

**CONTROL OF HOST REPRODUCTION BY SOCIAL PARASITE  
*SULCOPOLISTES SULCIFER* (HYMENOPTERA, VESPIDAE).**

**S. TURILLAZZI, R. CERVO & L. ZANOBETTI**

*Dipartimento di Biologia Animale e Genetica,  
Università degli Studi di Firenze,  
Via Romana 17, 50125 Firenze, Italy.*

**Summary :** An obligate permanent social parasite must be able to assume and maintain control over the invaded colony population as, lacking a worker caste of its own, its reproductive success depends on the labour of the host workers. The aim of this research is to establish whether the social parasite *Sulcopolistes sulcifer* can suppress ovarian development in the workers of the host species (*Polistes dominulus*). The dissection of workers from parasitized colonies kept under different experimental conditions in the laboratory and workers collected from colonies in the field indicated that this parasite is able to control the reproductive capacities of its host in a similar manner the dominant females of non-parasitized colony control those of her workers. It is still uncertain whether inhibitory pheromones are employed besides simple aggressive behaviour.

**Key words :** Social parasitism, *Polistes*, *Sulcopolistes*, ovaric development, reproductive control.

**Résumé :** Contrôle de la reproduction de l'hôte par le parasite social *Sulcopolistes sulcifer* (Hymenoptera, Vespidae).

Un parasite social obligatoire et permanent doit être capable d'assurer et de maintenir un contrôle sur la population de la société dans laquelle il s'est introduit dans la mesure où, ne possédant pas de propre caste ouvrière, son succès reproducteur dépend totalement du travail des ouvrières de sa société hôte. Le but de cette recherche est d'établir si le parasite social *Sulcopolistes sulcifer* est capable d'inhiber le développement ovarien chez les ouvrières de son espèce hôte (*Polistes dominulus*). La dissection d'ouvrières provenant de colonies parasitées gardées au laboratoire sous différentes conditions expérimentales et d'ouvrières appartenant à des colonies récoltées sur le terrain, montre que ce parasite est capable de contrôler les capacités reproductrices de son hôte de la même façon que les femelles dominantes des colonies non parasitées le font à l'égard de leurs ouvrières. Nous ne sommes toujours pas en mesure de dire si, en plus du comportement d'agression, des phéromones inhibitrices sont ou non mises en jeu.

**Mots-clés :** Parasitisme social, *Polistes*, *Sulcopolistes*, développement ovarien, contrôle reproducteur.

## INTRODUCTION

*Sulcopolistes sulcifer* is the obligate permanent social parasite of *Polistes dominulus*. It uses the nests and the workers of the host species to rear its own reproductives. Invasion of the host nest occurs towards the end of the pre- or the very beginning of the post-emergence period. Information on these social parasites is very scanty and limited to a few papers, the most important of which is by Scheven (1958). Recently we studied the invasion behaviour of this species in depth (Turillazzi et al., 1989) and confirmed that the parasite is very aggressive towards high ranked host foundresses, which are forced to leave the nest and sometimes suffer amputation of one or more legs by the parasite. The lower ranked foundresses, on the contrary, often remain on the nest and are dominated by the *Sulcopolistes*. Scheven already pointed out how the attitude of the parasite toward the host foundresses resembles the behaviour of the alpha female in the associative foundations of *P. dominulus* and that the intraspecific and interspecific dominance patterns are very similar.

This preliminary research aims to determine whether the parasites are actually able to control the host colonies by reducing the reproductive capacity of *Polistes* in a similar fashion as the alpha female of *Polistes* does on non-parasitized colonies.

## MATERIALS AND METHODS

We reared 18 non-parasitized foundations of *P. dominulus* in the laboratory in 15x15x15 cm glass boxes. The wasps were supplied with honey, water, *Tenebrio molitor* and fly larvae *ad libitum* and kept under L-D period with supplementary 100w bulbs during the day. Before the first worker emerged, we removed all the foundresses from 8 colonies (with several operculated cells) so that the immature brood was left by itself. We removed all the foundresses except for the alpha female from the remaining 10 colonies. We waited for the workers to emerge, which varied in number from 3 to 15 on the different colonies. Ten days after the last worker had emerged on each colony (according to Pardi (1946) a period of at least seven days is necessary for the egg to develop in the ovary), we dissected the adult population present on the nest in order to measure the ovarian development of each individual (Ovarian Index = O.I., average length of the six longest oocytes in the ovary).

