TRAIL SHARING BETWEEN CAMPONOTUS AND CREMASTOGASTER: SOME COMMENTS AND IDEAS

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The earliest report on the relationship between Camponotus lateralis Ol. and Cremastogaster scutellaris Ol. is given by Gené(1842). According to this author, the colonies of these two species are sometimes contiguous and the trails that connect the nests with the sources of food are held in common. Later Emery (1886, 1915)described the situation in greater detail and stated that the nests of the two species are always separate, but suggested that Camponotus, which chromatically mimics Cremastogaster, uses the trails of the latter in order to protect itself from myrmecophagous animals that are repelled by the characteristically unpleasant odour of Cremastogaster. The subsequent literature contains scattered observations on the relationship between these two species and also indicates the possibility of analogous relationships between other species of these two genera. Zimmermann (1934) implies that the relationship between Camponotus truncatus Spin. and Cr. scutellaris is sometimes like that between C. lateralis and Cr. scutellaris. Analogous situations have been postulated between Camponotus sicheli var. guancha Sant. and Cremastogaster nouallieri Em. on the island of Tenerife by Santschi (1919) and between Camponotus vitreus var. angustula Em. and Cremastogaster vandermeer-mohri Men. in Sumatra by Menozzi (1930). The case of Camponotus femoratus F. and Cremastogaster parabiotica For. cited by Wheeler (1921) is much more complex. These two species, which nest together in 90% of the ant gardens of British Guiana, forage together and regurgitate food reciprocally. More recently Goetsch (1942, 1951, 1953) and Kaudewitz (1955) have redescribed the relationships of C. lateralis and C. truncatus with Cr. scutellaris as a new type of social parasitism. By inducing Camponotus to follow false trails marked by 4% formol or HCOOH, Goetsch demonstrates that Camponotus is attracted to Cremastogaster by essentially olfactive releasers. Furthermore, both authors describe a kind of heterospecific dominance order in the initial stages of the relationship between two species, with Cremastogaster hostile towards Camponotus. The manifestations of hostility are accepted by Camponotus in the typically dominated position which these authors call "Demutstellung" or "Wartestellung". After Cremastogaster's initial phase of hostility, the two species seem to get used to each other and continue to forage together.

Since I have had ample opportunity to make field and laboratory observations on these three species and since my conclusions differ somewhat from what has hiterto been written, it seems useful to state my principal observations and conclusions. For simplicity's sake, I shall refer only to C. lateralis, the more common species, in the text, but, as far as I could see, the behaviour of C. truncatus is identical.

A. The nests of C. lateralis and Cr. scutellaris, though always separate, are often close together, and their boundaries may even interdigitate. This would seem to indicate that although the two species can certainly live independently, Cremastogaster holds a strong attraction over the founding females of Camponotus. When the latter select the site of a colony, they clearly take into account the location of Cremastogaster nests whenever possible. This is further confirmed by my observation near Sirolo (Ancona) the 17th of August, 1956 of a wingless female of C. truncatus following a trail of Cr. scutellaris for a good stretch. In nature the closeness of some nests and degree of interpenetration of boundaries in some cases would lead us to consider them as a single nest held in common if it were not that when the nests are broken, the two species attack each other violently. Furthermore, in artificial nests, I have neither succeeded in getting Cremastogaster to adopt newly fertilized females of Camponotus nor in obtaining the fusion of colonies of the two species at various degrees of development. In both cases fighting seems inevitable and, in the latter, it ends only with the extermination of one of the two species.

B. Cremastogaster and Camponotus forage together, and members of the latter species are usually tolerated if they are not too numerous. I devised a simple experiment in nature to cast a further light on the relationship between these two species. It consisted in placing large quantities of sweetened water on trails of Cremastogaster at spots near trophoporic field of other nectarivorous species. As soon as the third species arrived at the spot in sufficient numbers, fighting inevitably ensued between it and Cremastogaster, while Camponotus kept well out of the way and did not return to that portion of the trail until calm had been regained.

