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WHY A SLAVE ANT SPECIES ACCEPTS AND CARES FOR COCOONS OF ITS SLAVE-MAKER

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SUMMARY

In order to determine the role of early social experience on the ontogeny of cocoon recognition by a slave-ant species, laboratory experiments were carried out in *Formica cunicularia*, a common slave of *Formica sanguinea*. In a choice-test, adult *F. cunicularia* workers coming from a pure colony tended only the homospecific cocoons, whereas destroyed the heterospecific unfamiliar ones (*F. sanguinea* and *F. lugubris*). Subsequently, 3 groups of artificial colonies were set up with callow *F. cunicularia* workers of the same age experimentally removed from their cocoons. After a 15-day training period with homospecific cocoons (group C), *F. sanguinea* cocoons (group T), or in absence of any cocoons (group I), these workers were given a choice-test between *F. cunicularia* and *F. sanguinea* cocoons. The choice of the workers belonging to groups C and T was always directed towards the cocoons with which workers had become familiar during the training period. Moreover, early deprivation of cocoons disrupted the cocoon discrimination and care ability of ants belonging to group I. On the basis of these data and those recently obtained by us on nestmate recognition in the same species, we can assume that social experience immediately following eclosion of *F. cunicularia* workers can fully explain their enslavement in nature and, therefore, the interspecific altruism of this host species towards the parasite.

RESUME

Pourquoi une espèce esclave de fourmi accepte et prend soin de cocons de son esclavagiste

Afin de déterminer le rôle de l'expérience sociale précoce sur l'ontogenèse de la reconnaissance des cocons par une espèce esclave de fourmi, des expériences de laboratoire ont été réalisées sur *Formica cunicularia*, une espèce communément esclave de *Formica sanguinea*. Dans un test de choix, des ouvrières adultes de *F. cunicularia* provenant d'une colonie pure soignèrent uniquement des cocons homospécifiques, tandis qu'elles détruisirent les cocons hétérospécifiques, non familiers (*F. sanguinea* et *F. lugu-*

bris). Après quoi, 3 groupes de colonies artificielles ont été constitués avec de jeunes ouvrières de *F. cunicularia* de même âge, retirées expérimentalement de leurs cocons. Après une période d'entraînement de quinze jours avec des cocons homospécifiques (groupe C), des cocons de *F. sanguinea* (groupe T), ou en l'absence de tout cocon (groupe I), ces ouvrières furent soumises à un test de choix entre des cocons de *F. cunicularia* et de *F. sanguinea*. Le choix des ouvrières des groupes C et T fut toujours en faveur des cocons auxquels elles avaient été familiarisées au cours de la période d'entraînement. En outre, la privation des cocons rompit la discrimination des cocons et l'aptitude aux soins des fourmis du groupe I. Sur la base de ces données et de celles que nous avons obtenues récemment sur la reconnaissance des partenaires du nid chez la même espèce, nous pouvons soutenir que l'expérience sociale suivant immédiatement l'éclosion chez l'ouvrière de *F. cunicularia* peut expliquer son esclavage dans la nature et, par conséquent, l'altruisme interspécifique de cet hôte à l'égard de son parasite.

INTRODUCTION

Slavery (or dulosis) in ants is a form of social parasitism in which the slave-making species conduct group raids against nearby colonies, attacking the adults and stealing their brood. In the slave-makers' nest, the slaves emerging from the unconsumed portion of the captured brood behave as full members of the parasitic colony (WILSON, 1975 ; BUSCHINGER *et al.*, 1980 ; STUART, 1984). From such behaviour the interesting question of the origin of slave forms arises. The hypothesis that early olfactory learning accounts for the social integration of host and parasite has been advanced (cf. JAISSON, 1975 ; LE MOLI, 1980). On the other hand, substantial evidence of imprinting-like phenomena has been presented in several forms of ants' social behaviour (for a review see JAISSON, 1985). In particular, we first demonstrated (cf. LE MOLI and MORI, 1985) that early experience influences nestmate recognition and the direction of aggressive behaviour in *Formica cunicularia* which is in nature a common slave of the slave-maker *Formica sanguinea*. Early experience, therefore, explains the acceptance of parasite by host and may account for the integration of slave-workers in the natural dulotic societies.

Nevertheless, since the success of slave-making ants depends upon the ability of workers of the host species to accept not only adult workers of the raider but especially its brood, we here attempt to determine whether early learning is also involved in cocoon recognition and nursing behaviour by *F. cunicularia* workers.

