Insectes Sociaux, Paris
1981, Volume 28, n° 2, pp. 117-128

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QUANTIFICATION AND MODIFICATION OF WORKER SIZE VARIATION IN THE FIRE ANT *SOLENOPSIS INVICTA* (1) (2)

Lois A. WOOD and Walter R. TSCHINKEL (3)

Department of Biological Science, Florida State University, Tallahassee, FL 32306 U.S.A.

Reçu le 10 avril 1979. Accepté le 12 septembre 1979.

SUMMARY

Solenopsis invicta workers display a slight polymorphism over a size range of head widths from 0.45 mm to 1.50 mm. Those measuring through 0.80 mm were designated small, through 1.00 mm, medium, and through 1.50 mm, large. Mature field colonies have small, medium, and large worker ratios of 45 %, 42%, and 16 % respectively. Queens founding colonies in the lab produced initial broods of minim workers, the smallest and only individuals a queen rears by herself. As colony populations grew, size classes of larger ants accumulated until after 7 months, ants with head widths ranging in size from 0.50-1.50 mm were produced. Size class distributions were skewed such that small, medium, and large ants made up 88 %, 11 % and 1 % of the population, respectively. Newly mated queens were adopted into small (500 ants), medium (2000 ants), and large (15,000 ants) experimental colonies of field ants of three ranges of worker size variation (9 treatments). No effect of worker size variation on pupal production or pupal size was detected. The mean numbers and mean head width of pupae in their initial broods were: (1) greater than those of newly founded colonies (minims were lacking); and, (2) correlated to experimental colony size. Both pupal numbers and mean pupal size increased throughout the 4-month experiment even though worker number was kept constant.

ZUSAMMENFASSUNG

Quantifizeirung und Veränderung der Grösse der Arbeiter in der Ameisenspezies Solenopsis invicta

Arbeiterinnen der Ameise *Solenopsis invicta* zeigen einen mäßigen Polymorphismus mit einer Variation der Kopfbreite von 0.45 mm bis 1.50 mm. Arbeiterinnen bis 0.80 mm

(1) Publication no. 5 of the Fire Ant Research Team.

(2) The helpful criticism of D.S. SIMBERLOFF and L.G. ABELE are gratefully acknowledged.

(3) Send reprint requests to W.R. TSCHINKEL.

wurden als klein, bis 1.00 als mittel und bis 1.50 als groß bezeichnet. Erwachsene Kolonien bestehen durchschnittlich aus 45 % kleinen 42 % mittleren und 16 % großen Ameisen. Königinnen, die im Labor Kolonien gründen, produzieren nur « Pygmäen »-Arbeiterinnen in der ersten Brut, die kleinsten Arbeiterinnen im Leben der Kolonie. Wenn die Kolonien heranwachsen, erzeugen sie größere Ameisen, bis im Alter von 7 Monaten Kopfbreiten zwischen 0.50 und 1.50 mm erreicht werden. Die Größenverteilungen waren dann stark asymmetrisch, so daß die Kolonien aus 88 % kleinen, 11 % mittleren und 1 % großen Arbeiterinnen bestanden.

Frischbegattete Königinnen wurden im Labor von kleinen (500 Ameisen), mittleren (2000) oder großen (15,000) Kolonien mit Arbeiterinnen jeweils einer der drei verschiedenen Größenklassen adoptiert (9 Gruppen). Die Variation der Arbeiteringröße hatte keinen Effekt auf die Zahl oder Größe der produzierten Arbeiterpuppen. Andererseits waren die Zahl und Kopfbreite der Puppen in den ersten Bruten im Durchschnitt 1) größer als die von neu gegründeten Kolonien (Pygmäen-Arbeiterinnen fehlten), und 2) positiv mit des Koloniegrösse korreliert. Puppenzahl und Größe wuchsen beide im Verlauf des 4-monatigen Experiments an, obwohl die Zahl der Arbeiterinnen konstant gehalten wurde.

