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The roles of the queen, brood, and worker castes in the colony growth dynamics of the pharaoh ant *Monomorium pharaonis* (Hymenoptera: Formicidae)

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Abstract

Known for its high reproductive rate, sociotomy, and unique nesting habits, the Pharaoh ant *Monomorium pharaonis* (LINNAEUS, 1758) is one of the most successful tramp ant species. In this study, combinations of different caste groups were used to examine the effects of each caste on queen and worker population growth dynamics over time. The initial number of queens in an incipient colony significantly affected queen population growth and accounted for 42.2% of the overall variability over a six-month period. Queen population growth significantly decreased as the initial number of queens increased in the incipient colonies, and in most cases, each colony retained its original number of queens (eight). The brood quantity had little effect on queen population growth and was responsible for an increase of only 2.5% in the overall variability, and the worker number had no effect on queen population growth. Worker population growth was primarily affected by the initial queen number of the incipient colony, although the effects of queen, brood, and worker number on worker population growth were all significant. Overall, our results showed that the number of caste components required for colony success was much lower than expected: A mere 50 workers and one queen were sufficient for colony survival and productivity irrespective of the presence of brood.

Key words: Pharaoh ant, caste regulation, queen pheromones, sociotomy, colony budding, colony growth dynamics.

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Introduction

The Pharaoh ant *Monomorium pharaonis* (LINNAEUS, 1758) is a globally important species of pest ant in urban environments. In addition to being a nuisance, this species may serve as a mechanical vector of pathogenic organisms, especially in food-preparation facilities (EDWARDS 1986, YAP & LEE 1994, LEE & al. 2003) and medical care centres (BEATSON 1972, EDWARDS & BAKER 1981, WETTERER 2010). Pharaoh ants normally nest in artificial, highly disturbed habitats, such as between sheets of papers, in rubbish heaps, and in the walls of houses (EDWARDS & BAKER 1981, PASSERA 1994).

The Pharaoh ant is a highly polygynous species, and a colony may contain up to several thousand workers and hundreds of fertile queens (HÖLLDOBLER & WILSON 1990). The life span of a Pharaoh ant colony largely depends on the reproduction of the queens, which are the colony's only fertile members (BAJOMI & al. 2005). PEACOCK & al. (1955) showed that Pharaoh ant workers in queenless colonies could rear a sexual brood from the existing brood; this observation led later to the hypothesis that queens are unnecessary for new colony establishment.

Pharaoh ant colonies face energy investment trade-offs in the regulation of both colony size and caste ratio (SCHMIDT & al. 2011). The removal of queens from a colony can give rise to a sexual brood (PETERSEN-BRAUN 1975). The pheromones emitted by a mated queen can suppress and change the development of the colony members, such as preventing the rearing of a sexual brood (EDWARDS 1991). However, the worker caste forages for food to supply the nutrients needed for queen production and brood development, and the larvae have the ability to process solid food into digestible nutrients that can be readily consumed by all colony members, including the queens and workers (BØRGESEN & JENSEN 1995). Thus, the interactions among all castes and brood are crucial to guaranteeing new colony establishment and regulating the growth dynamics of the colony (BØRGESEN 1989).

Pharaoh ants are able to separate from their parental colonies and establish new colonies under certain circumstances, such as chemical or physical disturbance, sudden depletion of the food supply, or overcrowding (BUCZKOWSKI & al. 2005). Budding into smaller groups may ensure efficient food distribution and optimum colony growth because new queens can be produced independently (BUCZKOWSKI & BENNETT 2009).

The management of Pharaoh ants is often challenging due to their high reproductive rate, sociotomy (budding), and unique nesting habits (LEE 2002). A high reinfestation

Tab. 1: Colony source for 64 different combinations of queen number, brood quantity, and worker number.