MATERIALS AND METHODS

Response of F. cunicularia workers from a pure colony to homo- and heterospecific cocoons

In order to see if *F. cunicularia* possesses a natural tendency to care specifically for cocoons of its slave-maker *F. sanguinea*, *F. cunicularia* adults were given a laboratory choice-test between homo- and heterospecific (*F. sanguinea* or *F. lugubris*) worker cocoons. Since these workers were taken in the field from a pure colony, they were familiar with only their own cocoons.

Thirty artificial colonies (see LE MOLI and PASSETTI, 1978) each containing about 200 adult *F. cunicularia* workers were set up and divided into 3 groups. The ants of *group 1* received 5 cocoons of *F. cunicularia* (*Fc*) and 5 of *F. lugubris* (*Fl*), a species belonging to the *Formica rufa* group not related to *F. cunicularia*. The workers of *group 2* were supplied with 5 homospecific (*Fc*) and 5 *F. sanguinea* (*Fs*) cocoons. The cocoons supplied to the workers of *group 3* belonged to *Fs* and *Fl*. According to JAISSON (1975) all the cocoons used in this and in the following test were killed by freezing.

Following JAISSON and FRESNEAU (1978), the number of undamaged cocoons of both species was plotted against time (in days) for each group of colonies to obtain cocoon survival curves. As criterion of adoption we used a survival index for each kind of cocoon, which was obtained by the number of days elapsed multiplied by the number of undamaged cocoons pooled over the 13 days of observation. Thus each colony yielded two cocoon survival indices. Statistical comparisons of survival indices within groups were obtained with a 1-tailed Wilcoxson test to the matched pairs of indices in each group. Between group comparisons were made with a 2-tailed Mann-Whitney 'U' test.

Response of F. cunicularia workers eclosed in different social environments to homo- and heterospecific cocoons

Fifteen artificial colonies (see above), each containing about 200 newly-eclosed workers of *F. cunicularia* experimentally removed from their cocoons on the same day, were set up and divided into 3 groups. The *control group* (C) consisted of ants kept for a fortnight after eclosion (cf. LE MOLI and MORI, 1985) in the presence of 10 *Fc* worker cocoons. The *experimental treated group* (T) was set up with ants maintained for 15 days after eclosion with 10 *Fs* worker cocoons. During this period each damaged cocoon in both groups was replaced with an intact one. The *experimental isolated group* (I) consisted of callows isolated from all cocoons during the first fortnight after eclosion. After the exposure period, all cocoons were removed from the groups C and T, and a choice-test between *Fc* and *Fs* worker cocoons was carried out in colonies of the 3 groups. Survivorship curves of cocoons were obtained by the above described procedure, and a similar statistical analysis was performed to evaluate between group differences in the survival indices recorded in each of these colonies. Within group comparisons were obtained from a 1-tailed randomization test.

RESULTS

Response of F. cunicularia workers from a pure colony to homo- and heterospecific cocoons

The life span of *Fc* cocoons was found to be clearly higher in both that of *Fl* in group 1 ($p = 0.025$; *fig. 1a*), and that of *Fs* in group 2 ($0.01 < p <$

