

Research article

Social parasitism of *Polistes dominulus* by *Polistes nimphus* (Hymenoptera, Vespidae)

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Summary. Interspecific facultative social parasitism is well known in ants and in bumble-bees, but it is rarer in wasps. This form of parasitism is traditionally considered to be an intermediate stage in the evolution of obligate interspecific parasitism, where the parasites are no longer able to nest alone. We report field and experimental observations of a newly discovered facultative parasitic relationship between two closely related free-living *Polistes* species: *P. nimphus* and *P. dominulus*. *P. nimphus* foundresses sometimes usurp the nests of the larger *P. dominulus* before worker emergence. The invading queen takes over the nest with abundant abdomen stroking on the nest surface and is accepted by workers if they emerge 6 or more days after usurpation. Morphometric comparisons show that the usurper species, though smaller than its victims, has morphological adaptations consisting of larger heads, mandibles and front femora relative to their body size that may give it an advantage during nest invasion. This strategy is likely to be taken only after the foundress loses her original nest because invading *P. nimphus* queens have lower reproductive success than they would have had on their own nest. Overall, we found that *P. nimphus* usurpers use strategies of invasion similar to those of two obligate parasites, suggesting that this may be an example of one of the pathways by which social parasitism evolved.

Key words: *Polistes*, social wasps, social parasitism, interspecific facultative temporary parasitism.

Introduction

Individuals whose young need substantial care can benefit greatly if they can trick someone else into raising those young. Brood parasites may fool individuals of their own species, but, some of the most spectacular cases of trickery

involve individuals of one species fooling individuals of another species into raising their young. This brood parasitism is well known in birds such as cowbirds, honeyguides and cuckoos (Lack, 1968; Payne, 1977) and is also widespread in ants, and in some social bees and wasps (e.g. Wilson, 1971; Buschinger, 1986; Bourke and Franks, 1991).

Social parasitism in social insects often takes the form of a queen taking over the nest and workforce of another individual and forcing them to raise the usurping queen's young. Intraspecific social parasitism, usually called usurpation, occurs when a female has failed to nest successfully on her own. She usurps the queenship of another nest, then produces her own workers and subsequent reproductives. This form of social parasitism is facultative and temporary and has been documented in all three subfamilies of social wasps (for *Polistes*, see Klahn, 1988; Field, 1992; Cervo and Dani, 1996; for Vespinae, see Matura and Yamane, 1990; for Stenogastrinae, see Turillazzi, 1991). Interspecific parasitism may be temporary, but necessary, as is the case of many ants that need the workers of another species to begin a colony, but then produce their own workers. It may be permanent as is the case when the social parasite produces no workers, only reproductives, reared by the workers of the host. In most species, interspecific social parasitism is obligate, but the literature also contains widespread reports of sporadic facultative interspecific social parasitism.

Interspecific facultative temporary parasitism is restricted to social insects that go through a single queen workerless stage since colonies with a workforce would be impossible to invade. This kind of parasitism was first described in a Vespine wasp: queens of *Vespa dybowskii* André regularly usurp colonies of *V. crabro* Linnaeus (Sakagami and Fukushima, 1957). Since this first description, the reports on interspecific facultative parasitism in Vespinae wasps gradually increased, suggesting that it is rare but widespread in this subfamily (MacDonald and Matthews, 1975, 1984; Akre et al., 1977; MacDonald et al., 1980; Bunn, 1982; O'Rourke