Queen	Brood (g)	Worker	Subcolony	Queen	Brood (g)	Worker	Subcolony	Queen	Brood (g)	Worker	Subcolony	Queen	Brood (g)	Worker	Subcolony
0	0.0	50	1, 2, 3, 4	0	0.1	50	1, 2, 3, 4	0	0.3	50	1, 2, 3, 4	0	0.6	50	1, 2, 3, 4
0	0.0	100	5, 6, 7, 8	0	0.1	100	5, 6, 7, 8	0	0.3	100	5, 6, 7, 8	0	0.6	100	5, 6, 7, 8
0	0.0	200	1, 2, 3, 4	0	0.1	200	1, 2, 3, 4	0	0.3	200	1, 2, 3, 4	0	0.6	200	1, 2, 3, 4
0	0.0	500	5, 6, 7, 8	0	0.1	500	5, 6, 7, 8	0	0.3	500	5, 6, 7, 8	0	0.6	500	5, 6, 7, 8
1	0.0	50	1, 2, 3, 4	1	0.1	50	1, 2, 3, 4	1	0.3	50	1, 2, 3, 4	1	0.6	50	1, 2, 3, 4
1	0.0	100	5, 6, 7, 8	1	0.1	100	5, 6, 7, 8	1	0.3	100	5, 6, 7, 8	1	0.6	100	5, 6, 7, 8
1	0.0	200	1, 2, 3, 4	1	0.1	200	1, 2, 3, 4	1	0.3	200	1, 2, 3, 4	1	0.6	200	1, 2, 3, 4
1	0.0	500	5, 6, 7, 8	1	0.1	500	5, 6, 7, 8	1	0.3	500	5, 6, 7, 8	1	0.6	500	5, 6, 7, 8
4	0.0	50	1, 2, 3, 4	4	0.1	50	1, 2, 3, 4	4	0.3	50	1, 2, 3, 4	4	0.6	50	1, 2, 3, 4
4	0.0	100	5, 6, 7, 8	4	0.1	100	5, 6, 7, 8	4	0.3	100	5, 6, 7, 8	4	0.6	100	5, 6, 7, 8
4	0.0	200	1, 2, 3, 4	4	0.1	200	1, 2, 3, 4	4	0.3	200	1, 2, 3, 4	4	0.6	200	1, 2, 3, 4
4	0.0	500	5, 6, 7, 8	4	0.1	500	5, 6, 7, 8	4	0.3	500	5, 6, 7, 8	4	0.6	500	5, 6, 7, 8
8	0.0	50	1, 2, 3, 4	8	0.1	50	1, 2, 3, 4	8	0.3	50	1, 2, 3, 4	8	0.6	50	1, 2, 3, 4
8	0.0	100	5, 6, 7, 8	8	0.1	100	5, 6, 7, 8	8	0.3	100	5, 6, 7, 8	8	0.6	100	5, 6, 7, 8
8	0.0	200	1, 2, 3, 4	8	0.1	200	1, 2, 3, 4	8	0.3	200	1, 2, 3, 4	8	0.6	200	1, 2, 3, 4
8	0.0	500	5, 6, 7, 8	8	0.1	500	5, 6, 7, 8	8	0.3	500	5, 6, 7, 8	8	0.6	500	5, 6, 7, 8

rate has been reported for this species, as those colony members that survive the application of insecticides are able to resume breeding (OI & al. 2000). However, the colony growth dynamics of the Pharaoh ant under unfavourable caste ratios are not fully understood. The present study analysed how these ants successfully sustain themselves in partially killed colonies. Considering the highly varied composition of Pharaoh ant colonies that are prone to budding after being subjected to disturbances (PEACOCK & al. 1955, HÖLLDOBLER & WILSON 1990), we studied the effects of different combinations of queens, workers, and brood on colony growth dynamics over time.

Materials and Methods

Ant colonies: Pharaoh ant colonies were obtained from Urban Entomology Laboratory, Vector Control Research Unit, School of Biological Sciences, Universiti Sains Malaysia. They were originally from a single colony that was collected in Gelugor, Penang, Malaysia that had been cultured since 2000. Subsequently they were subcultured since 2009 and in this experiment, they came from eight subcolonies (Tab. 1). The colonies were maintained under environmental conditions of 26 ± 1 °C, 60 ± 5% relative humidity, and a 12-hour photoperiod.

