

## Production in the ant *Leptothorax unifasciatus* (Hymenoptera, Formicidae)

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### Abstract

The methods used so far for estimating production in ant societies are inadequate because elimination (notably mortality) is hardly taken into account if at all. We present a new method, and apply it to laboratory societies of the ant *Leptothorax unifasciatus* (Latreille). Production was studied at two levels of integration, those of the individual and the society, which differ in the part of biomass which is recycled or eliminated. Growing societies reared in the laboratory under fluctuating conditions were used for estimating brood production during an annual cycle. All individuals were counted and measured every two weeks. Larval survival was estimated from artificial cohorts. By means of a population dynamical model, the larval population was divided into three subpopulations, comparable to cohorts, the production of which was estimated by the classical "growth increment summation" method. Total larval survival was generally high (83%), but there was a high mortality in the prepupal and pupal stages so that the overall survival from egg to imago reached 65%. Losses of biomass during metamorphosis amounted to 19% of brood production. Recycled biomass and elimination represented 2% and 41%, respectively, of the production at the society level. This suggests that the supposed social advantage of recycling is virtually absent and that neglecting elimination can lead to an underestimation of production by a factor of 1.7.

**Keywords:** Individual production, society production, population dynamics, survival  
*Leptothorax unifasciatus*.

### Résumé

Les méthodes d'estimation de la production de sociétés de fourmis utilisées jusqu'à présent sont, la plupart du temps, inadéquates parce que l'élimination (notamment la mortalité) est rarement, ou pas du tout, prise en compte. Nous présentons une nouvelle méthode et l'appliquons à des sociétés de *Leptothorax unifasciatus* (Latreille) élevées en laboratoire. La production a été étudiée à deux niveaux d'intégration, soit le niveau individuel et le niveau de la société, lesquels diffèrent l'un de l'autre par la fraction de biomasse qui est recyclée ou éliminée. Des sociétés en phase de croissance, élevées au laboratoire dans des conditions semi-naturelles, ont été utilisées pour l'estimation de la production du couvain pendant un cycle annuel. Tous les individus ont été

comptés et mesurés toutes les deux semaines. La survie larvaire a été estimée à partir de cohortes artificielles. Grâce à un modèle de dynamique de population, la population larvaire a été divisée en trois sous-populations, comparables à des cohortes, dont la production a été estimée par la méthode classique de « la sommation de l'accroissement ». La survie totale larvaire s'est avérée généralement élevée (83 %), mais, en raison d'une forte mortalité dans les stades prénymphes et nymphes, la mortalité totale, depuis l'œuf jusqu'à l'imago, est réduite à 65 %. Les pertes en biomasse durant la métamorphose atteignent 19 % de la production du couvain. La biomasse recyclée et l'élimination représentent, respectivement, 2 % et 41 % de la production au niveau de la société. Ces éléments suggèrent que l'avantage social supposé du recyclage est virtuellement nul et que ne pas tenir compte de l'élimination peut mener à une sous-estimation de la production d'un facteur 1,7.

## 1. INTRODUCTION

This work originated in the assessment of an energy budget of the ant *Leptothorax unifasciatus* (Latreille) (MARTIN, 1990). Production is a very important parameter of an energy budget and enters into the calculation of various efficiency ratios allowing the comparison between species.

For a long time, production was assumed to be easy to estimate, given the "well defined" closed system of a nest (MACKAY, 1985). For the sake of convenience, an ant society was regarded as a superorganism, and production was considered to be the sum of new-born workers and sexuals (GOLLEY & GENTRY, 1964; JENSEN, 1977, 1978a; HORSTMANN, 1982; MACKAY, 1985).

A better and generally accepted definition of production is the biomass accumulated by a population per time unit (RIGLER & DOWNING, 1984). Thus production is the increment of biomass ( $\Delta B$ ) plus the materials secreted or lost in other ways than by respiration, i.e. elimination ( $\varepsilon$ ) (MACFADYEN, 1967; PETRUSEWICZ & MACFADYEN, 1970; SOUTHWOOD, 1978):

$$(1) \quad P = \Delta B + \varepsilon$$

Surprisingly enough, that part of production which is eliminated and not consumed by members of an ant society has been taken into account only partly if at all and in diverse ways. This seriously hampered discussions on energetics of ant societies in the past.

Moreover, the production of an ant society can be studied both at the individual level (*ind*) and at the society level (*soc*) and elimination has a different meaning at the two levels. In a society, a part of the biomass is recycled instead of being eliminated. This part ( $\varepsilon_{\text{rec}}$ ) must be taken into account at the individual level, but may be considered as part of the internal metabolism and can therefore be neglected at the society level. Thus

$$(2) \quad \varepsilon_{\text{rec}} = \varepsilon_{\text{ind}} - \varepsilon_{\text{soc}}$$

Therefore the difference between  $\varepsilon_{\text{ind}}$  and  $\varepsilon_{\text{soc}}$ , i.e. the recycling of energy by material-turnover otherwise lost in a solitary life, can be considered as a substantial advantage offered by social life.