and Kurczewski, 1984; MacDonald, 1989). Published observations of simultaneous occupation of the same nest by two different *Polistes* Latreille species are few. Snelling (1952) reported a colony of *P. fuscatus* Fabricius usurped by *P. apachus* Saussure. Two nests containing *P. metricus* Say and *P. fuscatus* were discovered by Hunt and Gamboa (1978): in both cases *P. metricus* seemed to be the intruder species. More recently, O'Donnell and Jeanne (1991) observed a colony of *P. instabilis* Saussure usurped by *P. canadensis* Linnaeus; and Giannotti (1995) observed a nest of *P. versicolor* Olivier usurped by *P. lanio* Fabricius. In European *Polistes* species, the only report of interspecific facultative usurpation is of 6 colonies of *P. gallicus* Linnaeus usurped by *P. dominulus* Christ (Cervo and Dani, 1996; Cervo, pers. obs.) found over four different years. However, none of these *P. gallicus* usurped colonies succeeded: they lasted no longer than the pre-worker stage of the colony cycle and they did not produce usurper reproductives. Recently, cases of interspecific occupation of a nest by two species, belonging to different genera, have been observed in Stenogastrine wasps by Turillazzi et al. (1997) in *Myschocyttarus* Saussure with *Polistes* by Prezoto and Nascimento (1999).

How social parasitism evolved in social insects has been much discussed (Emery, 1909; Taylor, 1939; Wilson, 1971; Michener, 1974; Buschinger, 1986; Bourke and Franks, 1991; Choudhary et al., 1994; Lowe et al., 2002). Since parasites must fool their hosts, they are often closely related (Emery, 1909; Wilson, 1971; Michener, 1974; Choudhary et al., 1994). The phylogenetic proximity between two species often means chemical and behavioural similarities that could favour the host exploitation. Some have speculated that sympatric speciation is commonly involved (Wilson, 1971; Buschinger, 1986), but a careful study found clear phylogenetic evidence arguing against sympatric speciation in *Polistes* (Choudhary et al., 1994).

The only obligate social parasites in the polistine wasps occurs in the subgenus *Polistes sensu stricto*. They are *P. sulcifer* Zimmermann, *P. semenowi* Morawitz, and *P. atrimandibularis* Zimmermann. The social parasites have very large heads, mandibles and forelegs, compared to their hosts and they use these weapons in taking over nests (Cervo, 1994). These three social parasite species are monophyletic, indicating that the social parasitism habit they share evolved once in their common ancestor (Choudhary et al., 1994). The sister group to the social parasites is a two-species clade containing *P. nimphus* Christ and *P. dominulus*. Recently, Cervo (1998) reported that *P. nimphus* can usurp nests of *P. dominulus*. Since these two species are the sister group of the social parasites, a detailed study of this rare behaviour may provide insights into the origin of socially parasitic behaviour. In this paper we report the incidence of interspecific usurpation, how the parasite integrates herself into the colony, her control over the host, her reproductive success, and morphological differences between host and parasite.

Materials and methods

Field study

The study site was located in Cavriglia, in central Italy, between Arezzo and Florence, at approximately 300 m elevation. At the end of April for three years (1995, 1996, 1998), we located all *P. dominulus* nests present in a given area (different each year), and individually marked their foundresses. Then we checked these *P. dominulus* nests weekly for the presence of *P. nimphus* females. Afterwards, the usurped nests were periodically checked to evaluate their success.

One nest was usurped by two *P. nimphus* females. To find out if these two females were related, we genotyped them. We used five polymorphic DNA microsatellite loci (Pdom 2, Pdom 17, Pdom 140, Pdom 7, Pdom 122) originally developed for *P. dominulus* (Henshaw, 2000) and used standard techniques for polymerase chain reactions (for methods see Strassmann et al., 1996).

Laboratory study

In Spring 1996, we collected *P. dominulus* and *P. nimphus* nests that had been begun by single females near the area where the field study was performed. All nests had only a single foundress and were in similar stages of brood development. We brought the colonies into the laboratory and placed them in glass boxes (15 cm³). They were supplied *ad libitum* with water, honey, *Tenebrio molitor* larvae and paper for building. The cages were maintained in a room with natural light and temperature and with additional illumination from 6.00 a.m. to 6.00 p.m., from a 100 W bulb 25 cm from each cage. Eleven *P. nimphus* foundresses, taken away from their nests, were used as 'usurpers' on as many *P. dominulus* nests whose foundresses have been removed (experimental colonies). As controls, another five *P. nimphus* foundresses were left on their original nests (control colonies). The experimental and control colonies were maintained in the laboratory for about three months. We randomly chose 5 out of the 11 experimental colonies to compare with the 5 control colonies for development and adult offspring emergence. *P. nimphus* foundresses were observed daily from 70 to 104 days after collection using instantaneous scans 15 s long every min for 30 min.

