

## Research article

# Nutritional function of replete workers in the pharaoh's ant, *Monomorium pharaonis* (L.)

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**Summary.** Queens of the pharaoh's ant *Monomorium pharaonis* (L.), like several other ant species, feed on larval secretions as their main nourishment and their fecundity is positively correlated with the number of large larvae present in the nest. The surplus of secretions produced by larvae is stored in a temporary caste of replete workers, which comprises young workers who remain in the nest and store liquid nourishment. Repletes are characterised by a conspicuously large gaster, caused by large amounts of liquid food stored in the crop, from which it may be regurgitated and distributed among colony members. In this study, repletes of pharaoh's ants were demonstrated to be functioning as buffers, smoothing fluctuations in availability of high quality food to the reproductive queens when larvae are scarce or missing, thus temporarily keeping up the egg production of queens.

In undisturbed two-queen colonies with 20 large worker larvae and 30 workers (15 young and 15 old workers), approximately 10 repletes developed (one replete per two larvae). Development of older workers into repletes, when some or all repletes had been removed from the colonies, demonstrated that their temporal polyethism exhibits great plasticity in this trait.

This study confirmed that, in pharaoh's ants, the regulation of fecundity depends not only on the food flow to the queen from larvae or from repletes but also on an unknown larval stimulus.

The term *crop repletes* is suggested for replete workers which use their crop to store nourishment, as opposed to *fat-body repletes*, which store nourishment in their fat body.

The presence of brood tending crop repletes in nests in several European ant species of *Leptothorax*, *Myrmica*, and *Lasius*, show that repletism is a common trait in ants, and that it may play an important role in regulation of nutrition in ant colonies, as demonstrated in *Monomorium pharaonis*.

**Key words:** Social regulation, liquid food storage, egg production, queen fecundity, larval secretions.

## Introduction

In flourishing laboratory-reared pharaoh's ant colonies, a number of brood-tending workers can be observed with distended gasters exposing the translucent stretched intersegmental membranes. These are replete workers, also called repletes, which develop and stay inside the nest as described by Wheeler (1926). In brood-producing colonies of pharaoh's ants the major crop content in repletes is a clear liquid solution, with a yellowish lipid drop floating on the top. In colonies with few or no larvae present, the crop content is lipid. Upon dissection, the crop content looks similar to the queens' crop content (pers. observation in a stereo microscope). However, the chemical composition of the contents in the crops has not been analysed.

Both workers and queens have been seen imbibing secretions from the larvae (Børgesen, 1989). Larvae are the only members of the colony which are able to swallow solid food and convert it into available nourishment for workers and queens. The fecundity of the queens is positively correlated to the number of large larvae (Børgesen and Jensen, 1995; Jensen and Børgesen, 1995). There seems to be a positive relationship between the presence of the repletes and the presence of large larvae in the colony. If larvae are removed from the colonies, the gaster crop of the repletes decreases in volume. This is followed by a significant decline in oviposition rate of mated reproductive queens. About 2–5 days later, the repletes have slender gasters similar to those of other workers. During the next few days, the egg yield of queens drops from 10–60 eggs per queen per day to a level of 4–8. This depends on the number of larvae present before removal, and on the number of queens in the colony.

Replete workers have been found in species of most sub-families of ants but their functions have in general been poorly understood. In starved populations of pharaoh's ants repletism of workers in relation to foraging has been described by Haack et al. (1995). In pharaoh's ants, replete workers under conditions of ad libitum feeding in the nests have been described only by Børgesen (1989). To find repletes in the nests, it is necessary to search for them among the crowd of hundreds or thousands of workers with normal sized gasters moving around in the brood clusters. The special use of workers as stores for larval-produced liquid seems not to have been investigated previously in any ant species. This paper describes the source of replete-crop contents, and the influence of the number of repletes on queens' egg production, oocyte number, and fat body development, in colonies of pharaoh's ants.