Experimental design: The colony demographic patterns of the Pharaoh ant were observed for 64 different combinations of queen number (0, 1, 4, and 8), brood quantity (0, 0.1, 0.3, and 0.6 g), and worker number (50, 100, 200, and 500) (Tab. 1). Fertile queens two to three weeks of age were used. Each queen was placed in a separate container for 24 hours and confirmed to be mated and to have laid eggs. The brood component (eggs, larvae, and pupae) was weighed to the nearest 0.01 mg using a digital analytical balance at an estimated ratio of 1:2:1 (BP 190 S Sartorius AG, Goettingen, Germany). Each combination was reared in a polyethylene container (13.0 × 11.5 × 6.0 cm), the inner sides of which were smeared with a thin layer of Fluon® (polytetrafluoroethylene suspension) (Wilmington, DE) to prevent the ants from escaping. A Petri dish (5.5 cm in diameter and 1.7 cm in height, with three small holes on the side) provisioned with folded corrugated paper (8 × 3 cm) was used as a harbourage. Water and 10% sucrose solution were provided ad libitum. Each colony was fed weekly with freshly killed late instars of the lobster cock-

Tab. 2: Analysis of variance results for *Monomorium pharaonis* queen and worker population growth under different combinations of queen number, brood quantity, and worker number. df = degrees of freedom; SS = sum of squares; MS = mean squares; F = F statistic; * = P < 0.05.

Source of variance	df	SS	MS	F	P
Queen population growth					
Queen	3	102.2	34.1	105.5	0.001*
Brood	3	5.4	1.8	5.6	0.001*
Worker	3	1.2	0.4	1.2	0.300
Queen × brood	9	6.9	0.8	2.4	0.016*
Queen × worker	9	9.2	1.0	3.2	0.002*
Brood × worker	9	4.4	0.5	1.5	0.147
Queen × brood × worker	27	20.7	0.8	2.4	0.001*
Error	128	41.4	0.3		
Corrected total	191	191.4			
Worker population growth					
Queen	3	109.6	36.5	97.4	0.001*
Brood	3	24.3	8.1	21.6	0.001*
Worker	3	8.8	2.9	7.8	0.001*
Queen × brood	9	12.7	1.4	3.8	0.001*
Queen × worker	9	17.6	2.0	5.2	0.001*
Brood × worker	9	32.4	3.6	9.6	0.001*
Queen × brood × worker	27	40.6	1.5	4.0	0.001*
Error	128	48.0	0.4		
Corrected total	191	295.1			

