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EXPERIMENTS ON THE SLAVE RAIDING BEHAVIOUR OF *FORMICA SANGUINEA*  
LATREILLE ON *FORMICA RUFIBARBIS* FABRICIUS  
(Hymenoptera, Formicidae)

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Summary: The raiding behaviour of *Formica sanguinea* on *Formica rufibarbis* is investigated in defined laboratory circumstances. Over a period of three months the mortality rate of the two species, the killing of the *rufibarbis* queen, the carrying behaviour by *sanguinea* of *rufibarbis* workers and the growing proportion of *sanguinea* and *rufibarbis* workers in the respective nests are observed.

Key-words: *Formicidae*, *Formica sanguinea*, *Formica rufibarbis*, *dulosis*, slave raiding behaviour, mortality, carrying behaviour, territoriality.

Résumé: Un nid de *Formica sanguinea* avec environ 5000 ouvrières et un nid de *Formica rufibarbis* avec environ 4000 ouvrières sont connectés dans des circonstances de laboratoire bien définies. Chaque nid compte 14 compartiments intérieurs avec un gradient de températures de 12 à 28 °C et un 15e compartiment extérieur, s'ouvrant sur une aire extérieure longue de 50 cm et large de 25 cm. Entre ces deux aires se trouve une troisième de 50 cm sur 50 cm. Les trois aires sont reliées par deux ponts, long de 30 cm et large de 1,5 cm.

Dès la mise en place des ponts 100 à 200 ouvrières de *sanguinea* passent par heure dans l'aire médiane. La bataille active avec les ouvrières de *rufibarbis* ne dure que quelques heures, *sanguinea* se bat en solitaire, *rufibarbis* à plusieurs en forme d'étoile et la défense de leur territoire est plus vigoureuse que l'attaque de *sanguinea*. Après cinq heures *sanguinea* se trouve déjà dans le compartiment extérieur de *rufibarbis*. Après une semaine la proportion moyenne d'ouvrières de *sanguinea* dans les compartiments de *rufibarbis* est de 21 %. La reine de *rufibarbis* s'est retirée dans le compartiment froid le plus éloigné, où *sanguinea* n'est pas encore pénétrée. Le 11e jour la reine se trouve dans le compartiment 7 et elle est activement attaquée; le 13e jour elle est en mauvaise condition, le 18e jour elle est morte et le 19e jour son cadavre est transporté dans le monde extérieur.

La mortalité cumulative des deux espèces est linéaire; jusqu'au 13e jour le coefficient de mortalité par jour pour

pour *rufibarbis* est 24,3 et pour *sanguinea* 8,6. Du 13e au 18e jour, pendant la lutte autour de la reine, la mortalité de *rufibarbis* monte à 50 par jour. Depuis lors jusqu'au 50e jour la mortalité de *rufibarbis* est 19,5 par jour et celle de *sanguinea* 13,7. Dès le 50e jour la mortalité de *rufibarbis* diminue à 10,5 par jour tandis que celle de *sanguinea* reste constante à 13,7.

Le système glandulaire de *sanguinea* dans l'attaque, la défense et la domination est clairement supérieur à celui de *rufibarbis*.

Le réflexe porteur de *sanguinea* joue à notre avis un rôle prépondérant dans son comportement esclavagiste. Dès le premier jour on voit des ouvrières de *sanguinea* transporter des ouvrières de *rufibarbis* du nid de *rufibarbis* dans le nid de *sanguinea*. L'efficacité du transport et l'orientation, probablement visuelle, en traversant les trous d'accès et les ponts, sont remarquables. Entre le 11e et le 15e jour la proportion moyenne de *rufibarbis* dans le nid de *sanguinea* est 11 %, nombre qui monte à 16 % entre le 20e et le 22e jour et diminue de nouveau à 9 % entre le 75e et le 82e jour. Rarement on observe le transport de couvin.

Le nid de *rufibarbis* continue à exister comme entité. Après 15 jours la proportion de *sanguinea* chez *rufibarbis* est 21 %, après 25 jours 26 % et après 75 jours 43 %. Cette augmentation est expliquée par la mortalité progressive des ouvrières de *rufibarbis* sans remplacement par de jeunes ouvrières.

Mots-clés: *Formicidae*, *Formica sanguinea*, *Formica rufibarbis*, *dulosis*, esclavagisme, comportement de portage, mortalité, territorialité.