INTRODUCTION

Polymorphism in social Hymenoptera can be interpreted as a function of two measurable characteristics of the adult females of any species : allometric growth and intracolonial size variation (WILSON, 1968). Elementary polymorphism is exhibited in all ants by differentiated queen and worker castes. Within the worker caste evolutionary changes in allometry and size-frequency distributions have brought about the emergence of subcastes. Morphometric studies of mature colonies have characterized several degrees of polymorphism, ranging from monomorphism through complete dimorphism.

A common polymorphism among social insects is that in which the first workers in a colony's life are often the smallest, and mean worker size increases with colony size and age. To name just a few examples of ant species in which this has been noted : *Œcophylla smaragdina* (COLE and JONES, 1948) ; *Myrmecia dispar* (GRAY, 1971) ; *Myrmica rubra* (BRIAN, 1957) ; *Harpagoxenus sublævis* (BUSCHINGER and WINTER, 1975) ; *Camponotus ligniperda* (LEUTERT, 1963) ; *Pheidole pallidula* (GOETSCH, 1937) ; *Monomorium pharaonis* (PETERSEN-BRAUN, 1977). Similar observations have been reported for the subject of this report, *Solenopsis invicta* (MARKIN *et al.*, 1972, 1973 ; GREEN, 1967). The phenomenon is not restricted to ants, for nests of *Vespula vulgaris* also produce larger workers as colonies grow (ARCHER, 1972).

In addition to an increase in mean worker size, the range of worker sizes also increases with colony growth in many ants, but less information is available on the development of this variation. A few experimental studies have examined colony parameters controlling worker size-variation, or its special case, the differentiation of soldiers. The first eggs of a colony-founding queen typically develop into minim workers, the smallest workers to appear in the colony's history. A commonly posed question is whether

the small stature and short life-span of minims or the large size of soldiers is determined in the egg (blastogenic) or environmentally (trophogenic). GOETSCH (1937) transplanted eggs from newly mated queens of *Pheidole pallidula* into older colonies and found that these eggs developed mostly into minims with an occasional somewhat larger worker. GREGG (1942) reared eggs in all-worker, all-soldier, and mixed colonies of *P. morrisi* and found that soldiers inhibited the production of more soldiers. He concluded that development to soldiers was extrinsically determined. PETERSEN-BRAUN (1977) reared eggs from juvenile queens of *Monomorium pharaonis* in older colonies and found that most of the resulting workers were minims but that some were slightly larger, implying a dominance of blastogenesis with a touch of trophogenesis. PASSERA (1977) found that even the eggs of founding queens of *Pheidole pallidula* can develop into soldiers if reared in the appropriate colonies. Soldier production in this species is inhibited when the percentage of adult soldiers is greater than about 4 % (PASSERA, 1977). All-worker colonies numbering 750 or more produce a higher percentage of soldiers than do smaller groups. HAVERTY (personal communication) found that differentiation to the soldier caste in the termite, *Coptotermes formosanus*, proceeded at a lower rate in smaller groups.

Solenopsis invicta colonies display slight polymorphism with considerable size variation. Worker head widths range from 0.45 mm (minims) to 1.50 mm (largest workers) and the size frequency distribution of a mature colony's worker population is skewed to the right. Field observations indicate that the proportion of major workers reaches a maximum in large colonies. HORTON and HAYES (1974) reported the presence of minor and major workers of undefined dimensions, but gave no information on frequency distributions, colony age or colony size. On the other hand, MARKIN *et al.* (1973) provided a timetable from the field of the appearance and proportions of 4 arbitrary size-classes of workers as defined by weight (minim, minor, media, major). KHAN *et al.* (1967) estimated the time until the first appearance of minor, media and major workers in the lab.

MATERIALS AND METHODS

Newly mated fire ant queens were collected in and around Tallahassee, Florida, U.S.A., from late August to late September 1977, and again in June 1978 during clear afternoons following rainstorms. Forty-eight queens were used to found incipient laboratory colonies and the remainder were used for adoption into experimental colonies composed of worker ants collected from field colonies. Plastic petri dishes with a continually moist plaster of Paris patty on the bottom served as nests. Each nest was placed in a Teflon (polytetrafluoroethylene) coated plastic box. Colonies were kept in a 28° C insectary and provided with an abundance of 0.5 M sucrose and freshly killed mealworms.

