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SHORT COMMUNICATION

The social parasite wasp *Polistes atrimandibularis* does not form host races

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Abstract

Parasites that exploit the parental behaviour of several host species may be selected to form distinct host-specific genetic lineages. This process is well documented in bird brood parasites, but not in insect social parasites. *Polistes atrimandibularis* is the only paper-wasp social parasite known to exploit four host species. It does not form genetically distinct host races according to analyses based on microsatellite loci. Also, there were no size-matching between parasites and host species. Instead, *P. atrimandibularis* queens seemed to be successful as parasites in this population only when they originated from nests of *P. dominulus*, the largest species. The other host species are a sink for *P. atrimandibularis* since adult females emerging from those nests appear too small to usurp colonies themselves. Traits that may help *P. atrimandibularis* infiltrate multiple species may include its nonaggressive usurpation tactics and its ability to acquire host cuticular hydrocarbon recognition labels.

Introduction

Parasites that exploit the parental behaviour of their hosts may be engaged in an arms race, so they may be selected to specialize on one or few closely related host species (Davies *et al.*, 1989). A parasite exploiting more than one host species may thus form separate genetic lineages or host races. This process is well documented in bird brood parasites like *Cuculus canorus* (the common cuckoo) which lays its eggs in other species' nests, and evolved distinct genetic lineages that mimic the egg pattern of its many different hosts (Brooke & Davies, 1988; Gibbs *et al.*, 2000). However, there is little evidence that the same process occurs in insect social parasites that usurp the colonies of other species and then monopolize most or all of the reproduction (Davies *et al.*, 1989; but see Packer *et al.*, 1995).

Among the more than 200 species of *Polistes* wasps currently described (Carpenter, 1997), three are known to be obligate social parasites: *Polistes sulcifer* (Zimmermann), *P. semenowi* (Morawitz) and *P. atrimandibularis* (Zimmermann). All three live in sympatry around the Mediterranean and Caspian Basin, although *P. atrimandibularis* is more common at high elevations, and the other two species are typically found at low elevations (Cervo & Dani, 1996). How social parasitism evolved in this group has been a matter of discussion (Cervo & Dani, 1996; West-Eberhard, 1996) but it is clear that they are monophyletic and that no parasite is their host's closest relative (Choudhary *et al.*, 1994; Carpenter, 1997). Previous work suggested that each social parasite exploited only one species, or a pair of sister species (Choudhary *et al.*, 1994; see shaded areas in Fig. 1). *P. sulcifer* and *P. semenowi* parasitize species in the sister clade to the social parasites: *P. dominulus* (Christ), and both *P. dominulus* and *P. nimphus* (Christ), respectively. *P. atrimandibularis*, on the other hand, was known to parasitize two more distantly related species *P. gallicus* (L.), and *P. biglumis* (L.).

The adaptations requiring host specificity in *Polistes* may include physical as well as chemical characteristics, because *Polistes* social parasites control their host colonies (Cervo & Lorenzi, 1996) by aggressive threats (Cervo

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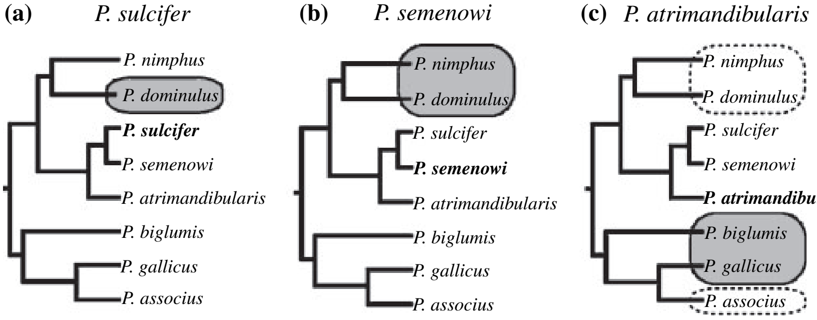

Fig. 1 Phylogenetic relationships of the three *Polistes* social parasites and their hosts. Bold squares: hosts described before 2001; dotted squares: recently described hosts of *P. atrimandibularis* (modified from Carpenter, 1997).

et al., 1990a), by altering their species-specific mixture of cuticular hydrocarbons to match the odour of the host colony after usurpation (Bagnères *et al.*, 1996; Turillazzi *et al.*, 2000; Fanelli, 2001; Sledge *et al.*, 2001; Lorenzi & Bagnères, 2002; Lorenzi *et al.*, 2004), and possibly also by employing pacification pheromones (Cervo *et al.*, 1990a).

