. In particular, an aggressive take-over with active invasion occurs (Stuart, 1984). In fact, during this process, not only the resident queen, but also many host workers were killed. Anyway, the usurping female was adopted by a large portion of resident workers. Finally, egg-laying by *Polyergus* successful usurpers, the subsequent eclosion of the brood, and its complete social integration in the newly-established mixed colonies were also recorded (Mori et al., 1995). It is worth

noting that the dulotic female was almost always (85.7%) adopted in both queenright and queenless colonies of *F. cunicularia*, whereas in the presence of *F. rufibarbis* it was generally killed in a short time. The failure in usurping the *F. rufibarbis* colonies supports the occurrence of host specificity in the European amazon ant, like in the American amazon ants (Hölldobler and Wilson, 1990). Free-living workers of *F. rufibarbis* have been described to be fiercely aggressive towards *P. rufescens* and these laboratory experiments confirm the high level of interspecific aggression (Habersetzer, 1993; Mori et al., 1994b). In fact, it seems likely that *F. rufibarbis* workers are more successful than *F. cunicularia* workers in defending their nest and therefore less suitable (Buschinger, 1991). This factor, together with ecological determinants, may favour the choice of *F. cunicularia* as host species by *P. rufescens*. In this connection, in the field we observed scouts of *P. rufescens* being attacked and killed by *F. rufibarbis* workers near their nest, and some raiding swarms rejected (cf. also Forel, 1874; Scortecchi, 1972). Moreover, in this slave-maker, host fidelity may be based on a chemically grounded tradition. In fact, if the parasite imprints on the host species present in the dulotic nest (which is also the more available), workers would raid colonies belonging to this species and young queens would try to usurpate colonies of the same species (Goodloe et al., 1987; Schumann and Buschinger, 1994).

In this kind of colony founding, that involves the adoption of *Polyergus* queen by adult *Serviformica* workers, the formation of an interspecific social bond is an enigmatic matter. Moreover, in this context, the care of the slave-makers' brood is devoted to adult slave-workers with no prior experience with this brood. Nevertheless, the capacity of the parasitic queen and her brood to gain acceptance by adult slave workers during host colony usurpation is one of the crucial steps in the evolution of slavery. Usurpation is the only system of colony founding adopted by this obligatory slave-maker. Such a strong specialization is guaranteed by morphological, physiological, and behavioural adaptations. In this context, not only the evolution of sharp mandibles and thick integument by queens but also the development of a sophisticated chemical strategy may have allowed *Polyergus* to become very efficient parasites. On the basis of laboratory experiments conducted both in *P. rufescens* (Mori et al., 1996) and *P. breviceps* (Zimmerli and Mori, 1993), it is proved that the attractiveness of *Polyergus* brood for slave species is due to an interspecific brood pheromone in addition to brood mimicry.

The reduction in aggression during host colony take-over is the likely result of the action of "appeasement" allomones by the *Polyergus* queen (Mori et al., 2000a). This particular strategy has also been found to occur in *P. breviceps* (Topoff et al., 1988), where it seems to increase usurpation success. In fact, the critic phase of take-over is the entrance into the target colony, since the parasitic queen must avoid the fierce defensive aggression of *Serviformica* workers. Therefore, the occurrence of chemical strategies during the initial phase of usurpation was investigated in the European amazon ant. We analyzed (cf. Mori et al., 2000a) the effect of the secretion of different glands (Dufour's, poison, pygidial, rectal, and

mandibular) on the behaviour of workers of its common host species, *F. cunicularia*. In order to offer these secretions to resident host workers, individuals of another *Serviformica* (i.e. *F. rufibarbis*) were daubed with these extracts, and introduced into colony fragments of *F. cunicularia*. The results of a set of laboratory "aggression test" (cf. Le Moli and Pazmigliani, 1981) showed that the secretion of the mandibular, pygidial, rectal, and poison glands do not alter the characteristic aggressive reactions generally performed by resident workers against alien ants. By contrast, the Dufour's gland seems to play a crucial role in the appeasement of residents of the target host colony. In fact, these experiments indicate that the aggressiveness of the *F. cunicularia* workers towards the workers of *F. rufibarbis*, daubed with the Dufour's extract, decreases drastically: at the beginning they tend to ignore the intruder, which is successively adopted. Thus, the secretion of the Dufour's gland is likely to act as an "appeasement" allomone towards the residents of the target host colony rather than as a "propaganda" substance, as occurs in *F. pergandei* and *F. subintegra* (Regnier and Wilson, 1971). This chemical strategy probably allows an easier invasion and usurpation of host colonies by newly-mated females of *P. rufescens* (Mori et al., 2000a).

