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# Pupae Transplantation to Boost Early Colony Growth in the Weaver Ant *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae)

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**Abstract**

*Oecophylla* ants are currently used for biological control in fruit plantations in Australia, Asia and Africa and for protein production in Asia. To further improve the technology and implement it on a large scale, effective and fast production of live colonies is desirable. Early colony development may be artificially boosted via the use of multiple queens (pleometrosis) and/or by adoption of foreign pupae in developing colonies. In the present experiments, we tested if multiple queens and transplantation of pupae could boost growth in young *Oecophylla longinoda* colonies. We found out that colonies with two queens artificially placed in the same nest, all perished due to queen fighting, suggesting that pleometrosis is not used by *O. longinoda* in Benin. In contrast, pupae transplantation resulted in highly increased growth rates, as pupae were readily adopted by the queens and showed high survival rates (mean = 92%). Within the 50-day experiment the total number of individuals in colonies with 50 and 100 pupae transplanted, increased with 169 and 387%, respectively, compared to colonies receiving no pupae. This increase was both due to the individuals added in the form of pupae but also due to an increased per capita brood production by the resident queen, triggered by the adopted pupae. Thus pupae transplantation may be used to shorten the time it takes to produce weaver ant colonies in ant nurseries, and may in this way facilitate the implementation of weaver ant biocontrol in West Africa.

## Introduction

The arboreal weaver ants (*Oecophylla smaragdina* and *O. longinoda*) are territorial and prevent intruders from accessing their nests. They forage for arthropod prey including many different insect pests in the canopy of their host trees (Way & Khoo, 1992; Peng & Christian, 2006; Van Mele, 2008). According to Dejean (1991) a colony with 12 nests can capture approximately 45,000 prey items per year and may in this way suppress insect pest populations.

*O. smaragdina* could increase economic benefit compared to commonly used conventional pesticides in Australian mango and cashew (Peng & Christian, 2005a; Peng et al., 2004) and Asian citrus orchards (Offenberg et al., 2013). Furthermore, weaver ants are known to improve the quality

of crops such as cashew nuts (Peng et al., 1995; Peng et al., 2004), citrus (Barzman et al., 1996) and mango (Sinzogan et al., 2008; Peng & Christian, 2005b). Therefore, *Oecophylla* is increasingly being utilized as a substitute to synthetic chemical pesticides as they are often equally or even more efficient in controlling pests and at the same time cheaper to use.

Several recent studies on applied weaver ant research have been carried out in Asia and Australia on *O. smaragdina*, however, the life history and the behavior of the African *O. longinoda* is less well documented. Emerging markets for organic and sustainably-managed African fruit (mango, citrus) and nut (cashew) products (Van Mele & Vayssières, 2007) asks for more research and investment in *O. longinoda* in West Africa, as also here the economic potential is high. For example, Dwomoh et al. (2009) showed that *O. longi-*

*noda* can be used to control pest hemipterans as effectively as insecticides in Ghanaian cashew plantation and were able to increase yields four-fold compared to plots without any control measures.

On top of the high potential as a biocontrol agent, *Oecophylla* is also used as a commercial food product (Sribandit et al., 2008) - a tradition especially well developed in Thailand and other Southeast Asian countries (Van Huis et al., 2013). The double utilization of the ants has led to an increasing interest in the development of *Oecophylla* management. For the effective implementation of *Oecophylla* ants in pest management and ant farming, several aspects need to be considered.

It is difficult to collect a queenright colony since the queen nest is well hidden in less accessible places (Peng et al., 1998). Established "wild" ant colonies produce several winged queens (flying ants) each year, which individually leave their colony and start new colonies alone. However, under natural circumstances, the mortality of these queens is high (> 99%) and they are therefore difficult to obtain. Furthermore, it takes, for the few survivors, approximately 2 years before their colony contains enough ants to be used for pest control (Vanderplank, 1960; Peng et al., 2004) or for ant larvae production (Offenberg & Wiwatwitaya, 2010). So far all implementation has been based on collection of wild colonies or natural establishment in orchards which also takes several years (Peng et al., 2005a).