Recently, it was discovered that a lowland population of *P. atrimandibularis* parasitizes three additional host species that it was not previously known to utilize: *P. dominulus*, *P. nimphus* and *P. associus* (Kohl) (Fanelli *et al.*, 2001; dashed circles in Fig. 1). *P. atrimandibularis* is so successful in fooling all of these host species that in a few cases the hosts tended and reared the parasite's larvae to maturity weeks after the usurping *P. atrimandibularis* disappeared from the colony (Fanelli, 2001). This finding challenges the hypothesis that the different *Polistes* social parasites are specialists on a single clade of hosts. Perhaps *P. atrimandibularis* manages to parasitize different hosts by forming specialized host races.

Using microsatellite loci developed for *P. dominulus* (Henshaw, 2000), we looked for evidence of population subdivision along three host lines, as well as for inbreeding as a result of assortative mating within host lines. We also measured the sizes of successful parasites in the two most common lowland host species, and we measured the daughter parasites that were produced in three host species to determine whether there was selection for morphological specialization. We detected no significant host-related population structure, and no size-matching between parasites and host species, but we found that successful parasites on nests were bigger than the parasite brood that emerged from the hosts *P. gallicus* and *P. associus*, but not *P. dominulus*.

Materials and methods

Collections and size measurements

As in the other two *Polistes* social parasites, *P. atrimandibularis* usurps its host colonies in late spring, prior to the emergence of the first workers. The parasite usurper soon starts to lay its own eggs in the colony, and will usually stay in the host colony until the end of its life cycle. The newly emerged parasites usually remain on the host colony until late summer, and then migrate to mountain peaks where they mate and overwinter (Cervo & Dani, 1996). We collected a total of 58 *P. atrimandibularis* females in a plain in northwestern Tuscany (Fanelli *et al.*, 2001), including 47 newly emerged females and 11 usurpers. Usurpers and newly emerged parasites can be distinguished by differences in their behaviour as well as by the worn wing tips of usurpers. The sample of newly emerged females was collected between 10 and 20 August 1999, and consisted of 23 females that emerged from eight nests of *P. gallicus*, 9 females that emerged from four nests of *P. dominulus* and 15 females that emerged from three nests of *P. associus*. The sample of usurpers was collected on 1 August 2001 and consisted of eight usurpers on *P. gallicus* colonies and three on *P. dominulus* colonies. These usurpers were all collected after their brood had started to emerge, indicating they were all successful social parasites. These sample sizes are large considering that *Polistes* social parasites are rare (Cervo & Dani, 1996).

All individuals were stored at −20 °C. Measurements were taken under a binocular microscope. The maximum head width and the length of the medial cell of the wing were quantified with an optical ruler, which allowed a maximum error of ca 1%. A unique function of size measure was extracted by Principal Component Analysis (93.6% of total variance explained). An ANOVA with a nested design was then employed to test the effect of host species and of nest of origin within host species. The *post hoc* LSD tests were Bonferroni-corrected for multiple comparisons.

Genetic analyses

We genotyped 32 newly emerged female parasites: 15 parasites from four nests of *P. gallicus*, nine from four nests of *P. dominulus*, and eight from three nests of *P. associus*. All individuals were genotyped at six polymorphic microsatellite loci developed for the nonparasitic species *Polistes dominulus*: Pdom2, Pdom7, Pdom121, Pdom122, Pdom127b and Pdom140 (Henshaw, 2000). With the exception of Pdom2, which had only three alleles, all the loci had seven to nine alleles. We extracted, amplified and scored the DNA following standard laboratory techniques (Strassmann *et al.*, 1996).