At the end of colony cycle, all inhabitants of experimental and control colonies were killed and dissected in order to evaluate ovarian development and fat body condition and to measure their head width and wing length. These parameters allowed us to separate females into two different castes: workers and gynes. Larger females with undeveloped ovaries and with copious fat bodies were classified as gynes. Gynes will mate and overwinter, then becoming the next year's foundresses.

Morphological analysis

In autumn 1998, we collected 21 gynes of *P. nimphus* at one of their hibernation sites on the slopes of Monte Nerone (Central Apennines) and 25 *P. dominulus* gynes at a hibernation site near Florence, Italy. A morphometric comparison was undertaken in order to highlight morphological characters of the usurper species that could give females an advantage during nest invasion. We measured six external body parts for each specimen: width of the head, mesonotum, first gastral sternum, width and length of the front femur, length of the tibia of the third pair of legs, and length, width and thickness of the mandibles. These measurements were taken with a binocular microscope equipped with an ocular micrometer. To normalize the data for wasp size we divided each measure by the wing length of each animal.

Results

Field study

Number of usurped nests and parasitism rate – *P. dominulus* is the predominant species in the study area. For example in 1995 we found 104 nests of *P. dominulus*, 24 of *P. nimphus* and 28 of *P. gallicus* in our study field.

We found, in total over three years, 8 nests (Table 1) of *P. dominulus* usurped by *P. nimphus*. Eight out of 518 nests, or 1.54% of *P. dominulus* nests were usurped by *P. nimphus*. Where we had numbers of *P. nimphus* in the same field (Table 1) we can determine the number of *P. nimphus* usurping other species relative to those remaining on their own nest. In 1995, 3 out of 27 (24 nests plus 3 usurping females) or 11.1% of *P. nimphus* were social parasites and in 1996 1 out of 89 (88 nests plus 1 usurping female), or 1.1%. In addition we also observed 3 other nests of *P. dominulus* usurped by *P. nimphus*, out of the study area, in the course of other studies. By contrast, we never found a single case of *P. dominulus* usurping a *P. nimphus* nest. This is true of the 112 nests of *P. nimphus* observed in this study (Table 1), and also of the many hundreds of nests we have followed over the last 20 years of field research (Cervo, unpublished).

Invasion period

Typically, usurpation occurred between the middle of May and the beginning of June, when the *P. dominulus* colonies are well established and the workers are near to emergence. No usurped nest had any workers at the time of invasion.

In one case, we found two females of *P. nimphus* on the same *P. dominulus* nest. These two females were full sisters. They shared at least one allele at all 6 loci we genotyped as would haplodiploid full sisters. Furthermore their average relatedness from these loci was that of full sisters.

Host foundress number and host foundress fate

In *P. dominulus*, colonies can be begun by single or multiple females (Pardi, 1942). In our population, about the half of the nests are founded by 2 or more foundresses (Cervo, unpublished). In our parasitized nests, the number of foundresses on the nest before usurpation was known in 7 cases. Two of the *P. dominulus* nests were founded by a single female, whereas another five were occupied by two (3 nests) or more

foundresses (one nest with 3 and one with 5 foundresses), indicating that *P. nimphus* usurpers surprisingly did not preferentially attack single foundress colonies. It is possible that some of the multiple foundress colonies could have lost their additional foundresses shortly before usurpation. The larger nests of multiple foundress groups undoubtedly make a more attractive target for usurpers.

Immediately after usurpation, in 5 of the 7 nests the usurper was alone on the nest until worker emergence. In the other two cases we found *P. dominulus* foundresses (three and one) together with dominant usurper.

