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Colony foundation in the ant *Carebara vidua*: the dispelling of a myth

Queenright colonies of ants can be founded by single queens (haplometrosis), multiple queens (pleometrosis) or by a queen with a complement of workers (fisson or swarming).[1,2] Usually in colony foundation by fission, a virgin queen mates, returns to the nest and then starts a new colony with the assistance of her sister workers, this colony being independent but within walking distance of the parent nest. However, for a long time it was widely held that *Carebara vidua* F. Smith, and other members of the genus, had an aberrant form of colony fission in which a few workers clung onto the virgin queen during the nuptial flight from the nest and assisted her, once she had mated, in founding a new colony.[3–6] This hypothesis was inspired by the extreme size dimorphism between the minute workers and the queen. It was argued that assistance to the queen was necessary because her mouthparts were too large to make direct feeding of the tiny larvae possible. However, Lowe[7] in Malaysia showed that workers of *C. lignata* did not assist queens in colony foundation and that queens were capable of feeding the larvae. Similarly, Lepage and Darlington[8] in Kenya showed that accompanying workers are not necessary for colony foundation in *C. vidua* and that newly mated queens in the field did not have workers with them. In the present paper we provide further evidence that workers do not assist the queen of *C. vidua* in colony foundation and, in addition, discuss how the mistaken belief about the mode of colony foundation in *C. vidua* developed from speculation to an accepted fact.

Observations were made in Mkuze Game Reserve (27°36′S, 32°13′E), northern Zululand. Heavy rain, the first of the season, fell in the last days of September 1987, and queens were found dispersing from several colonies soon afterwards (29 September – 1 October). Observations were made also after the first summer rains of 1988 (15 October). Queens emerging from two colonies were caught by hand after they had taken off and flown about a metre. The number of workers on each queen (including any dislodged onto the hand during capture) was recorded. A net was not used because it dislodged workers easily and made accurate counting of these workers impossible. Queens which had mated and were beginning to excavate a nest were examined also for workers and in addition were taken back to the laboratory for observations of colony foundation behaviour. In the laboratory they were housed in plastic Petri dishes filled with the local sandy soil and darkened by covering with disks of red Perspex. A regular check was kept on them, and the soil moistened with an atomiser once a week. Unfortunately, a fungal disease killed the queens before the eggs hatched, so it was not possible to confirm Lepage and Darlington's results[8] that *C. vidua* queens could rear larvae unaided.

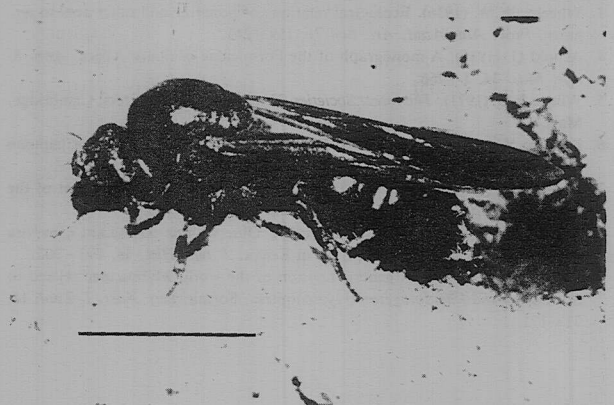

Fig. 1. Female of *C. vidua* at nest entrance surrounded by workers with some of them crawling over her. Scale line = 1 cm.

Alate queens were found emerging from different colonies in the field from 10h30 to 16h30. Males were seen emerging along with the queens at 12h30 and 14h00. Queens emerged from one nest over a period of three days, and from another over at least two days. Workers milled round the entrance hole, surrounding the emerging queens and crawling over them (Fig. 1).

Queens often buzzed their wings shortly before take-off, which dislodged many of the workers on them. Only 5% of queens caught in flight leaving Colony 1 had workers attached to them, whereas in Colony 2, 61% of queens had workers on them (Table 1). The discrepancy between colonies was a result of their location because Colony 1 was surrounded by short green grass, which obstructed the queens' take-off and caused more buzzing, whereas Colony 2 opened in bare ground.

Table 1. Number of *C. vidua* queens carrying workers after they had flown about one metre from the nest.

	Number of workers on queen							
	0	1	2	3	4	5	6	7+
Number of queens								
colony 1	58	3	0	0	0	0	0	0
colony 2	11	6	8	0	2	0	1	0

Once airborne, the queens rose 13 – 17 m into the air, about twice the height of the surrounding vegetation, and flew off on a straight course. Some were followed with binoculars for over 500 m before they were lost from sight. Once a queen had mated, she flew to the ground and shed her wings immediately by trapping them between her flexed mid- and hind-legs and pulling them down and backwards. She then wandered about and eventually began digging into the ground. There were few termite mounds in the vicinity and queens were not observed excavating nests where there were obvious signs of termite activity. During nest excavation, they used their forelegs and mandibles, covering themselves with soil from the hole as they bored downwards. Eventually all that remained was a rosette of sandy pellets, rather like those left by burrowing dung beetles. Of 21 queens observed in the field after they had shed their wings, none had workers attached to them.