Therefore, to make the *Oecophylla* technology accessible to non-specialists and to implement it on a large scale, cheap production of live colonies in ant nurseries is needed. Artificial rearing of colonies from newly mated queens may lead to a stable and quick production of *Oecophylla* colonies (Krag et al., 2010) and improve the chances of a wide implementation.

For an effective production of live weaver ant colonies in ant nurseries faster growth of young colonies is desired. Two different ways may be used to boost early colony growth. Firstly, *Oecophylla* (Peeters & Andersen, 1989) and other ant species (Bernasconi & Strassmann, 1999) are known to found new colonies with multiple queens (pleometrosis) in order to increase the probability of survival during the initial phase of colony development via a faster production of more workers. Secondly, the adoption of non-nestmate brood from other colonies may increase colony growth as several ant species are known to rob intraspecific brood from neighbor colonies and in this way accelerate colony growth by adding these robbed individuals to their worker force (Bartz & Hölldobler, 1982; Rissing & Pollock, 1987).

It is not known if *O. longinoda* uses pleometrosis during colony founding nor is it known if they accept and adopt pupae transplanted from foreign colonies. In this study we tested if more than one queen could be merged in founding colonies of *O. longinoda* (pleometrosis) and we tested the effect of pupae transplantation on the growth of newly founded colonies.

## Materials and methods

In a mango plantation in the Parakou area (09° 37' 01"N/02° 67' 08"E) of Benin 54 *O. longinoda* queens were collected after their nuptial flight with the use of artificial nests during the wet season in 2012. Artificial nests were made on 15 mango trees by rolling a single leaf together, fixing it with a plastic ring (1.3 cm in diameter) in the middle part and sealing the tip end with a paper clip. Nests were colonized by founding queens right after their nuptial flight as they constitute safe nesting sites (J. Offenberg, unpublished data). Nests were inspected 2-3 times a week and all queens were collected 1-3 days after their mating flight. At this developmental stage all colonies were composed of a single queen and her eggs, as no pleometrotic founded colonies were found. After collection, the queens and eggs were put into open cylindrical transparent plastic containers ($\Phi$ = 4.5 cm; height = 10.5 cm) with a mango leaf inside to increase humidity and sealed with mesh nylon materials at the open end.

The brood transplantation experiment was divided into two sub-experiments; one where queens were kept individually with their brood and transplanted pupae, and a second where two queens were artificially merged into one colony to test for pleometrosis, as has been observed for *O. smaragdina* (Peeters & Andersen 1989; Offenberg et al., 2012a; Offenberg et al., 2012b).

In the first experiment with single queen colonies, 30 fertilized queens were used, which were divided into three pupae transplantation treatments with 0 (control), 50 or 100 non-nestmate pupae being transplanted to each colony, resulting in 10 replicates per treatment. In the first six replicates pupae were transplanted to the queens 7-14 days after they were collected in the field whereas in the last four replicates, pupae transplantation took place the day after they were collected. Every time a new queen was collected in the field, it was sequentially allocated to one of the three treatments (i.e. the first mated queen no transplantation, the next 50 pupae transplantation, the third 100 pupae transplantation etc.).

In the second experiment with two queens per colony, colonies were divided into two pupae transplantation treatments with 0 (control) or 50 non nestmate pupae being transplanted, respectively, and with five replicates per treatment (= 20 queens in total). In both experiments transplanted nonnestmate pupae were obtained from a single mature *O. longinoda* colony. During transplantation, each colony was transferred to a cylindrical transparent plastic vial ($\Phi$ = 8 cm and height = 5 cm) with a mango leaf and the relevant number of pupae placed inside the vial. All colonies were kept at ambient temperature ranging between 24.3 °C and 29.7 °C (mean 27.5 °C) on a table protected from intruding ants by placing each table leg in a tray with water. During the experiment, all colonies were provided a few drops of pure water every day to allow the queens to drink. After the emergence of the first imago workers drops of 20% sucrose water were provided to

each colony every day. One week after emergence of imago workers, protein food in the form of canned cat food and fish was provided to all colonies *ad libitum*.

