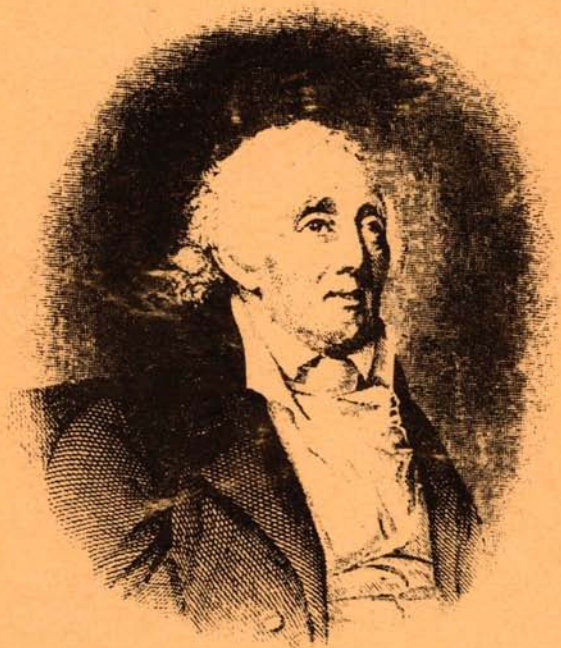


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ON THE STRATEGIES OF HOST NEST INVASION IN THREE SPECIES OF *SULCOPOLISTES*, SOCIAL PARASITES OF *POLISTES* WASPS

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Summary: *Sulcopolistes* are obligate and permanent social parasites of some European *Polistes*. The host nest invasion strategies employed by the three species of the genus were analysed in the laboratory where parasite females were offered host colonies. Invasion strategies range from a pacific, non-aggressive tactic to a violent one, with a relative plasticity within each species. The strategy employed by each parasite is possibly related to the length of host colonial cycle, to the way nest are founded and to nest characteristics at the moment of invasion.

Key words: wasps, *Sulcopolistes* spp., *Polistes* spp., social parasitism, host nest invasion strategies

Titre: Les stratégies d'invasion du nid de l'hôte utilisées par les trois espèces de *Sulcopolistes*, parasites sociaux des guêpes *Polistes*.

Résumé: Les *Sulcopolistes* sont des parasites sociaux permanents et obligatoires de quelques espèces européennes du genre *Polistes*. Nous avons analysé au laboratoire le comportement des femelles de trois espèces de ce genre au moment de l'invasion du nid de leurs hôtes. Les stratégies utilisées, qui vont d'une tactique pacifique, non agressive à une tactique violente (avec une certaine flexibilité à l'intérieur de chaque espèce), peuvent être mises en relation avec la durée du cycle colonial de l'espèce hôte, aux modalités de fondation du nid et à certaines caractéristiques de la colonie au moment de l'invasion.

Mots clés: guêpes, *Sulcopolistes* spp., *Polistes* spp., parasitisme social, stratégies d'invasion du nid de l'hôte

Introduction

The genus *Sulcopolistes* comprises the only three species of obligate social parasites: *S. atrimandibularis*, *S. semenowi* and *S. sulcifer*. As they lack a worker caste, they usurp the nest of some *Polistes* species and rely almost entirely on host workers for rearing their own brood of reproductives. All of them are

distributed almost exclusively in countries around the Mediterranean Basin.

S. atrimandibularis parasitizes *P. biglumis bimaculatus* (WEYRAUCH, 1937; BEAUMONT and MATTHEY, 1945; SCHEVEN, 1958), which in Italy lives over 800 m a.s.l., reaching an altitude of more than 200 m. A single fertilized female of this host species (where nest foundation is strictly haplometrotic) builds her nest in meadow lands, on small stones at ground level. Even after the emergence of her worker brood the foundress participates the most in extracolony activities (i.e. food collection). Due to climatic limitations, the whole colony cycle does not last more than 4 months (LORENZI and TURILLAZZI, 1986). More rarely *S. atrimandibularis* parasitizes *P. gallicus* (SCHEVEN, 1958; pers. obs.), a species where a single female founds the nest on shrubs and bushes or buildings in lowland (COLOMBINI, 1983).

