

# *Polistes* wasps and their social parasites: an overview

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Severe brood care costs have favoured the evolution of cheaters that exploit the parental services of conspecifics or even heterospecifics in both birds and social insects. In *Polistes* paper wasps, three species have lost worker castes and are dependent on hosts to produce their sexuals, while other species use hosts facultatively as an alternative to caring for their own brood. This paper offers an overview of the adaptations, strategies and tricks used by *Polistes* social parasites to successfully enter and exploit host social systems. Moreover, it also focuses on the analogous solutions adopted by the well-known brood parasite birds, and stresses the evolutionary convergence between these two phylogenetically distant taxa. A comparative analysis of life-history patterns, as well as of phylogenetic relationships of living facultative and obligate parasitic species in *Polistes* wasps, has suggested a historical framework for the evolution of social parasitism in this group. As with avian brood parasites, the analysis of adaptation and counter adaptation dynamics should direct the future approach for the study of social parasitism in *Polistes* wasps. The *Polistes* parasite–host system seems a suitable candidate for a model system in coevolutionary arms race studies, just as *Polistes* paper wasps have been considered for many years a model organism for sociobiological studies.

## Introduction

In many species, adults invest a large amount of energy to care for their own brood. For example, many animals build elaborate nests where they rear brood, usually for a significant amount of time, providing it with both food and protection. The high cost of parental care have induced some individuals to develop strategies to reduce time and energy involved in this activity by exploiting the work of conspecifics or even heterospecifics (Davies *et al.* 1989). Freedom from these parental care costs often permits females to redirect all foraging efforts to an increase in their own fecundity.

The form of exploitation is diversified: some individuals usurp only the nest structure, saving time to immediately start their own brood rearing; others exploit food or material stored in alien nests, using these resources for their own young; finally, others use the work of different individuals to rear their own brood and specialise in reproduction only. In this latter case, hosts spend time and energy raising parasitic young that have no genetic value for them, reducing or fully annulling their own reproductive success. These exploitation forms range from brief intrusions in alien nests to long parasite–host cohabitations that require elaborate tricks to fool their host. The simplest form of parasitic relationship

is facultative parasitism, in which the parasite exploits the parental services of conspecifics or heterospecifics as an alternative strategy to rear their own brood. For other species, called obligate parasites, the complete dependence on a heterospecific is the only available strategy to rear their young, as obligate parasites have completely lost the capacity to build a nest or to care for their own brood.

These parasitic strategies are widespread among species that usually build a nest, and whose young need substantial care before gaining independence. In fact, brood parasitism seems limited to those animal groups whose young hatch in a helpless state and are dependent on parents for food. These young have various degrees of morphological degeneration (e.g. altricial chicks in birds or apod larvae in insects) that make them unable to move, shelter, or feed themselves.

Obligate brood parasitism is widespread in birds and has independently evolved in seven avian groups (Payne 1977). Approximately 1% — corresponding to 95 species — of extant birds are brood parasites, and all but one (the black-headed duck) have altricial young. Although birds are the best known parasitic vertebrates, some cases of brood parasitism have been reported among freshwater fish (Sato 1986, Baba *et al.* 1990) and mammals (Jones 2005). Among invertebrates, social parasitism is common in social insects (Wilson 1971); it is widespread in Hymenoptera but unknown in Isoptera, although the latter is composed entirely of eusocial species.

The Hymenoptera — ants, bees and wasps — are holometabolus insects and, as with birds, their immature are unable to attend to their own needs. Thus, they require a large energetic investment by provisioning adults. Isoptera, alternatively, are hemimetabolus, meaning that after egg hatching, their immatures are independent and can immediately contribute to the colony. This remarkable difference in developmental patterns may explain the lack of parasitism in termites.

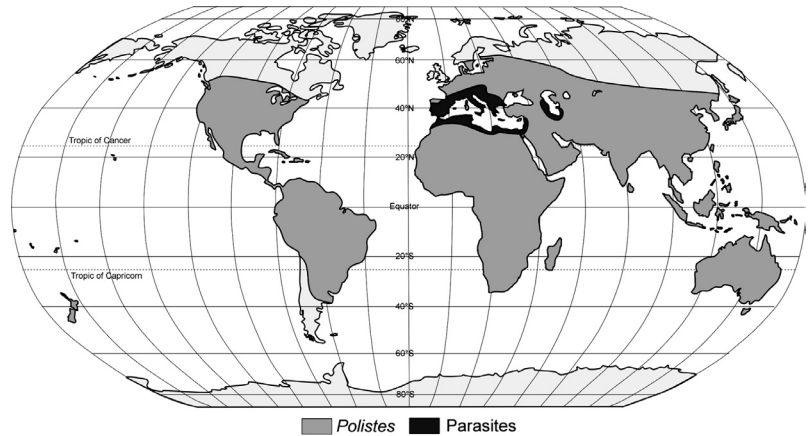
Social parasites are particularly common among ants, where more than 200 species have been described (Buschinger 1986, Hölldobler & Wilson 1990). Among bees, social parasitism is

widespread in primitively eusocial species such as bumblebees (*Psithyrus* genus consists entirely of obligate social parasites of *Bombus* species, Alford 1975) and allodapine bees (Michener 1974), but most recently studied in the highly eusocial Cape honeybee (Neumann *et al.* 2001, Moritz & Neumann 2002). Among wasps, obligate social parasites are known in the subfamilies of Vespinae (4 species) and Polistinae (3 species), but no cases are reported for the Stenogastrinae subfamily. Although, some cases of interspecific occupation of a nest by two species of hover wasps has been reported (Turillazzi *et al.* 1998). Facultative parasites are common in all these insect groups (Field 1992), but a recent review shows that ‘egg dumpers’ are also present in other insect orders (Tallamy 2005).

Both facultative and obligate, intraspecific and interspecific, avian brood parasites adopt a unique parasitic strategy: when nest owners are absent, the parasite quickly lays a single egg in a host nest and leaves without providing parental care. The host then incubates the parasitic egg with its own eggs, and raises the alien young, even if doing so it affects its own reproductive success.

Similar to birds, social insects perform facultative and obligate, interspecific and intraspecific parasitism, but they show a larger variety of parasitic strategies. The most intriguing of which is represented by slave-maker ants. Slave-maker ants steal pupae from host nests and use the captives as slaves in their own colony; these slaves work for their kidnappers and perform all the tasks necessary for colonial life (Hölldobler & Wilson 1990, D’Ettorre & Heinze 2001). Kleptoparasitism is known in some ants and bees (Wilson 1971); for example, meliponinae bees of the *Lestrimelitta* genus enter other nests to steal stored food (Sakagami & Laroca 1963). Females of some ant, bee, and wasp species are unable to found a nest and have lost the worker caste; they live in the host nest relying exclusively on host workers (Wilson 1971). The variety of parasitic strategies in social insects probably reflects the diversity of social organization and/or social behaviour of potential hosts.