The transparent plastic containers allowed daily inspection and counting of brood in their different developmental stages. The numbers of intrinsic eggs, larvae, pupae and imago workers (defined as the brood produced by the resident queens) and adopted workers, were counted 50 days after the pupae transplantation in all the colonies. At this point all adopted pupae and the oldest intrinsic brood had developed into imago workers. However, intrinsic imagines could be distinguished from adopted individuals due to the size difference between the pupae from the mature colony and the much smaller nanitic workers produced by the founding queens (Porter & Tschinkel, 1986; Peng et al., 2004). Based on the number of live adopted imago workers, the survival rate from transplanted pupae into imago workers was calculated [(no. of emerged workers / no. of transplanted pupae) x 100] and mean numbers of brood and pupae survival were compared with ANOVAs using JMP 8.0.1 statistical software. Due to the difference in the number of days from queens were collected until pupae were transplanted, the total number of days from queen collection until the experiment was terminated (50 days after pupae transplantation) was recorded for each colony and used as a covariate in the subsequent analyses.

## Results

In the single queen experiment the survival from transplanted pupae into imago workers ranged between 88 and 96% (mean % survival and SD = 92.05 and 2.52) and was not significantly affected by transplantation rate (mean % survival and SD, 50 pupae = 92.4 and 2.45, 100 pupae = 91.7 and 2.66; ANOVA including development time as a co-factor, $F_{(2, 17)}$ = 1.1; $p$ = 0.36) indicating that non-nestmate pupae were readily accepted by the queens and suggesting that pupae required no

or only minimal amount of nursing.

Fifty days after the transplantation, intrinsic imago workers were present in all colonies, however, with significantly more individuals in colonies with more pupae transplanted ($F_{(2,26)}$ = 147.1, p < 0.0001). The mean (SD) number of intrinsic workers was 31.2 (4.37), 44.8 (3.04) and 74.5 (8.25) in the colonies that received 0, 50 and 100 pupae, respectively (Table 1). Pupae transplantation also led to increased production of the remaining developmental stages of intrinsic brood. This was true both for the number of eggs, larvae, pupae, workers and their sum ($p$ < 0.0001 in all cases) at the end of the experiment (Table 1). The average total intrinsic production in colonies without added pupae was 46.5 (6.33) individuals during the first 50 days of colony development. In comparison, 50 pupae transplantation led to a 70 % increase in the per capita queen production, and a 100 pupae transplantation led to 190% increase compared with no pupae transplantation (Fig 1). Thus, the transplanted pupae stimulated the fertilized queen's egg production and increased her brood production with approximately 1.4 and 1.9% per adopted pupae, respectively.

In addition, the total colony size (all intrinsic brood plus adopted workers) was 46.5 (6.33), 125.2 (11.01) and 226.7 (15.32), respectively, in the colonies that received 0, 50 and 100 pupae. In comparison to the treatment without pupae transplantation, the total number of individuals increased 169% with 50 transplanted pupae and 387% with 100 transplanted pupae (Fig. 1). Thus, adopted workers led to a considerably increase in total colony size.

In the second experiment with two queens in each colony, one of the queens, in all cases, killed the other before the emergence of imago workers from the transplanted pupae, suggesting that pleometrosis induced in the laboratory is not possible. It should, however, be noticed that we found 5 claustral colonies with two queens out of a total of 87 collected in 2013 (all the others being singly founded)(I. Ouagoussounon,

**Table 1**: Mean (± SD) number of intrinsic brood (egg, larvae, pupae, imago workers and their total) produced by the resident queen in the colonies 50 days after the transplantation of pupae.