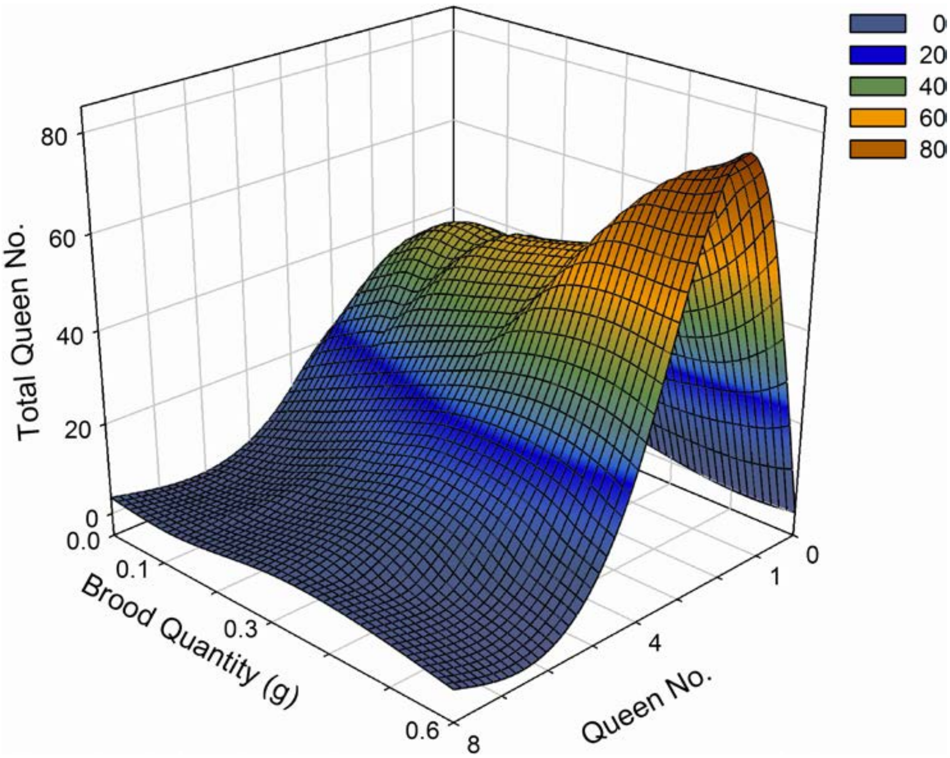

Fig. 1: The effects of queen number and brood quantity on queen population growth in incipient colonies of *Monomorium pharaonis* after six months.

roach (*Nauphoeta cinerea*, OLIVIER 1789), canned tuna fish (TC Boy Marketing Sdn. Bhd., Shah Alam, Malaysia), and hard-boiled egg yolk. Four replicates were performed for each combination.

Statistical analysis: The numbers of live queens (including alates) and workers (including the test individuals) in each container were determined by direct counting at one, two, three, four and six months post-introduction using a computer according to photographs of the containers. The numbers of queens and workers were subjected to Log_{10} transformation prior to analysis. Univariate analysis of variance (ANOVA) was used to evaluate the queen and worker population growth in the different caste combinations as well as the full factorial interactive effects of different numbers of different castes. Stepwise multiple linear regression analysis was used to determine the predictive power of the variables that could account for a significant proportion of the variance in the regression model of queen and worker population growth. All analyses were performed using SPSS at $\alpha = 0.05$ (SPSS version 11.5, SPSS Inc., Chicago, IL).

Results

Queen population growth: The main effect of the initial number of queens in an incipient colony on queen population growth was statistically significant ($F = 105.5$; $df = 3$; $P < 0.001$): Queen number was found to decrease significantly as the initial number of queens in the incipient colonies increased (Fig. 1; Tab. 2). The effect of the initial queen number accounted for 42.2% of the overall variability in queen population growth ($R^2 = 0.422$; $F = 103.743$; $df = 1, 142$; $P < 0.001$) (Tab. 3). A drastic increase in queen population growth occurred between the second and third month, between the third and fourth month, and between the fourth and sixth month for colonies that initiated with one queen and four queens, respectively (Fig. 2). As many as 120 queens were observed after six months for incipient colonies that initiated with one queen. In the incipient colonies that initiated with no brood, up to 54 queens were observed after six months as long as a queen or queens were present. However, queenless colonies produced few (≤ 21) or no queens after six months. Different brood quantities had little effect on queen population growth ($F = 5.6$; $df = 3$; $P < 0.001$), increasing the overall variability of this variable by only 2.5% ($\Delta R^2 = 0.447$; $\Delta F = 57.0$; $df = 2, 141$; $P < 0.001$). Worker number alone played no role in queen population growth ($F = 1.2$; $df = 3$; $P = 0.30$). However, statistically significant interactions were detected between queen number and worker number ($F = 3.2$; $df = 9$; $P < 0.01$), queen number and brood quantity ($F = 2.4$; $df = 9$; $P < 0.05$), and among queen number, brood quantity, and worker number ($F = 2.4$; $df = 27$; $P < 0.001$).

Worker population growth: The statistical analyses revealed that the main effects of queen number ($F = 97.4$; $df = 3$; $P < 0.001$), brood quantity ($F = 21.6$; $df = 3$; $P < 0.001$), and worker number ($F = 7.8$; $df = 3$; $P < 0.001$) on worker population growth were statistically significant. Furthermore, significant interactions were observed among queen number, brood quantity, and worker number (Tab. 2). Nevertheless, worker population growth was primarily af-