A further development of this study was the chemical analysis of the Dufour's gland secretion in *P. rufescens*, in order to verify possible similarities with the chemical communication system adopted by their host species. This secretion, in fact, might imbue the *P. rufescens* queen with an odour similar to the *Serviformica* one (changing its cuticular hydrocarbon profile), or reduce aggression until the usurper queen acquires the odour from the environment of the invaded nest. Indeed, the Dufour's gland is an extremely large and hypertrophied reservoir in queens of *P. rufescens* (if compared with that of workers and other formicine), further suggesting a role in pheromone production (Giovannotti et al., 1996).

The Dufour's gland is a sac-like structure closely associated with the sting of queens and worker castes of all social Hymenoptera (Billen, 1987). Although the primary purpose of the Dufour's gland in the Formicidae is not completely known, many recent studies in ants have shown that it performs various (probably secondary) functions, containing substances that serves as pheromones. In fact, the volatile compounds stored in the Dufour's gland frequently have a communicative function (Parry and Morgan, 1979): in some cases it is involved in alarm, recruitment or sexual attraction, as a source of trail pheromones or territorial markers (cf. Morgan, 1984; Hölldobler and Wilson, 1990; Billen and Morgan, 1998). Studies of the Dufour's gland secretion in various ant species show that many have a species-specific composition (Morgan, 1984; Hölldobler and Wilson, 1990). It is a source of hydrocarbons and its derivatives such as long-chain acetates or ketones (Blum and Hermann, 1978; Attygalle and Morgan, 1984; Morgan, 1984). In the ants of subfamily Formicinae it produces the most complex blend of saturated and unsaturated straight chain hydrocarbons among arthropods (Blum and Hermann, 1978).

The chemical composition of Dufour's gland in queens of both *P. rufescens* and its host *F. cunicularia* was analysed by

gas chromatography-mass spectrometry (Visicchio et al., 2000). In *P. rufescens* this gland contains a mixture of five esters. One of these, the decyl butyrate, was consistently present in large quantities (always more than 80%).

The Dufour's gland of *P. rufescens* and *F. cunicularia* queens were found to be qualitative different. This appears to be in contrast with a general rule according to which slave and slave-making species – usually closely related (Emery, 1909; Heinze, 1991) – among formicine ants possess Dufour's glands with similar secretions (Bergström and Löfquist, 1968). But during evolution related species have diversified repeatedly by creating variable mixtures of pheromones in the same exocrine gland particular to individual species (Hölldobler and Wilson, 1990). In fact, the patterns of Dufour's gland substances of both parasitic and host species appear to be species-specific, containing different substances. The major difference was that decyl butyrate, the predominant compound in *P. rufescens* females, is absent in *F. cunicularia*. If decyl butyrate present in *P. rufescens* does indeed act as an appeasement pheromone, it would represent a case of exploitation by illegitimate signallers of a smell unknown to the receiver and, in this case, attractive for them.

Behavioural assays, recently conducted to verify this hypothesis and consisting in laboratory "aggression tests" (cf. Le Moli and Pazmigiani, 1981), showed that decyl butyrate really acts as an appeasement allomone, since it reduces significantly the aggressive behaviour of *Serviformica* resident workers against heterospecific aliens and allows their presence into the target nest and even near the resident brood (Mori et al., 2000b). This last experiment confirms that the usurping queens of *P. rufescens* utilize this allomone to escape the defense of resident workers during the invasion of host colonies. This is in contrast with a repellent action recently assigned to the Dufour's gland content (D'Ettorre et al., 2000; Lenoir et al., 2001). We do not agree with these authors from both a methodological and an interpretative point of view. In fact, the repellent function of this secretion was tested using an experimental procedure in which feeding motivation, which is not involved during the usurpation, could indeed have affected the response of ants. Moreover, the "aim" of the usurping queen is not to drive away the residents but to address their cares towards herself to be adopted as soon as possible. This is in accordance with the behaviour really observed during host colony invasion in which in a few hours the parasite queen become accepted and groomed by resident workers (Mori et al., 1995).

