Insectes Sociaux, Paris
1984, Volume 31, n° 4, pp. 403-407

COLONY EFFICIENCY AND THE REPRODUCTIVITY EFFECT IN *LEPTOTHORAX ALLARDYCEI* (MANN)

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Reçu le 25 mai 1983. Accepté le 13 juillet 1984.

SUMMARY

The composition of colonies of *Leptothorax allardycei* (Mann) is examined. The number of total brood increases linearly with the number of workers in the colony. There is no evidence of the reproductivity effect in *L. allardycei*. The relative efficiency of colonies remains constant with increases in colony size. The implications for colony size are briefly discussed.

RESUME

Efficacité de la colonie et effet reproductif chez Leptothorax allardycei **(Mann)**

La composition des colonies de *Leptothorax allardycei* (Mann) est étudiée. L'importance numérique du couvain augmente linéairement avec le nombre d'ouvrières dans la colonie. Il n'y a pas de preuve d'un " reproductivity effect " chez cette espèce. Le rendement des colonies reste constant malgré l'augmentation de la population. Les conséquences pour la croissance de la colonie sont brièvement analysées.

INTRODUCTION

The manner in which the relative efficiency of colonies of social insects varies with colony size has a bearing on the evolution of insect societies. In bees there is information available on a variety of species (MICHENER, 1964, 1974). In these species a general pattern has emerged. Most species attain their highest efficiency (as measured by the production of immature stages per worker) at small colony sizes. The pattern of declining *per capita* production with increasing colony size has been termed the " reproductivity effect " (WILSON, 1971, 1974).

Among ants there is scanty information on colony size of species and the relation between colony size and the composition of the brood. Despite the importance of this information, the problems associated with obtaining reliable colony size data and brood data on soil nesting ants are difficult to overcome. For arboreal ants that nest in hollow twigs, such data are more easily obtained.

MATERIALS AND METHODS

Colonies of *L. allardycei* were collected from Sugar Loaf Key, Florida from 8-11 November 1979 and from 31 July to 7 September 1981. *Leptothorax allardycei* nests in hollow sawgrass *(Cladium jamaicense)* culms. Entire colonies were housed in plastic containers (COLE, 1980). An outline of the social behavior of *L. allardycei* is to be found in COLE (1981). The colony was allowed to move into observation nests constructed of two microscope slides held apart by a cardboard partition. The number of workers and brood was then counted under a dissecting microscope. The numbers of eggs, larvae and pupae were recorded. Prepupae, after the expulsion of the meconium, are included as pupae in the following presentation.

RESULTS

The number of brood in a colony was linearly related to colony size in both 1979 and 1981. In 1979 the relation between the number of brood (B) and the size of the colony (W), was $B = 0.61\ W + 7.65$ ($n = 12$, $r^2 = 0{,}52$, $p < 0.01$). In 1981 (see *fig. 1)*, the relation was $B = 1.15\ W + 7.74$ ($n = 28$, $r^2 = 0{,}74$, $p < 0.001$). Analysis of covariance shows that the relationship between the number of brood and the number of workers was different in 1979 and 1981 ($F_{1,37} = 12.29$, $p < 0.005$). In 1981 the relation between the number of workers and the number of each category of brood was calculated. For eggs the relation was $E = 0.22\ W + 1.06$ ($r^2 = 0.62$, $p < 0.001$). For larvae the relation to the number of workers was $L = 0.59\ W + 10.0$ ($r^2 = 0.47$, $p < 0.001$). For pupae the relation to colony size was $P = 0.29\ W + 1.14$ ($r^2 = 0.47$, $p < 0.001$).

A fraction of the colonies of *L. allardycei* are queenless. Unless the queenless colonies have 15 or more workers, they do not have any brood associated with them. In 1979, 7 of 21 (33 %) total colonies with more than 15 workers were queenless. In 1981, 2 of 41 total colonies (5 %) with more than 15 workers were queenless. This difference in the fraction of queenless colonies is statistically significant (percentage test, $t = 2.93$, $p < 0.01$).

DISCUSSION

Reproductivity is a term that refers to some measure of the production of immature stages (MICHENER, 1964). It has been used to refer to the numbers

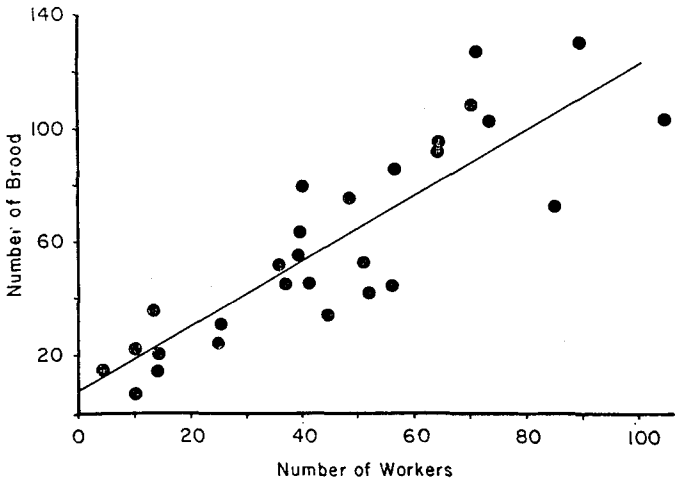

Fig. 1. — The relationship between total number of brood in *Leptothorax allardycei* colonies and the number of workers in the colony. The relationship is: (No. of brood) = 1.15 × (No. of workers) + 7.74 (r^2 = 0.74, p < 0.001).