## Methods and materials

**Experiment:** The pharaoh's ants came from colonies bred by Buschinger and Petersen-Braun since 1968, and were maintained as described by Børgesen (1989). All ants were taken from the same stock colony, having queens around 7 weeks old. Each of the 24 test colonies contained 2 queens, 20 last-stage worker larvae and 30 workers (15 newly emerged from their pupal skin, and 15 pigmented workers taken outside the nest area). The ants had 5 weeks to adapt to the experimental conditions. All eggs were removed, and all pupae and the few dead workers were replaced with the same number of large larvae and workers from the stock colony. This happened when the colonies were regularly given food and water, twice each week.

Two days prior to the experiment, all eggs were removed, and the replete workers were counted. At the beginning of the experiment, the eggs produced over the last two days were removed and counted. Four colonies were picked at random for dissection of queens (controls). The remaining 20 colonies were randomly assigned to one of two groups of 10 colonies each. In Group A, all larvae were removed. Group B colonies contained 20 large worker larvae per colony. Colonies were randomly numbered 1–10 in each group. All repletes in Colony 1 of both groups were removed and replaced with normal slender workers from the 4 control colonies (where the queens had been removed for dissection). In Colony 2, two repletes were left, in No. 3 colonies four repletes were left, and so on. The number of repletes per colony was thus progressively increased by 2 in each sequentially numbered colony. The surplus of a specific temporary caste was exchanged for the other kind of worker cast from the control colonies. At the start of the experiment, Colony 1 in both groups had 2 queens and 30 slender workers, while Colony 10 had 2 queens, 18 repletes, and 12 slender workers  $\pm$  larvae according to the group they belonged. After 90 hours the experiment was stopped. The eggs and repletes were counted, and the queens and some repletes were frozen and stored at  $-80^{\circ}\text{C}$  for later dissection.

*The size of workers* was estimated using a pair of callipers and magnified photos of several colonies, with graph paper covering the bottom of their boxes. The colonies were allowed to settle in the boxes for a few days before they were photographed. Pharaoh's ants have a monomorphic worker caste; the workers are almost of the same size, but have a cyclic weight and size gain related to the brood cycle. The largest workers (mean fresh weight of pupae = 0.3 mg) hatch at the same time as the new reproductives. The smallest workers (0.18 mg) hatch about 6 weeks after the mating of the young sexuals, when the queens are producing eggs at high rates (Petersen-Braun, 1973). The body size of the workers varies from 1.8–2.5 mm (Berndt and Eichler, 1987). The approximate size of replete and non-replete brood-tending workers was estimated here by measuring the length of ants photographed on graph

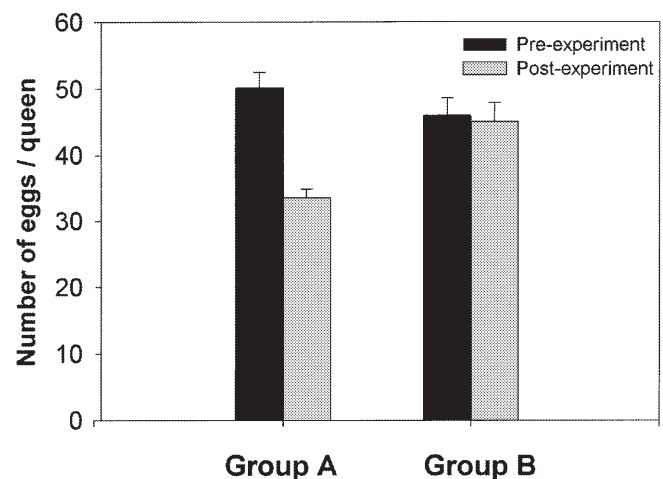
paper. The measuring method was chosen because killing repletes by ethylene acetate,  $\text{CO}_2$ , or ice, usually results in regurgitation of the crop contents of the repletes. This method somewhat under-estimates the total length, as the heavily loaded gasters bend more towards the floor of the nest than "normal-sized" non-replete gasters. Measuring the mid-body of the workers seemed to give more exact measurements. Repletes in ants are generally recruited from the largest workers (Hölldobler and Wilson, 1990; Tsuji, 1990; Hasegawa, 1993), but within the sample size of 23 repletes and 25 non-repletes no significant size difference between the two castes was detected. In future investigations, it would be better to measure length and width of the head of a sample of each caste.