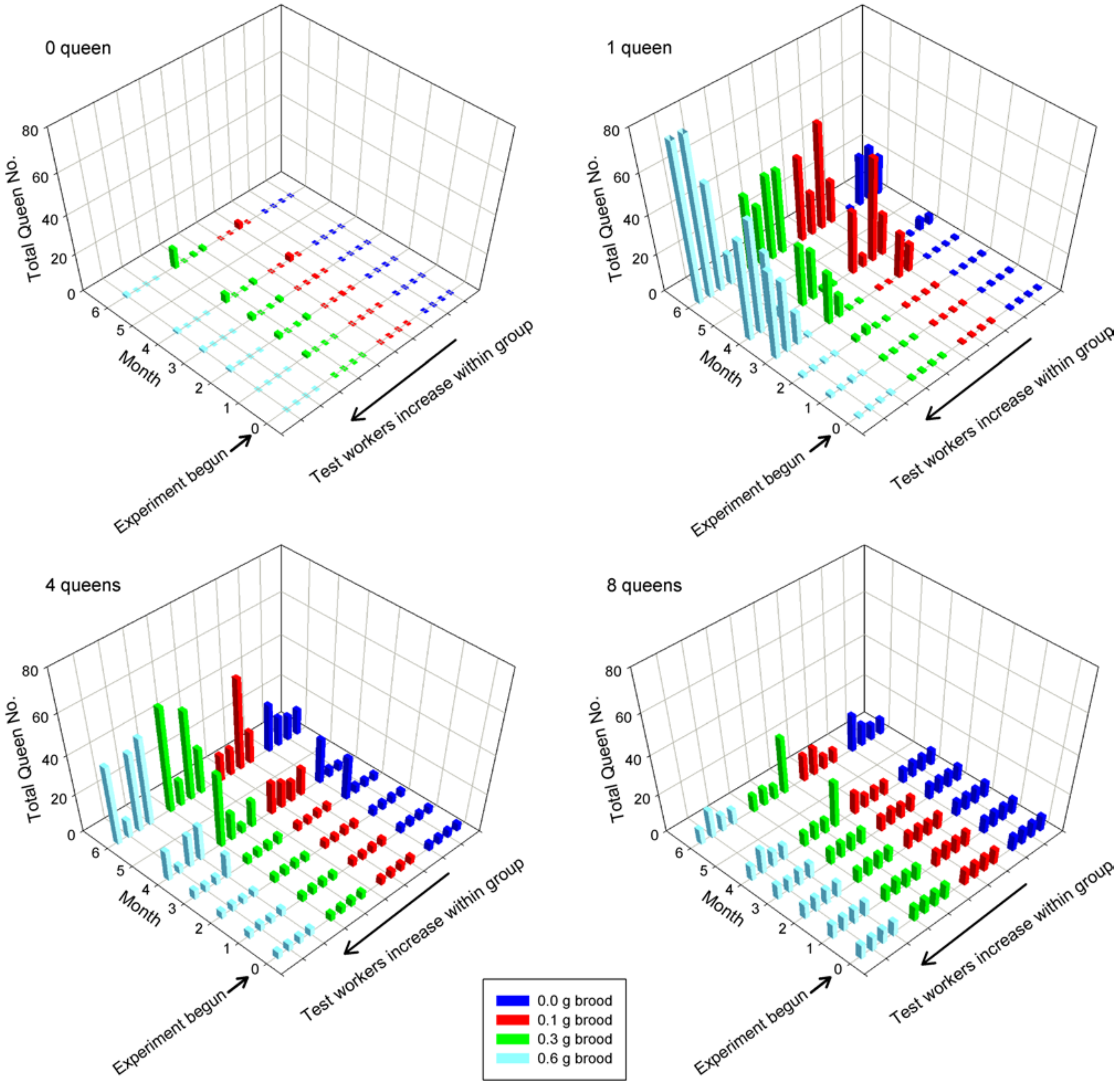

Fig. 2: The number of queens in incipient colonies of *Monomorium pharaonis* cultured using various queen number, brood quantity, and worker number combinations after one, two, three, four and six months.

fected by the initial queen number in an incipient colony (Tab. 3), as this variable accounted for 22% of the variance in worker population growth ($R^2 = 0.22$; $F = 52.19$; $df = 1; 190$; $P < 0.001$). Low, inconsistent worker numbers were recorded after six months in the incipient colonies that contained no queen, although worker numbers increased slightly during the first month, partly due to new worker emergence from the existing brood (Fig. 3). When the effects of brood quantity and worker number were added into the regression equation, they explained only an additional 6% and 2% of the variance in worker population growth, respectively (brood: $\Delta R^2 = 0.28$; $\Delta F = 35.69$; $df = 2, 189$; $P < 0.001$; worker: $\Delta R^2 = 0.30$; $\Delta F = 27.14$; $df = 3, 188$; $P < 0.001$). A preliminary statistical analysis found that the results were not affected by the possible genetic differences between colonies. As such, the colony effect was not accounted in the statistical analysis.

