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STIMULATORY INFLUENCE OF THE QUEEN AND KING ON SOLDIER DIFFERENTIATION IN THE HIGHER TERMITES *NASUTITERMES LUJAE* AND *CUBITERMES FUNGIFABER*

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SUMMARY

The influence of the reproductives on soldier production was studied in two species of higher termites, *Nasutitermes lujae* (Nasutitermitinae) and *Cubitermes fungifaber* (Termitinae). In both species, the royal pair has a stimulatory influence on soldier production. The soldier molts are two to three times more numerous when workers are reared with the reproductives. In *N. lujae,* the king and the queen have an apparently equal stimulatory influence. The reproductives act on both induction and orientation of the molts toward the soldier type. It can be now claimed that in *N. lujae,* in which the existence of an inhibitory soldier pheromone was recently evidenced, the proportion of soldiers results from the balance between the stimulatory influences of the reproductives and the inhibitory influences of the soldiers. The hypothetical nature of the royal stimulatory influence is discussed.

RESUME

Action stimulatrice de la reine et du roi sur la différenciation des soldats chez les termites supérieurs Nasutitermes lujae **et** Cubitermes fungifaber

L'influence des reproducteurs sur la production de soldats a été étudiée chez deux espèces de termites supérieurs, *Nasutitermes lujae* (Nasutitermitinae) et *Cubitermes fungifaber* (Termitinae). Dans les deux espèces, le couple royal stimule la production de soldats. Il se forme en moyenne 2 à 3 fois plus de soldats dans les élevages lorsque les reproducteurs sont présents. Chez *N. lujae,* le roi est aussi stimulateur que la reine. Les reproducteurs agissent à deux niveaux : ils induisent les mues et les orientent vers le type soldat. On peut maintenant affirmer que chez *N. lujae,* où une phéromone inhibitrice de soldats a été récemment mise en évidence, la proportion de soldats résulte de l'équilibre entre les actions stimulatrices des reproducteurs et les actions inhibitrices des soldats. La nature hypothétique de l'action stimulatrice royale est discutée.

INTRODUCTION

The proportion of soldiers in termite colonies is regulated in many species by inhibitory mechanisms which prevent the differentiation of competent individuals towards this caste when soldiers are already present in sufficient numbers (CASTLE, 1934 ; MILLER, 1942 ; LIGHT and WEESNER, 1955 ; NOIROT, 1955, SPRINGHETTI, 1969 ; NAGIN, 1972 ; RENOUX, 1972 ; HAVERTY and HOWARD, 1981 ; OKOT-KOTBER, 1985). An inhibitory pheromone secreted by the soldiers has recently been shown to slow down or to suppress the differentiation of new soldiers in a higher termite, *Nasutitermes lujae* (LEFEUVE and BORDEREAU, 1984).

However, as has been pointed out by GRASSE 1982, the social regulation of termite colonies cannot be explained solely by the inhibitory mechanisms. Such is likely to be the case in *Nasutitermes lujae* in which the variations observed in soldier production suggested that other factors are involved. Moreover, caste stimulation has been claimed to exist in the lower termites (MILLER, 1942 ; SPRINGHETTI, 1969, 1970).

The present paper reports on the role of the royal pair in soldier production in *Nasutitermes lujae* (Wasmann) which possesses a high percentage of soldiers, and in another higher termite, *Cubitermes fungifaber* (Sjöstedt), a species with a low percentage of soldiers.

MATERIAL AND METHODS

• *Nasutitermes lujae :* 13 arboreal nests of this monogynous species were collected in Ivory Coast at different times of the year and sent by plane to France where they were stored, until used, in large glass tanks filled with decayed wood in an air-conditioned room (T : 28°C, RH : 80 %).

The soldier + presoldier proportion was previously estimated to 18.7 ± 2.7 % ($\bar{x}$ ± SD) (LEFEUVE and BORDEREAU, 1984). Soldiers and presoldiers represented 36.0 ± 7.8 % of the small workers + soldiers + presoldiers population.

Soldiers develop from small workers of the first instar ($S^{w}1$) through an intermediary instar of presoldier (NOIROT, 1955). Small workers of the first instar can only differentiate to soldiers or to small workers of the second instar (SW2) which are easily recognizable with their brownish pigmented head. SW2 are very few in the nests and in our experiments we never observed their differentiation, only soldier molts occured.

Termites were reared according to GRASSE and NOIROT 1955 in glass tubes (180 × 18 mm) partially filled with sand and containing one piece of wood.