**Statistical methods:** Linear regression analysis, multiple regression analysis ( $R^2$ ), variance analysis (F), t-tests, paired tests whenever data occur in pairs as they exhibit greater power than non-paired tests (t), and Mann-Whitney U-tests (U') (Zar, 1996). Mean values are arithmetic means  $\pm$  S.E.

## Results

**Egg production before experiment:** The mean egg yield/ $\text{Q}/\text{day}$  after adjustment to test conditions for 5 weeks was  $50 \pm 2.3$  in Group A and  $46 \pm 2.6$  in Group B. There was no statistical difference between the groups. See Figure 1, and for statistical data see Table 1.

**Egg production at the end of the experiment:** A multiple regression analysis was performed with the change in egg yield as a function of the number of repletes at the start of the experiment and of the presence of larvae (see Table 1). According to the analysis the dependence of the egg yield on number of repletes and the presence of larvae is highly significant with both of the last two variables contributing significantly to the variance in egg production. The relationship between egg yield and each of the two variables within the groups were analysed by using paired t-tests as the experimental colonies occur in pairs of equal numbers of repletes. The tests indicated that in the larva-less group egg production declined significantly to  $34 \pm 1.4$  eggs / $\text{Q}/\text{day}$ , but there



**Figure 1.** The mean egg production  $\pm$  S.E. before and after the experiment. The difference in Group A without larvae is significant. In Group B colonies, which kept their larvae, there is no significant difference

was no decline in the group with larvae, which remained at  $45 \pm 2.7$ . See Figure 1 and Table 1.

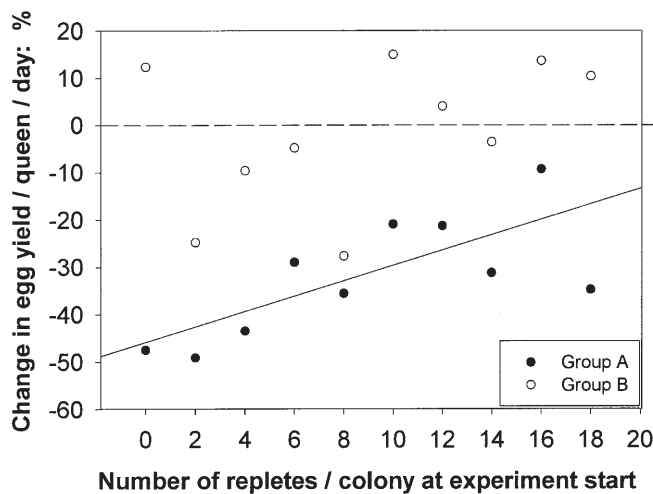
The change in egg production as a function of repletes in Group A (without larvae) is significant, and is positively related to the number of repletes. See Figure 2 and Table 1.

As the egg production per queen varied due to individual physiological conditions before the test, it is necessary to calculate the *relative change* in egg yield per queen in order to compare the effect of the treatment within and between the groups. The relationship between the relative change in egg production [ $Y = (\text{eggs per } \text{♀} \text{ per day prior to test}) - (\text{eggs per } \text{♀} \text{ per day at the end})$  as % of the egg yield per day prior to the experiment] and the number of repletes per  $\text{♀}$  at the start of the experiment ( $X$ ) was described by the linear equation:  $Y_{\text{Group A}} = 3.0 * X - 45.6\%$  of the egg production per  $\text{♀}$  per day prior to the experiment. In the group with larvae the relationship was not significant. The effect per replete in the larval group is about 3% of queens' original egg production per day i.e. about 1.5 eggs per replete per day as the daily egg production was about 50 eggs per  $\text{♀}$ . See Figure 2 and Table 1.