S. sulcifer is the social parasite of *P. dominulus* (WEYRAUCH, 1937; BEAUMONT and MATTHEY, 1945; SCHEVEN, 1958), a species which nidificates in lowlands and on hill sides and which exceptionally is found over 1000 m a.s.l.. It builds its nest in sheltered, hot places, such as fissures under roof slates, corrugated iron, scrap metal etc.. *P. dominulus* often exhibits associative foundation, i.e. several fertilized females build a nest together and form a dominance hierarchy (PARDI, 1942). After the emergence of the workers, the dominant female spends more time on the nest and relies on them for most of the colony activities (PARDI, 1951). The whole colony cycle of this species lasts over 6 months.

Occasionally *P. dominulus* is also parasitized by *S. semenowi*, a species that more often parasitizes *P. nimpha* (WEYRAUCH, 1937; BEAUMONT and MATTHEY, 1945; SCHEVEN, 1958). This host species resembles *P. dominulus* in its nesting habits, but colonies may be found at higher altitudes and foundations are more often solitary (CERVO, 1983; CERVO and TURILLAZZI, 1985).

Latest studies on social parasites of wasps and bees (see for references CERVO *et al.*, in press) show that invasion tactics of the different parasite species range from non aggressive intrusion, followed by cohabitation with the host queen, to violent combat that can lead to her death. Indeed, the comparison of the strategies employed by each species of parasite in invading the host nest may well help out the comprehension of the evolution of social parasitism.

Invasion experiments were performed by SCHEVEN (1958) with 2 females of *S. atrimandibularis*, 2 of *S. sulcifer* and 3 of *S. semenowi*. The author describes that an aggressive strategy is employed by all species. More recently, DEMOLIN and MARTIN (1980) described a pacific host nest invasion in the field by a female of *S. semenowi*, and DISTEFANO (1969) observed an aggressive usurpation of a *P. dominulus* nest by *S. sulcifer*.

Materials and methods

Female parasites were collected in the field or directly from usurped host nests at the beginning of the invasion period together with non usurped colonies of the host species. The colonies were placed in 15 cm sided glass containers in the laboratory. Within a fortnight, each *Sulcopolistes* female was introduced into a cage containing a colony of the host species and the invasion of the host nest was monitored and documented with the help of a video recorder. Observations were led on the usurpation by 4 females of *S. atrimandibularis*, 22 of *S. sulcifer*, and 3 of *S. semenowi*.

The stage of each host nest presented to the parasites is given in table 1.

In addition, data on the period of nest invasion and on the stage of usurped colonies were collected in the field with periodic checks.

| Parasite | Host | Pre-emergence | Post-emergence |
|---------------------|----------------------|---------------|----------------|
| <i>S. atrimand.</i> | <i>P. bigl. bim.</i> | 4 nests | |
| <i>S. semenovi</i> | <i>P. dominulus</i> | 1 nest | 1 nest |
| | <i>P. nimpha</i> | 1 nest | |
| <i>S. sulcifer</i> | <i>P. dominulus</i> | 13 nests | 7 nests * |

* For other two nests the stage of development was not definable.

Table 1. Stage of development of nests presented to parasites.

Results

An interval of 3-4 weeks occurs between the beginning of nest foundation and the arrival of the parasite in both *S. atrimandibularis* and in *S. sulcifer*. The former always invades nests in the pre-emergence stage, while the latter may parasitize colonies where workers have already emerged (12 colonies out of 26).

Invasion strategy of *Sulcopolistes atrimandibularis*

In all 4 cases observed, the parasite was absolutely non aggressive during the nest invasion, avoiding any contact with the foundress. Once the parasite landed on the nest in a moment when the foundress was absent, she rarely left it, whilst the host female performed short visits to her comb, occasionally attacking the invader. In this first phase the parasite was active only when she was alone on the nest. If her host was present she retreated to the back of the comb and remained inactive, and never attacked her. As the time passed the *Sulcopolistes* became more and more active even in the presence of the foundress until she finally dominated her.

Invasion strategy of *Sulcopolistes sulcifer*

In all the 22 cases observed the parasite proved to be extremely decisive and

aggressive in her invasion. The tactic employed in fighting her hosts, once the parasite had managed to rid them from the nest, was essentially to tackle them one at a time on the ground. Unsuccessful usurpation was observed when the colony experimentally presented to a parasite for invasion was composed of 17 adult host females (a post-emergence colony). Colonies of up to 11 females were conquered.