#### INTRODUCTION

The slave raiding behaviour of *F. sanguinea* has been explained in different ways. BUSCHINGER (1980) and coworkers published an extensive comparative study on the organization of Slave Raids in Dulotic Ants. In the case of *F. sanguinea* he mentioned the opinion of DOBRZANSKI (1961) who proposes that the raiding behaviour is a continuation of the foraging accomplished by the group of outside workers.

In laboratory experiments several authors observed the merging of interspecific and intraspecific colonies; KUTTER (1957) forged the term "eudulosis" for this phenomenon where the queen of the subdued nest is killed and the surviving brood and workers are integrated in the nest of the slave maker. BUSCHINGER prefers to interpret this phenomenon as "territorial interaction".

We propose some new experiments and quantitative results of the interaction of *sanguinea* and *rufibarbis* in laboratory circumstances.

#### MATERIALS AND METHODS

A nest of *F. rufibarbis*, with approximately 5000 workers and a nest of *F. sanguinea*, with approximately 4000 workers, are connected to an outside world. Each nest consists of 14 interior cells, mounted on a temperature gradient with a range of 12

to 28 degrees Celcius. Each nest opens on an exterior transitory 15th cell, connected to an outside area of 50 by 100 cm. This outside world is divided in three parts. The 15th cell of each nest opens on an area of 25 by 50 cm and between them is a third area of 50 by 50 cm. These outside areas are joined by bridges, 30 cm long and 1,5 cm large. In this way the contact between the two ant nests is made sufficiently difficult to avoid a too fast merging of the outside workers (Figure 1).

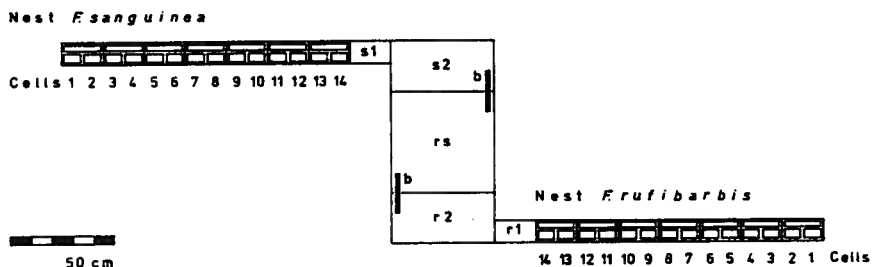


Figure 1: Experimental set-up for the connection of a *F. rufibarbis* to a *F. sanguinea* nest; r1: outside 15th cell of *rufibarbis*, r2: outside area of *rufibarbis*, rs: intermediate area, s1: outside 15th cell of *sanguinea*, s2: outside area of *sanguinea*, b: bridge.

## RESULTS

Immediately after the positioning of the bridges 100 to 200 workers of *sanguinea* are crossing per hour to the median area and soon afterwards a few sporadic workers reach the second bridge to the *rufibarbis* side. There is a visible initial fighting that lasts only for about five hours. *Sanguinea* is a solitary fighter, *rufibarbis* fights with two or more in a starlike fashion. After five hours *sanguinea* workers have penetrated the outside 15th cell of the *rufibarbis* nest. There is a mass arousal of the *rufibarbis* workers at the foot of their bridge and some workers show a display of standing high on their legs with a raised gaster. The *rufibarbis* workers are visibly disoriented. This phenomenon is explained by authors as LÖFQVIST (1968, 1973, 1976, 1977) and BILLEN (1982); the large amount of undecane and dodecylacetate, ejected by the *sanguinea* workers, have a disarming effect on the slave species.

To have an estimate of the effectiveness of this chemical alarm-defense system in *sanguinea* we counted all the dead workers of the two species over the three months of the experiment and constructed a cumulative mortality curve. This curve revealed well defined periods in the conquering of the *rufibarbis* nest by the *sanguinea* workers (Figure 2).

1. There is a first period of 13 days; the outside visible fighting lasts only some hours, inside the *rufibarbis* nest fighting continues around the *rufibarbis* queen. Normally the queen resides in

the cells 7,8,9 with a temperature around 24 °C. She is pushed back in the first cold cell on the 8th day of invasion; from the 11th till the 13th day she is pulled back in the cells 7 to 9. Till then the daily mortality rate of the *rufibarbis* workers is 24,3, nearly three times that of *sanguinea* which counts 8,6. 2. From the 13th to the 18th day there is a sharp increase in mortality in *rufibarbis*, an average of 50 workers a day; the mortality of *sanguinea* increases to 13,7, and this number remains constant for the remaining months of the experiment.