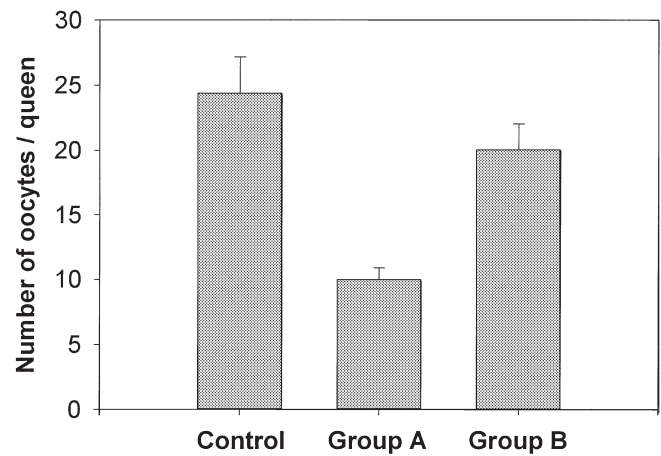
*Oocytes before experiment:* The dissected queens from the 4 control colonies had a mean of  $24 \pm 2.8$  oocytes per  $\text{♀}$  ( $n=8$ ).

*Oocytes after experiment:* The mean number of mature and vitelline oocytes in queens from Group A without larvae was  $10 \pm 0.9$  oocytes per  $\text{♀}$ . This is significantly less than the mean oocyte number of the control queens. In Group B the mean oocyte number of  $20 \pm 2.0$  oocytes per  $\text{♀}$  was not significantly different from the control queens' (Fig. 3 and Table 1).

In contrast to the positive effect of repletes on egg production in Group A, there was no significant relationship



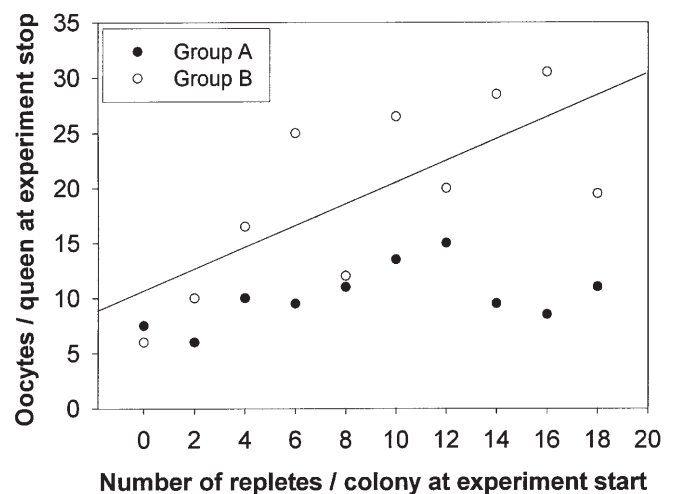
**Figure 2.** Correlation between the egg production/ $\text{♀}$ /24 hours (calculated as the difference in % of the mean production prior to the experiment) and the number of repletes at the start of the test. The queens' egg production increased significantly with the number of repletes in colonies without larvae (Group A:  $\bullet$  = boxes without larvae. Significant:  $P = 0.021$ ). The queens' egg production was unaffected by the number of repletes in colonies containing larvae (Group B:  $\circ$  = boxes with 10 larvae per queen. Not significant:  $P = 0.234$ )



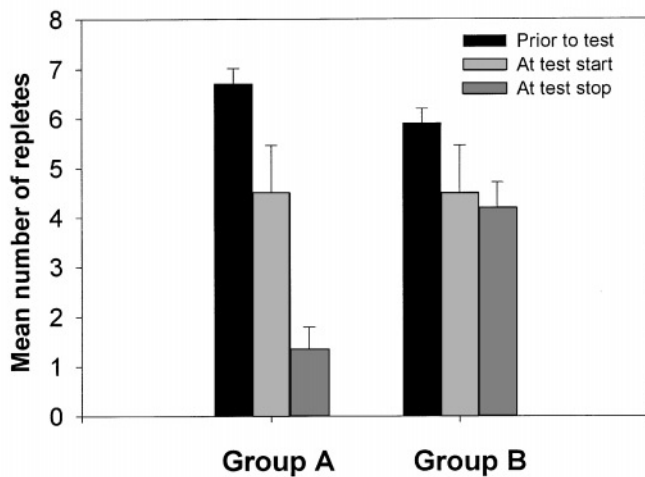
**Figure 3.** The mean number of oocytes per queen  $\pm$  S.E. at the end of the experiment

between the number of oocytes in queens and the number of repletes in their colonies. In the group with larvae, the correlation between the number of oocytes and the number of repletes was significantly positive. This difference between A-queens and B-queens with respect to stimulation and development of oocytes suggests an unknown factor directly related to the presence of large larvae (Fig. 4 and Table 1).