In this paper we investigate annual production in the ant *L. unifasciatus* which takes elimination into account. A new method of estimating production in ant societies is presented and used. Production is estimated at both the individual and the society levels. This enables us to quantify  $\epsilon_{\text{rec}}$  and  $\epsilon_{\text{soc}}$  and thus (1) to assess the importance of the social advantage of recycling ( $\epsilon_{\text{rec}}$ ) and (2) to evaluate, at the society level, the magnitude of the error made in estimating production when eliminated biomass ( $\epsilon_{\text{soc}}$ ) is neglected.

## 2. LIFE CYCLE AND ELEMENTS OF PRODUCTION OF *L. UNIFASCIATUS*

### 2.1. Life cycle

*L. unifasciatus* is a Central-European xerophilic species (GASPAR, 1971a, b). In Belgium, it lives in rather dry and sunny to semishaded areas. It forms small monogynous societies (about 500 workers when mature) which generally nest in rocky places, between schist flakes or stones. Its period of biological activity is interrupted by a hibernation from early November to late April (MARTIN, 1988, 1990), when brood consists mainly of small larvae and some eggs. Larval growth starts again at the end of hibernation and results in the appearance of the first prepupae and pupae in early June and of the first emerging workers in early July in the laboratory. It decreases from mid-August onwards and is even arrested in the largest larvae at that time (MARTIN, 1988). From mid-September onwards, the society announces the onset of hibernation in various ways: a decrease in the number of eggs, reduced alimentary rates, grouping of the society, progressive closing of the entrance and general decrease of activity.

### 2.2. Production at the individual level or gross production

Four individual categories, with various terms of production for each of them, should be considered:

a) queen: there is only one queen and her main production, egg-laying, will be incorporated into brood production;

b) brood: egg-laying by the queen, larval growth (including mortality), and products given to workers in stomodeal and proctodeal exchanges (LE MASNE, 1953; BRIAN, 1983; HÖLLDOBLER & WILSON, 1990);

c) workers: imaginal growth, pheromones, venom, nutrients delivered to larvae by means of trophic eggs (BRIAN, 1983; PASSERA, 1984; HÖLLDOBLER & WILSON, 1990) or post-pharyngeal gland secretions and trophallaxis (DELAGE-DARCHEN, 1976);

d) sexuals: fattening of female alates before their nuptial flight; this does not happen in male sexuals (MARTIN, 1990, 1992).

Depending on the ant species and the society's age, these four individual categories participate to various extents in the global production. In the case of growing laboratory societies of *L. unifasciatus*, brood production should play the most important role.

Stomodeal and proctodeal exchanges of larvae with workers have been observed within societies of *L. unifasciatus* (MARTIN, 1990). Collecting this fluid is virtually impossible in practice and was not done in this study. However, from the results of OHLY-WÜST (1977, in HÖLLDOBLER & WILSON, 1990), who studied these

exchanges in great detail in *Myrmica rubra* L., it appears that the contribution of these discharges might be important.

Imaginal growth is most probably zero with regard to increase in size (NIELSEN & JOSENS, 1972). But there is some growth of fat bodies, ovaries and glands in the young worker. Practically, this production does not accumulate and results in trophic eggs and nutritive secretions for first-instar larvae (BRIAN, 1983; HÖLLDOBLER & WILSON, 1990). Once again, it is very difficult to estimate this production, which is almost instantaneously consumed by larvae or workers (HÖLLDOBLER & WILSON, 1990; MARTIN, 1990). While imaginal growth can be significant, as shown in *Formica polyctena* Förster (HORSTMANN, 1982), in *L. unifasciatus* the difference in energy between emerging and older workers is very small (MARTIN, 1992). Moreover, laying of trophic eggs was seldom observed in our rearings.

Nothing is known about quantitative production of pheromones and venom (NIELSEN & JOSENS, 1972). For an ant society, these products virtually escape analysis.

Finally, the fattening of young queens before their nuptial flight is non-existent here because our growing societies did not produce any female alate during this study, although they did produce some males.

Thus in practice, only brood production (including reproductive eggs) can be estimated at the individual level. Even if this is an underestimation of gross production, it still merits a comparison with the net production.

Larval production, including elimination, would be easy to measure if cohorts could be recognized (RIGLER & DOWNING, 1984). This is not the case in most ant species. It is, however, possible to assess larval production, including elimination, provided that age classes or stages can be distinguished. Knowing the weight increment in each age class and the number of individuals passing through that age class, it is possible to sum up production for the whole larval life (WINBERG *et al.*, 1971; NIELSEN & JOSENS, 1972). This calculation was used by JOSENS (1973, 1982) for estimating termite production.

In our *L. unifasciatus* societies, egg-laying by the queen was more or less continuous during her biological activity period. As a result, the larval population could not be split into cohorts. In order to recognize age classes within the larvae, we designated three societies (L4, L5 and L6) with artificially created cohorts. Unfortunately the speed of larval growth in artificial cohorts and in other societies proved to be different. Therefore the Winberg method was not applicable in our case and we had to design another method, which is presented below.

### 2.3. Production at the society level or net production

As mentioned in the introduction, this level essentially differs from the previous one by the fact that part of the eliminated biomass is consumed and not lost. From gross production, we shall distinguish (a) the biomass totally recycled (trophic eggs, nutritive secretions, stomodeal and proctodeal trophallaxis by larvae), (b) the biomass partially recycled (dead workers, reproductive eggs, larvae, pupae and some sexuals partially eaten dead or alive, organism's tissues reserves) and (c) the biomass definitely lost (pheromones, venom, exuviae, swarming sexuals).