Finally, the structural appearance and development of the Dufour's gland show a clear age-dependent evolution that is in line with its behavioural function. At the moment of eclosion, young females have a gland with an empty lumen but thick lining epithelium, of which the active secretory cells are characterized by a well developed Golgi apparatus, abundant mitochondria and smooth endoplasmic reticulum. The basal plasmalemma shows deep invaginations that facilitate the uptake of precursors from the hemolymph, while intercellular contacts display conspicuous interdigitations in the apical cell part. The metabolic machinery for the elaboration of the appeasement substance is thus already fully active dur-

ing the first days of adult life, and results in the rapid accumulation of secretion in the lumen. After three weeks, the gland has a turgid appearance with a full lumen, and is lined with a considerably reduced epithelium, that does no longer display the cytoplasmic features of an actively secreting tissue. By this time, the gynes are ready for penetration into a slave colony, being loaded with large quantities of the appeasement allomone that are necessary at this initial stage of the usurpation process. Once the *Polyergus* queen has been adopted by the resident *Serviformica* workers, she does no longer need to keep her Dufour gland active, which becomes also apparent in its size reduction (Billen et al., 2001).

Raiding behaviour

Raiding is surely the most spectacular activity shown by slave-making ants. This is especially true for obligatory slave-makers, as *P. rufescens*. In fact, this parasite conducts incursions against colonies of the related genus *Formica*, from which they have been phylogenetically derived.

The raiding behaviour of some *P. rufescens* colonies in Northern Italy was studied both in the field and in the laboratory (Mori et al., 1991; Le Moli et al., 1993, 1994; Grasso et al., 1994, 1996, 1997).

These observations showed that the basic organization of a raid of this species comprises scouting, recruitment, pilage, and brood transportation. In fact, during the raiding expeditions, thousands of individuals form close-packed columns that reach and invade the target nest; after taking the host brood, homing raiders retrace exactly the outbound route in a looser formation.

Typically, the appearance of the first Amazon workers outside the nest in the early afternoon was followed in about 1 h by the increase of above-ground activity with the emergence of several hundreds of slave-makers which began to mill around the nest entrance. These individuals moved incessantly and occupied an area roughly circular, with a radius rarely extending beyond 1.5–2 m. Moreover, the number of these "circlers" increased throughout the afternoon, reaching a peak just prior to raiding. In the field, the phase of mass recruitment was almost always preceded or accompanied by scouting. The existence of scouting workers, that individually leave their nest in the early afternoon to explore the neighbouring area, was confirmed by recent field observations (Le Moli et al., 1994). The route of these individuals away from the mother nest is generally tortuous and time consuming and is followed by a return trip along a different and straighter path. Observations also showed that these workers recruit nestmates and lead raiding columns towards target host colonies, confirming their important role in the organization of slave raids. Moreover, the similarity between routes taken by scouts and raiders during outbound trips indicates the close connection between scouting and raiding activity. On the other hand, the possibility that some raids may occur without the influence of scouts can not be excluded, since Dobrzanska and Dobrzanski (1960, 1989) showed no relations between the so called "scouts" and raids.

For orientation, ants often use chemical trails. Evidence for a chemical-trail system has been reported also for the genus *Polyergus* (Talbot, 1967; Marlin, 1969; Topoff et al., 1984, 1985b; Hasegawa and Yamaguchi, 1994; Le Moli et al., 1994). In this connection, the factors involved in the orientation of scouts and raiders of the European amazon ant, and how these factors are used by raiders of this species during the different phases of slave-making expeditions were investigated in the field (Grasso et al., 1996, 1997).

This research revealed that the scouts of *P. rufescens* exhibit a vectorial orientation to return to the home nest (probably a path integration system similar to that described for *Cataglyphis* ants, see Wehner, 1992), whose angular component is measured on the basis of celestial cues such as the sun and, more important, an orienting factor perceived in the ultraviolet range (e.g. skylight polarization) (Grasso et al., 1996).