It has been suggested that similar selective pressures have driven the evolution of social/brood parasitism both in birds and insects



**Fig. 1.** Distribution of *Polistes* genus and of the three species of *Polistes* obligate social parasites.

(Davies *et al.* 1989, Brockmann 1993, Cervo *et al.* 2004a), but that each has developed different parasitic strategies. Aristotle first described cuckoo breeding behaviour 2300 years ago. Since then, enormous advances in our understanding of avian brood parasites have occurred. The study of social parasitism in insects has a much shorter history but the research in this area is progressing rapidly. As these two fields develop so does our awareness of analogous solutions adopted in response to similar selective pressures by phylogenetically distant taxa.

In this review, I provide a framework of the ecology, ethology, and evolution of social parasitism in *Polistes* wasps based on twenty years of research (*see* Cervo & Dani 1996). I also provide evidence for the evolutionary convergence of brood parasitic birds and wasps.

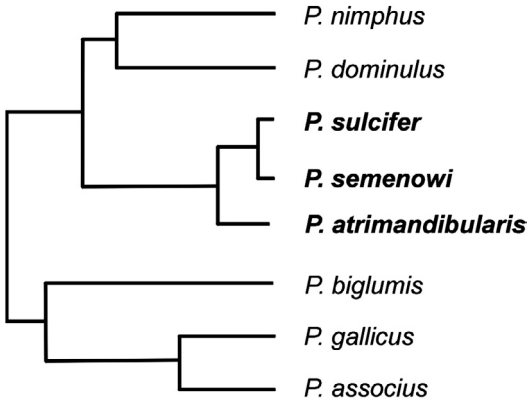
## Geographic distribution and phylogenetic relationships

There are more than 200 species in the genus *Polistes* (Akre 1982, Carpenter 1996). Species in this genus show a cosmopolitan distribution globally (Reeve 1991), although they are more concentrated in the tropics and are rarer in the colder areas of the world (Fig. 1). Among them, only three species of obligate social parasites have been described: *P. sulcifer*, *P. atrimandibularis*, and *P. semenowi*. The distribution of obligate social parasites is limited to areas around the Mediterranean and the Caspian basins (Fig. 1), where they are very rare. As other insect social

parasites (Wilson 1971), *Polistes*inquilines have a patchy distribution within their area, where they can be locally abundant. Overlapping with the obligate social parasites are six independent founding *Polistes* species: *P. dominulus*, *P. gallicus*, *P. nimphus*, *P. associus*, *P. bishioffi* and *P. biglumis*. All of them, except for the latter, are lowland species with simpatric distribution, while *P. biglumis* is strictly a mountain species. Each of them, except for *P. bishioffi*, represents the host species of at least one of the three obligate parasites.

The phylogenetic relationships of this group, investigated first by Carpenter *et al.* (1993) who performed cladistic analyses using allozyme data, did not support a close relationship between each parasite and its hosts, as was predicted by Emery's rule (1909). The latter, in its strict form, states that social parasitic species are more closely related to their hosts than to any other free-living species (Lowe *et al.* 2002).

Phylogenetic analysis of the same European *Polistes* species using mitochondrial 16S rRNA (Choudary *et al.* 1994) provided evidence for monophyly for the three species of social parasites (Fig. 2). These molecular data, together with their restricted distribution, suggest that social parasitism arose only once in *Polistes* genus, probably in the Mediterranean basin from a common ancestor. Moreover, the phylogenetic tree shows that the three species of obligate social parasites are more closely related to *P. nimphus* and *P. dominulus* than to *P. gallicus* and *P. biglumis* (Fig. 2). An analysis performed using morphological, molecular, and behavioural



**Fig. 2.** Phylogenetic relationships among European *Polistes* species. The names of obligate social parasite species are set in boldface.

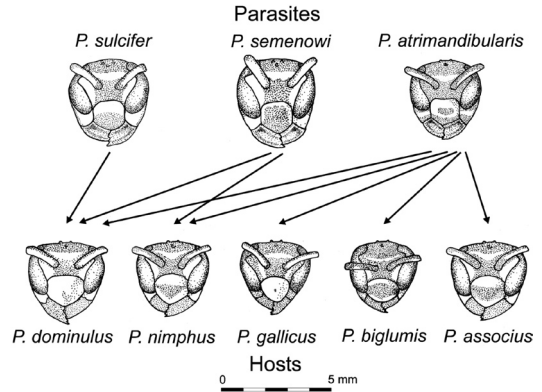
data (Carpenter 1997) confirms this phylogenetic reconstruction.

Studies on other insect social parasite–host pairs have both supported and rejected Emery’s rule (for Vespinae: Varvio-Aho *et al.* [1984], Carpenter & Perera [2006]; for allodapine bees: Lowe & Crozier [1997]; for bumblebees: Pamilo *et al.* [1987]; for ants: Bourke & Franke [1991], Ward [1996], Savolainen & Vepsäläinen [2003], Sumner *et al.* [2004]), suggesting that this rule cannot be generalized for social parasitism in the Hymenoptera. The molecular phylogenetic reconstructions of groups containing social parasites suggest that, in insects, social parasites can evolve through both allopatric and sympatric speciation (Lowe *et al.* 2002).

## Parasitic relationship among European *Polistes* wasps

### Obligate parasites

Recently, we acquired additional information about the parasitic relationships between *Polistes* social parasites and their hosts. The previous scheme of parasitic relationship reported by Cervo and Dani (1996) has been changed (Fig. 3) according to the new findings in *P. atrimandibularis* (Fanelli *et al.* 2001). *Polistes atrimandibularis* was known to be the social parasite of *P. biglumis* and *P. gallicus* (Scheven 1958, Cervo *et al.* 1992), two non-sympatric species, with



**Fig. 3.** Parasitic relationships among the three species of *Polistes* obligate social parasites (at the top) and their host species (at the bottom). The lines match each parasite species with its respective host species.

the former a typical mountain species. Now, we know that the latter parasite can successfully usurp and exploit three more host species (*P. dominulus*, *P. nimphus*, *P. associus*) than was previously reported. Therefore, this parasite can be considered a generalist, in contrast to the other two *Polistes* inquiline species. Host specificity seems to be a widespread condition among insect social parasites (*see* Wilson 1971); e.g. parasitic ants are generally specialized on a single species. Nevertheless, not all the species of insect social parasites are specialists (*see* Bogusch *et al.* 2006).

It has been proposed that one of the results of arms race between the parasite and its host is the specialization of the parasite to just one host species (Timms & Read 1999). A successful parasite–host interaction requires parasite specialization in the host communication mechanisms in order to better deceive the host recognition system (Buschinger 1986). Therefore, each parasite species should not be effective on more than one host species. For example, *P. sulcifer* exclusively usurps *P. dominulus* (Fig. 3), even in areas where additional species are present (Cervo & Turillazzi 1996). This specific host selection was confirmed using choice laboratory experiments in which a *P. sulcifer* female was offered different nests of the most common European species (Cervo & Turillazzi 1996).

