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Social dominance and trophallaxis in bigynic societies of Polistes gallicus (L.)

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SEZIONE III

(Botanica, zoologia, fisiologia e patologia)

Zoologia. — *Social dominance and trophallaxis in bigynic societies of* Polistes gallicus (L.). Nota di MARIA TERESA MARINO PICCIOLI e LEO PARDI, presentata (*) dal Corrisp. L. PARDI.

RIASSUNTO. — Miele radioattivo (I^{131}) è stato somministrato a femmine α o β di 14 società iniziali biginiche di *Polistes gallicus* (L.) (Vespidae, Hymenoptera), in cui la gerarchia era ben definita ($\alpha > \beta$). Gli scambi trofallatici fra i due adulti sono bidirezionali ($\alpha \rightleftarrows \beta$), ma la β tende a cedere in quantità maggiore e più rapidamente liquidi per rigurgito della α. La dominazione con contatto $\alpha > \beta$ anche con antennazione, non comporta necessariamente trasferimento di liquido e il liquido eventualmente rigurgitato non è sempre radioattivo, quindi non sempre proviene dallo «stomaco sociale».

The use of radioactive tracers in the study of trophallaxis in social insects was first investigated in domestic honeybees (Nixon and Ribbands, 1952). Since then this method has been used to analyze the nature of the trophallactic exchange between various forms (juveniles-adults, males-females, sterile-fertile females) of Hymenoptera (bees, ants, wasps) and Isoptera. However, none of the above research has concentrated on the direction of nourishment between two adults of equal caste but of a different hierarchical position.

Pardi (1946, 1947, 1948) reported a preferential direction of liquid nourishment from subordinates to dominants in *Polistes gallicus* (L.) confirmed by various authors in other species (for example, *P. fuscatus* Fabr. [West, 1969]), and this was true also for solid foods in *Polistes* (Morimoto, 1960) and *Mischocyttarus* (Jeanne, 1972). Pardi's findings, however, were based only on ethological observations and it was thus decided to confirm the validity of these observations through the use of radioactive tracers. Given the increasing interest in the analysis of hierarchical organization in *Polistes* and Vespidae in general (cf Wilson, 1971, pp. 7–26), it was deemed useful to report in full a series of experiments heretofore mentioned only briefly (Pardi, 1974).

MATERIALS AND METHODS

Our study was conducted on 14 α–β pairs of female *P. gallicus* (L.) raised in captivity. Each wasp was marked α or β accordingly and then isolated for 24 h without food. Using a capillary tube and carefully avoiding any external contamination, one of the partners was then offered a mixture containing 0.25 ml of the radioactive isotope I^{131} (100 μCi/ml in a NaI carrier-free solution) in 0.75 ml of diluted honey. The quantity of radioactivity absorbed was immediately determined and the wasp then returned to her nest and companion where domination behavior and trophallactic exchange

(*) Nella seduta del 10 maggio 1980.

were observed. The tracer was administered to the α female (*α* tests) in nine experiments, and to the β female (*β* tests) in five experiments. The level of radioactivity in both wasps was measured using a spark counter with a 2″ crystal well of NaI activated to Tl. Each wasp was measured in the same geometrical space for 2 min and no less than 1000 impulses, correcting for background count and decay.

The wasps were given radioactive food in the morning (with the exception of experiment 3 begun in the afternoon), and their level of radioactivity measured throughout the day after every buccal and/or dominance contact (from 2 to 6 readings). Controls were also made in the absence of observed contacts, at the times indicated below each diagram.

Each diagram records the level of radioactivity of each tracer-fed wasp (continuous line) and her partner (dotted line) as well as the combined radioactivity of each pair (dashed line), all expressed as a percentage of the initial radioactivity of the tracer-fed wasp. Also shown is the time elapsed between administration and measurement of the tracer (below), continuity of the observations (heavy line, continuous; no line, wasps together but unobserved;] [, wasps separated). Hierarchical behavior is qualified above (>, dominance; ∞>, several dominance acts; >>, strong dominance or aggressivity; ∞>>, several aggressive dominance acts; → or ←, presumed one-way exchange based on observation alone; —, buccal contact with direction of exchange unknown). The area above the dashed line represents the radioactivity lost by each pair through decay and elimination of the radioactivity liquid either by regurgitation on or off the nest or by defaecation. The shaded area thus represents the radioactivity transmitted by the tracer-fed wasp to her companion.