The sharp increase in *rufibarbis* mortality expresses the killing of their queen; on the 13th day she is cripple, on the 18th day she is dead, and from that moment the mortality of the *rufibarbis* workers drops to 19,5 a day, till the 53d day of the experiment; then it drops further to 10,5, even lesser than the constant mortality of *sanguinea*, 13,7 a day. The slight increase of *sanguinea* mortality is probably caused by the start of a new brood cycle, beginning around the 13th day.

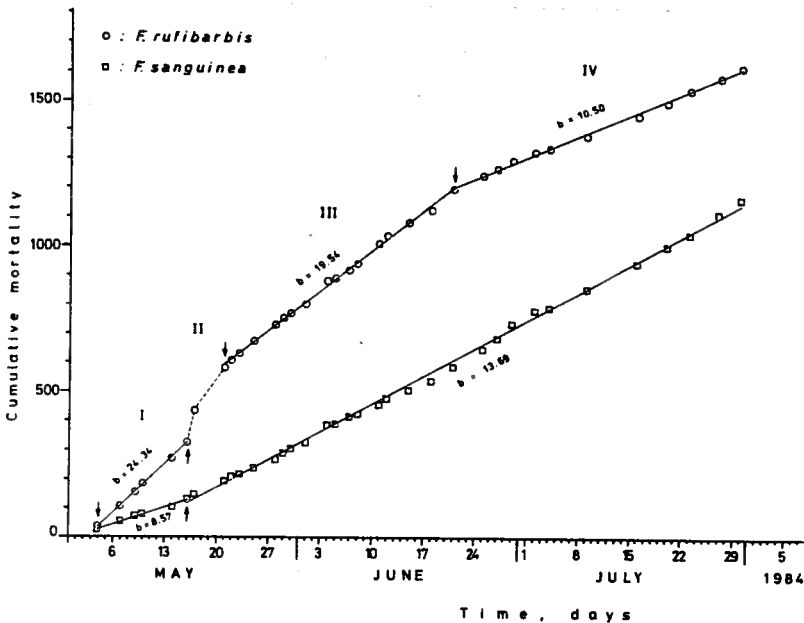


Figure 2: Cumulative mortality of *F. rufibarbis* and *F. sanguinea* during the whole length of the experiment. Mortality is linear between critical points (arrows), regression-coefficients are given (b). The meaning of the periods (I-IV) is given in the text.

What is happening meanwhile? On observing the *sanguinea* nest before the experiment we stated that certain *sanguinea* workers show a strong carrying reflex. They run in straight lines to the feeding area, solicit a feeding or drinking worker and

carry it back to the nest in the typical *Formica* fashion (HÖLDOBLER, 1974).

From the first day of contact between *sanguinea* and *rufibarbis* we observed continually the so called taxi's and picking up these workers we found always a *sanguinea*, carrying a *rufibarbis* to the *sanguinea* nest. There exists a remarkable, probably visible orientation of the *sanguinea* workers: a *rufibarbis* worker solicited and taken in the outside 15th cell of the *rufibarbis* nest is carried in straight lines through the connecting holes, over the two bridges in the *sanguinea* nest.

In day-time observation we only noticed the transport of a couple of larvae out of the *rufibarbis* nest to the *sanguinea* nest. There is an inverse transport. On the 20th day, after the disappearance of the *rufibarbis* queen, we observe *sanguinea* workers carrying *rufibarbis* workers in the nest of *rufibarbis*. In the *rufibarbis* nest brood is always present and on the 30th day males and young workers of *sanguinea* are present in the *rufibarbis* nest. What means that part of the brood of *sanguinea* has been transported to the *rufibarbis* nest, probably during the night; we never observed it. The *rufibarbis* nest has become part of the territorium of *sanguinea*.

What about the proportion of *rufibarbis* and *sanguinea* workers in the respective nests? We took regularly samples of at least 50 workers out of each cell and outside areas, and counted the proportion of the *rufibarbis* and *sanguinea* workers (figure 3).