*P. semenowi* is reported as a social parasite of two sympatric and sister species, *P. nimphus* and

*P. dominulus* (Fig. 3). However, while reports on *P. dominulus* are very well documented (unpublished data by our research group), reports on *P. nimphus* are very scattered, and only two parasitized nests were found, one by Scheven (1958) and one by Demolin and Martin (1980). It is very likely that the parasitic relationship between *P. semenowi* and *P. nimphus* is an accidental and rare event, and the general ability to parasitize several host species seems to be unique to *P. atrimandibularis*.

In addition to having the ability to parasitize a broad range of hosts, *P. atrimandibularis* can parasitize them all in the same locality. Our studies on *P. atrimandibularis* showed that it is not the lack of common host nests that induces a shift towards new hosts (Fanelli *et al.* 2001). In addition, field data showed that the parasite has the same success in usurping all three host species (Fanelli *et al.* 2001), which suggests that *P. atrimandibularis* is a true generalist. When a *Polistes* generalist parasite coexists with a specialist one — e.g. *P. atrimandibularis* and *P. sulcifer* in our studied areas (Fanelli *et al.* 2001; R. Cervo pers. obs.) — there is an overlap in the host species chosen, as both parasitize *P. dominulus*. Alternatively, the two specialist parasites, *P. sulcifer* and *P. semenowi*, who both use the same host species (*P. dominulus*), are not found in sympatry (R. Cervo pers. obs.).

The limited number of hosts used by *P. sulcifer* and *P. semenowi* could be due to their large body size, which limit usurpable host species (Cervo & Turillazzi 1996). Alternatively, Fanelli *et al.* (2005) suggested that the broader range of host species found in *P. atrimandibularis* results from the lack of size constraints of this species: *P. atrimandibularis* is smaller than the other two social parasites (R. Cervo unpubl. data), and is the only parasite compatible in size with the smaller European *Polistes* species (*P. gallicus*, *P. associus*, *P. biglumis*).

Generalists, as well as specialists, are known among avian brood parasites, where the number of hosts can range from 1 to 100 for cuckoos (Rothstein & Robinson 1998) and from 1 to 200 for cowbirds (Lanyon 1992). Traditionally, it has been hypothesised that the first brood parasite was a generalist, which increased host encounter probability. As hosts developed defence strate-

gies, however, brood parasites had to specialize (Rothstein & Robinson 1998). An alternative view is presented by molecular analysis on cowbirds (Lanyon 1992), where host specificity is suggested as the primitive condition, and generalism as the derivative.

Among the generalist avian brood parasites, the common cuckoo, *Cuculus canorus*, shows a well-studied pattern of host use. It is known that individual females of this parasite tend to specialize on one particular host species, and lay eggs that match the eggs of their respective hosts. This means that *Cuculus canorus* is sub-divided into separated host races, which are referred to as gentes (De Brooke & Davies 1988). Although genetic studies have been carried out to explore how the difference in egg mimicry is maintained (Gibbs *et al.* 1996, Marchetti *et al.* 1998), only recently has it been shown that females are involved in host-specific race formation (genetic factors for colour pattern are linked with mitochondrial DNA), while males maintain the genetic cohesion within species by randomly mating with females (Gibbs *et al.* 2000).

The generalist nature of *P. atrimandibularis* gives us the opportunity to test whether host specific races are present in an insect social parasite. In other words, we tested whether *P. atrimandibularis* is truly a generalist or individual female exploits just one host species. The specialization at an individual level could explain the long-term use of several host species of this parasite. The process of specialization at an individual level could be accelerated by parasite phenotype matching with one host. As expected, there is a difference in the size of parasites reared from different host species (Fanelli *et al.* 2005), as brood cell sizes differ markedly among host species. The emerging parasite population differs in size, with smaller individuals emerging from nests of *P. gallicus* and *P. associus* and larger from *P. dominulus* nests. Although these findings could suggest host race formation, with smaller parasites usurping only smaller host species, *P. atrimandibularis* usurpers do not match body size with host species (Fanelli *et al.* 2005); all successful parasites were large and matched in size with the parasites emerging from *P. dominulus* (Fanelli *et al.* 2005). Moreover, microsatellite genetic analysis, on *P. atrimandibularis* females



who enclosed on nests of different host species show no evidence for genetically distinct host races (Fanelli *et al.* 2005). We suggested (Fanelli *et al.* 2005) that the lack of host genetic differentiation in *P. atrimandibularis* is due to the usurpation method used by *Polistes* parasites, namely to deceive the host chemical cue recognition system by allowing the parasites to acquire any colonial odour after usurpation (Sledge *et al.* 2001, Lorenzi *et al.* 2004, Lorenzi 2006). On the contrary, the cuckoo strategy — based on a specific egg colour pattern — is more rigid and requires a genetic egg pattern mimicry. However, a recent study (Bogusch *et al.* 2006) demonstrates that exactly as in avian cuckoos, each female of two generalist cuckoo bees species tends to attack just one host species.

### Facultative parasites

Recently, it has been reported that *P. nimphus* is a peculiar relative of other free-living *Polistes* wasps, as it is the only known species that regularly performs successful interspecific facultative temporary parasitism (Cervo 1998, Cervo *et al.* 2004b). Until now, very little was known about this intermediate form of parasitism, in which a foundress of an independent nesting species usurps a colony of another species. Observations of the contemporary occupation of the same nest by two different *Polistes* species are few and sporadic. Snelling (1952) discovered one colony of *P. fuscatus* usurped by *P. apachus* without furnishing any additional information on this example. Hunt and Gamboa (1978) reported two nests occupied by *P. metricus* and *P. fuscatus*. O'Donnell and Jeanne (1991) observed the development of one colony of *P. instabilis* usurped by *P. canadensis* and Giovannotti (1995) noticed one nest of *P. versicolor* usurped by *P. lanio*. Reports on interspecific facultative parasitism are more common with European species. *P. dominulus* foundresses are able to usurp colonies of *P. gallicus* (Cervo & Dani 1996, unpubl. data) and *P. nimphus* invade colonies of *P. dominulus* (Cervo 1998, Cervo *et al.* 2004b). The interspecific relationship between *P. dominulus* and *P. gallicus* was never successful: none of the 6 mixed *P. dominulus*–*P. gallicus*

colonies that I checked lasted beyond a very initial stage of the colony cycle and did not produce workers or reproductives.

The parasitic relationship between *P. nimphus* and *P. dominulus* represents a real example of the second step of parasitism in Taylor's scheme (Taylor 1939), with *P. nimphus* usurpers successfully exploiting *P. dominulus* colonies (Cervo *et al.* 2004b). *Polistes nimphus* seems to be specialized on usurping *P. dominulus* nests, even when another potential host, *P. gallicus*, is present in the same area. If the simplest form of interspecific parasitism (facultative) requires phylogenetic proximity (Fig. 2), followed by chemical and behavioural similarity between the two involved species, we can understand the unsuccessful interspecific usurpations of *P. dominulus* of *P. gallicus*, and the lack of usurpation attempts of *P. gallicus* by *P. nimphus* (see Fig. 2).