For this species, our study is based on the comparison of soldier production during 30 or 45 days in groups of 200 SW1 reared in the presence or, as controls, in the absence of the royal pair. For each nest which always contains only one reproductive pair, one experiment with queen or/and king and 5 to 9 controls were carried out ; reproductives were never used for more than one experiment.

• *Cubitermes fungifaber :* 26 nests of this monogynous species were collected in the forests near Abidjan and the experiments were carried out in Ivory Coast.

Soldiers develop from workers through an intermediary presoldier instar (NOIROT, 1955). The soldier + presoldier proportion is 1.6 ± 0.17 % ($\bar{X}$ ± SD) (NOIROT pers. com.).

Groups of 300 workers were reared either in the presence (26 groups) or in the absence (91 groups) of the royal pair, in plastic boxes (5 cm in diameter, 1.5 cm tall), partially filled with forest humus. Soldier production was estimated after 2 to 6 months of rearing.

Results were analysed with the statistical t and χ^2 tests.

RESULTS

I. Nasutitermes lujae

Results are summarized in *table I.*

1. *Influence of the queen*

Twelve experiments were carried out with physogastric queens. Mortality levels of the controls and of the experimental groups were generally low and did not differ significantly (t test, p = 0.36 at 4 weeks, p = 0.19 at 6 weeks). After 4 weeks of rearing, soldier production in experimental groups (200 SW1 + 1 queen) was higher than in controls (200 SW1) in 7 cases whereas soldier production in the experimental groups was equal to or lower than that of the controls in 4 cases. In one case, soldier production in the experimental group was very high (68.5 %) but the control was lost. After 6 weeks of rearing, all the experimental groups produced a significantly higher percentage of soldiers than the control groups (t test, p = 0.004). Soldiers produced in all groups were morphologically normal, no intercaste was observed.

Thus the presence of a physogastric queen stimulates the soldier differentiation in *Nasutitermes lujae.* The mean number of soldiers produced in the presence of the queen is about twice that obtained in orphan groups.

2. *Influence of the king*

The king does not become physogastric and often leaves the royal chamber during air transportation of the nest, it was found in only four nests. The king also very definitely stimulates soldier differentiation (*table I*). After 6 weeks of rearing, its stimulatory influence is of the same order of importance as that of the queen.

3. *Influence of a royal pair*

With one royal pair, soldier production was comparable to that obtained with one queen or with one king alone (*table I*).

Table I. — Soldier production in *Nasutitermes lujae* expressed in percentage ($\overline{X} \pm SD$) in different experimental groups : orphan groups of 200 small workers of the first instar (SW1) as controls and groups of 200 SW1 containing either one queen (Q), one king (K), or one royal pair (Q + K) as experimental groups. For each nest, 5 to 9 controls were carried out. Dates correspond to the beginning of rearing which lasted for 30 (D. 30) or 45 (D. 45) days. R is the ratio test soldier production/ control soldier production. The mortality rate is in brackets.

Tableau I. — Production de soldats chez *Nasutitermes lujae* (exprimée en poucentages ($\overline{X} \pm DS$) dans des élevages témoins de 200 petits ouvriers du premier stade (SW1) et dans des élevages tests de 200 petits ouvriers associés à une reine (Q), un roi (K) ou un couple royal (Q + K). Pour chaque colonie, 5 à 9 élevages témoins ont été réalisés. La date correspond au jour de mise en élevage. La production de soldats a été estimée après 30 (D. 30) ou 45 (D. 45) jours d'élevage. R représente le rapport de production de soldats entre l'élevage test et l'élevage témoin. Les nombres entre parenthèses expriment le taux de mortalité.