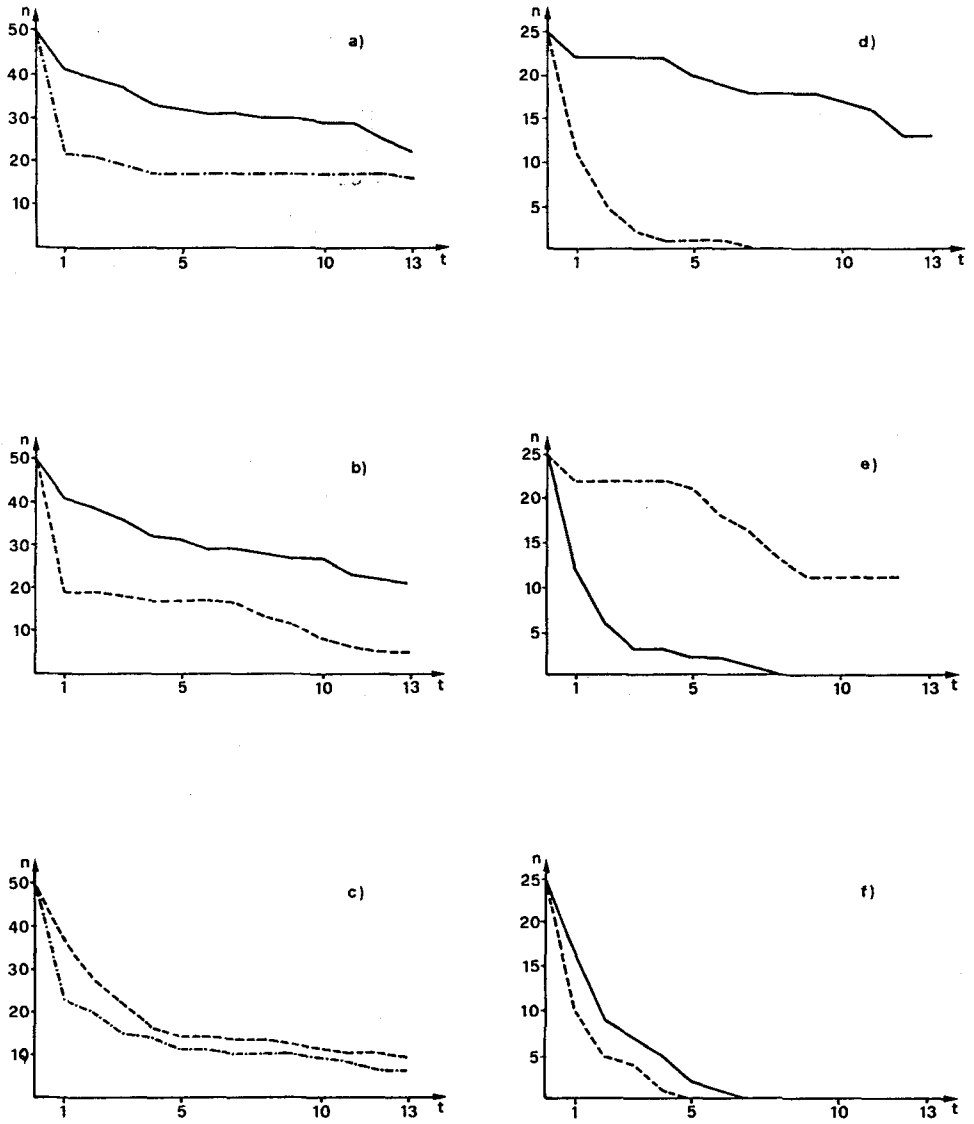

Fig. 1. — Response of *F. cunicularia* workers to homo- and heterospecific cocoons. The survivorship curves of cocoons were recorded from choice-tests of: a-c) workers taken in the field from a pure colony; d-f) workers reared for a fortnight from eclosion respectively with homospecific cocoons (d), *F. sanguinea* cocoons (e), and without cocoons (f).
n = number of intact cocoons; t = time in days.
———— = cocoons of *F. cunicularia*; —·—·—·— = cocoons of *F. lugubris*; - - - - - - - - - - = cocoons of *F. sanguinea*.

Fig. 1. — Réponse des ouvrières de *F. cunicularia* à des cocons homo- et hétéro-spécifiques. Les courbes de survie des cocons ont été enregistrées à partir de tests de choix: a-c) d'ouvrières prises dans la nature dans une colonie pure; d-f) d'ouvrières élevées pendant une quinzaine de jours après l'éclosion respectivement avec des cocons homospécifiques (d), des cocons de *F. sanguinea* (e), et sans cocons (f).
n = nombre de cocons intacts; t = durée en jours.
———— = cocons de *F. cunicularia*; —·—·—·— = cocons de *F. lugubris*; - - - - - - - - - : cocons de *F. sanguinea*.

0.025 ; *fig. 1b*). In contrast, in group 3 the difference between heterospecific cocoon survival indices was not significant, since both kinds of alien cocoons rapidly disappeared (*fig. 1c*). The comparisons of the series of survival indices between groups showed that there was no difference between life span of *Fc* cocoons in groups 1 and 2. No difference was found between survival indices of *Fs* and *Fl* cocoons among the 3 groups. This discrimination between familiar and alien cocoons was very rapid, since similar results were shown by statistically comparing data collected on the 5th day of observation.

Response of F. cunicularia workers eclosed in different social environments to homo- and heterospecific cocoons

The comparisons of *Fc* and *Fs* survival indices within group showed that the life span of homospecific cocoons was clearly higher ($p = 0.032$) than that of heterospecific ones in group C (*fig. 1d*). However, workers of group T (*fig. 1e*) took care of *Fs* cocoons and destroyed those of their own species ($p = 0.032$). Finally, the ants of group I destroyed both kind of cocoon at comparable rates (*fig. 1f*). The difference between *Fc* versus *Fs* survival indices was not significant.