*Mating, fat body and gaster crop:* The queens were all mated with a supply of spermatozoa in their spermatheca and had well developed fat bodies. The gaster crop extended to the distal edge of the first tergite, which is normal for egg laying queens. There was a tendency for the crops to be slightly larger in some queens of Group B, but no significant differ-



**Figure 4.** The relation between number of oocytes per queen and the number of repletes per colony. The number of oocytes in queens with no access to larvae for 90 hours was unaffected by the number of replete workers (Group A:  $\bullet$  = boxes without larvae. Not significant:  $P = 0.267$ ). The queens number of oocytes increase significantly with the number of repletes in queens having larvae in their colonies. (Group B:  $\circ$  = colonies with 10 larvae per queen. Significant:  $P = 0.011$ )



**Figure 5.** The number of repletes  $\pm$  S.E. in relation to absence (Group A) or presence (Group B) of larvae

ence of the crop size could be seen within or between the two groups.

*Repletes before experiment:* All repletes seemed to develop from the young workers, as they were all paler in colour compared to non-repletes. The mean number of repletes per queen, after the 5 weeks of adjustments, was  $6.7 \pm 0.31$  in Group A, and  $5.9 \pm 0.30$  in Group B. The difference between the two groups was not significant. Figure 5 and Table 1.

*Repletes after experiment:* There were significant changes in the number of repletes remaining in the colonies in both groups A and B, but the changes and the significance were greater in Group A than in Group B. See Table 1.

In colonies A1 to A5 there were no repletes when the experiment was stopped. In A6 to A9 there were between 2 and 3 left, and in colony A10 there were 3.5 repletes per queen. Thus, in all Group A colonies there were far less repletes remaining than were given to the colonies at the start of the experiment.

In colonies B1 and B2, there were more repletes after the test than were originally given. Some of these newly-developed repletes were older individuals which were almost black in colour compared to repletes in general. This indicates that temporal polyethism with regard to this function is very labile. In colonies B3–B6, the number remained the same, whilst in B7–B10, there were fewer repletes than at the start. The mean number of repletes after the test was 4.2 per ♀ which is close to the “natural” level of 5.9 per ♀ in Group B prior to the test. See Fig. 5. This suggests that in two queen colonies the number of repletes is regulated to a ratio of approximately one replete worker to two large larvae.

*Size of brood tending workers:* There was no significant difference between replete and non-replete workers body length ( $2.24 \pm 0.02$  mm and  $2.22 \pm 0.02$  mm respectively) nor in thorax ( $0.73 \pm 0.01$  mm. and  $0.71 \pm 0.01$  mm respectively). Gaster length and width were significantly different between

**Table 1.** Data for statistical tests. Group A: The larvae were removed from the colonies. Group B: The larvae were present in the colonies