Date	200 SW1		200 SW1 + 1 Queen				200 SW1 + 1 King			
	D. 30	D. 45	D 30	R	D. 45	R	D. 30	R	D. 45	R
01-25-84	—	—	68.5 (0.0)	—	—	—	—	—	—	—
05-30-84	18.4 ± 3.7 (11.9 ± 5.9)	— —	76.8 (9.5)	4.2	—	—	—	—	—	—
07-04-84	13.5 ± 4.4 (1.2 ± 2.4)	— —	36.6 (1.5)	2.7	—	—	—	—	—	—
10-17-84	12.7 ± 4.7 (6.0 ± 1.7)	— —	10.2 (1.5)	0.8	—	—	—	—	—	—
12-04-84	9.8 ± 5.3 (10.8 ± 3.0)	11.5 ± 6.6 (17.4 ± 4.1)	19.0 (10.5)	1.9	32.1 (19.0)	2.8	—	—	—	—
02-01-85	7.8 ± 1.9 (4.6 ± 0.9)	13.8 ± 2.0 (12.7 ± 4.4)	5.8 (5.0)	0.7	21.0 (12.0)	1.5	10.1 (11.0)	1.3	23.9 (20.5)	1.7
04-15-85	24.7 ± 6.6 (1.8 ± 0.7)	30.6 ± 7.9 (8.9 ± 2.4)	45.0 (0.0)	1.8	54.1 (8.5)	1.8	—	—	—	—
04-29-85	8.9 ± 3.5 (9.9 ± 1.5)	11.2 ± 3.5 (18.2 ± 4.7)	30.8 (15.5)	3.5	40.8 (20.5)	3.7	20.9 (6.5)	2.4	39.0 (17.5)	3.5
05-23-85	18.1 ± 5.2 (3.8 ± 2.2)	28.2 ± 5.1 (10.2 ± 3.0)	6.1 (1.0)	0.3	35.0 (10.0)	1.2	—	—	—	—
06-10-85	11.9 ± 2.7 (13.3 ± 2.3)	20.0 ± 4.5 (24.9 ± 1.1)	46.0 (1.0)	3.9	62.0 (21.0)	2.9	—	—	—	—
07-09-85	25.0 ± 2.9 (6.8 ± 1.8)	31.1 ± 4.0 (30.8 ± 4.7)	39.7 (13.0)	1.6	44.7 (29,5)	1.4	35.4 (9.5)	1.4	55.6 (28.0)	1.8
08-22-85	26.9 ± 5.8 (6.3 ± 2.3)	29.9 ± 2.8 (14.6 ± 3.6)	26.0 (2.0)	1.0	39.1 (10,5)	1.3	22.2 (1.0)	0.8	34.5 (14.5)	1.2

	200 SW1		200 SW1 + 1 Q + 1 K			
	D. 30	D. 45	D 30	R	D. 45	R
01-30-85	12.1 ± 4.0 (11.3 ± 1.8)	15.5 ± 3.0 (14.8 ± 0.6)	21.8 (3.5)	1.8	45.9 (14.0)	3.0

II. Cubitermes fungifaber

Results obtained from 26 colonies are summarized in *table II.*

It was observed that the proportion of groups producing soldiers was higher in those containing the royal pair than in controls and the χ^2 test showed that this difference was highly signifiant ($\chi^2 = 12.4787$, $p = 0.0004$). Moreover, of the 13 colonies which produced soldiers with the royal pair (series 1), 10 controls produced soldiers and 37 controls produced no soldiers. Of the 13 colonies which produced no soldiers with the royal pair (series 2), 5 controls produced soldiers and 39 controls produced no soldiers. The χ^2 test shows that these controls of series 1 and 2 are not significantly different ($\chi^2 = 1.622$, $p = 0.2028$). So it can be concluded that the increased proportion of groups producing soldiers actually arises from the presence of the royal pair and not from the colony.

If results are expressed in percentages (*table III*), it can be seen that soldier production in controls is very low, but the presence of the royal pair allows for a threefold increase (t test, $p = 0.0056$).

Table II. — Soldier production in *Cubitermes fungifaber* expressed in number of producing or non producting soldiers groups after 2 to 6 months of rearing in orphan groups of 300 workers or in groups of 300 workers with one royal pair.

Tableau II. — Production de soldats chez *Cubitermes fungifaber* après 2 à 6 mois d'élevage dans des groupes orphelins de 300 ouvriers ou des groupes de 300 ouvriers contenant un couple royal. (Production exprimée en nombre d'élevages produisant ou non des soldats).

	Workers	Workers + royal pair
Groups producing soldiers	15	13
Groups producing no soldiers	76	13

Table III. — Soldier production in *Cubitermes fungifaber* expressed in percentages.

Tableau III. — Production de soldats chez *Cubitermes fungifaber* exprimée en pourcentages.

Duration of rearing (months)	Orphan groups (300 workers)	300 workers with one royal pair
2 — 3	0.059 (n = 28)	0.21 (n = 8)
3 — 4	0.016 (n = 21)	0.17 (n = 6)
4 — 5	0.119 (n = 28)	0.19 (n = 7)
5 — 6	0.071 (n = 14)	0.13 (n = 5)
X ± SD	0.066 ± 0.042	0.175 ± 0.034

Thus, in this species with a low percentage of soldiers, the royal pair also has a significant stimulatory influence on soldier production.