A. - Incipient lab colonies

The number of workers produced by all 48 colonies was recorded every week for the first 10 weeks and then every 2 or 3 weeks after that for a total of 7 months. Distribution of workers sizes was determined in the following manner: The live workers were placed in the top sieve of a stack of U.S.A. Standard Testing Sieves (geological sieves) whose mesh size decreased from top to bottom. The inner walls of the sieves were coated with Teflon (polytetrafluoroethylene) so that the ants could not climb back up. A warm light over the top sieve encouraged the ants to make their way through the lowest sieve they could fit through and to accumulate there. This process was also hastened by banging the sieves occasionally to keep the ants moving. The head widths of ants trapped in the bottom pan and the three smallest sieves were 0.45-0.80 mm, in the medium-sized sieves, 0.85-1.10 mm, and in the largest sieves 1.15-1.50 mm. These were designated small, medium and large, respectively.

B. - Experimental colonies

The experimental colonies were designed to test the effects of colony size and worker size variation on the numbers and sizes of pupae in initial and subsequent broods produced by a newly mated queen. Colonies were of three sizes (500, 2000, and 15,000 ants) designated small, medium, and large, respectively, and three levels of polymorphic make-up (ants measuring: (1) 0.45-0.80 mm; (2) 0.45-1.10 mm; and, (3) 0.45-1.50 mm) defining 9 unique treatments. Nest size was proportional to worker number to maintain a constant density at approximately 1 ant/mm^2. The original number of adults in each experimental colony was maintained by replacing dead workers with ants from the original field colony. Once queens were established, colonies were observed every 2 to 3 days for eggs and larvae. Following production of the first brood of pupae, colonies were monitored weekly, at which time pupae were removed, counted, measured and discarded. The head width of each pupa was measured to the nearest 0.05 mm. under a Wild dissecting microscope (50 X objective) using an ocular micrometer. A mean head width was calculated for each week's brood from every colony.

C. - Data analysis

A packaged Analysis of Covariance (ANCOVA) computer program was utilized for testing whether treatments significantly affected the results of the experiments. This test compares linear regressions, and is appropriate since curve-fitting programs indicated linear functions. The distribution of worker sizes in a brood was analyzed by calculating a *'skewness index'*, a modification of the skewness coefficient descibed by Snedecor and Cochran (1967). This index: (1) facilitated comparison of small and large samples; and, (2) indicated that the sample deviated significantly ($p < 0.01$) from normality when its value was 2.5 or greater.

Abb. 1. — Durchschnittliche Anzahl Arbeiterinnen in jungen, wachsenden Laborkolonien, dargestellt als die Summe der mittleren Anzahl in jeder Größenklasse.
Die durchschnittliche Anzahl von Ameisen jeder Größenklasse wurde jeweils zu der (den) mittleren Anzahl (en) der darunterliegenden Größenklasse (n) addiert, so daß zu jedem einzelnen Zeitpunkt der Abstand zwischen zwei Linien die mittlere Anzahl Ameisen dieser Größenklasse angibt. Die Anzahl der Ameisen nahm mit Heranwachsen der Kolonien in allen Größenklassen außer der kleinsten (Pygmäen) zu. Verbindungslinien für die zahlenmäßig gering vertretenen Größenklassen wurden nicht eingezeichnet.