### Morphological specializations of usurpers to parasitic life

#### Obligate parasites

Parasites can evolve several morphological features to improve their capacity to exploit hosts. Few morphological specializations to parasitic habit are reported in brood parasite birds, as no interactions occur between parasite females and parental hosts since most brood parasites approach host nests very stealthily during the host's absence (reviewed by Rothstein & Robinson [1998]). After a quick egg deposition, they leave the host nest, fully delegating egg incubation and young care to host parents. In cuckoos, female plumage is less conspicuous than male plumage to facilitate this stealthy approach, while the bright colours of the males help them to attract host attention which favours female nest entry (Duckworth 1991). In insects, social parasites must enter a host society and be accepted as a colony member. Therefore, their morphological specializations are more conspicuous. The latter are used to improve both their fighting equipment to enter host colony (e.g. enlarged mandibles or strong sting), and their means (e.g. specialized glands for chemicals production) to mimic the hosts' chemi-

cal communication (see Wilson 1971, Buschinger 1986). Many insect social parasites have evolved a large set of morphological modifications (see Wilson 1971) resulting from the reduction or lack of colonial activity, such as nest building (e.g. loss of wax glands in bees) and foraging (e.g. lack of the pollen baskets, reduction of wing venation as well as eyes and mouth parts).

The evident morphological features of the three *Polistes* obligate social parasites were sufficient to taxonomically separate them (in the *Sulcopolistes* genus) from the *Polistes* species, even before their parasitic habit was recognized (Zimmermann 1930). Eventually, Carpenter (1991) synonymized *Sulcopolistes* with their hosts. All the three species of *Polistes* obligate social parasites are morphologically adapted for fighting, and for having an advantage during nest invasion. The overall body size is similar in *Polistes* parasites and in their respective principal hosts, but some body parts (head, first femur and posterior tibia) are significantly more developed in the parasite than in its host (Cervo [1994] for *P. sulcifer* and *P. atrimandibularis*; R. Cervo [unpubl. data] for *P. semenowi*). The enlarged first femur, as well as the longer posterior tibia, could be useful during invasion fights, as well as later when the parasite must maintain its dominant position within the host colony. The thickened cuticle and the close fit among abdominal segments in *P. sulcifer* females prevent host sting penetration (Cervo 1994). Mandibles, an exaggerated trait of obligate social parasites, although similar in length in parasites and host, are significantly larger and thicker in the former (Cervo [1994] for *P. sulcifer* and *P. atrimandibularis*; R. Cervo [unpubl. data] for *P. semenowi*). The typical groove that runs along the mandibles of all *Polistes* parasites may be needed to strengthen this enlarged mouth part (Cervo 1994). Mandibles are essential for the parasites: they are used as a weapon to injure hosts that resist parasite intrusion (Turillazzi *et al.* 1990). A different interpretation has been proposed for *P. atrimandibularis* by Schwammberger (2001), who suggests that enlarged mandibles and thickened cuticle may be an adaptation to conspecific competition for access to host resources.

In contrast to Vespinae obligate social parasites, whose sting is more stout and curved than

that of the host queens (Reed & Akre 1982, Ondricek-Fallacheer 1992), the sting of *Polistes* social parasites is not different from that of host foundresses (Cervo 1994). This is expected because no parasite sting use occurs during usurpation struggles. No morphological features connected to the reduction in some colonial activity has been found in *Polistes* obligate social parasites (Cervo 1994), suggesting a low level of specialization of these inquiline.

### Facultative parasites

Since in facultative parasites the parasitic behaviour represents an alternative strategy to brood care that is not always adopted, morphological specializations are not expected. No specific studies on this aspect have been carried out for facultative conspecific parasites in *Polistes* wasps. However, preliminary field data show that head size of *P. dominulus* conspecific usurpers are significantly larger than that of the legitimate nest owners (data for 5 pairs, R. Cervo [unpubl. data]). Although, data are few, they suggest that body size can be a decisive factor for a successful conspecific usurpation.

For all sporadic cases of mixed *Polistes* colonies reported in the literature, the usurper species is always bigger than the usurped ones (O'Donnell & Jeanne 1991, Giannotti 1995, Cervo & Dani 1996). More information is available for *P. nimphus* foundresses who, besides founding their own nest, they are able to usurp conspecific colonies (R. Cervo pers. obs.) or those of *P. dominulus* (Cervo *et al.* 2004b). Although *P. nimphus* is smaller than the species it parasitizes (*P. dominulus*), it shows enlarged mandibles and front femurs that, as with obligate *Polistes* parasites, can be used as usurpation tools (Cervo *et al.* 2004b). These enlarged body parts may allow *P. nimphus* to successfully usurp both solitary and associative foundations of *P. dominulus* (Cervo *et al.* 2004b).

The similarity in "fighting equipment" between *P. nimphus* and three species of obligate social parasites allows for some speculations. Firstly, *P. nimphus* may show these peculiar morphological traits as they are better offensive weapons to successfully usurp another colony.

Secondly, *P. nimphus* may represent the oldest host species exploited by obligate parasites, but is no longer parasitized because, in the arms race with the parasites, it developed defensive characters to prevent parasite usurpation. These defensive features may be currently used as offensive tools to usurp *P. dominulus* nests. In support of this perspective is the rare number of reports of *P. nimphus* being used as host species by obligate social parasites (2 nests usurped by *P. semenowi* and 3 usurped by *P. atrimandibularis*), in spite of its belonging to the same sister clade. Finally, *P. nimphus* could represent the living species most closely related to the ancestor of obligate *Polistes* parasites, and its morphological features render this species a less attractive target for the obligate parasites.

## Usurper behavioural adaptations to parasitic life

### Obligate parasites

Although the behaviour of brood parasitic birds and insect social parasites is different, some similar solutions to the same parental constraints have been adopted in both groups. Firstly, host nest location and proper timing are essential for successful parasitism in avian brood parasites as well as in *Polistes* parasites. Brood parasitic birds often search for host nests by following hosts and observing their behaviour. The parasitic females then wait the right time to lay their eggs. If the parasite lays its egg before the host starts its own deposition, the latter would abandon the nest or eliminate the parasite egg. Alternatively, if it lays its egg too late, its nestling would be at a disadvantage relative to the host nestlings (Lotem *et al.* 1995). Similarly, *Polistes sulcifer* usurpers actively look for established host nests and, once in proximity, choose the more suitable one by means of chemical cues, as showed by laboratory experiments (Cervo *et al.* 1996). The ability to chemically detect the correct nest without landing on it, provides a clear advantage for the parasites. In this way, they avoid initiating usurpation attempts of colonies unsuitable in terms of host species and colony stage (Cervo *et al.* 1996). An early usurpation may cause hosts

to abandon the colony and build a new one. A late usurpation, after workers emerge, may fail as many workers can prevent usurper entry. In fact *Polistes* parasites, as in other insect social parasites, arrive on the host colonies in a well-defined temporal window, approximately one month after host nest foundation (Cervo *et al.* 1990a, 1990b, Cervo & Turillazzi 1996, Zacchi *et al.* 1996). At this time, the parasite has a sufficient time to reproduce and to exploit host worker force for rearing its brood.