C. Unquestionably Camponotus follows the olfactive trails of

Cremastogaster to reach the same sources of food. This is easily demonstrated by Bonnet's simple experiment and confirmed in nature by the fact that Camponotus continues to use Cremastogaster trails even in the coldest nights or after the warm weather has ended, when Cremastogaster no longer leaves the nest, whereas Camponotus is never seen before Cremastogaster , even on trails that are used year after year. Nevertheless I was never able to induce Camponotus to follow false trails traced with 4% formol or HCOOH as Goetsch (l.c.) claims to have done. On the contrary, when I traced a curved trail from the Camponotus nest to a deposit of sweetened water, Camponotus, ignoring the false trail, consistently followed a straight line to the new source of food by photomenotactic orientation (demonstrated by the mirror experiment). This result is not unexpected if one reflect that all our present knowledge of trail substances indicates that they are highly specific. If Camponotus had such a broad releasing capacity, it would be highly exceptional and would permit it to follow trails made by other species of ants.

D. The relationship between Cremastogaster and Camponotus is generally characterized by remarkable tolerance or even indifference. I witnessed manifestations of hostility only occasionally, in particular near the nest or the source of food or when Camponotus was present in large numbers. The reaction of Camponotus to contact with Cremastogaster is almost always one of hasty escape, soon followed by a return to the trail at a nearby point. This behaviour is graphically represented in fig. 1.

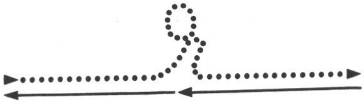


Fig. 1. Track of a Camponotus upon meeting a Cremastogaster on an olfactory trail.

I have never observed Camponotus in the exact position described by Goetsch and by Kaudewitz as "Demutstellung" and "Wartestellung". However, when the temperature is rather low, Camponotus sometimes reacts to contact with its hosts by immobilizing itself in a tanatotic position rather than by escaping.

E. Thus we see that Cremastogaster has a double and antithetical effect on Camponotus. On the one hand a larger number of the former on a trail will leave a stronger odour more easily recognizable by Camponotus, and, on the other, larger numbers of Cremastogaster will further delay each Camponotus on the trail. At this point we can ask what the optimum situation for Camponotus may be, and how their possibility of using the trail is affected by the variation in number of the Cremastogaster. Let us pose:

L = length of the trail
$2n$ = number of Camponotus
$2m$ = number of Cremastogaster
V = speed of Camponotus
v = speed of Cremastogaster
d = delay of a Camponotus upon meeting a Cremastogaster

Since it has been shown experimentally that the relation $V > v$ always holds, it is taken that the Camponotus will be delayed only by meeting Cremastogaster coming from the opposite direction.

We shall suppose that the ants are distributed uniformly over a trail traversed in both directions so that n Camponotus meet the m Cremastogaster coming from the opposite direction.

First let us consider only the negative effect of the Cremastogaster that delay the Camponotus with each encounter, and let us choose as a first hypothesis the case of a single Cremastogaster on the trail. In the interval of time d the single Cremastogaster will cover the portion of the trail $\lambda = dv$, on which $\frac{ndv}{L}$ Camponotus will be found. In this period, however, it will not only meet the $\frac{ndv}{L}$ Camponotus that are on tract λ, but also all those that are on the tract $\lambda_1 = dV$ that are able to reach tract λ in a period of time $\leq d$. The number of these will be $\frac{ndV}{L}$. Thus the total number of Camponotus encountered by the single Cremastogaster in time d will be $\frac{nd}{L}(v+V)$.

After a certain amount of time, the number of Camponotus off the trail because of encounters with Cremastogaster will remain constant because each new encounter will correspond to the return of another Camponotus previously put off the trail. Therefore at any moment the number n_1 of Camponotus on the trail is given by

$$n_1 = n - \frac{nd}{L}(v+V) = n\left(1 - \frac{d}{L}(v+V)\right) = n(1-h)$$

where $h = \frac{d}{L}(v+V)$.

h is a constant of the model that satisfies the relation $0 < h < 1$. In fact, from $n_1 < n$ it follows that $h > 0$, and from $n_1 > 0$ it follows that $h < 1$. Note that $h < 1$ implies that $\frac{d}{L}(v+V) < 1$ and therefore $d(v+V) < L$. In other words, the length of the trail must always be greater than the product $d(v+V)$.

Now let us consider the case in which m Cremastogaster travelling in the same direction are uniformly distributed over a trail of length L at a given moment of time. The whole trail L can be subdivided into k tracts, each one having the length dv. Thus $k = \frac{L}{dv}$.