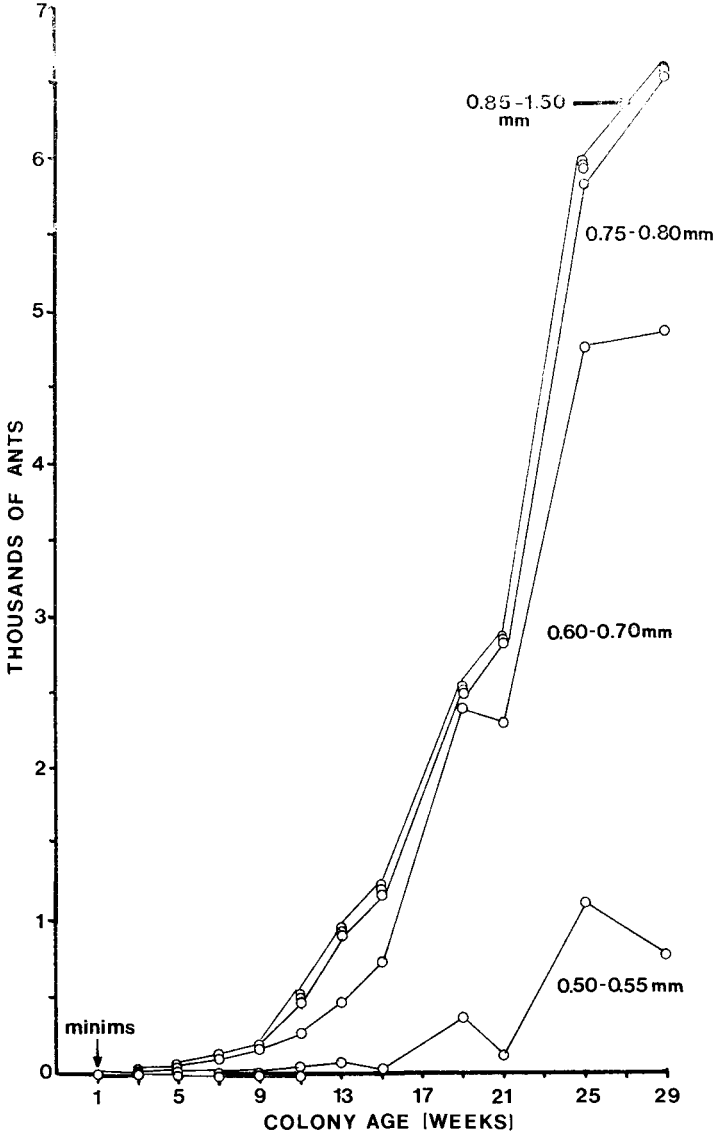

Fig. 1. — The average number of ants in growing, incipient laboratory colonies expressed as the sum of the mean numbers of ants in each size class.
The average number of ants in each size range was added to the average number(s) in the size range(s) below so that, at any given time, the interval between two lines indicates the average number of ants in that particular size range. All size classes other than minims accumulated ants as colonies grew. Lines separately bounding less-represented size classes were not drawn in.

RESULTS

A. - Incipient colonies

The populations of both the sieved and unsieved colonies increased throughout the experiment so that by the end of 7 months, the colonies reached mean population sizes of about 6 200 and 8 000, respectively. The first brood of all colonies emerged by 36 days. It was composed entirely of minims, the smallest size class (0.45 mm in head width) a queen ever produces. Minims were absent after 3 months. One-month-old colonies (from first adult workers) have population sizes of around 100 ants with head widths ranging in size from 0.45 to 0.70 mm. At 3 months of age, colonies averaged 1 000 ants with head widths ranging from 0.45 to 1.00 mm. The modal size class established at this time (0.60 to 0.70 mm) persisted as the modal class through the rest of the experiment. These data are summarized in figure 1.

The accumulation of larger size classes is not haphazard and proceeds gradually. Most colonies numbering less than 100 ants had worker size distributions in which the mode and the mean coincided or the mean was slightly higher than the mode. This produces skewness indices with a low or negative value. As colonies grew to between 100 and 300 ants and accumulated their first medium-sized ants (0.75 to 0.80 mm), indices gradually increased until some showed significant skew. Most colonies between the sizes of 300 and 1 000 were significantly skewed, and some displayed the highest skewness indices of all because there were only a few ants in the newly represented upper medium size range (1.05 to 1.10 mm). After colonies grew to over 1 000 ants, all of the size distributions were significantly ($p < 0.01$) skewed.

B. - Experimental colonies

Colony size and elapsed time both affected pupal production. Initial broods, from which minims were absent, emerged between 37 and 70 days after queens were adopted. The number and mean head width of worker pupae in initial broods were both correlated to colony size, but not to worker size variation.