A way to delay the arrival on host nests is to postpone the overwintering exit. A peculiar behaviour of *Polistes* parasites is that they spend the winter on mountains (Cervo & Dani 1996). Soon after emergence from host nests, males and females of obligate parasites migrate to the tops of high mountains, where mating occurs and where inseminated females remain for overwintering for several months, often under a thick blanket of snow and ice (R. Cervo pers. obs.). Severe climatic conditions extend parasite diapause for about one month in comparison with that of congeneric lowland hosts (R. Cervo unpubl. data), allowing the parasites to reach lowland host colonies when they are developed enough to be successfully usurped. Moreover, since *Polistes* obligate parasites are rare, altitudinal migrations promote encounters between sexes and favour matings between non-relatives (Cervo & Dani 1996) as reported for other rare insect species (Thornhill & Alcock 1983). Altitudinal migration constraint may explain the patchy distribution of these parasites, as well as of the higher parasitic pressure on host populations living at the foot of mountains.

It is well known that brood parasitic birds are remarkably fecund, capable of laying a large number of eggs per season (e.g. over 100 in a species of *Molothrus*, see Rothstein & Robinson 1998). This high fecundity leads them to parasitize many host nests, as the parental foraging efforts of one host pair cannot fulfil the reproductive capacity of a single parasite. Although no specific studies have been carried out on the fecundity of insect obligate social parasites, the available data for *Polistes* suggest that parasite fecundity is not higher than that of a single host foundress (Lorenzi *et al.* [1992] for *P. atrimandibularis*). However, it is clear that a



colony supplies sufficient rearing opportunities to assure the reproductive needs of one parasite. Therefore, while the single-egg-per-nest strategy of most of avian brood parasites leads them to have no contact with hosts, social insect parasites become members of host societies in order to exploit them for the entire colonial cycle.

The three species of obligate *Polistes* social parasites show similar life cycles, even though there are remarkable differences in their parasitic strategies. They differ in the amount of aggression used to enter host colonies: *P. sulcifer* and *P. semenowi* females adopt an aggressive strategy to invade host colonies, fighting with the hosts (Cervo *et al.* 1990a, Turillazzi *et al.* 1990, Zacchi *et al.* 1996); whereas *P. atrimandibularis* females enter the host colony using a non-aggressive strategy, at least when they parasitize *P. biglumis* (Cervo *et al.* 1990b) and *P. gallicus* (R. Cervo unpubl. data). This passive strategy consists of initial submission to frequent attacks of the host queen, followed by a gradual increase of dominant acts on the host performed by the parasite. The parasites also differ in their tolerance to the host queen: *P. sulcifer* females generally drive off or kill the host queen (Turillazzi *et al.* 1990), whereas *P. semenowi* and *P. atrimandibularis* cohabitate with the dominant individual for some time (Cervo *et al.* 1990b, 1992, Lorenzi *et al.* 1992, Zacchi *et al.* 1996, Fanelli 2001).

After successfully avoiding host recognition systems by adopting host chemical profiles as well as chemically invisibility (review by Lorenzi [2006]), the parasites live as nestmates and become queens of the host colonies (Cervo 1990, Cervo & Dani 1996). As soon as parasites take possession of host nests, they destroy some of the host's immature brood: most eggs and small larvae are devoured, whereas older larvae and pupae suffer less destruction (Cervo 1990, Turillazzi & Cervo 1996). Emptying cells for egg deposition may be the main factor inducing host brood destruction in usurper females, even if host brood eating may also allow the parasite to acquire host specific cuticular hydrocarbons to elude the host nestmate recognition system (as suggested for a myrmecophilus spider; Elgar & Allan 2004). Host egg eating, before egg deposition, is also a widespread strategy in avian brood

parasites, where it might increase incubation efficiency (Payne 1977, Davies & De Brooke 1998). In addition, both in birds and in insect parasites, egg removal may provide an energetically rich meal for their egg production period (Davies & De Brooke 1988, Cervo 1990).

Immediately after *P. sulcifer* and *P. semenowi* usurpers take possession of a colony, they perform very intense stroking of the nest surface with the ventral part of the gaster (Turillazzi *et al.* 1990, Zacchi *et al.* 1996). *Polistes atrimandibularis* does not perform the abdominal stroking behaviour, or performs it less frequently relative to the other parasitic species (Cervo *et al.* 1990b). However, this behaviour decreases during the first few hours after invasion (Turillazzi *et al.* 1990, Zacchi 1995). Exaggerated abdominal nest stroking, combined with prolonged licking of the host's body and frequent trophallactic interactions, are likely linked to the parasite's integration into the host colony (Cervo *et al.* 1990b, Turillazzi *et al.* 1990, 2000).

The behaviour of usurper females of the three species of *Polistes* parasites differs during the colonial cycle. *P. sulcifer* and *P. semenowi* females behave as true social parasites, limiting their activities to host control and egg laying (Cervo 1990, Zacchi 1996). A peculiar behaviour performed by usurpers of both these species is "abdominal drumming", first described on *P. sulcifer* (Cervo 1990), and later observed in *P. semenowi* (Zacchi 1996), but never performed by any host species or by *P. atrimandibularis* (Cervo 1990). Even if we did not know the function of this behavioural pattern, it is remarkable that it is only performed by females of two parasite species. Alternatively, *P. atrimandibularis* is a peculiar parasite for its active defence of the colony against predators or potential usurpers (Cervo 1990, Cervo *et al.* 1990c, Fanelli 2001). Interestingly, it has been suggested that great spotted cuckoos (*Clamator glandarius*) provide parasitized nests with protection against predation (Arias-de-Reyna 1998, Soler *et al.* 1999).

But, the most distinguishing behavioural trait of *P. atrimandibularis* is its extra-colonial activity, during which it usurps other host nests (secondary nests). From these "secondary nests" the parasite takes away larvae and pupae, and uses them as food for feeding larvae on the "primary

nest", used for reproductive purposes only (Cervo *et al.* 1990c). Predatory behaviour on secondary nests, first described on *P. biglumis* (Cervo *et al.* 1990c), has been reported on host colonies of the other lowland species (Cervo *et al.* 1992, Fanelli 2001). Pillaging reduces or even nullifies host reproductive success on secondary nests, but provides advantages on primary ones (Cervo 1990, Cervo *et al.* 1990c, Schwammberger 1998, Fanelli 2001). The only case where an avian host benefited from parasitism was reported by Smith (1968): parasite nestlings of the giant cowbird (*Molothrus oryzivorus*) remove harmful ectoparasites from their host nestmates.

It is possible that the predator behavior of *P. atrimandibularis* is analogous to the documented great spotted cuckoo behaviour of destroying eggs and young in host nests from which cuckoo eggs have been rejected, the so called "avian mafia" effect (Zahavi 1979, Soler *et al.* 1995). Future research on *P. atrimandibularis* predatory traits should shed light on the factors influencing this behaviour.