Concerning the raiders, they were shown to use different cues (chemical trail, sun's position and probably the polarized light pattern) during the various phases of raiding expeditions. In fact, during the outward journey, the ants at the head of the raiding column do not follow previously deposited chemical trails but orient by celestial cues. Raiders in the middle of the column use celestial factors but are also strongly affected by the recruiting activity of the ants that precede them. During the return trip, raiders follow exactly the same path used during the outbound journey. They rely both on the chemical trail (previously deposited by them during the outward trip) and on celestial cues. The latter allow the ants to assume the correct home direction while following the chemical trail. Perception of the ultraviolet band of the light spectrum is of crucial importance for the orientation of the raiders, during both the outbound and inbound journeys. This supports the hypothesis that *P. rufescens* workers, like other ant species, perceive the pattern of polarized skylight in the ultraviolet range (Grasso et al., 1997). Concerning the chemical trail, recent laboratory experiments showed that the glands involved in the nestmates' recruitment and in the trail laying are the Dufour's gland and the hindgut, respectively (Visicchio, 2000).

The raiding column was sometimes longer than 10 m, wider than 50 cm at its head and 20 cm at the middle. It advanced steadily, at a mean speed of about 1.5 m/min, without disturbing other ants' nests which they passed by, but sometimes stopping to search a *Serviformica* nest entrance. They fanned out and began circling as in the recruiting activity at the dulotic mother colony and digging around stones, in grass and leaves. When a target colony was located, the penetration was almost always immediate. Several raiders gathered in front of the entrance and began to move the little stones that blocked it and to dig the soil. The behavioural pattern of excavation, that allowed an easier mass-entrance and was very frequent during the raids, is peculiar to the raiding context (Mori et al., 1991), since in the mixed colonies the Amazons left this labour to their slaves (Sakagami and Hayashida, 1962).

The action of *P. rufescens* at the target colony is fulmineous and, generally, without battle. In fact, when a target

nest was located, immediately after the removal of the stones that block the entrance, the raiders penetrated it and pillaged cocoons and big larvae in few minutes. Sometimes, the raiders emerged carrying mature adult *Serviformica* workers in the "pupa-like" position (Mori et al., 1991). Unfortunately, in the dulotic colony, it was not possible to determine whether they were killed by the residents or incorporated into the labour force (this would be a rare case of 'eudolosis', *sensu* Kutter, 1957). The action inside the *Serviformica* nest could be so rapid likely because the raiders use pheromones that prevent the organization of defence by the host species and disperse the defenders (Regnier and Wilson, 1971; Czechowski, 1977; Buschinger and Maschwitz, 1984; Hölldobler, 1984). In this connection, recent laboratory experiments showed that *P. rufescens* uses "propaganda" allornones. In fact, the secretion of its mandibular glands causes the typical panic reactions by *Serviformica* residents at the moment of nest invasion (Visicchio, 2000).

Raiding activity was quite regular, with raid-free days occurring only when it was raining or the sky was completely overcast (Mori et al., 1991; Le Moli et al., 1994). Simple, compound, and multiple raids were conducted only against *F. cunicularia* colonies, confirming the occurrence of host specificity phenomenon. Moreover, the mean value of total time devoted to raiding activity (i.e. the time between the raid onset and the return of the raiders to the mother nest) was 50 min.

Another interesting phenomenon is the occurrence of intraspecific attacks with sack involving several colonies of *P. rufescens* (Le Moli et al., 1993; Grasso et al., 1994). Even if dulotic ants when raiding mixed colony of their conspecifics "intend" to raid a given slave species, since the booty consisted primarily of *Polyergus* brood, we considered these raids to be real intraspecific dulotic attacks. Laboratory observations confirmed this hypothesis. In fact, the majority of the raided brood was reared to eclosion by *Serviformica* workers of artificial dulotic colonies, and emerging *Polyergus* workers were perfectly integrated in the adoptive mixed colonies. In fact, no intolerance or aggression was recorded between residents and newly eclosed ants, but young *Polyergus* lived clumped together with *Polyergus* coming from the raiding colony and were cared for and fed by the slaves.

We suggest that intraspecific raids in *P. rufescens* are a consequence of territorial competition connected with a dense slave-maker population and they influence the spatial distribution of *Polyergus* colonies. Territorial intraspecific raids with capture and enslavement of brood could be also interpreted in an evolutionary context. In fact, intraspecific territorial competition with opportunistic brood capture is considered an important preadaptation for the evolution of slavery in leptothoracine and tetramorine ants (Wilson, 1975; Alloway, 1980; Pollock and Rissing, 1989; Schumann, 1992). Our observations on *P. rufescens* support the hypothesis that functional intraspecific slavery, as a consequence of territorial competition, could be considered an important evolutionary precursor of interspecific slavery also in formicine ants (Alloway, 1980; Topoff et al., 1984; Pollock and Rissing, 1989; Le Moli et al., 1993).