Under our experimental conditions, soldier production did not increase with time. This could mean that soldier differentiation occurs preferably in young individuals. However, as only 10 % of the normal soldier proportion was produced, it may be that the rearing conditions were not optimal for this delicate humivorous species.

DISCUSSION

1. The stimulatory influence of the reproductives

The data presented here indicate that soldier production is strongly stimulated by the reproductives in the higher termite *Nasutitermes lujae* as well as in *Cubitermes fungifaber*. It must be remarked that the stimulatory effect the reproductives have over small populations of 200-300 workers may be much greater than their effect over whole colonies of several thousands of individuals. However, this stimulatory action may be not strictly proportional to the size of the population, in particular if, as we suggest, it is of pheromonal nature and mediated by chemoreception (see § 3). Two other cases have been reported in the lower termites, *Kalotermes flavicollis* (SPRINGHETTI, 1969, 1970) and *Prorhinotermes simplex* (MILLER, 1942). Moreover, in HOWARD'S study (1983) concerning the influence of juvenile hormone analogues on soldier production in *Reticulitermes flavipes*, a stimulatory effect of the reproductives could also be noticed. In contrast, in *Zootermopsis angusticollis, Z. nevadensis* (LUSCHER 1973) and in *Macrotermes michaelseni* (OKOT-KOTBER 1985), the reproductives had no apparent stimulatory influence. However, in *Macrotermes*, whether young swarming imagoes or mature reproductives were tested is not known.

Soldier production can be increased on average by twofold in *Nasutitermes lujae*, by threefold in *Cubitermes fungifaber*, when the reproductives are present. The soldier molts are 5 to 6 times more numerous in *Kalotermes flavicollis* (SPRINGHETTI, 1969, 1970) and about 3 times more numerous in *Prorhinotermes simplex* (MILLER, 1942) when pseudergates are reared in the presence of a royal pair. However, it is difficult to compare our results obtained in the higher termites with SPRINGHETTI' and MILLER'S results because the lower termites may easily differentiate supplementary reproductives when the royal pair is absent. So in the controls of *Kalotermes* and *Prorhinotermes*, there is a bias against soldier differentiation. For instance, in *P. simplex*, 9.5 % of the soldiers were produced in 200 pseudergates reared with a royal pair, and only 3 % in orphan groups. However, in the latter case, 14.5 % of the pseudergates differentiated to supplementary reproductives. Moreover, in the study on *Kalotermes*, mol-

ting specimens were removed from their group until the depletion of the group, a condition which suppresses the social regulation and emphasizes the bias previously noted.

Our study shows that, in *N. lujae,* the queen and king have similar stimulatory effects on the differentiation of the workers into soldiers. Such is not the case in *K. flavicollis* where the king is much less efficient than the queen.

2. Variations in solder production

In *N. lujae,* soldier production varies greatly with the nests. Under our experimental conditions, this production depended on the competence of the small workers and on the stimulatory power of the reproductives. The soldier's inhibitory action is also a regulating factor, but as the first soldiers do not appear until after 3 weeks of rearing, this factor cannot significantly intervene in our tests.

The competence of the workers in the soldier differentiation is observed in control groups in which the workers are free from the stimulatory or inhibitory influences possibly exerted by the other castes. In these controls, for any given nest, soldier production did not vary greatly, indicating intracolony homogeneity. In contrast, there is a great intercolony variation as control soldier production between different nests may vary from 8 to 27 % after 30 days of rearing. It is known that the competence of the individuals in the soldier differentiation varies within the instar. According to the species, the individuals are more competent at the beginning of the instar (*Macrotermes,* OKOT-KOTBER, 1982) or at the end of the instar (*Kalotermes,* SPRINGHETTI, 1972 ; *Zootermopsis,* LUSCHER, 1974). At the time of experimentation, the small worker populations of *N. lujae* can be of different ages according to the social environment and therefore can provide fewer or more soldiers. In this species, worker competence in soldier differentiation seems to increase with age since the small workers reared at the time of the opening of the nest produce fewer soldiers than the small workers from the same nest inhibited by soldiers for several months before rearing (LEFEUVE and BORDEREAU, 1984).

The stimulatory influence of the queen and the king also varies extensively between the different nests. This does not appear to be related to the variations of small worker competence. The more pronounced stimulatory actions were observed in small worker populations which produced a moderate number of soldiers in controls.