## Facultative parasites

Conspecific parasitism has been viewed as a precursor to the evolution of interspecific parasitism both in birds and insects (Taylor 1939, Hamilton & Orians 1965, Wilson 1971, Payne 1977, Brockmann 1993), suggesting that obligate parasitism could have arisen from facultative intraspecific parasitism. Brockmann (1993) stressed that similar selective pressure favours intraspecific parasitism in both these groups.

Much of the work on facultative interspecific parasitism in *Polistes* wasps indicates that this strategy is usually performed by individuals 'making the best of a bad situation' (the lost of their own colony), an interpretation which is supported by the low profitability of this behaviour (*see* Cervo & Dani 1996). Although, the same was suggested for conspecific avian brood parasitism (Yom-Tov 1980), some authors have emphasized that this form of parasitism may represent an fitness maximizing alternative reproductive strategy, pursued by females that are capable of taking care of their own young (*see* Petrie & Møller 1991). Available informa-

tion on *Polistes* interspecific usurpation is too scarce to support the choice between these two alternatives. However, *P. nimphus* (a facultative parasite of *P. dominulus*) shows some features common to obligate social parasites, such as morphological specializations and mountain overwintering (Cervo *et al.* 2004b), suggesting that *P. nimphus* interspecific usurpers may choose a parasitic strategy rather than starting their own nests (Cervo *et al.* 2004b).

Behavioural patterns of facultative *Polistes* parasites follow those of obligate parasites. Both intraspecific and interspecific facultative usurpers use violence to enter a host colony and kill the host queen, as has been confirmed by dead foundresses found at the feet of usurped nests (*see* Cervo & Dani 1996, Cervo *et al.* 2004b). Facultative interspecific parasites time their arrival on the host nests in a similar way as obligate parasites (Cervo *et al.* 2004b). Behavioural tests provide evidence for successful chemical integration of facultative parasites within host colonies (Lorenzi 2006), which is most likely obtained through intense stroking behaviour performed after nest appropriation (Cervo & Turillazzi 1989, Dani *et al.* 1992, Cervo & Lorenzi 1996a, Van Hooser *et al.* 2002, Cervo *et al.* 2004b).

## Parasite brood adaptations to parasitic life

### Obligate parasites

An evolutionary enigma is why hosts accept and care for unrelated brood. This intriguing puzzle has been extensively studied in avian brood parasites, where it is now largely solved. Unfortunately, studies on insect social parasites have not yet focused on this subject. It is expected that parasitic larvae have evolved several tricks in order to conceal their identity from hosts and to attract host attention to be fed.

Important adaptive features of cuckoo eggs, such as thick eggshells, mimetic colour patterns, short incubation times, and small size relative to the size of the parasite, provide some of the better examples of coevolution in vertebrates (Lotem & Rothstein 1995). Cuckoo egg mimicry induces

hosts acceptance, as has been experimentally demonstrated by Davies and De Brooke (1988). However, egg mimicry is not a universal trait of parasitic birds. Mimicry in parasitic eggs is lacking in all but one cowbird species (*see* Rothstein & Robinson 1998), probably due to the darkness of the nesting sites chosen by hosts, rendering egg colour unimportant (Fraga 1983).

The famous concave back of cuckoo nestlings permits the cuckoo chick to obtain all host parental effort, as it allows the cuckoo to push the host eggs or chicks out of the nest. In general, nestling mimicry is absent or scarcely developed in cuckoos (Lotem 1993), while it is almost perfect in cowbirds that are raised alongside the host chicks (Fraga 1998). Lotem (1993) suggested that the host inability to recognise cuckoo nestlings, raised alone in its own nest, may be explained by the high cost for the host when it imprints on parasitic nestling during its first breeding attempt.

In insect societies, the efficient host nestmate recognition system — based on chemical cues — has selected for parasites to develop brood mimicry to avoid brood detection and rejection by hosts. Some ant studies, show that parasitic immature brood, chemically resemble the host immature brood (Howards *et al.* 1990, Kaib *et al.* 1998, Akino *et al.* 1999, Elmes *et al.* 1999, Schonrogge *et al.* 2004, Johnson *et al.* 2005), thus allowing integration into the host colony. In other cases, some larvae of myrmecophilus beetles secrete appeasement substances from the tip of their abdomen to escape the host aggression (Hölldobler & Wilson 1990).

Recently, we have found an unexpected result for immature brood of *Polistes* social parasites: both eggs (Dani *et al.* 2004) and larvae (R. Cervo *et al.* unpubl. data) of *P. sulcifer* do not use the same chemical signatures adopted by adult parasites (*see* Lorenzi 2006) to be accepted by the host colony. In fact, the cuticular profile of both eggs and larvae do not match that of the respective immature stages of the host (Dani *et al.* 2004; R. Cervo *et al.* unpubl. data). Moreover, *P. sulcifer* larvae do not even promote their acceptance with low levels of hydrocarbons (R. Cervo *et al.* unpubl. data), which might give them chemical invisibility (Lenoir *et al.* 2001). A series of behavioural assays on larva recognition

showed that parasite larvae are detected and tolerated by hosts that did not experience parasites (R. Cervo *et al.* unpubl. data). The same host tolerance was reported for some *P. atrimandibularis* eggs that were experimentally transferred into *P. biglumis* unparasitized nests (Lorenzi & Filippone 2000). It is interesting to note that the chemical profile of parasite larvae of different colonies is less variable than that among host larvae, and that the parasite larvae chemical pattern is tolerated more by hosts than that of non-parasitic species (R. Cervo *et al.* unpubl. data). These results suggest that the parasite larvae cuticular pattern, even if not mimetic with host larvae, may be neutral for the hosts, thus facilitating their acceptance into host colonies. Despite this cuticular diversity, *P. sulcifer* larvae are well integrated into the host society and are fed and protected by host workers (Cervo *et al.* 2004a).

It is surprising that the hosts, besides tolerating the parasite brood, feed it even more than their own brood. The capacity of the parasitic brood to monopolize host parental care is widespread among avian brood parasites, but rarely investigated in social insect parasites. Larvae of some myrmecophilous beetles (*Atemeles pubicollis* and *Lomechusa strumosa*), for example, are able to induce ants to preferentially care for them and to neglect their own brood (Hölldobler & Wilson 1990); and larvae of *Apis mellifera capensis* (Beekman *et al.* 2000) receive more food when they are fed by host workers than by workers of their own species. But the best-known examples of host parental care manipulation by parasites are reported for brood-parasite birds. A *Cuculus canorus* chick is fed at the same rate as a whole host-clutch (De Brooke & Davies 1989), even if it is alone in the nest. To receive more food by the host, the cuckoo chick stimulates the feeding activity of the foster parents using both a visual signal — its large red gape — and a vocal signal — a very strong begging call comparable to that of the whole host clutch (Davies *et al.* 1998, Kilner *et al.* 1999). These traits allow the parasite chick to grow faster by receiving more care than any host chick.