Concerning the sanguinary ant, recent findings on the basic organization of slave-raids (Mori et al., 2000c) are generally consistent with those from previous research on this facultative slave-maker. In particular, these data support the absence of a division of labour among workers for slaves and food searching, since the same individuals are raiders during the slave raids and foragers during the food harvesting (see also Dobrzanski, 1961; Czechowski, 1977). It is confirmed that there is no special functional group of individuals specialized in searching for slaves. In fact, marked workers were observed both foraging and raiding and many of them were seen close to host colonies that were raided within the following two days. Moreover, after detecting a target colony, they went back rapidly to the mother nest, as previously described also by Czechowski (1977).

The basic organization of slave-raids of *F. sanguinea* observed in Northern Italy is quite similar to that described for *P. rufescens*. Scouting is essential to find host colonies and recruit the nestmates at the dulotic nest, since the location of a host colony was followed by a raid in a short time. In fact, when scouting was completed, there was a conspicuous emergence of slave-makers from the dulotic nest followed by the leaving of platoons of workers and finally the formation of a swarm (10 to 12 m long, 30 to 50 cm wide) consisting of about a thousand *F. sanguinea* accompanied by few dozens of slaves. We never observed slaves in the slave swarms of *P. rufescens* (Mori et al., 1991; Le Moli et al., 1994). The density of raiding *F. sanguinea* increased gradually and many raiders typically moved forward and back from the mother to the foreign nest. This two-way movement is probably connected with raider recruitment and orientation.

When the raiders located the target colony, they gathered in front of the entrance and began to move the little stones that blocked it and to dig in the soil. Fierce and prolonged fights involving many slave-makers and residents were recorded near the attacked colonies. During the combats many individuals of both species died and sometimes *F. sanguinea* workers transported the killed or injured adult ants of the host species back to the mother colony.

After the penetration of the host colony by slave-makers, many *Serviformica* residents burst from the nest, scattering in all directions and succeeding in escaping with brood. The inside raiding action of *F. sanguinea* was not rapid, and sometimes the first raiders with the booty appeared above ground some hours later. Therefore, they probably found the brood chambers with difficulty and ran into a fierce resistance by the resident population. This differs from the rapid action of *P. rufescens* raiders inside the host colonies and is probably due to the use of different weapons and raiding strategies by facultative and obligatory slave-makers. Worker pupae were mostly captured, but also reproductive brood was pillaged. This is of interest, since this may be predatory and not raiding behaviour. Moreover, many raiders returned to the mother nest with a prey (generally a small insect) captured around the target host colony during the raid (Mori et al., 2000c).

Digging and fighting at the target nest are characteristic of slave-raids organized by the sanguinary ants. Probably the transport of killed residents to the dulotic colony depends on

the actual trophic situation in the mixed colony. Previous studies on the raiding behaviour of species belonging to the *sanguinea* complex showed that these raiders rout their opponents, but no raiders carrying killed ants were described (Wheeler, 1910; Talbot and Kennedy, 1940; Dobrzanska and Dobrzanski, 1962; Marikowski, 1963; Dobrzanska, 1978). The only exception is *F. wheeleri*, in which slave raids often resulted in the killing and retrieval of adult ants from the invaded colony (Topoff and Zimmerli, 1991).

Coming back home, the raiding swarm of *F. sanguinea* followed the same trail as the outbound trip both during successful and unsuccessful raids. Not only the journey there and back was almost always coincident but it was run over again several times in different days. This is probably due to the following of a resistant chemical trail deposited by the raiders from the dulotic to the attacked nest. Czechowski (2000) observed that the raiders tend to simplify the back route.

Simple, continuous and simultaneous raids were observed in late morning or early afternoon of warm and sunny days. Weather conditions influenced raiding activity: in fact, at the moment of raid onset, the sky was completely clear or only slightly cloudy; by contrast, in the raid-free days, it was raining or the sky was completely overcast. This seems to support the hypothesis that *F. sanguinea* workers, like those of some *Polyergus* species (Topoff et al., 1984; Grasso et al., 1996, 1997), use the position of the sun and polarized light, in addition to chemical cues, for scouting and orienting during raiding activity.