Results

α test (Fig. 1).

Transfer of radioactivity varied greatly. In four tests the α ceded little (6) or no (1, 2, 3) radioactive liquid to the β, despite several fairly unaggressive α > β dominance acts and occasional buccal contacts (where direction could not be ascertained). In three tests (4, 5, 7) the α transferred a small quantity of radioactive liquid to the β which it dominated frequently and aggressively. Also numerous were buccal contacts where the direction of transfer was ethologically clear (α → β or β → α). In two tests (8, 9) the level of radioactivity in the β exceeded that in the α, thus indicating a marked transfer from α to β. In both instances the α was much less aggressive than that of tests 4, 5 and 7.

It should be noted that the initial transfer in all the α-tests occurred 20 to 90 min ($\bar{X}$ = 40 min 8/10) after the wasps were reunited and the aliquot of lost radioactivity (that not traceable in the wasps) was relatively high.

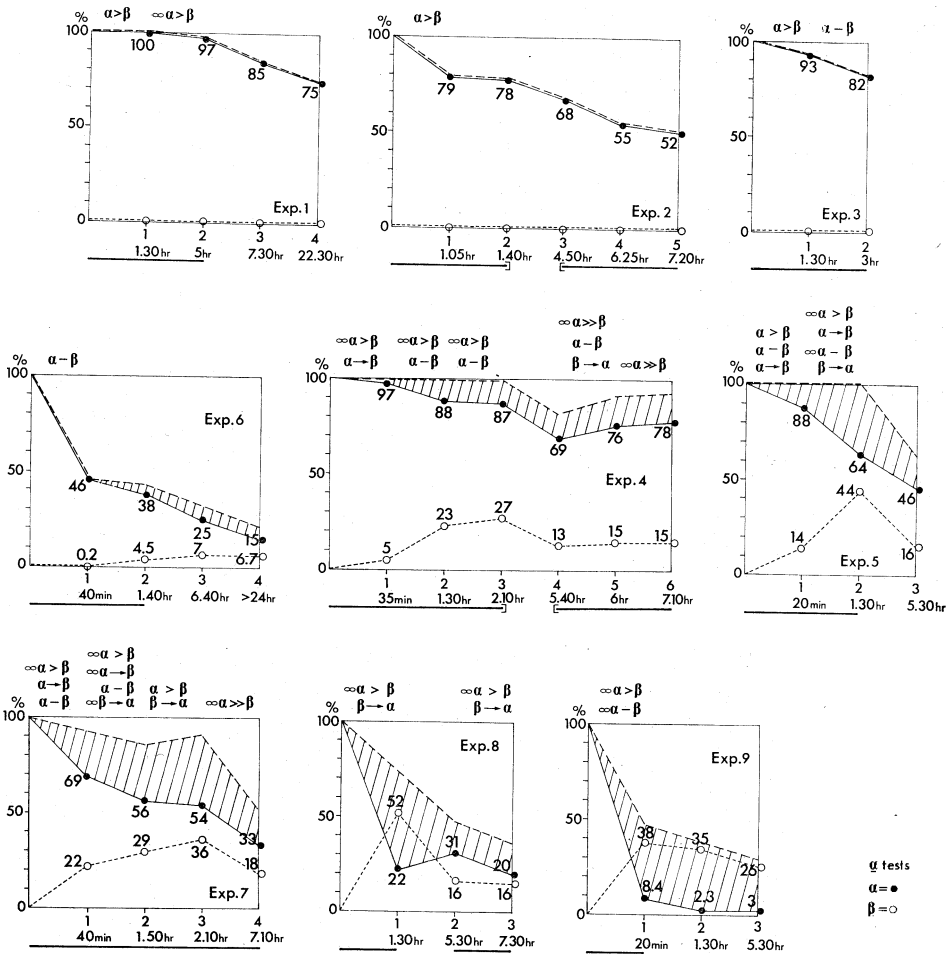

Fig. 1. – Tests in which the radioactive tracer was administered to the α (see text for further explanation). Ordinate: radioactivity level. Abscissae: successive measurements.