As for these variations concerning either the worker competence or the stimulatory influence of the reproductives, we were unable to detect any relationship with a seasonal cycle. However, because of the small sample size this should not be interpreted as conclusive evidence that these variations do not occur.

3. Nature of the stimulatory action of the reproductives

The stimulatory action of the royal pair on soldier differentiation was suggested to be pheromonal in nature by several authors, but no proof has been given until now. It is known that the juvenile hormone (JH), the hormone of the corpora allata, is highly involved in termite soldier differentiation (LUSCHER, 1974 ; NIJHOUT and WHEELER, 1982). Considering this preponderant role of JH, LUSCHER (1975) suggested that the reproductives would induce soldier formation via a primer pheromone activating the corpora allata, and OKOT-KOTBER (1980) claimed that this allatotrope pheromone must act during the competence period.

In *N. lujae,* it is clear that weakly competent individuals which would be inhibited by the first produced soldiers and maintained as small workers in controls, were induced to molt by the reproductives, So the royal pair does not only influence the nature of the molt of the individuals which are just about to molt, but also triggers the molts. This suggests that the action of the reproductives on the small workers may be prothoracicotropic as well as allatotropic. Since the JH prothoracicotropic action, known in many insects, has also been observed in termites (WANYONYI, 1974 ; OKOT-KOTBER, 1985), the assumed action of the reproductives on prothoracic glands might be carried out through the mediation of the corpora allata.

Finally, it should be recalled that the first LUSCHER hypothesis (1972), taken up by MYLES and CHANG (1984), was that JH itself could act as a primer pheromone. In this context, we can say that JH analogues can mimic the action of the reproductives in *N. lujae* and therefore have a prothoracicotropic effect (BORDEREAU, to be published). However, new experimentation is necessary to determine whether haemolymphatic JH of the reproductives (LANZREIN *et al.*, 1985) are actually partially excreted and distributed among the colony.

It has recently been demonstrated in *Nasutitermes lujae* that the soldier caste was regulated by a primer pheromone from the soldier frontal gland (LEFEUVE and BORDEREAU, 1984). With the new results brought to light in this report on *Nasutitermes lujae* and *Cubitermes fungifaber,* it is now possible to assert that the soldier proportions result from the balance between the stimulatory action of the reproductives and the inhibitory action of the soldiers.

The regulatory mechanisms of the soldier caste are very probably pheromonal in nature. However, only the soldier inhibitory pheromone had been evidenced until now. Our investigation points again to the homeostasis of the termite society and shows that the role of the king in this phenomenon has certainly been too much neglected in the past. The variations in the soldier proportions probably express the adaptation of the colonies to the environment for the best reproduction of the species.

In this context, we can say that the worker origin of the soldiers, present in many species, is highly advantageous since the regulation of this improductive soldier caste occurs in active individuals which are able to participate in the growth of the society until their transformation into soldiers. The energetic resources of the colonies can therefore be used to greatest avantage for the reproduction of the species.

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References

CASTLE G.B., 1934. — The damp-wood termites of the Western United States, genus *Zootermopsis* (formerly, *Termopsis*). In C.A. KOFOID *et al., Termites and Termite Control,* 2nd rev. ed., pp. 273-310. Univ. of Calif. Press, Berkeley.

GRASSE P.-P., 1982. — *Termitologia. I, Anatomie, Physiologie, Reproduction des Termites Masson ed.,* Paris, 676 p.

GRASSE P.-P., NOIROT Ch., 1955. — La fondation de nouvelles sociétés par *Bellicositermes natalensis* Hav. *Ins. Soc.,* 2, 213-220.

HAVERTY M.I., HOWARD R.W., 1981. — Production of soldiers and maintenance of soldier proportions by laboratory experimental groups of *Reticulitermes flavipes* (Kollar) and *Reticulitermes virginicus* (Banks) (Isoptera : Rhinotermitidae). *Ins. Soc., 28,* 32-39.

HOWARD R.W. 1983. — Effects of methoprene on binary caste groups of *Reticulitermes flavipes* (Kollar) (Isoptera, Rhinotermitidae). *Environ. Entomol., 12,* 1059-1063.

LANZREIN B., GENTINETTA V., FEHR R., 1985. — Titres of juvenile hormone and ecdysteroids in reproductives and eggs of *Macrotermes michaelseni :* Relation to caste determination. In *Social Insects.* WATSON J.A.L., OKOT-KOTBER B.M., NOIROT Ch. Eds., Pergamon Press, Oxford, pp. 307-327.