In the field we collected 8 *P. dominulus* colonies which had recently been invaded (less than a week) by *S. sulcifer*. The colonies were reared in glass boxes in the laboratory under the same condition as the non-parasitized colonies. Four of the colonies were left with only the parasite (colonies P), whilst the other four had parasite plus one foundress (of unknown rank) (colonies P+F). Here again we waited for the workers to emerge (which ranged from 6 to 10) and ten days after the last worker emerged we dissected all the adult population. If a wasp had egg equal to or longer than the smallest egg found in a cell (43 division = 1.4mm, calculated on 40 eggs) she was considered as a potential egg layer. Approximately 7 hrs 30 min behavioural observations were performed on the parasitized colonies (the focal animals were foundresses and/or parasites).

We also collected 11 parasitized and 6 non-parasitized colonies in the field at different stages of the season. The adult females on the nest were dissected in order to measure the ovarian index of the workers and the foundresses as well as that of the parasite.

## RESULTS

Figure 1 gives the ovarian indexes for females from parasitized and non-parasitized colonies reared in the laboratory.

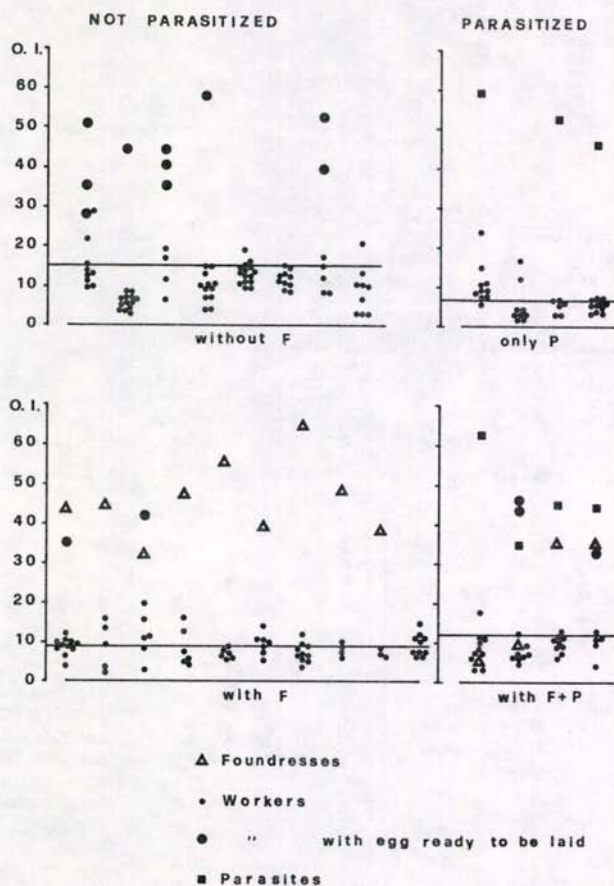


Fig. 1. - Ovarian index (O.I.) of females from parasitized (with or without host foundress) and non-parasitized (with or without alpha foundress) colonies reared in the laboratory. The horizontal lines refer to the average ovarian index of workers from each experimental stock. One division on the ordinate scale correspond to 0.032 mm.

Fig. 1 - Index ovarien (O.I.) des femelles provenant de sociétés élevées au laboratoire, parasitées (pourvues ou non de fondatrice) et non parasitées (pourvues ou non de fondatrice alpha). La ligne horizontale correspond à l'index ovarien moyen des ouvrières pour chaque lot expérimental. Une division de l'échelle des ordonnées correspond à 0.032 mm.