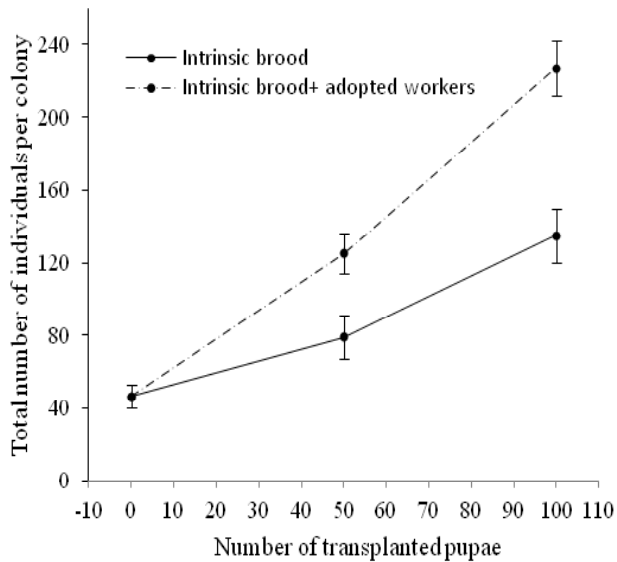| Transplantation (no. of pupae) | Eggs per colony | | Larvae per colony | | Pupae per colony | | Workers per colony | | Total intrinsic production per colony | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean (SD) | Two-way ANOVA | Mean (SD) | Two-way ANOVA | Mean (SD) | Two-way ANOVA | Mean (SD) | Two-way ANOVA | Mean (SD) | Two-way ANOVA |
| 0 | 7.3 (4.06) | | 4.3 (2.11) | | 3.7 (4.03) | | 31.2 (4.37) | | 46.5 (6.33) | |
| 50 | 16.8 (4.71) | $F_{(2, 26)}$ =58.3 P < 0.0001 | 10.5 (5.62) | $F_{(2, 26)}$ = 25.1 P < 0.0001 | 6.9 (5.26) | $F_{(2, 26)}$ = 23.3 P < 0.0001 | 44.8 (3.04) | $F_{(2,26)}$ =147.1 P < 0.0001 | 79.0 (11.74) | $F_{(2, 26)}$ =165.1 P < 0.0001 |
| 100 | 25.3 (3.59) | | 17.6 (4.81) | | 17.6 (4.67) | | 74.8 (8.25) | | 135.0 (14.83) | |
| Total development time (days) | | $F_{(1, 26)}$ = 8.9 P < 0.0001 | | $F_{(1, 26)}$ = 5.8 P = 0.023 | | $F_{(1, 26)}$ = 0.3 P = 0.60 | | $F_{(1, 26)}$ = 0.06 P = 0.80 | | $F_{(1, 26)}$ = 4.0 P = 0.056 |
| Whole model | | $F_{(3, 26)}$ =43.6 P < 0.0001 | | $F_{(3, 26)}$ =19.6 P < 0.0001 | | $F_{(3, 26)}$ =15.8 P < 0.0001 | | $F_{(3, 26)}$ =98.2 P < 0.0001 | | $F_{(3, 26)}$ =113.2 P < 0.0001 |

**Fig. 1**: The mean (± SD) number of individuals (egg, larvae, pupae and imago workers) per colony, 50 days after the transplantation of pupae.

unpublished data), suggesting that pleometrosis is sometimes used under natural conditions as also described by (Dejean et al.,2007). Because all queens were involved in fatal fights, no further analyses were conducted on this experiment.

**Discussion**

The results showed no difference in survival between queens receiving 50 pupae and queens receiving 100. Pupae in both treatments were readily accepted by the queen ants and more than 88% were reared to the imago stage. This means that potentially colonies may be boosted with even higher numbers of pupae and boosting can take place before the emergence of the first workers as a worker force is not needed for nursing. Offenberg et al. (2012b) and Peng et al. (2013) obtained similar results with a mean survival rate of 84%, when transplanting 30 and 60 non-nestmate pupae to *O. smaragdina* queens in Darwin, Australia. Also in that case survival was unaffected by transplantation rate. The same pattern may not hold true if larvae were transplanted instead of pupae as they need to be fed and groomed by members of the receiver colony. Larvae may well be accepted by receiver colonies, as described by Krag et al. (2010) for *O. smaragdina,* however, it is questionable if they can be added in high numbers as with pupae, because of their need for food, which is available in only limited amounts, especially in very young colonies with only a single queen and no worker force. A further advantage to colonies adopting pupae from mature colonies derives from the fact that young ant colonies, in order to reserve resources, produce only smaller and slimmer workers (nanitics) with an associated narrow task repertoire compared to older and larger colonies that produce larger major workers (Peng et al., 2004). After pupae transplantation the workers eclosing from the transplanted pupae are of a larger size as

they originated from a mature colony. As a consequence these transplanted individuals may conduct wider tasks compared to the nanitic imago workers intrinsic to the young colonies. If larvae were transplanted these may turn into smaller imagines due to food shortage if they are transplanted prior to the determination point of their final size. This is not the case with pupae as they have already attained their final size.