By definition, recycled biomass must not be taken into account at the society level, being part of the internal metabolism of the society. The most difficult problem arises from the biomass partially recycled and partially lost for good.

But in our laboratory societies, which were fed to satiety, consumption of male sexuals and dead or alive larvae was never observed; these accumulated among nest refuses. Only a few reproductive eggs were partially eaten.

Therefore, since dead biomass is definitely lost and partial recycling limited to reproductive eggs, production at the society level is well defined. It is restricted to the annual increase in the society biomass plus larval and adult mortality plus swarming sexuals. All of them are quantifiable.

### 3. MATERIAL AND METHODS

#### 3.1. Rearing societies in the laboratory

Seven societies (L1 to L7) of *L. unifasciatus* were reared in the laboratory under fluctuating conditions (no heating, no artificial lighting – MARTIN, 1988) throughout an annual cycle (from April 1987 to April 1988, table I). Each society was cultured in a plaster nest (8 × 7 × 2 cm) adapted from JANET (1893). A single darkened room (5 × 3 × 0.2 cm) was connected through a tunnel (0.3 cm in diameter) with a foraging tray 24 × 35 × 3 cm. The societies were fed to satiety with *Drosophila* flies and a 0.3 M sucrose solution enriched with vitamins (Alvityl Plus, Triosol S.A., Brussels). Such a sucrose concentration was shown to be optimal for rearing *Myrmica* (BRIAN, 1973).

TABLE I. – Size (number of individuals) and composition of the experimental societies.

Society	Date	Eggs	Larvae	Workers	Queen
L1	13 Apr 87	3	219	89	
	16 Apr 88	1	296	212	
L2	13 Apr 87	7	520	167	
	16 Apr 88	1	514	327	
L3	14 Apr 87	1	291	158	
	16 Apr 88	1	398	252	
L4	21 Apr 87	23	262	278	
L5	21 Apr 87	20	214	140	
L6	21 Apr 87	4	44	34	
L7	14 Aug 87	0	262	307	

In three societies (L1, L2 and L3), workers, eggs and larvae were counted and the brood was photographed (black and white film, Ilford Pan F 50 ISO; scale 1:1) twice a month while CO<sub>2</sub> anaesthetized. This procedure did not seem to have any deleterious effect: the number of workers in each society approximately doubled after one year, just as in the following years, when these manipulations were no longer performed (MARTIN, 1990). It allowed us to shorten the handling and to measure larval sizes later on the negatives.

In three other societies (L4, L5 and L6), we created artificial cohorts. We first eliminated all the eggs and small larvae at a given time, leaving only some large larvae in the nests. We then allowed eggs to accumulate, and 15 days after the first larval hatching all the remaining eggs were removed. This installed the first cohort. Subsequently laid eggs were eliminated until the larvae of the first cohort were big enough to allow the development of a second cohort. These three societies were handled in the same way as the first three ones and allowed us to assess larval survivorship curves.

The seventh society (L7) was reared to assess the relation between larval size and weight.

### 3.2. Reproductive eggs and brood production

#### 3.2.1. Principle

The total amount of production that we shall measure ( $P_T$ ) is the sum of reproductive egg-laying ( $P_E$ ) and larval growth until prepupation ( $P_L$ ), when larvae have achieved their maximal energy content:

$$(3) \quad P_T = P_E + P_L$$

Given our fortnightly censuses we shall consider that larval production is itself the sum of three terms: (a) production by the larvae that hatched since the last census, 14 days before ( $P_{LE}$ ), (b) production by the larvae that remained at the larval stage since the last census ( $P_{LL}$ ), and (c) production by the larvae that started prepupation since the last census ( $P_{PL}$ ):

$$(4) \quad P_L = P_{LE} + P_{LL} + P_{PL}$$

Provided these three subpopulations can be distinguished, their production is easy to estimate because they may be considered as cohorts. During each time interval from  $t$  to  $t + 1$ , production of any cohort can be calculated by:

$$(5) \quad P = N(t, t + 1) [m(t + 1) - m(t)]$$

where  $N(t, t + 1)$  is the average number of individuals in the cohort between times  $t$  and  $t + 1$  and  $m(t)$  and  $m(t + 1)$  are the mean individual body masses at times  $t$  and  $t + 1$  (RIGLER & DOWNING, 1984).

Brood mortality, or elimination ( $\varepsilon_{ind}$ ), is equal to the number of individuals that died between  $t$  and  $t + 1$  with a mean body mass  $m(t, t + 1)$  (WINBERG *et al.*, 1971):

$$(6) \quad = [N(t + 1) - N(t)] m(t)$$

where  $N(t)$  and  $N(t + 1)$  are the number of individuals at times  $t$  and  $t + 1$ .

But how can  $N(t, t + 1)$  and  $m(t, t + 1)$  be estimated for each subpopulation? The census of an ant population provides only the numbers of individuals in the various stages, but not the sizes of the subpopulations as required for the estimation of production or mortality, which depend on the population dynamics.