Discussion

The results showed that the incipient colonies that were initiated with a higher number of queens contained a lower number of queens at the end of the study. This result was particularly evident when the incipient colonies were initiated with eight queens. These colonies generally retained close to their original number of queens, although their demographics improved significantly over time. The release of high levels of sexual pheromones from the initial queens has been hypothesised to suppress the production of new queens (BERNDT & NITSCHMANN 1979, VARGO & FLETCHER 1986, 1987, VARGO & PASSERA 1991, KLOBUCHAR & DESLIPPE 2002, BOULAY & al. 2009). In the Pharaoh ant, the sexual larvae have been observed as being attacked and killed by the workers in the presence of the queens (EDWARDS 1991). This phenomenon also has been

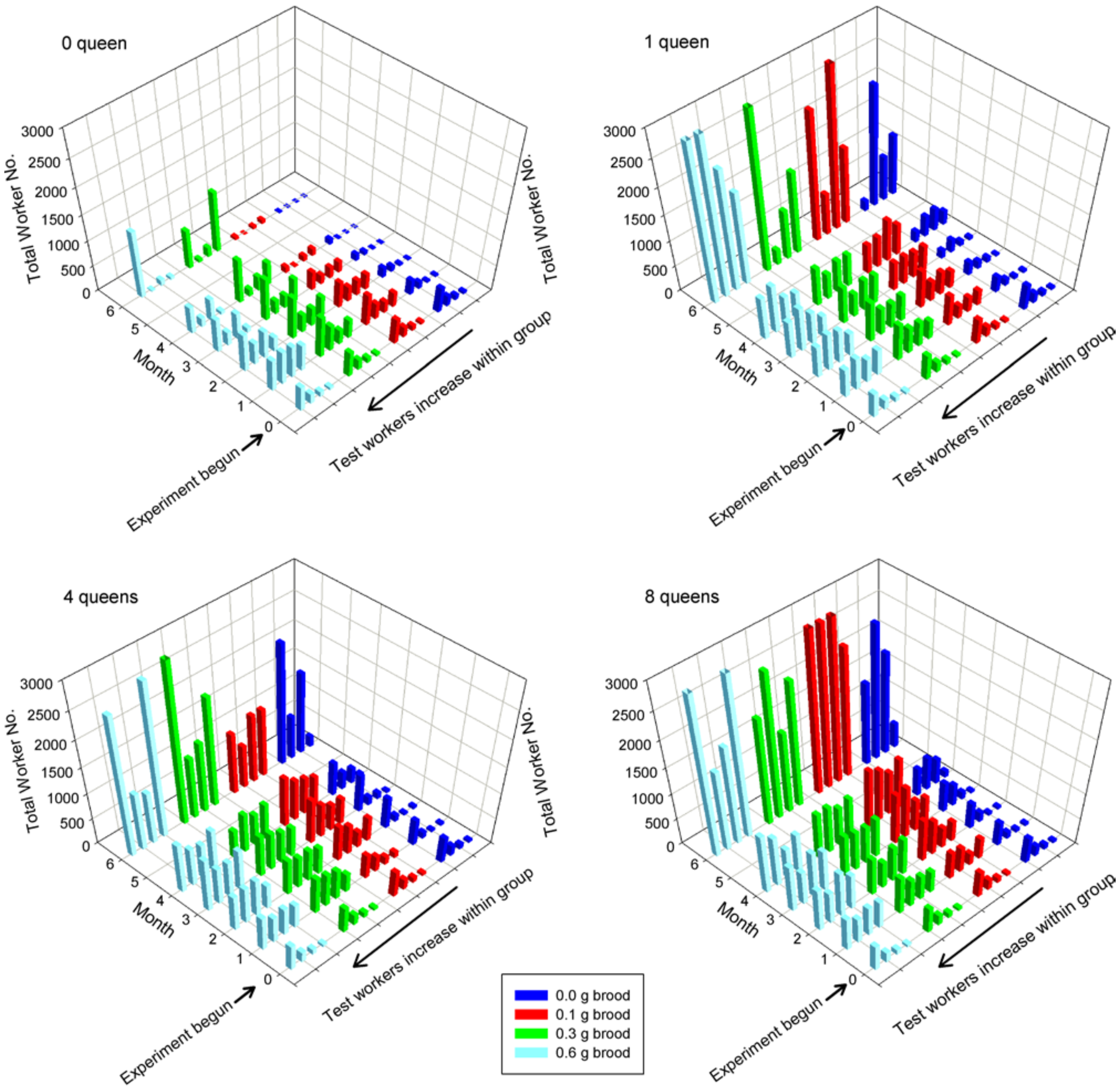

Fig. 3: The number of workers in incipient colonies of *Monomorium pharaonis* cultured using various queen number, brood quantity, and worker number combinations after one, two, three, four and six months.

observed in the Argentine ant, *Linepithema humile* (MAYR, 1868) (VARGO & PASSERA 1991, PASSERA & al. 1995), and in the red imported fire ant, *Solenopsis invicta* (BUREN, 1972) (KLOBUCHAR & DESLIPPE 2002).

It has also been suggested that the workers evaluate the presence of queens based on the quantity of eggs in the colony (EDWARDS 1987). Edwards observed that only workers were produced in the presence of a large quantity of eggs. This observation might explain why the incipient colonies that were initiated with eight queens, which could produce a large quantity of eggs, contained a lower number of queens at the end of the study. In contrast, the incipient colonies that were initiated with one queen or four queens contained approximately 2- to 11-fold more queens than the original number at the end of the study. In these colonies, workers could recognise the presence of a small quantity of eggs; thus, more queens were produced (EDWARDS 1987). Previous studies have also shown that the removal of the queens induces the formation of queen larvae in Pharaoh ant colonies (PETERSEN-BRAUN 1975, EDWARDS 1987, 1991).