To better understand the history of usurpation on each nest and the mating system of *P. atrimandibularis* in this lowland population, we assessed the kin structure of the newly emerged parasites in each nest. We estimated relatedness among the newly emerged parasites using the computer programme Relatedness 5.06 (Goodnight & Queller, 1999) and assessed the number of matrilines necessary to account for their genotypes based on Mendelian principles of inheritance. For relatedness estimations, we calculated the background allele frequencies from all of the genotyped individuals because there was no evidence for population differentiation (see below). Colonies were weighted equally for allele frequency calculations. Standard errors and 95% confidence intervals were calculated by jackknifing over loci for estimates within colonies and over colonies for population estimates.

We evaluated population structure, including differentiation between host races, and inbreeding, using the hierarchical *F*-statistics calculated in the computer programme Relatedness 4.2c, as well as an Analysis of Molecular Variance (AMOVA) as implemented in the computer programme Arlequin (Schneider *et al.*, 2000). For the AMOVA analysis, we selected one individual from each nest because genotypes within nests are not independent. Relatedness 4.2c accounts for this nonindependence in its calculations, so all of the samples were used for analyses with this programme.

Results

Host-related size differences

Both nest of origin and host species affected the size of the newly emerged parasite adults (Nested ANOVA: $n = 47$, host species: $F_2 = 16.220$, $P < 0.001$, nest of origin (nested in host) $F_{12} = 6.076$, $P < 0.001$) (Fig. 2). The significance of the nest of origin suggests that sizes must be in part a phenotypic consequence of environmental parameters linked to nest location (average temperature, humidity, food availability, and other environmental variables). However, the effects of nest position and host species are not independent because the different host species have different nesting-site preferences (Pardi, 1941; Fanelli, Pers. Obs.). The female parasites raised by *P. dominulus* were bigger than the ones raised by *P. associus* and *P. gallicus* (ANOVA *post hoc* LSD test Bonferroni-corrected: $P < 0.001$ in both cases), while these latter two were undistinguishable ($P =$ n.s.).

The adult females that usurped nests of *P. dominulus* were not different from those that usurped nests of *P. gallicus* (independent-samples *t*-test: $t_9 = -0.7$, $P =$ n.s.). However, overall, usurping parasites were bigger than the newly emerged daughters ($t_{56} = 4.355$, $P < 0.001$). In particular, they were bigger than the parasite brood raised by *P. gallicus* and *P. associus* (ANOVA *post hoc* LSD test Bonferroni-corrected $P < 0.001$ in both cases) but undistinguishable from the parasite brood raised by *P. dominulus* (ANOVA *post hoc* test Bonferroni-corrected $P =$ n.s.) (Fig. 2). In summary, there was no matching of sizes between *P. atrimandibularis* and its different host species. However, only the bigger parasites were successful usurpers in any species, and they were significantly bigger than the brood raised on *P. gallicus* and *P. associus*, but equal in size to the brood raised on *P. dominulus*. Based on the size-function extracted by PCA, only one individual raised in a *P. associus* colony and two individuals raised in a *P. gallicus* colony fell in the size class of successful usurpers.

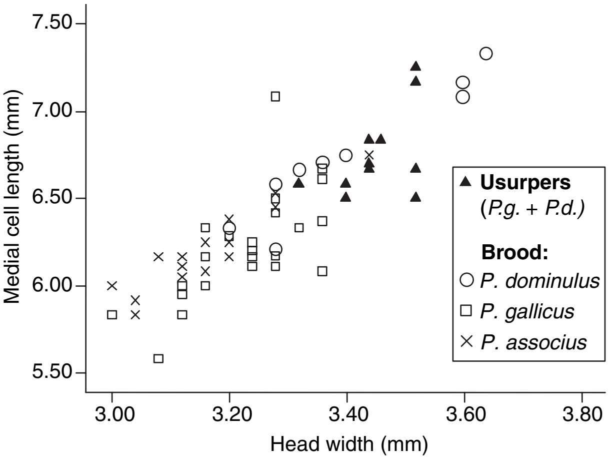

Fig. 2 Sizes of *P. atrimandibularis* that successfully usurped nests of *P. gallicus* and *P. dominulus*, and sizes of female brood emerged from three different host species. For display purposes, the overlapping points have been separated by adding or subtracting 0.05 mm from the medial cell length.