When the parasite headed for the nest she approached the host but never attacked first, always waiting for the host to make the first move. The final result of the attack was the removal of the foundresses and some of the workers. Once on the nest, the *Sulcopolistes* female rarely abandoned it, regardless of the number of host living there. The time a host stayed away from the nest depended on her position in the dominance hierarchy: whilst alpha sometimes never retreated to the nest, lower ranking females were more likely to come back. When they did, they submitted to acts of domination by the parasite and, in akinesis, were meticulously licked all over their legs and body.

Invasion strategy of *Sulcopolistes semenowi*

In 3 usurpations by *S. semenowi* on nests of *P. dominulus* and in one of *P. nimpha* the parasite displayed a strongly aggressive behaviour and entered into battles with the dominant females.

All the three species probably employ both behavioural and chemical devices to submit and control hosts (TURILLAZZI *et al.*, in press; CERVO *et al.*, in press).

| | <i>P.dominulus</i> | <i>P.bigl.bim.</i> | <i>P.gallicus</i> | <i>P.nimpha</i> |
|----------------------|--|--------------------|--------------------|-------------------|
| habitat* | L/H | M | L/H | L/H |
| nest site | sheltered places | stones in meadows | bushes | bushes |
| foundation^ | AP/PL | AP | AP | AP/PL |
| length of col. cycle | 6 months | 4 months | 6 months | 6 months |
| social parasite | <i>S.sulcifer</i> <i>S.semenowi</i> | <i>S.atrimand.</i> | <i>S.atrimand.</i> | <i>S.semenowi</i> |

Table 2 : Characteristics of the colonies of the host species.

* H= hill sides, L= lowland, M= mountain.

^ AP= haploretrotic, PL= pleometrotic.

Discussion

Our observations on the invasion strategies employed by *Sulcopolistes* females when invading the nest of their hosts agree with those of SCHEVEN (1958), with the exception of *S. atrimandibularis*, but contrast with those of DEMOLIN and MARTIN (1980) on *S. semenowi*.

SCHEVEN observed 2 females of *S. atrimandibularis* aggressively usurping *P. b. bimaculatus* nests in an advanced stage of the post-emergence period. The phenomenon observed by SCHEVEN may have been a different situation from the proper invasion the parasite performs at the beginning of the season (when she strictly invades pre-emergence colonies) and may possibly be related to the conquest of "secondary" nests (CERVO *et al.*, 1988) during the season.

Owing to such a brief season suitable for colony life in the mountain environment (Tab. 2), the *P. b. bimaculatus* foundress carries out great part of the colonial activities even after the workers have emerged. It is therefore imperative that a *S. atrimandibularis* female keeps the foundress on the nest after usurpation without killing or wounding her, so that she will do all the colony work in the remaining month before brood emergence and most of it during the post-emergence period. However, it would not benefit the parasite to usurp the colony later on in the season (when the colony work force is larger) since any delay in the short colonial cycle imposed by the alpine climate would seriously jeopardize offspring production. Parasite behaviour may differ when she invades nests of *P. gallicus* a monogynic lowland species. We did not find the foundress in the only colony of this host species parasitized by *S. atrimandibularis*, nor did SCHEVEN (1958) in another two.

In *P. dominulus*, a species living on flat land, the workers (and before them auxiliary females) carry out almost all of the external and internal colony work. Thus *S. sulcifer* can afford to immediately physically dispose of the alpha female and just keep the individuals which will contribute to the nest work force.

As far as *S. semenowi* is concerned our observations differ from those of DEMOLIN and MARTIN (1980) who report a case of non violent invasion of a bigynic nest of *P. nimpha* by this parasite. Invasion strategy may differ in relation to the stage of development of the colony.

Data available to date suggest that the *Sulcopolistes* exhibit a relatively plastic behaviour when usurping host colonies. Invasion strategy seems correlated to the length of the colonial cycle of the host species in each particular environment and specifically to the nest characteristics and the number and caste of the adult population present at the time of invasion, as well as to the life history of the parasite herself.

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