If m, the number of Cremastogaster, is greater than k, on a single tract dv there will be more than one Cremastogaster. The first of these meets a Camponotus which leaves the trail and return after time d and therefore after all the Cremastogaster that follow the first at a distance of less than dv have gone by. Therefore of all the Cremastogaster on a single tract dv, only the first has any effect on the Camponotus and therefore on the problem in question. From this it follows that whenever $m \geqq k$, the number of Cremastogaster encountering Camponotus at any moment will always be k.

Now let us examine the situation over a period of time d. The first Cremastogaster leaves $n_1 = n\,(1-h)$ Camponotus on the trail for the first Cremastogaster of the following group to meet. This Cremastogaster in turn will leave $n_2 = n_1(1-h) = n(1-h)^2$ Camponotus on the trail. Since when $m \geqq k$, the total number of Cremastogaster t hat interact are k, the Camponotus remaining on the trail will be $n_k = n\,(1-h)^k$. **[1]**

Instead, when $m < k$ we have $n_m = n\,(1-h)^m$. **[2]**

Both functions of n are represented graphi cally in figure 2.

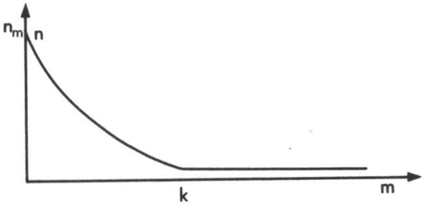


Fig. 2. Variation of the number of Camponotus (n) with the variation of the number of Cremastogaster (m) on a trail, considering only the negative effect of the latter.

Since $1-h<1$, then $n\,(1-h)^m$ is a function that tends towards O for $m \longrightarrow \infty$. However when $m \leq k$, the function n_k no longer depends on m and will therefore be represented by a straight line parallel to the abscissa axis.

Wilson (1962) has already demonstrated that the number of ants attracted to a trail is in direct proportion to the amount of trail substance emitted and therefore to the number of marker ants present on the trail. In our case we can therefore write that $n = a\,m$, in which a is a proportionality coefficient. Making the proper substitutions in **[1]** and **[2]** we set

$$n_k = a\ m\,(1-h)^k \quad \text{when } m \geqq k$$
$$n_m = a\ m\,(1-h)^m \quad \text{when } m<k.$$

Let us study the two functions separately, $n_k = a\,m$ and $n_k = c\,m$, in which $c = a(1-h)^k$ is a constant in relation to m, with $c<a$. These functions are represented in fig. 3. Instead, in the second case, we shall have the equation $n_m = a\ m\ b^m$, in which a and b are constants in relation to m and $b<1$. The corresponding curve is given in figure 4.

In fact when $m=0$, $n_m=0$, and when $m \rightarrow \infty, n_m \rightarrow 0$. The maximum point of the function has the abscissa $\bar{m}=-\frac{1}{\log(1-h)}$, and its value will be $n_m=-\frac{a}{e\log(1-h)}$. By superimposing the two curves we obtain the two possible graphs shown in figure 5.

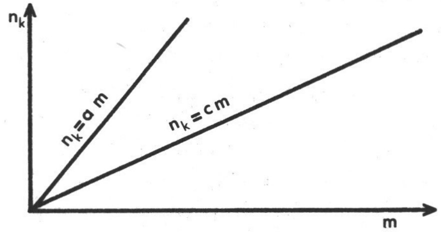


Fig. 3. Variation of the number of Camponotus on a trail as an effect of the variation of the number of Cremastogaster considering only the olfactory attraction and according to the equation $n_k=cm$.

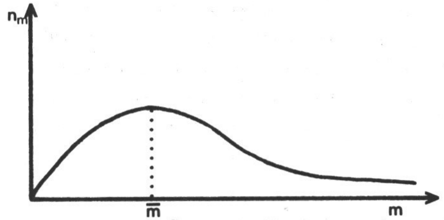


Fig. 4. Variation of the number of Camponotus in function of the number of Cremastogaster according to the equation $n_m=amb^m$