Larvae play an important role in nutrient digestion, storage, and enrichment in ant colonies (LIM & al. 2005). Larvae process solid, proteinaceous food into digestible nutrients that can be readily consumed by all colony members (CHONG & al. 2002). Pharaoh ant queens rely mainly on the anal and labial secretions of larvae as their main source of nourishment. In addition, larval liquid secretions are thought to contain fecundity-stimulating substances that may promote the ovarian development of the queens (BØRGESEN 1989). This phenomenon has been reported in other species, including *Solenopsis invicta* (see TSCHINKEL 1995)

Tab. 3: Stepwise multiple regression of the caste ratio effect on *Monomorium pharaonis* queen and worker population growth. B = unstandardised coefficients; SE = standard error; t = t value; r^2 = R squared; df = degrees of freedom; F = F statistic.

Dependent variable	Details of included variables					Significance of final regression model			
	Variable	**B**	**SE**	**t**	**P**	**r^2**	**df**	**F**	**P**
Queen population growth	Constant	3.77	0.12	32.14	< 0.001	0.42	1,142	103.74	< 0.001
	Queen	-0.23	0.02	-10.19	< 0.001				
	Constant	3.60	0.14	26.75	< 0.001	0.45	2,141	57.00	< 0.001
	Queen	-0.23	0.02	-10.38	< 0.001				
	Brood	0.70	0.28	2.52	< 0.05				
Worker population growth	Constant	6.47	0.12	56.23	< 0.001	0.22	1,190	52.19	< 0.001
	Queen	0.19	0.03	7.22	< 0.001				
	Constant	6.14	0.14	44.21	< 0.001	0.28	2,189	35.69	< 0.001
	Queen	0.19	0.03	7.49	< 0.001				
	Brood	1.31	0.34	3.91	< 0.001				
	Constant	6.29	0.17	38.86	< 0.001	0.30	3,188	27.14	< 0.001
	Queen	0.19	0.02	7.62	< 0.001				
	Brood	1.31	0.33	3.98	< 0.001				
	Worker	-0.01	0.00	-2.75	< 0.01				