Nest invasion success

In 4 out of 10 nests (considering also the additional nests found outside the study area) for which we were able to check the success of nest invasion, the usurpers remained on the nest only 5–21 days (11 days on average) after the invasion. In one case the former owner was found again on the nest after the *P. nimphus* female disappeared. On the other 6 usurped nests the *P. nimphus* usurper remained on the nest to the end of the colony cycle.

Success of parasitized colonies

In the usurped colonies that retained the *P. nimphus* queen, young maturing in the nest belonged to both species; host and parasite brood consisted of both males and females.

Nest invasion strategy

That *P. dominulus* foundresses usually disappear from their nests leaving only *P. nimphus* usurpers suggests that at some point *P. nimphus* fights the *P. dominulus* queen and excludes her from the nest. There was indirect evidence for such aggression. We found 3 dead females of *P. dominulus* near two of the usurped nests: a dominant female under a nest with two missing wings, and the bodies of two foundresses under the nest with 5 *P. dominulus* foundresses and one was missing both antennae and a leg. These missing body parts may indicate a struggle. These data and the observation that the *P. dominulus* hosts remained on two nests argue against the idea that *P. nimphus* was simply adopting abandoned nests.

Laboratory study

Usurpation experiments

Initially, we tried to force interspecific usurpation by introducing a *P. nimphus* foundress into a cage containing a *P. dominulus* nest with its owner. None of these attempts (N = 6) were successful; in all these experiments the *P. dominulus* queen successfully defended her nest against the intruder, even when they were left in the cages for several days. During the fights both the wasps often employed their mandibles, while neither used their sting.

In a second set of experiments, we introduced a *P. nimphus* queen into a cage with a *P. dominulus* nest from which we had previously (30 min before) removed the owner, thus simulating a normal absence of the foundress on a foraging trip. In all cases (N = 12), the usurper immediately landed on

Table 1. Interspecific usurpation rate of *P. nimphus* on *P. dominulus* in the study area

Year	N° of <i>P. dominulus</i> nests	N° of nests usurped by <i>P. nimphus</i>	%
1995	104	3	2.9
1996– I field	77	2	2.6
1996– II field	311	1	0.3
1998	26	2	7.6

the free nest, but, as soon as the owner was reintroduced into the cages, the original owner fought with the usurper and, in a short time, reconquered the nest. Of course in both these experiments neither female could leave the close proximity of the nest so these experiments do not necessarily represent the natural situation.

Finally, we tried another technique. We removed the foundresses from 11 *P. dominulus* nests and offered each to a *P. nimphus* foundress. Ten of these nests were adopted by *P. nimphus* foundresses within a few days (range 1–5). In two cases, before worker emergence, the *P. nimphus* usurper was found dead in the cage without any evident cause 3 and 18 days after usurpation. This allowed us to follow usurped nests.

Usurpation success

In two experimental nests, we observed host workers (3 and 6 of them respectively) kill the usurper soon after their emergence, which occurred 1 and 4 days after invasion. In the remaining usurped nests ($N = 6$) no overt conflict between usurper and host workers (born at the earliest six days after the invasion) was observed and they were successfully reared in the laboratory for about three months.

Parasitized colony success

In all cases, the individuals emerging from usurped colonies ($N = 5$) belonged to both species (Table 2). Dissection of females born on 5 usurped colonies and reared in the laboratory, showed that both workers and gynes of the usurper species emerged from usurped nests, whereas only workers of the host species were found. However, from 2 out of 5 usurped colonies males of the host species emerged also (24 and 10 males respectively).

The mean number of *P. nimphus* females (including females that died during the colony cycle and so could not be dissected), emerging from the usurped colonies (5.6 ± 4.3) was significantly lower (Mann Whitney U test, $U = 0$, $p < 0.005$) than from the control colonies of *P. nimphus* (36.6 ± 20.5). On average, the total reproductive success (males + gynes) of a *P. nimphus* usurper on *P. dominulus* nest was significantly lower than that of a *P. nimphus* foundress on its own nest (Table 2). As Table 2 shows, the number of gynes

was lower in usurped colonies than it was in normal *P. nimphus* colonies, and a trend for male numbers went in the same direction.