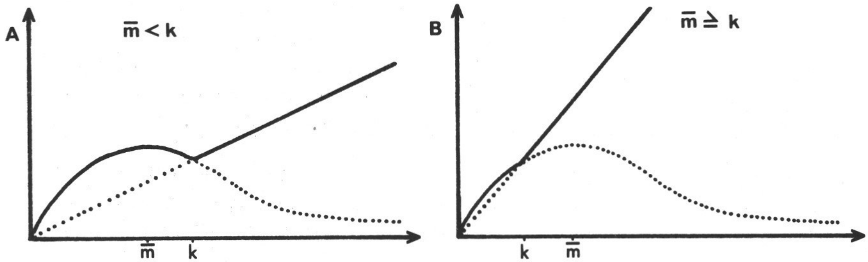
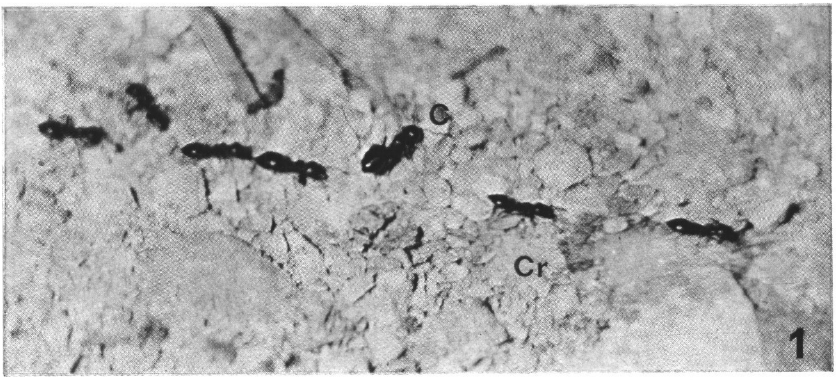


Fig. 5. Graphic representation of the two possible models expressing the variation in number of Camponotus on an olfactory trail of Cremastogaster, taking into account both the positive and negative effect of the latter.

A mathematical study of the rank relation between m and k shows that the relation $\bar{m}<k$ always holds. In fact, from $-\frac{1}{\log(1-h)}<k$ it follows that $h>1-e^{-\frac{1}{K}}$. On the other hand $h=\frac{dv}{L}+\frac{dV}{L}=\frac{1}{k}+\frac{1}{k'}$ in which $\frac{1}{k'}>\frac{1}{k}$ since $V>v$. Since it has already been stated that $\frac{1}{k}>1-e^{-\frac{1}{K}}$, it is clear that $\frac{1}{k}+\frac{1}{k'}>1-e^{-\frac{1}{K}}$. Therefore model A of figure 5 is the only valid one.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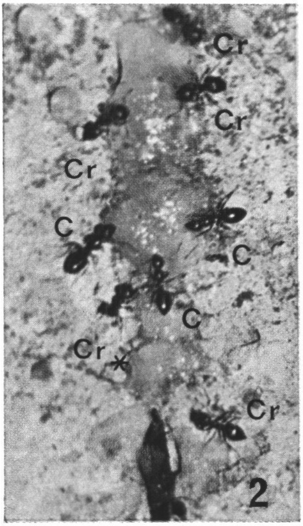
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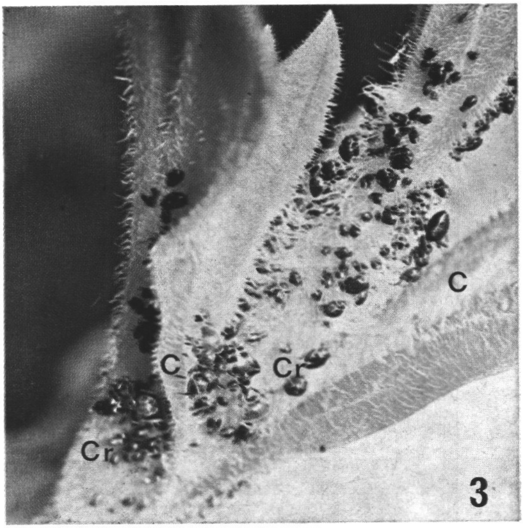
C
C
Cr
Cr
3

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Explanation of plate

1. A Camponotus lateralis worker (C) off a Cremastogaster scutellaris trail after encounter with the Cremastogaster Cr.

2. Camponotus lateralis (C) and Cremastogaster scutellaris (Cr) foraging together on a sweetened water deposit near the Cremastogaster nest. Note the Cremastogaster marked with an asterisk clearly in alarm position and biting the leg of a Camponotus.

3. Some Camponotus lateralis (C) and Cremastogaster scutellaris (Cr) workers together attending an aphid colony on Silene alba (Miller).