According to Redondo (1993), parasite supernormal stimulation compensates its scarce mimicry and assures its acceptance. In other parasite

birds, a chick is raised alongside the host chicks and it has to compete with them for food. It succeeds by using its larger body, loud begging calls, and exaggerated visual signal of its gape. A similar cohabitation occurs in *Polistes* parasitized nests, since parasitic and host larvae share the same comb, and the host workers feed both of them. However, we have shown that parasitic larvae are visited and fed more frequently than host larvae (Cervo *et al.* 2004a). This differential parental care ensures the relatively fast growth of parasite larvae and causes the slowly growth of the host larvae reared in the same comb (Cervo *et al.* 2004a). These findings suggest that *P. sulcifer* parasite larvae, in some way, manipulate the behaviour of the host tenders.

Behavioural observations of parasitized colonies have shown that the *P. sulcifer* usurper does not influence the nursing activities of host workers (Cervo *et al.* 2004a), the question on how parasitic larvae are able to elicit more care is still open. The parasite larvae might, as with parasitic birds, gain host attention by exaggerating those key characteristics usually used by young to solicit food. Myrmecophiles beetles larvae mimic and amplify behaviour usually performed by ant larvae to solicit food (Hölldobler & Wilson 1990). Analysis of *Polistes* larvae behavioural patterns, using artificial transparent plastic cells, showed that parasite larvae do not differ in their behavioural repertoire from host larvae (Cervo *et al.* 2004a). For example, both types of larvae perform a similar protrusion towards the cell opening (R. Cervo unpubl. data) when host workers walk on the comb.

Adult-brood communication has been poorly investigated in social insects, but some evidence has suggested the existence of 'hungry signals' in hornets, bees, and ants (Ishay & Landau 1972, Yamane 1976, Huang & Otis 1991, Pereboom *et al.* 2003, Creemers *et al.* 2003, Kaptein *et al.* 2005). Unfortunately, this possibility has not been addressed in *Polistes* wasps, where colony-level organization of larval nursing is practically unexplored. If hungry signals exist in *Polistes* wasps, it is possible that they are amplified by parasitic larvae in order to exploit the host tenders, as occurs in cuckoo chicks. Parasitic larvae could send such a signal more frequently to obtain more food, but while also avoiding host

detection. The latter strategy would support the Holen and co-workers' idea (2001) that selection may favour parasite signal intensity to closely match that of the host to avoid detection and rejection.

We have begun to explore whether *Polistes* larvae communicate their needs to adults. Larval starvation experiments, performed on *P. dominulus*, did not provide clear evidence for the existence of hungry signals in *Polistes* larvae (Cotoneschi *et al.* 2004), but additional experiments are needed before excluding this possibility. Many signals could be employed by parasitic larvae in manipulating the feeding activity of host tenders. Preliminary data exclude that parasite larvae facial markers (R. Cervo unpubl. data) might over-stimulate the nursing behaviour of host workers, but rather suggests that parasite larval head size may be involved in host parental care manipulation (R. Cervo unpubl. data). Moreover, *Polistes* parasitic larvae may use chemicals to induce hosts to feed them more often than host larvae. Further work is necessary to clarify the proximate mechanisms underlying this interesting host-parasite relationship that allows *P. sulcifer* larvae to be fed at an increased rate and consequently to grow faster than the host larvae.

In fact, the developmental time of *P. sulcifer* immature brood is much shorter than that of its host *P. dominulus* (on average 25 days vs. 33 days) (Cervo *et al.* 2004a, 2004b), and it is shorter relative to all other *Polistes* species (range 33–70 days) for which the immature development time is known (Strassmann & Orgren 1983, Reeve 1991). The speed of *P. sulcifer* development is due to a rapid larval growth period and to a very short egg hatching time (3–5 days). Parasite pupal stage length is not reduced relative to that of host pupae in unparasitized nests. As *P. dominulus* pupal stage is the shortest among all *Polistes* species, it is probably impossible to shorten it further (Cervo *et al.* 2004a).

A very fast egg hatching time is reported for cuckoo birds. Indeed, it is the fastest hatching time of all avian species. The rapid hatching time in the cuckoo is the result of a prolonged egg stay in mother's oviduct, where it begins the embryo development (Lack 1968, Vermon 1970, Whyllie 1975, Payne 1977). No information is available for the mechanisms responsible for the

very short egg hatching time in *P. sulcifer* (Cervo *et al.* 2004a). The advantages of a reduced hatching time, and of a manipulative feeding strategy, in avian brood parasites are linked to competition with host nestlings and food provisioning, respectively. Alternatively, the fast growth of parasite immature brood in *Polistes* parasites allows the usurper to obtain high offspring production using the same cells for more than one generation (Cervo *et al.* 2004a), despite the delay in parasite egg deposition (Cervo & Turillazzi 1996).

The “selfishness” of *Polistes* parasitic larvae could be related to the most remarkable feature of these parasitic species — the lack of a worker caste — as proposed by Nonacs and Tobin (1992). Parasites could have lost the worker caste as a consequence of host caste determination system based on the amount of food given during the larval stage (O’Donnell 1998): if parasitic larvae can manipulate host workers into providing more food during their development, they would develop into reproductives rather than into workers.

### Facultative parasites

Conspecific brood parasitism in birds seems to be far more widespread than previously believed (Yom-Tov 2001). Its wide expression is probably due to the relative ease with which this strategy can be performed among conspecifics. Rejection of conspecific parasitic eggs has been rarely reported, possibly because it is hard for conspecifics to detect parasitic eggs with the same features as their own eggs (Rothstein 1990). The situation in insect facultative parasites is more complicated: they have to overcome the same host recognition system as obligate social parasites. Since in *Polistes* wasps the immature brood and adults have a unique colonial odour (R. Cervo *et al.* unpubl. data, C. Cotoneschi *et al.* unpubl. data), alien conspecific brood is immediately detected and eliminated (Lorenzi & Filippone 2000, R. Cervo *et al.* unpubl. data). No work has focused on the mechanisms used by *Polistes* conspecific usurpers to make their own brood acceptable within an alien colony. However, the low reproductive success of conspecific

facultative usurpers in *Polistes* wasps (*see* Cervo & Dani 1996) suggests that these brood are not well integrated into alien colonies. On the other hand, the successful reproduction of *P. nimphus* on *P. dominulus* colonies indicates that *P. nimphus* brood is tolerated within congeneric colonies (Cervo *et al.* 2004b) and suggests the need of future investigation.