The number of *P. nimphus* workers that emerged from the usurped colonies was, on average, significantly lower than it was in control colonies (Table 2). But the mean number of workers emerging from control colonies (16.6 ± 12.9) was not significantly different (Mann-Whitney U test, n.s.) from that emerging from usurped colonies if both *nimphus* and *dominulus* workers (7.6 ± 5.7) are included.

Reproductive control of the host workers

Dissection of *P. dominulus* workers that emerged from the experimental colonies showed that none had developed ovaries.

Behaviour in the pre-emergence phase

Analysis of the behaviour of *P. nimphus* when usurping shows that the usurper performed all the behavioural patterns exhibited by a foundress on its own nest before worker emergence, although some frequencies varied. Abdomen stroking behaviour (Dani et al., 1992) was significantly more frequent (Mann Whitney U test, $U = 382$ $p < 0.001$) in usurpers ($N = 8$) than in foundresses ($N = 5$), even though it decreased within the first 7 days after the invasion (Fig. 1). In addition, resting time was longer (Mann Whitney U test, $U = 459$, $p < 0.005$) and their absence from the nest was reduced as well ($U = 515$, $p < 0.03$).

Behaviour in the host post-emergence phase

For this analysis data were split in three groups according to the number of host workers (1–2; 3–6; 7–15 workers), and the two nests where usurpers were killed were not used, so we had 6 usurpers and 5 foundresses on their own nests. Behaviour of *P. nimphus* usurpers did not significantly differ from that of *P. nimphus* on its own colony after workers emerged (Mann Whitney U test n.s.).

The frequencies of dominations and trophallaxis between the usurper and the host workers were not significantly higher than between foundresses and their daughters in the control nests.

Table 2. Mean number (and S.D.) of workers and reproductives (gynes and males) emerged from 5 *P. nimphus* nests (control nests) and 5 *P. dominulus* nests usurped by *P. nimphus* females reared in laboratory

	<i>P. dominulus</i> usurped nests ($N = 5$)		<i>P. nimphus</i> control nests ($N = 5$)		Mann-Whitney U test p
	Mean	S.D.	Mean	S.D.	
<i>P. n.</i> workers	2	2	16.6	12.9	< 0.05
<i>P. n.</i> reproductive females	3.4	2.3	14.8	9.8	< 0.05
<i>P. n.</i> males	8.6	5.7	15.2	11.5	n.s.
Total <i>P. n.</i> reproductives	12	5.7	30	12.6	< 0.05
<i>P. d.</i> workers	5.6	3.8			
<i>P. d.</i> reproductive females	–	–			
<i>P. d.</i> males	6.8	10.5			

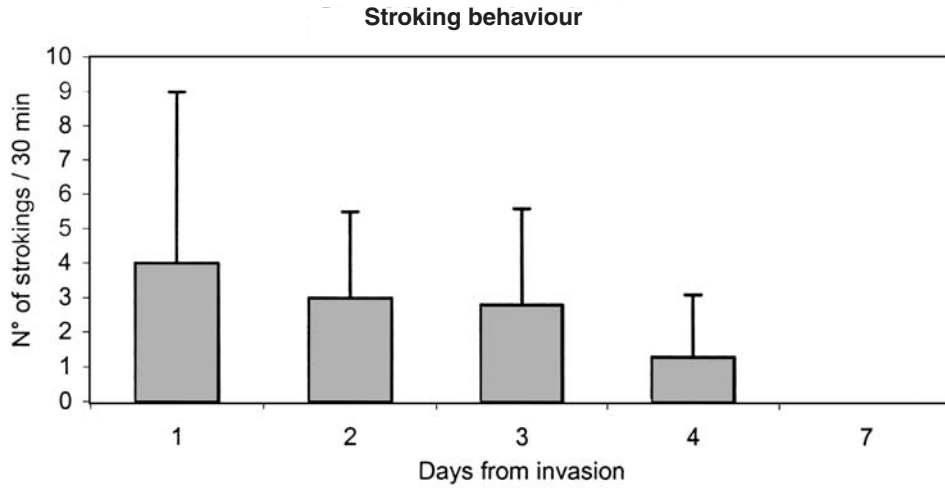


Figure 1. Frequency of stroking behaviour performed in the laboratory by *P. nimphus* usurpers during the first seven days after host nest invasion