Among the brood that emerged from all hosts, the mean head width was 3.24 mm ± 0.02SE and the mean wing length was 6.33 mm ± 0.05SE. The selection differential (Lande & Arnold, 1983; Brodie & Janzen, 1996) for being a successful lowland usurper was $s = 0.527$ for head width (*t*-test not assuming equal variances $t = 7.357$, d.f. $= 36.173$, $P < 0.001$) and $s = 0.531$ for wing length ($t = 4.64$, d.f. $= 21.478$, $P < 0.001$).

Population structure and relatedness

We found limited, but inconclusive evidence for host specialization. Inbreeding (F_{IS}) was −0.0723 and did not differ from 0, while F_{ST} was 0.0567 and was marginally significantly different from 0 when the standard error was calculated by jackknifing over loci (Table 1). However, F_{ST} was not significantly different from 0 when the standard error was calculated by jackknifing over nests (Table 1), nor was it significantly different from 0 in the AMOVA analysis (Table 2). Thus, there was no evidence

Table 1 Inbreeding coefficients of the brood of *P. atrimandibularis* raised by three different host species.

Coefficient	Value	SE	95% CI (loci)	95% CI (nests)
Individuals (F_{IS})	−0.0723	0.0697	0.179	0.222
Host species (F_{ST})	0.0567	0.0216	0.0558	0.065
Population (F_{IT})	−0.0115	0.0719	0.1848	0.096

Confidenceintervals were calculated by jackknifing over loci and over nests (total $n = 32$, nine colonies).

Table 2 The AMOVA for parasite brood emerged from different host species.

Variance component	Variance	Total (%)	ϕ-statistics	P
Individuals (F_{IS})	−0.11837	−5.68	−0.06001	n.s.
Host species (F_{ST})	0.10964	5.27	0.05265	0.055
Population (F_{IT})	2.09091	100.42	−0.00420	n.s.

Results include the partitioning of the variance, estimates of standard *F*-statistics and significance estimates (total $n = 32$, nine colonies).

to support assortative mating nor does it seem likely that there was genetic differentiation among host lineages, particularly given that the size data indicate that parasites emerging from species other than *P. dominulus* are not successful.

Newly emerged daughter parasites in the same colony were related by 0.687 ± 0.125 CI on average, which is not statistically different from 0.75 expected for haplodiploid full sisters. Likewise, all of the daughter genotypes in each colony were consistent with a single matriline. This indicates that the *P. atrimandibularis* usurpers were singly mated, and that no usurpation from a second parasite took place, or that if it did, all brood of the previous usurper were removed.

Discussion

Polistes atrimandibularis has recently been found to parasitize three lowland host species not previously recorded. This study finds no consistent evidence for the development of host-related genetic differentiation in *P. atrimandibularis*. There was no evidence for morphological differences between successful usurpers on different hosts. Nor could we find evidence for genetic differences or assortative mating by parasites reared by different hosts (F_{ST} was small and not significant by two of three tests). Despite the lack of specialization, these parasites succeeded in reproducing in their host colonies.

Polistes social parasites may be better at fooling several species into taking care of their young than are cuckoos because of the nature of the recognition signal. Birds that are hosts to cuckoos recognize their eggs, which have a specific and fixed pattern. A parasitizing cuckoo must match that pattern, so there is strong selection for host race formation. Social wasps recognize their nestmates by their cuticular hydrocarbon profiles and these can be acquired and manipulated after the parasite joins the colony (Bagnères *et al.*, 1996; Turillazzi *et al.*, 2000; Fanelli, 2001; Sledge *et al.*, 2001; Lorenzi, 2003; Lorenzi *et al.*, 2004). This means that usurpation in wasps is inherently more plastic than usurpation in cuckoos. It should be easier for wasps to parasitize multiple species and to do so without the formation of host races.