The salient result arising from the comparisons between groups is that there was no difference between *Fc* (group *C*) and *Fs* (group T) cocoon survival indices. Moreover, the comparisons of *Fc* survival indices showed a significant difference between groups C and T, and between groups C and I (in both cases $p = 0.008$), but no difference was found between groups T and I. Concerning the *Fs* cocoons, a significant difference of survival indices occurred between groups T and C, and between groups T and I (in both cases $p = 0.008$). On the contrary, no difference existed between groups C and I for these cocoons. Again, similar results were shown by statistically comparing data collected on the 5th day of observation.

CONCLUSION - DISCUSSION

F. cunicularia workers coming from a pure colony in nature always discriminate (*fig. 1a, b*) homospecific cocoons from those of heterospecifics (*F. lugubris ; F. sanguinea*). In fact, they did not care for both kinds of alien cocoons but rapidly destroyed them at comparable rate (*fig. 1c*), according to JAISSON's observations (1975) in the closely related species, *F. fusca*. This behaviour means that *F. cunicularia* workers do not possess a natural tendency to care for cocoons of *F. sanguinea* compared with other heterospecific ones, although there are odour similarities between this slave species and its slave-keeper (BERGSTRÖM and LÖFQVIST, 1968).

One the contrary, the social environment at the emergence of *F. cuni-*

cularia workers strongly influences the cocoon recognition and care behaviour of adults. In fact, workers of group C (*fig. 1d*) and T (*fig. 1e*) familiar during the sensitive period with a particular kind of cocoon, rapidly destroy unfamiliar cocoons, both homo- and heterospecific (*F. sanguinea*), while those familiar are kept intact much longer. Moreover, workers of group I (*fig. 1f*) maintained in total absence of cocoons during the training period, showed no capacity to recognize any type of cocoon nor to perform parental cares. Therefore, it is evident that early experience soon after eclosion is determinant for subsequent cocoon discrimination and nursing behaviour by adult ants of this species.

These results, together with those previously obtained on the development of aggressive behaviour in *F. cunicularia* (LE MOLI and MORI, 1985), explain the integration and the subsequent heterospecific altruism towards brood and adults of slave-workers in the natural societies of dulotic ants.

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References

BERGSTRÖM G., LÖFQVIST J., 1968. — Odour similarities between the slave-keeping ants *Formica sanguinea* and *Polyergus rufescens* and their slaves *Formica fusca* and *Formica rufibarbis*. *J. Insect Physiol., 14,* 995-1011.

BUSCHINGER A., EHRHARDT W., WINTER U., 1980. — The organization of slave raids in dulotic ants - A comparative study (Hymenoptera ; Formicidae). *Z. Tierpsychol., 53,* 245-264.

JAISSON P., 1975. — L'imprégnation dans l'ontogénèse des comportements de soins aux cocons chez la jeune fourmi rousse (*Formica polyctena* Först.). *Behaviour, 52,* 1-37.

JAISSON P., 1985. — Social behaviour. In : Kerkut G.A., Gilbert L.I. (eds), *Comprehensive Insect Physiology, Biochemistry and Pharmacology, vol. 9, Behaviour,* pp. 673-694. Pergamon Press, Oxford, XVI + 735 pp.

JAISSON P., FRESNEAU D., 1978. — The sensitivity and responsiveness of ants to their cocoons in relation to age and methods of measurement. *Anim. Behav., 26,* 1064-1071.

LE MOLI F., 1980. — On the origin of slaves in dulotic ant societies. *Boll. Zool., 47,* 207-212.

LE MOLI F., MORI A., 1985. — The influence of the early experience of worker ants on enslavement. *Anim. Behav., 33,* 1384-1387.

LE MOLI F., PASSETTI M., 1978. — Olfactory learning phenomena and cocoon nursing behaviour in the ant *Formica rufa* L. *Boll. Zool., 45,* 389-397.

STUART R.J., 1984. — Experiments on colony foundation in the slave-making ant *Harpagoxenus canadensis* M.R. Smith (Hymenoptera ; Formicidae). *Can. J. Zool., 62,* 1995-2001.

WILSON E.O., 1975. — *Leptothorax duloticus* and the beginnings of slavery in ants. *Evolution, 29,* 108-119.