Krag et al. (2010) showed that *O. smaragdina* non-nestmate larvae showed chemical insignificance (i.e. were without colony specific odor) as they were adopted by colonies containing mature workers (but no queens). Subsequently it was found that also *O. smaragdina* pupae seems to be chemical insignificant and that the presence of queens in the colonies did not hinder adoption of foreign brood as transplanted pupae developed into imagines in queenright colonies (Offenberg et al., 2012b). From the present study we conclude that the same holds true for *O. longinoda* suggesting that chemical significance does not develop until beyond the pupal stage as also suggested by Lenoir et al. (2001), to be the case for other ant species. Also the present study shows that the presence of the maternal queen does not preclude adoption of foreign brood.

The addition of pupae to the colonies did not only increase colony size with the numbers added. In addition, the transplantation of pupae stimulated the fertilized queen´s own egg production and thereby increased the intrinsic brood production of the colonies. Thus, the presence of brood at the pupal stage (or beyond), increased egg laying rates. This seems to be adaptive to queens as younger brood is associated with expenditures to the queens in terms of nursing time and food allocation, whereas pupae will soon eclose and develop into workers that can take over the nursing of brood and forage for food. This result follows the findings by Gibson & Scott (1990) and Offenberg et al. (2012b), showing that pupae increased egg laying in *Camponotus spp.* and *O. smaragdina* queens, respectively. On the other hand, other researchers have shown that only the number of late stage larvae is responsible for queen fertility in e.g. *Monomorium pharaonis* and *Solenopsis invicta* (Tschinkel, 1988; Børgesen & Jensen, 1995; Cassill & Vinson, 2007). This suggests that different mechanisms may operate in different ant species. Further, the triggering of an increased fecundity in the present study shows that egg laying rates in *O. longinoda* are plastic and can be manipulated via the presence of pupae and/or workers.

In the present study, the total population size (all brood stages) in the colonies that received 0 pupae was 1.99 times higher (mean = 46.5 ± 3.6 SE) compared to the results obtained by Offenberg et al. (2012a) in the hapleometrotic colonies of *O. smaragdina* (mean = 23.3 ± 2.0 SE) after 68 days. This lower production in *O. smaragdina* was likely affected by the fact that the colonies in that study were transported under cold conditions at the start of the experiment which may have delayed their development. On the other hand, the total population size (all brood stages) after 68 days was 1.6 times

higher in the pleometrotic *O. smaragdina* (Offenberg et al., 2012a) colonies (mean = 74.9 ± 10.5 SE) compared to the haplometrotic colonies in this study (mean = 46.5 ± 3.6 SE). This highlights the strong effect of multiple queens in founder colonies.

Under natural circumstances, it takes approximately two years before a colony contains enough ants to be used for pest control (Vanderplank, 1960; Peng et al., 2004) as each colony is expected to occupy approximately 10 trees in the receiver plantation (Peng et al., 2004). This minimum colony size may be achieved more quickly by boosting the growth via pupae transplantation. In the present study colony size increased up to almost 5-fold in only 50 days and with only a single pupae transplantation event. Multiple transplantations with potentially even higher numbers of pupae being transplanted may lead to much higher boosting, considerably shortening the otherwise slow development to an acceptable colony size. Secondly, it is evident that the biological control efficiency of weaver ants depends on the density of the worker ants (Van Mele et al., 2007; Peng & Christian, 2005b, 2007). Thus, keeping high densities of *O. longinoda* is essential in biocontrol programs and may be accomplished by pupae transplantation during critical periods.

This study suggests that queen right *O. longinoda* colonies accept foreign brood and that pupae transplantation facilitate colony growth. This knowledge may ease the implementation of the weaver ant technology in Africa where the ants can be used to control pest species on various crops. Future studies should test if the immediate presence of pupae will trigger higher egg-laying rate by the queen before the pupae emerge as workers. Also it would be interesting to test if pupae transplantation and the following higher numbers of larger workers will lead to the production of a larger intrinsic worker caste in receiver colonies compared to colonies that develops naturally.

## Acknowledgements

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