Seven dealated queens from the field were placed in soil-filled plastic jars, eight centimetres deep, and began to burrow within ten minutes. They worked their way to the bottom of the jars, where they each formed round chambers 18 – 25 mm in diameter. They were later transferred to plastic Petri dishes, in which they rebuilt their cells. They moved about relatively little in the chamber and laid small, ovoid eggs averaging 0,39 mm in length (range = 0,35 – 0,44 mm, s.d. = 0,02 mm; n = 50). The eggs stuck to the queens' abdomens and to each other, forming irregular masses. When the egg masses became large, they remained on the floor of the chamber.

The crops of eight virgin queens that were dissected contained a yellow lipid-like substance and were extremely large, averag-

ing 24,1% of whole fresh body mass (range = 21,9 – 27,5%, s.d. = 5,4%).

Our observations confirm those of Lepage and Darlington,[8] that *C. vidua* queens do not carry workers to new nests to assist with colony foundation. Even shortly after take-off from the parent nest, there were few if any workers on the queens (Table 1). Our observations differed from those of Lepage and Darlington in two respects. Firstly, they observed *C. vidua* alate queens in Kenya dispersing from nests for only short distances at little over a metre above the ground, whereas we observed them flying considerable ditances, high above the ground (>15 m). The reasons for this contrast in dispersal behaviour are not clear, but may be related to differences in the structure of the vegetation or the density of termite mounds at the two sites. Secondly, none of the queens observed in Zululand dug into termite mounds when founding a colony, unlike the Kenyan individuals. Although termite mounds were uncommon at the site where we observed *C. vidua*, termites were common underground and their presence could conceivably have influenced where a queen dug. However, we obtained no evidence that termites did influence the site of colony foundation.

It is remarkable how an attractive hypothesis can be transformed into an accepted fact. Arnold[4] in 1916 was the first to speculate on colony foundation in *C. vidua* and described it in the following way:

> It is probable that the dense tufts of hairs on the tarsi of the female serve an important purpose—that of enabling some of the minute workers to attach themselves to the body of the female when the latter is about to leave the parent nest. Several specimens of the female have been taken by me with one or more workers biting on to the tarsal fimbriae. I am inclined to suspect that the young queen cannot start a new nest without the help of one or more of the workers from the old nest, on account of the size of her mouth-parts, which would probably be too large and clumsy to tend the tiny larvae of her first brood, and that it is therefore essential that she should have with her some workers which are able to feed the larvae by conveying to them the nourishment taken from the mouth of the queen.

Wheeler,[3] in a paper published in 1936 on the relationship of ants to termites, agreed with the ideas presented by Arnold and in addition presented a drawing of a museum specimen of a winged queen of *C. vidua* with two workers attached to her tarsi. This queen was probably collected while emerging from her natal nest, before the workers were shaken off. Wheeler states categorically, with no supporting proof, that 'the rearing of the minute larvae after hatching from the eggs . . . cannot be carried on by the same method of oral regurgitation as that employed by other colony-founding ants in which the difference in size between the female and her first brood of offspring is less excessive'. He disagreed with Arnold that the workers transported to the new nest are able to feed the larvae from substances regurgitated by the queen, because 'there is no reason to assume that the colony-founding queen leaves the parental nest with a supply of liquid food in her crop'. Instead, he proposed that the transported workers preyed on termites in the vicinity or utilized as food some of the eggs produced by the queen. The results of the present study show that in fact the queen leaves the nest with a considerable quantity of liquid in her crop.

It was Wheeler's article that provided the source for the perpetuation of this mistaken idea of colony foundation in *C. vidua*. Wilson[5] in 1971, in his influential book on social insects, reproduced Wheeler's drawing of the queen with attached workers. Although Wilson does not state categorically that the workers assist the queen in founding a colony, Arnold's original idea is presented in a convincing manner, as follows:

> . . . The workers of *Carebara* are so much smaller [than the queen] that some catch a ride with each queen on her nuptial flight. The queen enters a termite nest after the nuptial flight and is presumably assisted by her little sisters in the rearing of the first brood.

Brian[6] brings the myth of colony foundation in *C. vidua* to fulfilment by stating that '*Carebara* queens . . . have such small workers that they can cling to their legs during nuptial flights and be ready to help (Wheeler, 1936), thus cutting out much risk and time'. Both Wilson and Brian appear to have been unaware of the findings and remarks of Lowe,[7] which were published in 1948, well before the books of these two authors appeared. Ettershank,[9] however, was aware of Lowe's paper and relegated Wheeler's popularization of colony foundation in *Carebara* to its rightful place as speculation.

It is surprising that the myth of colony foundation in *Carebara* developed at all as it does not make sense that there would be selection for the production of large, costly queens that are totally dependent on one or two tiny vulnerable workers clinging to them when they leave the nest. These workers would have to survive the nuptial flight, the digging of the hole by the queen, and the period between egg laying and the production of the first brood.

In myrmicine ants, reproductives leaving the nest are usually surrounded by workers (H. Robertson, personal observations), presumably to protect them from predators. In the process, workers frequently walk over the reproductives and even bite them. In *C. vidua*, because of the extreme size dimorphism between workers and reproductives, it is inevitable that during the release of alates, queens (and males) sometimes take off with workers still on them, but this apparently has no adaptive significance.

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