	Statistical data:	Statistically significant: (P $\leq$ 0.05)
Difference in egg production between A and B before experiment:	$U' = 128, n_1 = n_2 = 10, P > 0.1$	No
Difference between egg production in A before and after experiment:	$t = 6.664, df = 9, P < 0.001$	Yes
Difference between egg production in B before and after experiment:	$t = 0.453, df = 9, P = 0.661$	No
Dependence of change in egg yield on number of repletes and presence of larvae: (Multiple regression analysis)	$R^2_{Adjusted} = 0.659, P < 0.001$ $t_{Repletes} = 2.681, P = 0.016$ $t_{Larvae} = 5.591, P < 0.001$	Yes Yes Yes
Group A: Relation between change in egg prod. and number of repletes/♀: $Y_{Group A} = 3.0 * X - 45.58$	$F = 8.163, df = 1 + 8 = 9, P = 0.021$	Yes
Group B: Relation between change in egg prod. and number of repletes/♀: $Y_{Group B} = 2.1 * X - 11.09$	$F = 1.657, df = 1 + 8 = 9, P = 0.234$	No
Change in oocytes in A before and after experiment:	$t = -6.317, df = 26, P < 0.001$	Yes
Change in oocytes in B before and after experiment:	$t = 1.205, df = 26, P = 0.239$	No
Group A: Relation between number of oocytes and number of repletes/♀: $Y_{Group A} = 0.4 * X + 8.27$	$F = 1.314, df = 1 + 18 = 19, P = 0.267$	No
Group B: Relation between number of oocytes and number of repletes/♀: $Y_{Group B} = 1.7 * X + 12.25$	$F = 8.037, df = 1 + 18 = 19, P = 0.011$	Yes
Difference between number of repletes in A and B before experiment:	$t = 1.978, df = 18, P = 0.063$	No
Change in number of repletes in A during experiment:	$t = 5.026, df = 9, P < 0.001$	Yes
Change in number of repletes in B during experiment:	$t = 3.221, df = 9, P = 0.01$	Yes
Difference between thorax length of repletes and non-repletes:	$U' = 595, n_1 = 23, n_2 = 25, P = 0.502$	No
Difference between gaster length of repletes and non-repletes:	$U' = 942, n_1 = n_2 = 25, P < 0.001$	Yes
Difference between gaster width repletes and non-repletes:	$U' = 940, n_1 = n_2 = 25, P < 0.001$	Yes

the two worker castes. In repletes, gasters were 40% longer ( $0.88 \pm 0.02$  and  $0.63 \pm 0.01$  mm respectively and 35% wider than non-repletes ( $0.58 \pm 0.01$  and  $0.43 \pm 0.01$  mm. See Table 1.

## Discussion

The differences in egg yield (Fig. 2) and number of oocytes (Fig. 4) *between* Group A and Group B clearly demonstrated the positive relationship between the fecundity of pharaoh's ant queens and the presence of larvae, i.e. queens without larvae produce significantly fewer eggs than do queens with larvae in their nest.

The difference in egg yield *within* both groups shows the positive relationship between fecundity and the number of repletes. The changed pattern in replete numbers of both groups during the experiment similarly shows the positive relationship between the presence of larvae and the number of developed repletes.

In the multiple regression analysis the dependence on larvae was far more significant than the dependence on repletes (Table 1), but it should be borne in mind that there are only 2 levels of numbers of larvae (0 and 10 larvae/♀) in this experiment so the significance level should be interpreted with caution. Børgesen and Jensen (1995) found, however, that the effect of larvae on fecundity of queens is around 4.6 eggs per larva per day. When larvae were absent, the number of repletes helped the queen sustain egg laying but not as effectively as larvae. Repletes sustain an egg production of 1/6 compared to the egg production based on nourishment directly from the larvae, i.e. 1.5 eggs per replete per day/((4.6 eggs per larva per day) \* 2) = 0.14 or 1/6 repletes per larvae. The repletes turned into workers with slender gasters within a period of about 5 days after disappearance or moulting of last instar larvae. This period corresponds approximately to the time of a larval stage. In periods with no or few of the last stage larvae, the buffer capacity of a large cast of repletes contribute keeping up the egg production until the second instar generation of larvae turn into last instar which produce large amounts of the secretions needed for queen nourishment.

The difference in number of oocytes *within* each group confirms a previously observed physiological effect of the large larvae by Børgesen and Jensen (1995) (Fig. 4). The absence of larvae inhibit the uptake of vitellogenin by the ovarioles of the queen and thus the development of oocytes. The regulation of fecundity in pharaoh's ants thus depends on two larval factors – the food flow to the queen (directly from the larvae or indirectly via the repletes) and an unknown larval or pharate-pupal stimulus.