LEFEUVE P., BORDEREAU C., 1984. — Soldier formation regulated by a primer pheromone from the soldier frontal gland in a higher termite *Nasutitermes lujae. Proc. Natl. Acad. Sci. USA, 81,* 7665-7668.

LIGHT S.F., WEESNER M.F., 1955. — The production and replacement of soldiers in incipient colonies of *Reticulitermes hesperus* (Banks). *Ins. Soc., 2,* 347-354.

LUSCHER M., 1972. — Environmental control of juvenile hormone (JH) secretion and caste differentiation in Termites. *Gen. comp. Endocr., Suppl., 3,* 509-514.

LUSCHER M., 1973. — The influence of the composition of experimental groups on caste development in *Zootermopsis* (Isoptera). *Proc. VII Cong. IUSSI,* London, 253-256.

LUSCHER M., 1974. — Kasten und Kastendifferenzierung bei niederen Termiten. In *Sozialpolymorphismus bei Insekten,* SCHMIDT G.H., ed, Wissenschaftliche Verlagsgesellschaft MBH, Stuttgart, 694-739.

LUSCHER M., 1975. — Pheromones and polymorphism in bees and termites. In *Pheromones and Defensive Secretions in Social Insects,* NOIROT Ch., HOWSE P.E., LEMASNE G., eds., *Proc. Symp. IUSSI,* Dijon, pp. 123-141.

MILLER E.M., 1942. — The problem of castes and caste differentiation in *Prorhinotermes simplex* Hagen. *Bull. Univ. Miami, 15,* 3-27.

MYLES T.G., CHANG F., 1984. — The caste system and caste mechanisms of *Neotermes connexus* (Isoptera : Kalotermitidae). *Sociobiol., 9,* 163-321.

NAGIN R., 1972. — Caste determination in *Neotermes jouteli* (Banks). *Ins. Soc., 19,* 39-61.

NIJHOUT H.F., WHEELER D.E., 1982. — Juvenile hormone and the physiological basis of insect polymorphismus. *Quat. Rev. Biol., 57,* 109-133.

NOIROT Ch., 1955. — Recherches sur le polymorphisme des Termites supérieurs (Termitidae). *Ann. Sc. Nat. Zool., 17,* 400-595.

OKOT-KOTBER B.M., 1980. — Competence of *Macrotermes michaelseni* (Isoptera, Macrotermitinae) larvae to differentiate into soldiers under the influence of juvenile hormone analogue (ZR-515, methoprene). *J. Ins. Physiol., 26,* 655-659.

OKOT-KOTBER B.M., 1982. — Correlation between larval weights, endocrine gland activities and competence period during differentiation of workers and soldiers in *Macrotermes michaelseni* (Isoptera, Termitidae). *J. Ins. Physiol., 28,* 905-910.

OKOT-KOTBER B.M., 1985. — Mechanisms of caste determination in a higher termite, *Macrotermes michaelseni* ,Isoptera, Macrotermitinae). In Caste Differentiation in Social Insects, WATSON J.A.L., OKOT-KOTBER B.M., NOIROT Ch. eds., Pergamon Press, Oxford, pp. 268-306.

OSTER G.F., WILSON E.O., 1978. — Caste and ecology in the social insects. Monographs in population biology. (Princeton University Press, Princeton, NJ), vol. 12, 352 p.

RENOUX J., 1975. — Le polymorphisme de *Schedorhinotermes lamanianus* (Sjostedt) (Isoptera - Rhinotermitidae). *Ins. Soc., 21,* 35-44.

SPRINGHETTI A., 1969. — Influenza dei reali sulla differenziazione dei soldati di *Kalotermes flavicollis* Fabr. *Proc. VI Cong., IUSSI,* Bern, 267-273.

SPRINGHETTI A., 1970. — Influence of the king and queen on the differentiation of soldiers in *Kalotermes flavicollis Fabr. Monitore Zool. Ital.* (N.S.), *4,* 99-105.

SPRINGHETTI A. 1972. — The competence of *Kalotermes flavicollis* pseudergates to differentiate into soldiers. *Monitore Zool. Ital.* (N.S.), *6,* 97-111.

WANYONYI K., 1974. — The influence of the juvenile analogue ZR-515 (Zoecon) on caste development in *Zootermopsis nevadensis* (Hagen) (Isoptera). *Ins. Soc., 21,* 35-44.