#### 3.2.2. Estimation of mean numbers of individuals in the subpopulations

Population dynamics between two censuses at times  $t$  and  $t + 1$  may be described by the matrix model:

$$(7) \quad \begin{pmatrix} E(t+1) \\ L(t+1) \\ P(t+1) \end{pmatrix} = \begin{pmatrix} S_{EE}(t)q_E(t) & 0 & 0 \\ S_{LE}(t)[1-q_E(t)] & S_{LL}(t)q_L(t) & 0 \\ 0 & S_{PL}(t)[1-q_L(t)] & S_{PP}(t) \end{pmatrix} \begin{pmatrix} E(t) \\ L(t) \\ P(t) \end{pmatrix} + \begin{pmatrix} F(t) \\ 0 \\ 0 \end{pmatrix}$$

or, more compactly:

$$(8) \quad \bar{N}(t+1) = \bar{T}(t) \bar{N}(t) + \bar{F}(t)$$

$\bar{N}(t)$  is the population vector whose elements are the numbers of individuals in the various stages at time  $t$ : eggs ( $E$ ), larvae ( $L$ ) and prepupae plus pupae ( $P$ );  $\bar{F}(t)$  is the fecundity vector, where  $F(t)$  is the number of eggs laid between times  $t$  and  $t + 1$ ; and  $\bar{T}(t)$  is the matrix describing the transitions of

individuals between stages from time  $t$  to  $t + 1$ , where  $q_I(t)$  is the proportion of individuals in stage  $I$  at time  $t$  that are destined to remain in that stage until time  $t + 1$ , and  $s_{IJ}(t)$  is the survival rate associated with the transition from stage  $J$  at time  $t$  to stage  $I$  at time  $t + 1$ .

In model (7),  $E(t)$ ,  $L(t)$  and  $P(t)$  are known (they were measured every two weeks);  $s_{LL}(t)$  was measured in societies L4, L5 and L6 (with artificial cohorts) and is assumed to be identical in societies L1, L2 and L3;  $s_{EE}(t)$  and  $s_{LE}(t)$  were determined from information in the literature (see 4.1.3.); and  $s_{PL}(t)$  and  $s_{PP}(t)$  were determined as explained below. Model (7) thus reduces to a system of three equations which can, in principle, be solved for the three unknowns  $F(t)$ ,  $q_E(t)$  and  $q_L(t)$ . Determination of the subpopulation sizes required for the estimation of production is then straightforward. Thus, for instance,  $q_L(t)L(t)$  is the size at time  $t$  of the larval subpopulation that is destined to remain at the larval stage until  $t + 1$ , while  $s_{LL}q_L(t)L(t)$  is its size at time  $t + 1$ .

Model (7) is incomplete in that it does not include the adult stage. An additional complication arises from the fact that only the overall survival rate from larvae to adults,  $s_{AL}$ , was measured in the artificial cohorts, but not its two components  $s_{PL}$ , the survival rate from the larval to the prepupal stage, and  $s_{PP}$ , the survival rate during pupal stage. In fact, the situation described by the model is the most complex one. In practice, it can often be simplified, knowing the species life cycle. Six periods can be distinguished in the annual cycle of *L. unifasciatus*.

(1) *First period (weeks 17-22): no hatching, larval growth, no prepupation*

Because there is neither egg hatching nor prepupation during this period,  $q_E(t) = q_L(t) = 1$ .  $F(t)$  is then calculated simply from the equation for  $E(t + 1)$  in (7):

$$(9) \quad F(t) = E(t + 1) - s_{EE}(t)E(t)$$

(2) *Second period (weeks 23-24): no hatching, larval growth, prepupation*

During this period,  $q_E(t) = 1$ .  $F(t)$  is calculated as above by (9), and  $q_L(t)$  is calculated from the equation for  $L(t + 1)$  in (7):

$$(10) \quad q_L(t) = L(t + 1) / [s_{LL}(t)L(t)]$$

The equation for  $P(t + 1)$  can then provide an estimate of  $s_{PL}(t)$

$$(11) \quad s_{PL}(t) = P(t + 1) / \{[1 - q_L(t)]L(t)\}$$

(3) *Third period (weeks 25-28): hatching, larval growth, prepupation, no imaginal emergence*

In this period, all three unknowns are involved, so that the survival rates  $s_{PL}(t)$  and  $s_{PP}(t)$  must be known. We assumed these to be both equal to the rate  $s_{PL}(t)$  as estimated by (11) for the previous period. We then find from the equations for  $P(t + 1)$ ,  $L(t + 1)$  and  $E(t + 1)$ , respectively:

$$(12) \quad q_L(t) = 1 - [P(t + 1) - s_{PP}(t)P(t)] / [s_{PL}(t)L(t)]$$

$$(13) \quad q_E(t) = 1 - [L(t + 1) - s_{LL}q_L(t)L(t)] / [s_{LE}E(t)]$$

$$(14) \quad F(t) = E(t + 1) - s_{EE}q_E(t)E(t)$$

(4) *Fourth period (weeks 29-32): hatching, larval growth, prepupation, imaginal emergence*

It is in this period that the situation is most complex, since new adults begin to appear. Rather than including adults in model (7), which would add more assumptions on parameter values, we solved

the problem indirectly by estimating the number of larvae,  $M(t)$ , that are destined to metamorphose during each time interval.