In the fire ants, *Solenopsis invicta*, Tschinkel (1995) found that an unknown factor from the pharate-pupal stage stimulates ovarian development and egg-laying in the queen 60–170% more than other brood stages. This fecundity-stimulating factor is correlated to the shedding of the gut contents (meconium) in the process of becoming a pupa. The factor is collected from the anus of the pharate-pupae and

delivered to the queen by a specialised group of workers that shuttles back and forth between the pharate pupae and the queen. In the pharaoh's ants, the queens themselves are particularly keen about collecting anal exudates from meconium-passing brood, as described by Børgesen (1989). It is thus very likely that the meconium exudate contains the fecundity-stimulating substance which stimulate the egg production of the queen. The regulation of new eggs in the nest is thus in accordance with the number of potential brood-nursing workers, which may be available shortly after the young larvae hatch from these eggs. The significance of this positive feed-back regulation between queens and larvae, which reinforces the queen's fecundity in periods of undisturbed settlement, may be an adaptation to the opportunistic way of life of tramp species described by Passera (1994). Further investigations are needed to see if this is a general trait in ants.

In the group without larvae (A), the flow of food was from the repletes to the queen, but the rate of food flow was not sufficient to maintain the egg yield of the queens at 100% (Fig. 5). This is because there were not enough repletes present in most colonies. There were, however, still 2–3 repletes left in some of the colonies which had more repletes added than would have developed "naturally". This suggests that the food flow, and thus the fecundity of the queen, is controlled by the repletes, which regulate by economising on the larval secretions to the queen, when larvae are absent.

In the group with larvae (B) the flow of food was primarily from larvae to repletes. The observed loss or gain of repletes, depending on their initial number, suggests that both larvae and queens regulate the number of repletes in a colony. Replete number would depend on the net food gain on the flow of food from the larvae to queens and repletes minus the flow of food from repletes to queens.

The repletes of the pharaoh's ant seem to be recruited among young workers, but older workers, having slender gasters, also showed behavioural plasticity towards this trait. Beside caring for eggs, larvae and pupae, these repletes thus have an important function improving the fitness of the colony when large larvae and normal food is scarce. Repletes seem to be important in surviving unfavourable climatic or social conditions, functioning as a buffer, smoothing the oscillations in food supplies to the queens in particular, but also in the supplies to other nest mates.

Relatively few animal species store food by any other mechanism than as fat. Pharaoh's ants store nutritional resources in several ways: 1) Larvae can be cannibalized (Ohly-Wüst, 1977). 2) Solid food is stored in piles in special areas of the nest (Petersen-Braun, 1973; Haack et al., 1995). 3) Liquid food is stored in the crops of repletes. 4) Excess fat or protein is stored in the fat body. To differentiate between the two ways of storing food inside the body (in the crop or the fat body); I suggest the first kind of workers is called *crop repletes* and the second *fat-body repletes*.

A mode of obtaining food similar to that of pharaoh's ant queens is described for *Leptothorax acevorum* queens by Bourke (1991). Personal observations direct into the nest chambers of several *Leptothorax* species kept under semi-

natural conditions in my home, show that when larvae are present, there are several brood-tending crop repletes in all species observed: *L. acevorum*, *L. muscorum*, *L. interruptus*, *L. tuberum*, and *L. nylanderii*. These species live in small colonies in unstable ecological conditions, and must be able to move the entire nest population quickly to new nest sites when endangered. During the transport, the workers hold the repletes high up over their head as described by Möglich and Hölldobler (1974). Other commonly occurring European species like *Myrmica rubra*, *M. ruginodis*, *M. scabrinodis*, *Lasius mixus*, *L. flavus*, and *L. niger* also show brood-tending crop repletes when there is brood in the nests. This observation comes from excavations of nests in my garden and other places. I am convinced, however, that when people start looking for crop repletes they will find them in many, if not in most, species. In future investigations, it would be of great interest to know if, in stable conditions, the same individuals remain "specialised" as repletes for long periods or if there is some turn over in this function. Furthermore, the real ratio of repletes in field colonies or complete laboratory colonies should be studied as the values of this investigation only correspond to very artificial experimental conditions.

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