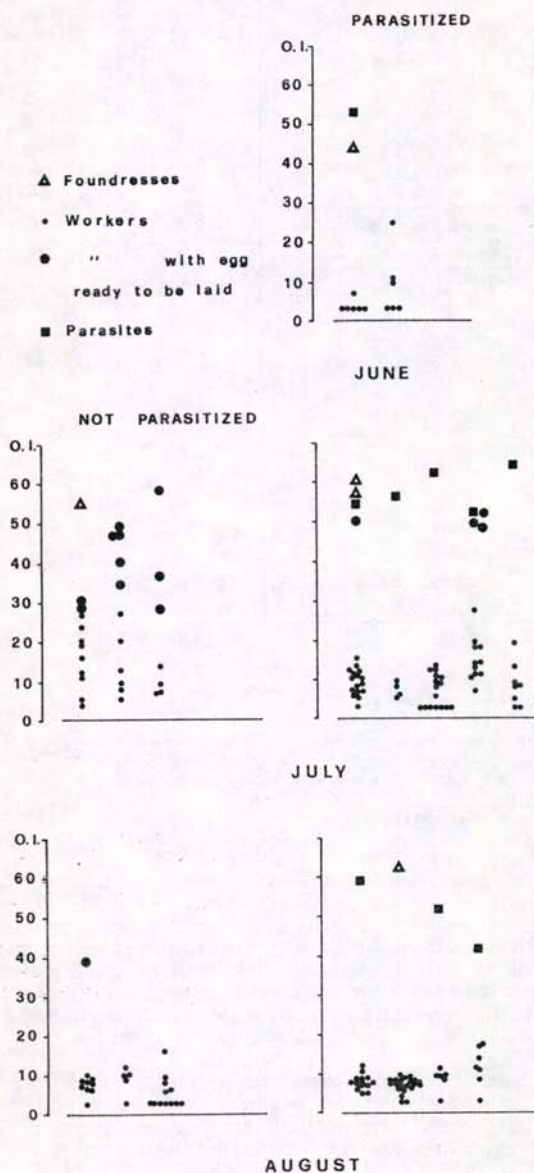


Fig.2 - Ovarian index (O.I.) of females from two parasitized colonies collected in June and of females from non-parasitized and parasitized colonies collected in July and August in the field. In one parasitized colony collected in June and in one collected in August the *Sulcopolistes* female flew away on collection.

Fig.2 - Index ovarien (O.I.) des femelles provenant de deux colonies parasitées récoltées en Juin et de celles provenant de colonies non parasitées et parasitées récoltées en Juillet et en Août sur le terrain. Dans l'une des colonies parasitées récoltées en Juin et dans l'une de celles récoltées en Août, la femelle de *Sulcopolistes* s'est enfuie lors de la récolte.

In the non-parasitized colonies, the average ovarian index of workers from nests with no foundress was significantly higher than that of workers from colonies where a foundress was present (Mann-Whitney test,  $p < 0.05$ ), as Pardi (1946) observed in the same species. In non-parasitized colonies with no foundress 10 workers (out of 89) had at least one egg ready to be laid in their ovaries, but only 2 workers (out of 71) showed the same condition in colonies with a foundress.

In the parasitized colonies the average ovarian index of the workers was lower in the P colonies than in the P+F colonies (Mann-Whitney test,  $p = 0.057$ ). Only 3 workers had well developed ovaries (with at least one egg ready to be laid) and these were all from P+F colonies.

There are no significant differences between the average ovarian index of workers from parasitized colonies and non-parasitized colonies when a *Polistes* foundress was on the nest (Mann-Whitney test, n.s.).

Two out of four host foundresses from parasitized colonies had degenerated eggs in their ovaries and none of the eggs were ready for deposition.

The ovarian indexes of females from parasitized and non-parasitized colonies collected in the field at different stages of the season for the most part confirmed the data obtained in the laboratory colonies, even though in some cases the situations were very different (Fig. 2).

The main difference in the behaviour of the parasites and foundresses in the P+F colonies concerns the time spent outside the nest, which was considerably lower in the parasites. The behaviour of the parasites in P and P+F colonies was very similar but in the latter the parasites directed their dominance activity more towards the foundresses than the workers, even in the post-emergence period. Table 1 gives an idea of this difference, especially considering that the foundresses spent a higher percentage of time out the nest than any of the workers, and that the number of workers varied from 3 to 10.

N° of nest	observation time (sec)	dominance activity		N° of Ws
		on F (sec)	on Ws (sec)	
3	6555	131	0	3-6
4	6409	133	184	1-10
5	9142	52	49	3-10
6	10498	206	53	6-10

Table 1 - Dominance activity (in seconds) of *Sulcopolistes* towards Foundress (F) and Workers (Ws) of nests P+F.

Tableau 1 - Durée des actes de dominance (exprimée en secondes) manifestés par les femelles de *Sulcopolistes* à l'égard des fondatrices (F) et des ouvrières (Ws) des nids P+F.

## DISCUSSION

From these preliminary data it seems that on the host nest *Sulcopolistes sulcifer* achieves reproductive control in the same manner as the leader female of a nonparasitized colony. The repression of the reproductive capacity of the host females is appreciable in both laboratory and field colonies, in spite of some exceptions. It should also be remembered that the laboratory data refer to a rather precocious phase of the post

emergence period when the worker population does not exceed fifteen individuals. On one end of the scale the parasite exerts total control over its host's ovaries even in some of the more mature colonies, whilst on the other on some non-parasitized colonies the workers had developed ovaries in spite of the presence of a foundress. The greater amount of dominance activity directed towards the foundresses in P+F colonies could explain the higher ovarian development in the workers, as the parasite controls these individuals less. As yet there is no decisive evidence whether the parasite exerts its control by purely behavioural methods or also adopts pheromonal mechanisms. Indeed, it can be argued on the one hand that the control mechanisms the parasite employs are more efficient than those used intraspecifically, and/or on the other that *Sulcopolistes* is capable of deceiving the host workers that they are related to their usurper, in order to force them to rear a totally unrelated brood. Experiments and observations on this matter are at present in progress.

#### ACKNOWLEDGEMENTS

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