The total number of new adults which appeared during the entire annual cycle is known. It is deduced from the numbers of live and dead workers at each census. Dividing this total number by the overall survival rate from the end of the larval stage to imaginal emergence,  $s_{AL}$ , which is known too, we obtain the total number of larvae before prepupation over a whole year. It is possible to calculate the numbers of larvae destined to metamorphosis,  $M(t)$ , during the second and third periods:

$$(15) \quad M(t) = [1 - q_L(t)] L(t)$$

where  $t$  refers to either the second or the third period.

These numbers must be subtracted from the total number of larvae before prepupation to obtain the number of larvae destined to metamorphosis during the fourth period.

Once  $M(t)$  is estimated for the fourth period, it is easy to deduce  $q_L(t)$  for this period:

$$(16) \quad q_L(t) = M(t)/L(t)$$

$q_E(t)$  and  $F(t)$  are estimated as above by equations (13) and (14).

(5) *Fifth period (weeks 33-42): hatching, larval growth, no prepupation*

During this period,  $q_L(t) = 1$ , and  $q_E(t)$  and  $F(t)$  are found as above by (13) and (14).

(6) *Sixth period (weeks 43-16): hibernation*

During this period,  $q_E(t) = q_L(t) = 1$  and  $F(t) = 0$ .

### 3.2.3. Estimation of mean individual body mass in the subpopulations

Once the size of each subpopulation is known, the total larval population at each census is divided into its three subpopulations assuming a direct relation between larval size and age. The mean individual body mass in each subpopulation is then calculated from the size histograms and the relation between body mass and length. The latter was obtained independently from a society (L7) reared especially for that purpose.

### 3.3. Conversion of dry weights into calorific equivalents

The conversion was made from calorimetric values obtained with a Phillipson microbomb calorimeter (PHILLIPSON, 1964; PETRUSEWICZ & MACFADYEN, 1970; PAINE, 1971; PRUS, 1975). This calorimeter requires at least 1 mg (dry weight) of material. Twenty-four societies were collected in the field and used, among others, for calorimetric measurements. However, the small size of the societies (30 to 591 larvae and 62 to 679 workers) and the tiny size of the individuals compelled us to group the samples for getting only one measurement for each category.

### 3.4. Body mass losses in resting stages

Knowing the total numbers and energy contents of larvae before prepupation and of new adults which appeared over a whole year, it is easy to estimate the body mass lost during metamorphosis (the problem is conceptually identical to the estimation of production). The body mass lost during hibernation was estimated by weighing a society before and after hibernation. A loss by starvation is unlikely since the societies were fed to satiety.



## 4. RESULTS AND DISCUSSION

### 4.1. Validity of the method

#### 4.1.1. Rate of larval development

As already mentioned, the rates of larval growth in artificial cohorts (societies L4, L5 and L6) and in other societies (L1, L2 and L3) proved to be different. In the societies with artificial cohorts, some of the larvae that measured 1.20 mm in April completed their development in September and some after hibernation. In the other societies, all the larvae that measured 1.20 mm in April and even in the first weeks of May became workers in September.

This means that, paradoxically, larval growth was much faster in undisturbed societies than in artificial cohorts. This is surprising because the creation of cohorts involved elimination of individuals and, consequently, should have reduced competition for food among larvae. The creation of cohorts did not involve anaesthesia by CO<sub>2</sub> during longer periods of time than in undisturbed societies, and actually fewer manipulations were required in cohort societies than in undisturbed ones. Therefore a differential effect of anaesthesia is unlikely to explain the differences in larval growth between the two types of societies. These differences were probably due to perturbations in the structure of the larval populations. As a result, the Winberg method could not be applied.

#### 4.1.2. Age-independent mortality

Our method assumes that larval mortality is independent of age. The survivorship curve of an artificial cohort (fig. 1) shows that, except for the hibernation period, mortality (as measured by the slope of the curve) was very

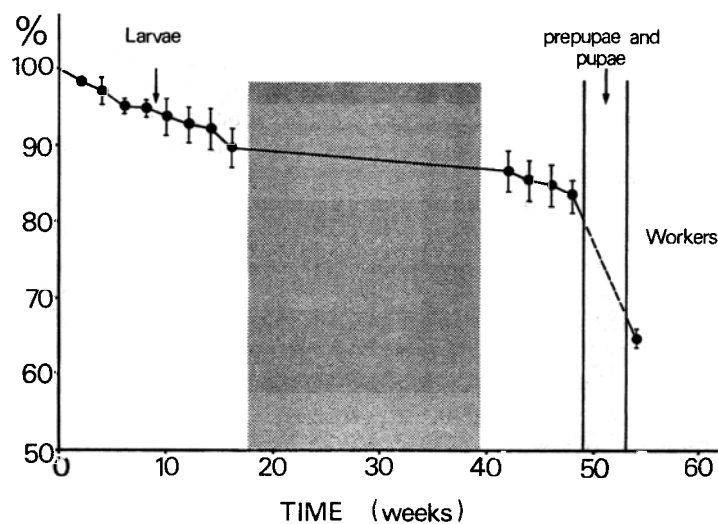


FIG. – Survivorship curve from hatching to imaginal emergence: average ( $\pm$  s.e.) of three cohorts constituted from eggs laid in spring and hibernating once as larvae (shaded area).

similar at the beginning and at the end of the larval stage. Thus the hypothesis seems valid.