Successful usurpers of all studied lowland host species were bigger than nearly all of the newly emerged brood, indicating selection for increasing size. Only 3 of 28 females of *P. atrimandibularis* emerging from nests of *P. gallicus* or *P. associus* fell in the size category of successful usurpers (Fig. 2). *P. dominulus* is the largest host, and has larger colonies (Fanelli, 2001; Cervo, unpublished data). The brood produced in this host species matched the size of successful lowland usurpers, so selection is acting on this lowland population of parasites to increase its average sizes and to prefer the host *P. dominulus*.

The most likely explanation for the disappearance of smaller individuals from the population is that they are less successful host usurpers. However, on a few nests in the population the brood of *P. atrimandibularis* was in rare cases raised to maturity weeks after the usurping parasite had disappeared (Fanelli, 2001). We have no information on the sizes of these latter early-disappearing usurpers, so we cannot exclude that these were the smaller parasites, which would thus have enjoyed a higher fitness than our data suggests. Moreover, we cannot exclude that the smaller parasites do not die but have dispersal abilities correlated to their size (see Vogt *et al.*, 2000), so that after the winter diapause they remain at higher altitudes and invade nests close to their over-wintering sites. However, *P. dominulus* is a typical lowland host, so we would still expect the larger individuals invading *P. dominulus* to increase in frequency in the lowland population.

Our selection hypothesis could be contradicted if the parasite females that usurp the suboptimal hosts *P. gallicus* and *P. associus* in the lowlands produced males rather than females, and if small males were successful in attracting mates. However, there is no evidence that parasites produced more males on *P. gallicus* and *P. associus* than on *P. dominulus* (Fanelli, 2001). Moreover, the males of all social parasites including *P. atrimandibularis* occupy mating territories and aggressively defend them against male competitors (Beani, 1996). Hence, larger sizes are presumably associated with higher fitness in males, and a parasite female that produced smaller males on the suboptimal host species would still incur a fitness cost.

Polistes atrimandibularis did not seem to preferentially use *P. dominulus* as a host in the lowlands, even though it was the only host where *P. atrimandibularis* was likely to rear a successful next generation. Indeed, the opposite seemed to be the case because *P. dominulus* was the most abundant host in the area, but was successfully invaded at lower rates than other species (Fanelli, 2001; Fanelli *et al.*, 2001). Our data are so sparse that we cannot determine whether or not *P. atrimandibularis* was simply less successful at invading *P. dominulus*. There may be a maladaptive lack of preference for the most profitable host species because *P. atrimandibularis* has only recently invaded this lowland environment and is not at equilibrium. If the recent invasion hypothesis is true, it underscores a main conclusion of this study, that successful host exploitation by *Polistes* social parasites requires less specialization than had been thought.

However, the ability to parasitize *P. dominulus* may reflect ancestral abilities. We can now say that all three social parasites parasitize their sister clade (*P. dominulus* and *P. nimphus*), which supports the view that social parasitism not only arose once in these wasps, but that the original social parasite used its closest relative as host, in accord with Emery's Rule (Lowe *et al.*, 2002). As both social parasites and clades evolved and speciated, *P. semenowi* and *P. sulcifer* remained on the original host clade. We now know that *P. atrimandibularis* has also remained partially on this clade, or at least retained the ability to recolonize it.

The most profound shift in host use was in the ability of *P. atrimandibularis* to parasitize species outside the original host clade: *P. biglumis*, *P. gallicus*, and *P. associus*. As noted above, the ability to change hydrocarbon profiles may have facilitated such a shift, but this does not explain why the other two social parasites have not similarly expanded their host range. One possibility is that their larger sizes make them less able than *P. atrimandibularis* to utilize smaller hosts. Another possibility is the peculiar behaviour, which characterises *P. atrimandibularis*. This parasite, differently from the other two, not only uses a nonaggressive usurpation tactic (Cervo *et al.*, 1990a) but also contributes to the rearing of immature brood by plundering larvae and pupae from other nests in the surroundings (Cervo *et al.*, 1990b). Whatever the explanation, it is clear that *P. atrimandibularis* has the ability to defeat host defenses and usurp an unusually broad set of hosts, and it appears to do so with a generalized strategy rather than through a set of specialized strategies adapted to each host.

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