β test (Fig. 2).

In all five tests the β always ceded radioactive liquid to the α, with the difference that twice (10, 11) the α became more radioactive than the β, once (12) the α and β reached approximately the same level, and twice (13, 14) the α did not reach the level of radioactivity of the β. The initial transfer occurred 1 to 25 min ($\bar{X}$ = 13 min 2/10) after the two wasps were reunited, and the aliquot of lost radioactivity was nil or much lower than in the α tests.

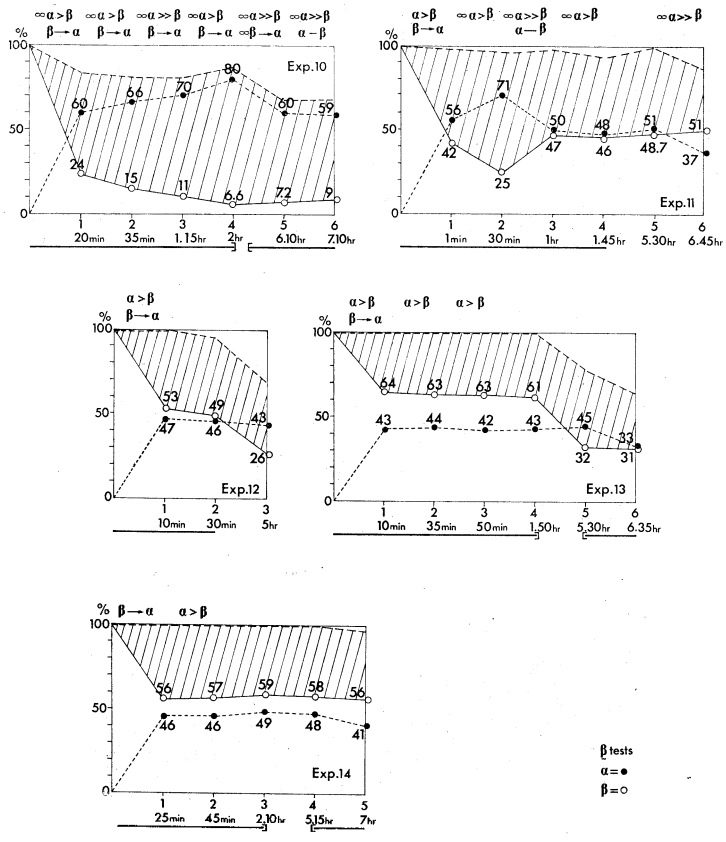

Fig. 2. – Tests in which the radioactive tracer was administered to the β (see Fig. 1 and text for further explanation).

Discussion

These tests clearly demonstrate not only the existence of a bi-directional trophallactic exchange in initial bigynic societies ($\alpha \rightleftarrows \beta$) but also reveal an asymmetry in the intensity of liquid flow. In fact, the β cedes with greater ease to the α than vice-versa, as can be seen in Fig. 3 which gives the level or radioactivity of each companion in the first three measurements.

The time elapsing between reunion and initial contact differs significantly in the α and β tests. While tracer-fed β females are immediately solicited after reunion by the α females, which become radioactive within an average of 13 min 2/10, tracer-fed α females contaminated the β only after an average of 40 min 8/10 (Mann-Whitney U test, $P < 0.030$). This indicates a reluctance of the α to cede, which is confirmed by the varying levels of lost radioactivity in the two series of tests (Fig. 4). This is low and constant in the *β* tests, higher and on the increase in the *α* tests. While the difference