and *Camponotus pennsylvanicus* (DE GEER, 1773) (GIBSON & SCOTT 1990). EOW & al. (2004) reported that at least 1000 eggs, or approximately 0.1 g of brood, were needed to produce a queen in Pharaoh ant colonies. In the present study, however, the regression coefficients for brood were low, which indicates that the brood quantity present at the beginning of the experiment did not have a strong impact on the queen population growth. Furthermore, the broodless incipient colonies that contained queens began to produce new brood after one month due to the youth and fertility of the queens used in this study. In this situation, the role of nourishment allocation within the colonies may have been taken over temporarily by the workers; BØRGESEN (2000) reported that Pharaoh ant workers are capable of storing liquid food in their crops for distribution to the queens in the absence of the brood. The present results suggest that brood is not necessary needed to start a colony. Queen and worker population growth rates in the incipient colonies that were initiated without a queen or queens were low, even in those colonies initiated with numerous workers and brood. Although PEACOCK & al. (1955) showed that Pharaoh ant workers were able to rear a sexual brood from the existing brood, the results obtained in the current study suggest that the rearing of a sexual brood by the workers was rare without the presence of a queen or queens continuously laying eggs.

In this study, the number of queens was found to be inconsistent after six months for the incipient colonies that were initiated with no queen. The few queens that were found in the initially queenless colonies were hypothesised to have emerged from the eggs that had been effectively developed into sexual brood. It has also been suggested that the caste of female larvae was already determined in the eggs by the time they were separated from the main colonies at the beginning of the study (EDWARDS 1991). Furthermore, because of the inconsistency of the number of queens produced in initially queenless colonies, the worker population growth was also found to be inconsistent after six months (Fig. 3). This result further suggests that Pharaoh ant colonies are unlikely to bud from their parental colonies if colony fragmentation involves only workers and brood that cannot effectively develop into sexual brood.

Workers conduct the majority of tasks in the colony, including nest defence, foraging, and caring for the queen and brood (ROBINSON 1992). However, worker number had no effect on queen population growth and had a limited effect on worker population growth in the present study. PETERSEN and BUSCHINGER (1971) reported that Pharaoh ant colonies could be established successfully from one mated queen and a group of 300 workers. However, interactions between genetic and environmental differences might contribute to the differences observed between Pharaoh ant populations (GOODISMAN & al. 2008, LINKSVAYER & WADE 2009), and different numbers of workers (50, 100, 200, and 500 workers) were therefore tested in the present study. The statistical results showed that incipient colonies initiated with different numbers of workers had comparable queen and worker population growth. It was therefore revealed that a mere 50 workers and a queen were sufficient for colony survival and productivity. According to OI & al. (2000), Pharaoh ant colonies are prone to budding and establishing new colonies if chemical treatment does not eliminate the population. This scenario explains why Pharaoh ant management is challenging and why management programs often fail. OI & al. (2000) achieved control of multiple colonies of Pharaoh ants in the laboratory using bait containing the metabolic inhibitor hydramethylnon, but reinfestation occurred after four weeks. BUCZKOWSKI & al. (2005) reported that the application of repellent insecticides such as cypermethrin and permethrin resulted in colony budding and worsened the state of infestation. The application of a slow-killing insecticide bait such as juvenile hormone analogue is more effective at achieving Pharaoh ant colony elimination, as the workers have sufficient time to pick up the toxin and distribute it among the other colony members (i.e., queens and brood) (EDWARDS 1975, WILSON & BOOTH 1981, VAIL & WILLIAMS 1995, VAIL & al. 1996, OI & al. 2000).

The information obtained in this study further illustrates the vital role of a queen or queens in guaranteeing new colony establishment and growth after a budding event. Future work should evaluate the potential of caste-precision bait technology, which only targets a specific caste of ant, as a way to ensure more sustainable pest management without causing undesirable environmental, economic, or sociological impacts.

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