Fig. 1. — Relation entre le nombre total de couvain chez *Leptothorax allardycei* et le nombre d'ouvrières. La relation est: (Quantité de couvain) = 1,15 × (Quantité d'ouvrières) + 7,74 (r^2 = 0,74, p < 0,001).

of a particular immature stage, the total weight of an immature stage or increase in weight of a given immature stage. In this paper, I refer to the reproductivity of *L. allardycei* as the total number of pieces of brood of a colony.

The significance of reproductivity is that it provides some indication of the ability of a colony to produce sexual forms. MICHENER (1964) shows that the relationship between colony size and reproductivity is similar to the relation between colony size and the number of sexuals produced. The reduction in reproductivity per worker with increasing size of a social insect colony has been called the " reproductivity effect ". MICHENER (1974) points out that while certain bees, e.g. *Bombus, Pseudagapostemon* (MICHENER, 1964), and *Braunapis* (MICHENER, 1971) do not show the reproductivity effect, it is generally true for a wide variety of social insects. MICHENER (1964) showed such a relationship in *Lasioglossum rhytidophorum, L. imitatum, Polybia bistriata, P. bicyttarella, Apis mellifera* and *Myrmica rubra* (for some quantities).

The reproductivity effect can also be produced, in principle, if there is a linear relationship between colony size and reproductivity. The only requirement, as MICHENER (1964) has pointed out, is that the y = intercept of the regression be positive (thus if the relation between reproductivity, *R*, and

colony size, W, is $R = mW + b$, then $R/W = m + B/W$). If b is positive the reproductivity per worker will asymptotically decline from $m + b$ to the slope of the line.

In *L. allardycei* the relationship between reproductivity and colony size is linear with slopes of 0.61 (1979) and 1.15 (1981). This difference is likely due to seasonal variability in colony size. In both cases the y-intercept of the relation between colony size and reproductivity is positive. Thus, in principle, one obtains a declining relationship between reproductivity per worker and colony size.

However there is a concommittant effect which more convincingly suggests that reproductivity is independent of colony size. *Figure 2* shows the reproductivity per worker as a function of the number of workers. The overall average number of pieces of brood per worker is 1.32. The 95 % confidence limits on this ratio are plotted in *figure 2*. When the number of workers and brood is large the confidence limits are fairly narrow, but as the size of the colony declines below 20 workers the confidence limits broaden markedly. Because the ratio is bounded below by zero but unbounded above, the upper confidence limit seems to increase more than the lower confidence limit.

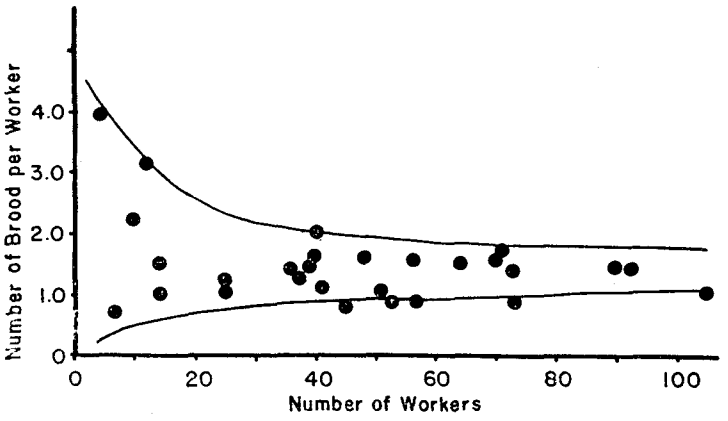

Fig. 2. — The relationship between the total number of brood per worker and the colony size. The mean number of brood per worker is 1.32. The lines represent the 95 % confidence limits on this ratio. Most points lie within the confidence limits of a constant ratio of brood per worker.

Fig. 2. — Relation entre la quantité totale de couvain par ouvrière et la taille de la colonie. La quantité moyenne de couvain par ouvrière est 1,32. Les lignes représentent la limite de confiance de 95 % sur ce ratio. De nombreux points se situent à l'intérieur des limites de confiance d'un ratio constant de couvain par ouvrière.

Thus it is not enough to note that the reproductivity per worker seems to take an upward turn at small colony size. Such a relationship is to be expected simply as a result of ratios in small samples.

As the large majority of points lie within the 95 % confidence limits, there is little question that there is no reproductivity effect in *L. allardycei.* In *Leptothorax curvispinosus* (WILSON, 1974) the number of larvae per worker and the number of eggs per worker both clearly decline as a function ot the total number of workers. However, the individual values lie almost entirely within the confidence limits of a constant ratio of .38 eggs per worker and .8 larvae per worker.

The significance of the reproductivity effect is that declining efficiency has implications for the evolution of both colony size and sociality. If smaller colonies are more efficient at reproduction, there should be selection for smaller colonies. In addition, as colonies become larger, it may become advantageous for a group of workers to leave a eusocial colony and reproduce on their own.

Opposing these selective pressures may be increased survivorship among larger colonies (WILSON, 1974). If larger colonies are less subject to predation or have a higher degree of internal homeostasis, they may have higher probability of surviving to reproduce. Because there is no reproductivity effect in *L. allardycei,* the workers ought to be indifferent to colony size, provided colony size does not correlate with survivorship.

The evolution of eusociality may be promoted by the reproductivity effect because it is evidence for a disproportionately large payoff to workers that stay with the queen and help produce her offspring. This may be significant in promitive eusociality. In advanced eusocial species the evolutionary options are not so straightforward. The option of reproducing on one's own is not usually viable for a worker of an advanced eusocial species. Thus the lack of evidence of a reproductivity effect in *L. allardycei* may suggest that colony size is limited by extrinsic factors such as nest site or interactions with other species of sawgrass inhabiting ants (COLE, 1982).

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