#### 4.1.3. Estimation of survival rates

Our method assumes that survival rates are known independently. The survival rates of growing larvae,  $s_{LL}$ , were estimated from artificial cohorts, and were assumed to be equal to those of undisturbed societies. It is possible to calculate these rates directly for societies L1, L2 and L3 during the first period of the annual cycle. For the three fortnights of the first period, they are 98, 96 and 99% for these societies, versus 97, 99 and 99% for the artificial cohorts. The great similarity between these values makes the hypothesis acceptable.

On the other hand, artificial cohorts did not provide any information on the survival rates within the egg stage,  $s_{EE}$ , and from the egg to the larval stage,  $s_{LE}$ .

Egg survival,  $s_{EE}$ , was not measured in this study. BRIAN (1951) pointed out that *Myrmica* first-instar larvae ate a significant number of eggs. Egg survival in *Myrmica* depended on social and trophic conditions and was of the order of 50% (BRIAN, 1965). PLATEAUX (1970) made similar observations in *Leptothorax nylanderi*. Egg mortality in *L. unifasciatus* was also assumed to result essentially from egg eating in the egg cluster by newly hatched larvae before they were carried away by workers. Accordingly, egg survival was assumed to be equal to 1 before the first hatchings (first and second periods) and, according to BRIAN's figures, equal to 0.5 from the appearance of the newly hatched larvae (third to fifth periods). In the absence of information on the survival rate at hatching,  $s_{LE}$ , we estimated this as the average of egg and larval survival rates, i.e.  $s_{LE} = (s_{EE} + s_{LL})/2$ . Note that any error made in the estimation of  $s_{EE}$  and  $s_{LE}$  has a negligible effect in the estimation of production because the dry weight of an egg is less than 2% of that of a larva before prepupation (MARTIN, 1990).

## 4.2. Survivorship

Survivorship from hatching to prepupation amounted to 83.1% (fig. 1). It decreased considerably during metamorphosis, falling to 64.6% over a period of only just above one month. As the censuses were spaced out every 2 weeks, i.e. a period longer than the lifetime of prepupae (6 to 7 days), it was not possible to determine exactly at which stage mortality was at its highest. However, the number of dead pupae observed both in the laboratory and in the field suggests that mortality was highest at the pupal stage (pupal sloughing might be the most critical stage).

On the whole, our results are remarkably close to those obtained by BRIAN (1965) for *Myrmica rubra* in which 100 larvae gave 84 prepupae, 74 pupae and 66 workers. These figures also indicate that mortality was high during metamorphosis since the survival rate from prepupation to imaginal emergence was 78.6% versus 77.3% in our own results.

In fact, survival varied quite a lot among societies. Overall survival from hatching to imaginal emergence varied from 49 to 76% (table II), and this variation was mainly due to survival during metamorphosis.

Social organisation of ants is likely to allow an optimal improvement of the conditions for brood rearing. As the investment loss due to the high prepupal and pupal mortality is far from being negligible for a society, this suggests that the development of these stages is largely outside the worker's control.

TABLE II. – Survival rates from hatching to imaginal emergence ( $s_{AL}$ ) and from the end of larval growth to imaginal emergence ( $s_{AP}$ ) of larval cohorts in societies L4, L5 and L6.

Society	$s_{AL}$	$s_{AP}$
L4	76.9%	91%
L5	49.0%	60%
L6	66.9%	81%
Mean	64.3%	77%

### 4.3. Production

#### 4.3.1. At the individual level

Brood production at the individual level was estimated at 2 576, 4 844 and 2 785 Joules in societies L1 (197 prepupating larvae produced), L2 (314 prepupating larvae produced) and L3 (178 prepupating larvae produced), respectively. The mean calorific contents are quoted in table III and detailed results are given for our society L2 in table IV.

TABLE III. – Dry weight and energy content of castes and stages (from MARTIN, 1992).

	Dry weight ( $\mu\text{g}/\text{ind}$ )	Energy content (Joules/ind)	Energy content (Joules/mg)
Egg	4.9	0.13	25.9
Young third-instar larva	28.6	0.8	26.8
Worker's prepupa	294	8.2	26.3
Worker's pupa	250	7.7	30.6
Emerging worker	209	6.1	29.2
Older worker	214	5.7	26.5
Male alate's prepupa	433	11.2	25.5
Male alate's pupa	207	4.6	22.4
Emerging male alate	159	3.4	21.5

It appears from this table that the contribution of eggs to total brood production is almost negligible (about 2%). This confirms our suggestion that any error in the estimation of survival rates at the egg stage and at hatching has no consequences on the estimate of total production. It appears also that production was irregular because of various factors. The zero production of weeks 19-20 (end of April) was observed in the three societies and was related with low nocturnal temperatures ( $<12^{\circ}\text{C}$ ). The striking peak of weeks 29-30 (July) occurred only in society L2 which at that time had accumulated a high proportion of larvae of 1-1.5 mm (fig. 2), which is the size with the fastest growth.

Male sexuals were produced in small numbers: for the three societies studied, they represented 6% of all the larvae starting prepupation on average. Finally, as mentioned previously, our societies did not produce any female sexual during the study, probably because they were too young (actually they produced numerous queens in 1990, when their size reached about 500 workers).