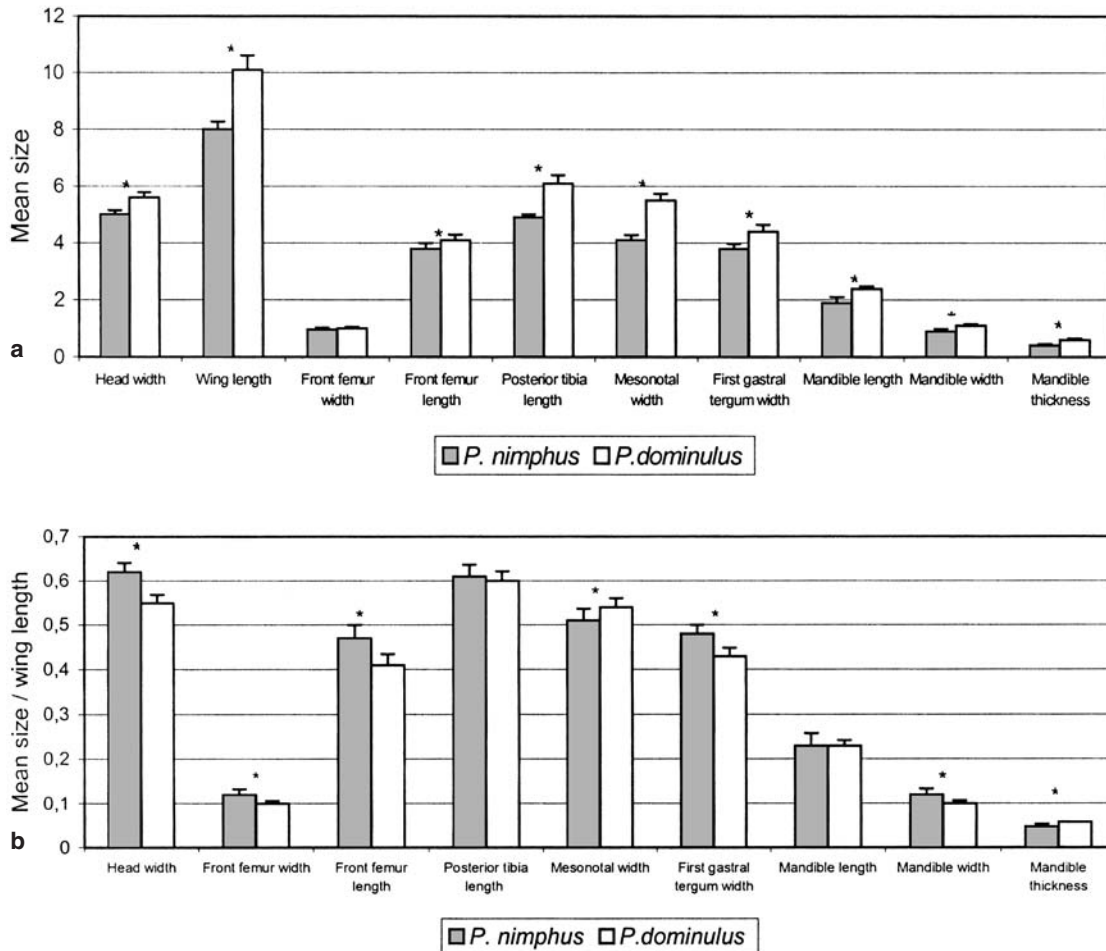


Figure 2. (a) Comparison between the mean size of seven body parts of the *P. nimphus* (N = 21) and *P. dominulus* (N = 25) gynes; (b) Comparison between the average size of the same external body parts of *P. nimphus* (N = 21) and of *P. dominulus* (N = 25) females normalized for wing length. *p < 0.001 (t test)