In contrast with previous observations on this species (Huber, 1810; Forel, 1874; Wasmann, 1891; Wheeler, 1910; Escherich, 1917), raiding behaviour in the sanguinary ant is not occasionally but it is a frequent behaviour (e.g. 26 raids distributed over 23 days occurred in a season, Mori et al., 2000c) and constitutes an important part of colony activity, as is the rule in the obligatory slave-makers. Even if several colonies of different genera lived in the area of study, according to Emery's rule, most colonies raided by *F. sanguinea* belonged to the phylogenetically closely related species of the subgenus *Serviformica*, i.e. *F. fusca* and *F. cunicularia*. Nevertheless, in contrast with observations in *P. rufescens* (Mori et al., 1991; Le Moli et al., 1994), in *F. sanguinea* the possibility of raiding several host species, together with the presence of both *Serviformica* slaves in the dulotic colonies, shows the absence of host specificity. Moreover, previous laboratory experiments indicated that probably early social environment does not influence the choice of the host (Mori et al., 1992). When colonies of *Lasius emarginatus* were attacked and raided, no adults of this species were seen in the dulotic nest. This seems to imply that *F. sanguinea* organizes not only slave raids, but also predatory expeditions with the only aim of supplying the dulotic colony with food.

These field observations show that *F. sanguinea* is a very efficient predatory species and its dulotic behaviour may be regarded as a continuation and expansion of its common foraging and predatory activity. Moreover, a strong aggressiveness and a pronounced retrieving behaviour joined to an effective chemical alarm-defence system enable the san-

guinary foragers to subdue individuals of the host species and to bring back to the dulotic nest their brood and adults (see also Ceusters, 1985; Czechowski and Rotkiewicz, 1997).

Finally, the results of these field observations support the evolutionary dulotic route proposed for the *Formica* ants long ago by Darwin (1859). It begins with brood predation for food in alien colonies of the same or different species, and led to the obligatory slavery of the Amazon ants of the genus *Polyergus* through the facultative dulosis of the *Raptiformica* species, like those belonging to the *F. sanguinea* complex (see also Topoff and Zimmerli, 1991). Nevertheless, other evolutive causes, as the territorial competition (cf. Wilson, 1975), could be involved in the development of this phenomenon. In fact, an unequivocally accepted theory on the beginnings and evolution of dulosis is still lacking.

Conclusion

Many aspects of colony life of both *F. sanguinea* and *P. rufescens* have been investigated and clarified during the last years by field and laboratory studies.

Firstly, the data confirm the different degree of specialization reached by *F. sanguinea* and *P. rufescens* in the evolutionary context of social parasitism. In fact, the two slave-makers show different behavioural strategies both in colony formation and raiding activity.

In particular, the variety of possible strategies of *F. sanguinea* newly-mated females for colony founding, together with data concerning its slave-making activity, provides evidence of a behavioural plasticity in this parasitic species and confirms its nature as a facultative slave-maker.

By contrast, the next steps in the dulotic progression, as shown by *P. rufescens*, involve more sophisticated mechanisms for subduing the host. This was confirmed also by laboratory experiments to test the fighting techniques used by the facultative and obligatory parasites against *Serviformica* individuals (Grasso et al., 1992). In fact, *F. sanguinea* engaged in prolonged combats with the opponents and used the mandibles to kill them. *P. rufescens* at first reacted only to the attack of the slaves and probably used pheromones to stop their aggression. Afterwards, if the attacks were repeated, it actively killed the slaves with its sharp mandibles. Moreover, this slave-making species founds new colonies only through usurpation, confirming its nature as obligatory parasite.

Reproductive strategies and raiding behaviour of both slave-makers are now less obscure. Moreover, new interesting questions arise from the data presented here. For example, the mechanisms and cues of orientation in *P. rufescens* have been studied in detail, but this phenomenon is quite unknown in *F. sanguinea* foragers and raiders. Moreover, progresses have been done in the chemical identification of glandular contents used by *P. rufescens* raiders during the different phases of raids and by queens during usurpation, but no evidence of similar glandular sources have been shown in *F. sanguinea*, both during raiding and colony founding.

Finally, further studies on imprinting-like phenomena involving parasites and hosts, intraspecific dulosis, territorial competition and predation in these and other slave-makers of the *sanguinea* complex and the *Polyergus* genus, could provide an universally accepted theory on the origin and evolution of slavery in formicine ants.

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