Annual production at the individual level, when biomass losses in the resting stages were taken into account, was estimated at 1 770, 3 505 and 1 894 Joules in societies L1, L2 and L3, respectively (table V). Thus respiration on average dissipated 19% of brood production during metamorphosis.

TABLE IV. – Production in Joules per fortnight of society L2. Production of eggs ( $P_E$ ), hatching larvae ( $P_{LE}$ ), growing larvae ( $P_{LL}$ ), prepupating larvae ( $P_{PL}$ ) and total brood production ( $P_T$ ). Data were lacking for the fortnight 25-26; the overall values obtained for the weeks 25-28 were shared out between the two fortnights.

Weeks	$P_E$	$P_{LE}$	$P_{LL}$	$P_{PL}$	$P_T$
17-18	0.78		.15		361.93
19-20	2.93		.00		2.93
21-22	1.40	–	.50	–	210.90
23-24	1.92	–	.91	4.87	622.70
25-26	6.89	1.57	.14	5.38	285.98
27-28	6.89	1.57	.14	5.38	285.98
29-30	17.88	85.45	.93	239.18	1 373.44
31-32	23.63	11.16	.07	51.27	358.13
33-34	14.95	5.46	.34		275.75
35-36	10.86	16.19	.97		371.02
37-38	2.57	0.00	.09		258.66
39-40	1.14	0.00	.13		394.27
41-42	1.79	0.59	.93		42.31
Annual total	93.61	121.97	4322.30	306.08	4844.00

A – sign indicates periods when the subpopulation is lacking.

#### 4.3.2. At the society level

Production at the society level was estimated at 1 833, 3 267 and 1 939 Joules for societies L1, L2 and L3 respectively. Details about each category (larvae, prepupae, pupae, swarming sexuals and workers) are given in table VI. Elimination was calculated assuming a recycling restricted to consumption of reproductive eggs only. The latter was estimated at 38.5, 45.1 and 38.1 Joules for the societies L1, L2 and L3 respectively, i.e. less than 2% of  $P_{soc}$ .

#### 4.3.3. Individual versus society level

A comparison between  $P_{ind}$  and  $P_{soc}$  shows similar values for the three societies (table VI). At this point of the discussion, this is not entirely unexpected because, according to equations (1) and (2),  $P_{ind}$  differs from  $P_{soc}$  by  $\varepsilon_{rec}$ , the part of biomass that is recycled instead of being eliminated. Since  $\varepsilon_{rec}$  is here restricted to some reproductive eggs and thus almost negligible (<2% of  $P_{soc}$ ),  $P_{ind} \approx P_{soc}$ . As a result, the supposed social advantage ensuing from the recycling of energy by material turnover is nearly non-existent.

In the field the societies are probably never fed at satiety and therefore  $\varepsilon_{rec}$  might be somewhat higher than in our laboratory societies. However, during our field samplings numerous carcasses of unconsumed pupae were observed among nest refuses.

#### 4.4. Comparison with other studies

Quite a few works in the ant literature deal with production, but in most cases they concern some limited aspects, such as production of sexuals or new-born workers only (BRIAN *et al.*, 1967; BRIAN, 1972; NIELSEN, 1972a, b; BRIAN & ELMES, 1974; BOOMSMA *et al.*, 1982; FRANKS, 1985; BACKUS & HERBERS, 1992), or increase

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1.7. Under conditions of food shortage, since more eliminated biomass might be recycled, the error on production should be somewhere between 1.0 and 1.7.

Ants have always been assumed to constitute a special group within insects, spending a disproportionate amount of energy in maintenance costs (PETAL, 1972, 1978) and having particularly low production efficiencies (10%, HUMPHREYS, 1979). Only JENSEN (1977, 1978a) expressed doubts about these assertions on the basis of a careful energy budget in *Formica pratensis* Retz. Our results point out that a re-estimation of production in ants is necessary; such a re-estimation will probably result in higher production efficiencies and provide the beginning of an answer to the question: do ants differ significantly from other insects by their energetic efficiencies?

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TABLE V. – Biomass lost during metamorphosis and hibernation in societies L1, L2 and L3. Annual production at the individual level ( $P_{ind}$ ) is compared with annual production at the society level ( $P_{soc}$ ). All figures in Joules.

Society	Loss in metamorphosis	Loss in hibernation	Total loss	$P_{ind}$	$P_{soc}$
L1	539.4	266.1	805.5	1 770	1 833
L2	804.5	534.7	1 339.2	3 505	3 267
L3	482.1	408.6	890.7	1 894	1 939

TABLE VI. – Annual production ( $P$ ) in Joules at society level in societies L1, L2 and L3.  $\Delta B$ : change in the biomass,  $\epsilon_{soc}$ : elimination at the society level.

		Eggs	Larvae	Prepupae + pupae	Workers	Swarming sexuals	Total
L1	$\Delta B$	-0.4	358.3		701.1		1 059.0
	$\epsilon_{soc}$	0	317.7	348.7	102.6	5.3	774.3
	$P$						1 833.3
	$\epsilon_{soc}/P$						42%
	$\Delta B$	-0.8	100.9		912.0		2 012.1
	$\epsilon_{soc}$	0	495.3	396.3	233.7	129.	1 254.4
	$P$						3 266.5
	$\epsilon_{soc}/P$						38%
	$\Delta B$	-0.	577.0		535.8		1 112.7
	$\epsilon_{soc}$	0	348.3	308.1	153.9	15.8	826.1
	$P$						1 939.5
	$\epsilon_{soc}/P$						43%

in larval biomass during a few weeks (DLUSSKY & KUPIANSKAYA, 1972; PORTER & TSCHINKEL, 1985).