Morphological differences between usurper and usurped species

Even though *P. nimphus* females are significantly smaller overall than *P. dominulus* (Fig. 2a), the width of their front femur is not significantly smaller than that of *P. dominulus* (0.98 ± 0.06 vs. 1.01 ± 0.5 Student's *t* test, $t = 1.9$, n.s., $N = 21$ *P. nimphus*, 25 *P. dominulus* foundresses). Figure 2b shows the comparison between the relative size of the external body parts of *P. nimphus* and of *P. dominulus* females normalized for winglength. In this case, the morphometric comparison shows that relative head width, width and length of front femur and width, but not thickness or length, of the mandibles are significantly larger in *P. nimphus* than in *P. dominulus* (Fig. 2b).

Discussion

The parasitic relationship between *P. nimphus* and *P. dominulus* here described represents an example of the second step of parasitism in Taylor's progression from free-living to parasitic (Taylor, 1939): interspecific, facultative and temporary parasitism. It occurs between two different and closely related species (Choudhary et al., 1994). Females of *P. nimphus* may found their own nests but they are also able to usurp nests of the same species (Cervo, pers. obs.) or of another species. This socially parasitic relationship is temporary: the dissection of *P. nimphus* females emerging from *P. dominulus* nests showed that *P. nimphus* usurpers produce more workers, not just reproductives. *P. nimphus* parasitism of *P. dominulus* may give us clues as to how obligate social parasitism arose.

Even though the facultative interspecific parasitism rate of *P. nimphus* is very low, ranging between 1.1% and 11.1% depending on the year, it is not very different from that of *Polistes sulcifer*, the obligate social parasite of *P. dominulus* in the same population. In 1995 we found 3 *P. nimphus* usurpers and 2 *P. sulcifer* on 104 *P. dominulus* nests. But, of course, *P. nimphus* also has many pure *P. nimphus* nests.

P. nimphus usurps *P. dominulus* nests and not another potential host, *P. gallicus*, which is present in the same area. Although *P. gallicus* could represent an easier target, since it is smaller than both *P. nimphus* and *P. dominulus*, it is phylogenetically farther from *P. nimphus* (Choudhary et al., 1994) and so it might be more difficult to gain acceptance from the emerging workers by fooling them with chemical signals. *P. gallicus* and *P. biglumis* are a sister clade to the group containing *P. nimphus* and *P. dominulus* and the 3 monophyletic obligate social parasites (Choudhary et al., 1994). This could explain the observations of unsuccessful interspecific usurpations of *P. dominulus* on the more distantly related *P. gallicus* (Cervo, pers. obs.; Cervo and Dani, 1996).

The behaviours *P. nimphus* uses are similar to *Polistes* usurping conspecifics as well as to obligate social parasites. Most interesting in this regard are the morphological differences between the two species: *P. nimphus* has relatively enlarged mandibles and front femurs which can help with

fighting off a larger host. Enlargement of these body parts is typical of the morphological traits found in obligate social parasites in *Polistes* (Cervo, 1994). In absolute terms, these body parts are not larger in *P. nimphus* than they are in *P. dominulus*, whereas in other facultative parasites are usually larger than the species they parasitize (O'Donnell and Jeanne, 1991; Giannotti, 1995).

The enlarged fighting body parts, the dead *P. dominulus* found under some nests and the continuing presence of *P. dominulus* foundresses with *P. nimphus* usurper on some colonies all argue that *P. nimphus* foundresses are not simply taking over abandoned *P. dominulus* nests. Such nests would only be available for a short time since ants and other predators quickly empty unattended nests. However, we cannot exclude the possibility that sometimes *P. nimphus* females adopt abandoned nests. In the laboratory we only succeeded in getting *P. nimphus* to adopt orphaned *P. dominulus* nests and not those with foundresses present. This does not mean that this is the only circumstance for usurpation in the field where *P. nimphus* females without nests will be much more motivated to usurp, and the female losing the battle for the nest can leave its vicinity.