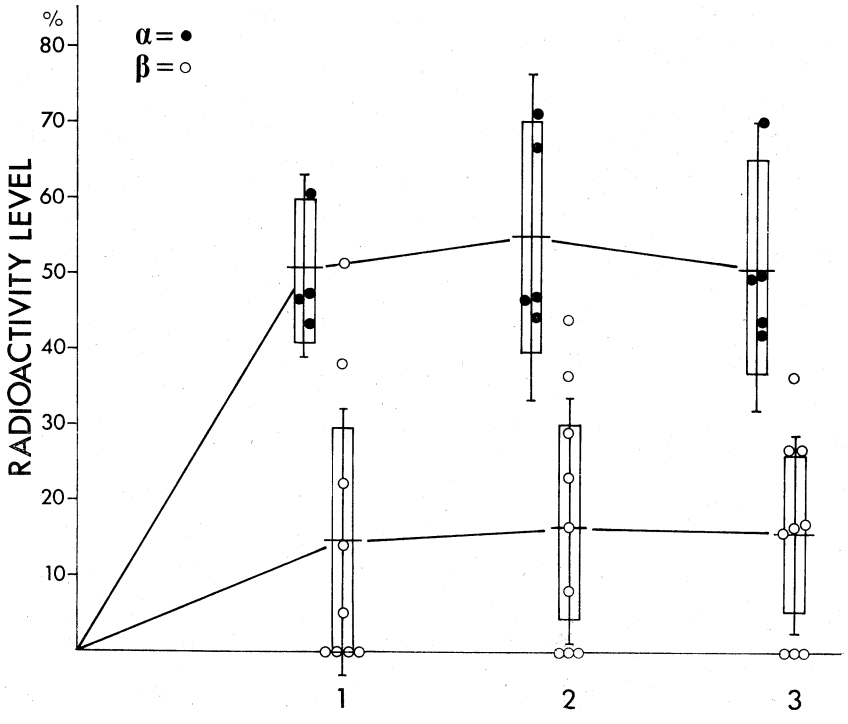

Fig. 3. – Level of radioactivity reached in the partners of tracer-fed wasps in the first three measurements.

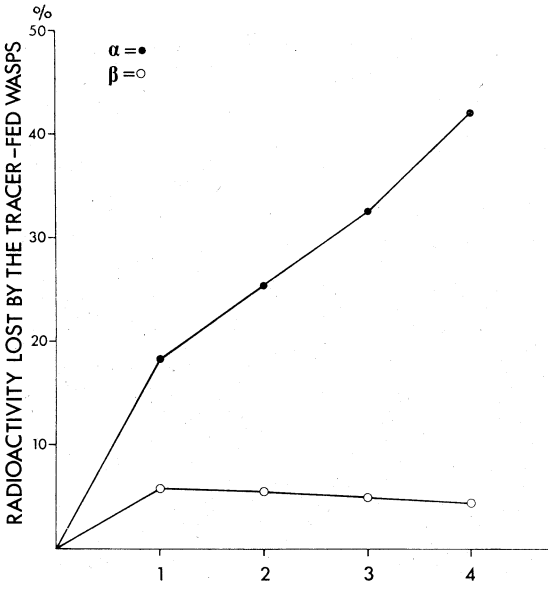

Fig. 4. – Radioactivity lost in both series of tests in the first four measurements.

between the mean values of the α and β tests is not significant in the first and second measurements (Mann-Whitney U test, $P > 0.10$), it is in the third ($P = 0.046$) and fourth ($P = 0.016$) measurements. Given their tendency to withhold the radioactive liquid, the α females obviously lose most of the liquid on the nest or by excretion. In contrast, the β females lose most of the liquid through transfer to the α.

Dominance with contact (for example, accompanied by antennation) does not always involve transfer of liquids from the subordinate to the dominant wasp. On the other hand, the wasps were clearly seen to transfer drops of liquid which did not contain any significant amount of radioactivity, as shown by immediately testing the wasps. This confirms that the liquids exchanged arise not only from regurgitation from the social stomach but also from the salivary glands [I^{131} is non-metabolizable and thus not absorbed by these glands].

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