The production of a society as a whole has only been studied in works dealing with energy budgets. To date, most of them have defined the production of a society as the sum of new-born workers and sexuals (GOLLEY & GENTRY, 1964; JENSEN, 1977, 1978a; HORSTMANN, 1982; MACKAY, 1985). This definition is only valid if (1) societies are mature so that there is no annual change in egg and larval biomass, and the annual increase in the society biomass is restricted to new-born workers and sexuals only, and (2) all dead larvae and pupae are consumed and reinvested in the society. In wild *L. unifasciatus* societies, this is not true: there is always some energy that is not recycled (e.g. carcasses of unconsumed pupae among nest refuses).

PETAL (1967, 1972) estimated production in a quite different way and defined it as "the increase in biomass due to the young generation". The main advantage of her method is the possibility of following production through time and, in this way, is similar to ours. However, elimination is not taken into account.

Given equation (2) and the discussion in 4.3.3., the magnitude of the error made in estimating production when eliminated biomass is neglected depends on the amount of biomass which is recycled instead of being eliminated. The latter is supposed to depend mainly on food supply. In our laboratory societies,  $\epsilon_{rec}$  was virtually zero and  $\epsilon_{soc}$  amounts to 41% of the production on average (table VI) so that neglecting this quantity means that production is underestimated by a factor of

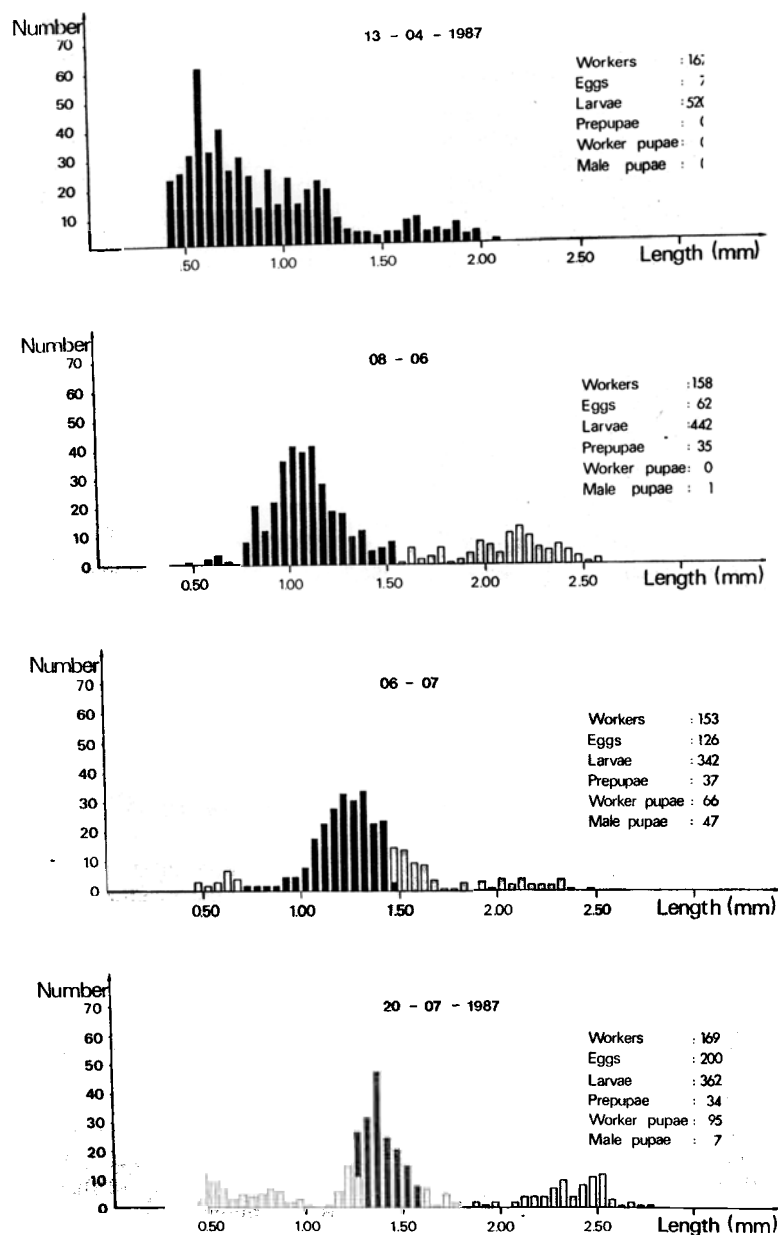


FIG. 2. - Distribution of larval sizes in society L2 at the end of hibernation (week 16, mid-April) and changes in this distribution from week 24 to 30 (early June to late July, i.e. from the beginning to the end of prepupations). The three larval subpopulations (see 3.2.1. and 3.2.2.) are shown: (a) the white bars on the left of histograms are the larvae that hatched since the last census, (b) the black bars are the individuals that were and remained larvae, and (c) the grey bars on the right of histograms are the individuals that became prepupae before the following census.



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