### Concluding remarks and future directions

In wasps, as in birds, interspecific nest parasitism is traditionally thought to have evolved via conspecific parasitism (Taylor 1939, Hamilton & Orians 1965, Payne 1977, Yamauchi 1995, Cervo & Dani 1996). Research has addressed questions regarding the evolution of obligate interspecific parasitism in birds using theoretical models (Yamauchi 1995, Magali & Sorci 2001) and comparative analysis (Krüger & Davies 2002). The latter approach based on the comparison of life-history patterns of living facultative and obligate parasitic species in *Polistes* wasps (Table 1) can be used to develop a working framework on the evolutionary history of social parasitism. Based on the characteristics of intraspecific and interspecific parasitism (Table 1), I hypothesize that the original obligate parasite performed a violent usurpation and eliminated the host queen, as is shown by *P. sulcifer* and by facultative *Polistes* parasites today. The next stage, represented at the present by *P. atrimandibularis*, involved a more passive tactic that, while avoiding aggressive encounters with the host queen, allowed the parasite and the host to coexist. According to this perspective, an intermediate step is shown by *P. semenowi*, in which an aggressive strategy is followed by queen–parasite cohabitation. The passive tactic is reported as derived in the cladistic optimization of behavioral traits performed by Carpenter (1997).

The cohabitation between parasite and host queen must have led the parasite to suppress host queen reproduction, as it is currently performed by *P. atrimandibularis* (Cervo & Lorenzi 1996b). The maintenance of morphological fighting characteristics in *P. atrimandibularis*, despite their sneaking invasion tactic, may be



linked to the aggressive behavior performed during pillaging of secondary nests (R. Cervo pers. obs.) or during conspecific competitions (Schwammburger 2001). Alternatively, offensive characters could be retained in prudent parasites.

Evading the host's colony recognition system seems to be a critical factor for parasitism to occur. It has been suggested that parasite pressure is one of the important factors favouring efficient nestmate recognition ability in *Polistes* wasps (Lorenzi *et al.* 1996). Chemical integration is a strategy shared by parasites, although its achievement is probably reached through different modalities in different parasites (*see* Lorenzi 2006). An exaggerated abdominal stroking behavior is a common to all parasitic stages (facultative and obligate ones), except in *P. atrimandibularis*, suggesting that this behavioral pattern represents a primitive behavior for attaining parasite integration into host colonies.

A comparison of the number of interacting species in a host-parasite system may help to establish the most probable evolutionary pathways of host specialization. The relationships among European *Polistes* suggest that the original *Polistes* parasite was probably specialized on a single host species and that over time, parasites became more generalist, thus gaining the ability to parasitize an increasing number of species. The broader range of host species exploited by *P. atrimandibularis* shows that, contrary to what was previously assumed (Buschinger 1989), a generalist parasite is able to evade the recognition system of multiple host species — even

those belonging to different clades — and suggests that the capacity of breaking nestmate recognition systems of several hosts is a derived condition.

The parasite-host relationships in *Polistes* wasps (Fig. 3) suggest, as a plausible scenario, that the ancestral social parasite used to usurp a species belonging to its closest clade (*P. dominulus* and *P. nimphus*). This suggests the intriguing possibility that *P. nimphus* represents an old host that is no longer exploited. However, while *P. sulcifer* and *P. semenowi* still use hosts of this clade, *P. atrimandibularis* has extended its host range to include parasitizing species outside the original clade (Fanelli *et al.* 2005). In this comparative perspective, the plundering behavior on secondary nests — showed only by *P. atrimandibularis* — seems to be a subsequent adaptation in the stage of obligatory and permanent parasitism. In other words, once specialized in usurpation, and in the maintenance of control over colonies of the host species, a parasite could increase its reproductive success by using this ability to plunder other nests to obtain food for the brood (Cervo 1990). The cladistic approach used by Carpenter (1997) also states the plundering behavior of *P. atrimandibularis* as a derived trait.

Finally, the altitudinal migration habits of interspecific parasites assure lowland nesting area abandonment, favouring effective outbreeding, which results in high evolutionary potential for these parasitic species.

However, the deep differences in behavioural patterns among the three living obligate para-

**Table 1.** Main behavioral patterns in facultative intra- and interspecific parasites (based on *P. nimphus* parasite of *P. dominulus*) and in the three species of obligate interspecific parasites (*P. sulcifer*, *P. semenowi*, *P. atrimandibularis*).

Parasitism stages	Intraspecific temp. and facultative	Interspecific temp. and facultative	Interspecific obligate and permanent		
			<i>P. sulcifer</i>	<i>P. semenowi</i>	<i>P. atrimandibularis</i>
Morphological adaptations	No	Yes	Yes	Yes	Yes
Usurpation tactic	Violent	Violent	Violent	Violent	Passive
Host queen cohabitation	No	No	No	Yes	Yes
Stroking behavior	Yes	Yes	Yes	Yes	No
Chemical integration	Yes	Yes	Yes	Yes	Yes
Number of host species	—	1	1	1(2)	Several
Secondary nests	No	No	No	No	Yes
Altitudinal migrations	—	Yes	Yes	Yes	Yes

sitic species (Table 1) could also suggest that *P. atrimandibularis* and the other two parasites have engaged two different evolutionary routes leading to inquilinism rather than representing different stages of the same evolutionary pathway. Both *P. sulcifer* and *P. semenowi* show specialized adaptations to parasitic life such as host specialization and lack of some activities (defence and nest foraging). On the other hand the peculiar generalist habit of *P. atrimandibularis* together with its capacity of plundering host nests suggests a different but efficient way to exploit its host.

This review, based on the available literature on *Polistes* parasites, has shown that these parasites have evolved many elaborate adaptations and intricate tricks to deceive the host, and has uncovered similarities with avian brood parasites. At the same time, this paper emphasizes how studies on defensive mechanisms and counter-adaptations among *Polistes* hosts are lacking (but see Nessi & Lorenzi 2004). It is well known that host–parasite systems are dynamic, with a continuous arms race between parasite and host resulting in a rapid coevolution of the antagonists (Dawkins & Krebs 1979, Thompson 1994). Avian brood parasites have always induced intense interest as models for coevolutionary processes, and have generated a remarkable amount of research (see Rothstein & Robinson 1998). As far as social insect parasites are concerned, ants have been suggested to be a potential model organism for the study of evolutionary arms races (Davies *et al.* 1989). Only recently have studies on slavemaking ants provided support of the existence of coevolutionary processes between social insect parasites and their hosts (Foitzik *et al.* 2001, Foitzik *et al.* 2003). Moreover, a recent review (Brandt *et al.* 2005) underlines how, in a social insect parasite–host system, similar characteristics of the two antagonists make it an optimal model for coevolutionary processes study.

*Polistes* social parasites and their hosts fulfill many important characteristics for the study of coevolutionary dynamics, and may satisfy these requirements even better than avian brood parasites (see Brandt *et al.* 2005). Although *Polistes* parasites are monophyletic, they are phylogenetically close to their hosts. They are rare species,

but are locally abundant and exert strong selective pressure on host populations. Moreover, and different from other parasite–host systems, *Polistes* parasites and their hosts have similar population sizes, generation times, and evolutionary potential.

In conclusion, *Polistes* obligate parasites provide as good a model for coevolutionary arms race studies, as *Polistes* paper wasps have provided — for many years — a model organism for sociobiological studies (see Reeve 1991, Turillazzi & West-Eberhard 1996). To achieve this goal, theoretical and empirical work on host counteradaptations have to be integrated with the present knowledge on *Polistes* social parasitism. This will help highlight the dynamics of host–parasite systems.

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