Our data show that usurpation in facultative parasites typically occurs in the same period in which obligate social parasites usurp their host colonies (Cervo and Turillazzi, 1996; Zacchi et al., 1996), when the *P. dominulus* colonies are well established and the host workers are near emergence. Both rely on the host worker force to maximize their reproductive output, but while the obligate parasites lay only reproductive eggs, *P. nimphus* females produce their own workers before producing reproductives.

Our field and laboratory data show that there is variation in the success of female *P. nimphus* usurpers on host colonies. Newly emerged host workers killed two usurpers in the laboratory experimental colonies, and four usurpers of the field colonies disappeared a few days after usurpation. Our data suggest that the workers accept their new queen only when the usurper arrives more than 6 days before their emergence. Nests where the emerging workers detected an invading queen are not as successful both in *P. nimphus* usurping *P. dominulus*, and also in within-species usurpations in *Polistes fuscatus* (Klahn, 1988). This could be because the usurping queens need to chemically fool the emerging workers to get them to work. *P. nimphus* interspecific usurpers as well as *P. sulcifer* and *P. semenowi* obligate parasites (Turillazzi et al., 1990; Zacchi et al., 1996) perform an intense stroking behaviour as soon as they invade the nests of the host species. This behavior seems to be involved in the chemical strategies necessary to enter a foreign colony (Dani et al., 1992; Cervo and Dani, 1996; Turillazzi et al., 2000). Recently, Van Hooser and co-workers (2002) showed that, in *P. fuscatus*, there is a positive correlation between tolerance by host workers and the length of time that the invader is on the nest before the workers emerge (also indirectly correlated with abdominal stroking time). In our study it seems that a six-day period before worker emergence is required for successful domination by *P. nimphus* queens. This facultative usurper probably attains chemical integration into the host

society before worker emergence and, probably, 6 days are necessary for the usurper to assume the host odour or/and to cover the colony with her scent, integrating it into hydrocarbon profile already present. The chemical strategies used by obligate *Polistes* parasites to integrate themselves into the host colony are known (Bagnères et al., 1996; Turillazzi et al., 2000) and some data is now available for the chemical strategy employed by *P. nimphus* when it usurps *P. dominulus* colonies (Lorenzi et al., submitted). It will be interesting to compare the chemical integration strategy in this facultative parasite to understand its level of specialization as well as the evolution of chemical integration strategies. However, even if facultative parasites are not always successful, this strategy seems to be viable for some usurpers. A *P. nimphus* female can obtain reproductive success as shown by the males and reproductive females that emerged from some usurped *P. dominulus* nests. It is possible that *P. nimphus* foundresses adopt this strategy after having lost their own nests and when the colonies of the usurped species are common (as it was in our field site). We do not know where the usurping *P. nimphus* females in our study came from. In three cases, we found an abandoned or damaged nest (probably belonging to *P. nimphus*) near the usurped *P. dominulus* colony suggesting that the usurpers could be foundresses that lost their own nests. On the other hand, we cannot exclude the possibility that *P. nimphus* usurpers are females that choose not to begin their own nests, as is the case for obligate social parasites. This hypothesis is supported by numerous findings of *P. nimphus* females hibernating at the top of mountains (more 1000 mt a.s.l.), where they do not nest and begin the season later after migrating down from the mountains. The altitudinal migration from the emergence sites and the hibernation at high altitude is typical of the three species of *Polistes* obligate social parasites (Cervo and Dani, 1996; Cervo et al., 1998). Though *P. nimphus* is not the only free-living species that we found overwintering at the top of mountain, it certainly is the most abundant. In obligate social parasites as well as in *P. nimphus*, hibernation in such conditions could delay the end of diapause and then favour usurpation of developed colonies of the same or other species in the valley below (Cervo, 1990).

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