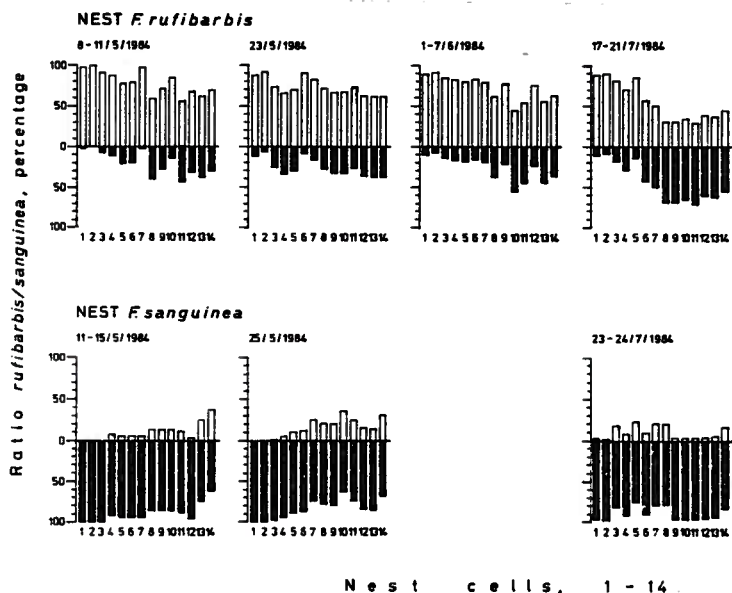


Figure 3: Histogram of the proportions of *rufibarbis* (shaded bars) and *sanguinea* (black bars) in the respective nest cells.

Between the 5th and 10th day the mean proportion of *rufibarbis* workers in the *sanguinea* nest is 11 %; this number increases to 16 % on the 20th to the 22d day and it decreases to 9 % between the 75th and 82d day. In the same three periods of sampling the mean presence of *sanguinea* in the *rufibarbis* nest is 21 %, 26 % and 43 % (Figure 4).

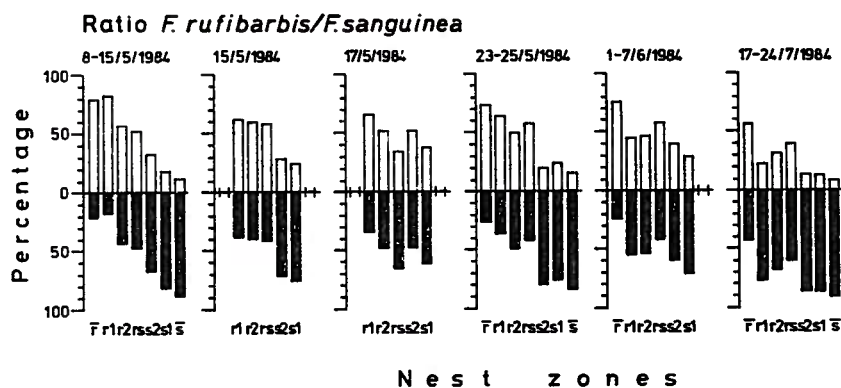


Figure 4: Histogram of the proportion of *rufibarbis* (shaded bars) and *sanguinea* (black bars) in the respective nest zones; r: mean presence in the *rufibarbis* cells, s: mean presence in the *sanguinea* cells, r1: outside 15th cell of *rufibarbis*, r2: outside area of *rufibarbis*, rs: intermediate area, s1: outside 15th cell of *sanguinea*, s2: outside area of *sanguinea*.

The *rufibarbis* nest continues to exist as an entity but in a decreasing way; the cumulative mortality of the *rufibarbis* workers is responsible for this situation, it is decreasing in this period. Therefore we made an absolute count of the *rufibarbis* and *sanguinea* proportions for the last sample (Table 1).

17-24/7/1984	<i>rufibarbis</i>	<i>sanguinea</i>	Totals
<i>rufibarbis</i> nest	1157	861	2018
outside world	162	514	676
<i>sanguinea</i> nest	376	3807	4183
Totals	1695	5182	6877

Table 1: Absolute numbers of the distribution of *F. rufibarbis* and *F. sanguinea* in the two connected nests near the end of the experiment.

## DISCUSSION

In our opinion territoriality does not wholly explain the observed phenomena. The proposition of DOBRZANSKI (1961) shows attractive aspects. The raiding behaviour is a continuation of the foraging. A behavioural pattern, consisting in a strong aggressiveness (DOBRZANSKA, 1959; LÖFQVIST, 1977) and a pronounced carrying behaviour (HÖLLDOBLER, 1974) joined to an effective chemical alarm-defense system by means of the Dufour gland, enable the *sanguinea* foragers to subdue other species, and to bring back to the nest not only brood but even workers of the slave species.

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