The number of pupae in each experimental colony's brood fluctuated week by week, but the mean numbers increased every time. The mean number of pupae produced was always lowest in small colonies, intermediate in medium colonies, and highest in large colonies. Four of the large colonies produced a few reproductives during the course of the experiment.

The mean head width of worker pupae was always greatest in large colonies, intermediate in medium colonies, and lowest in small colonies (fig. 2). The differences in mean head width were significant (ANCOVA; $p < 0.005$) but the rates of increase in mean head width were similar in all 3 colony sizes.

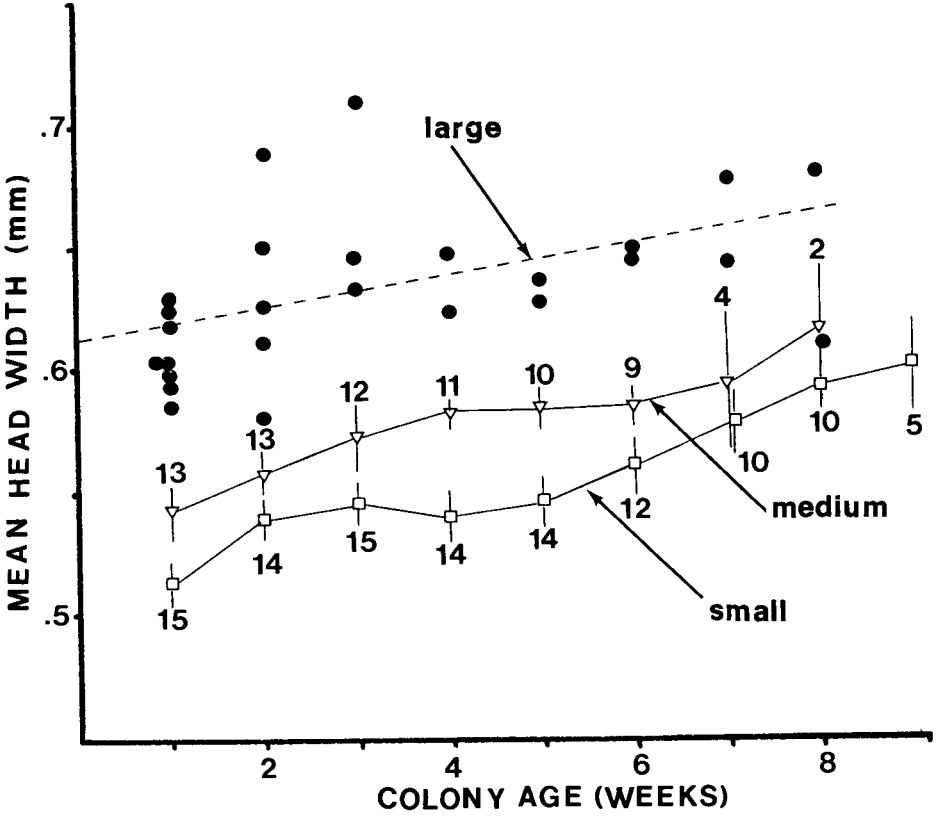

Fig. 2. — Mean head width of pupae produced by all experimental colonies as a function of elapsed time.
Mean pupal head widths of broods from both small and medium colonies were averaged each week and plotted along with one standard error bars and number of colonies sampled. The linear regressions are: small colonies, $y = .01\ x + .51$, $r = .56$; and, medium colonies, $y = .01\ x + .54$, $r = .52$. The linear regression through the individual records from large colonies is, $y = .04\ x + .61$, $r = .43$.

Abb. 2. — Durchschnittliche Kopfbreite von Puppen aus allen Experimentalkolonien in Abhängigkeit vom Alter der Kolonien.
Die durchschnittlichen Kopfbreiten von Puppen aus kleinen und mittleren Kolonien wurden wöchentlich ermittelt und mit 1 Standardabweichung eingetragen. Die jeweilige Anzahl von Völkern ist angegeben. Die Regressionsgleichungen lauten: für kleine Kolonien: $y = 0{,}01\ x + 0{,}51$; für mittlere Kolonien: $y = 0{,}01\ x + 0{,}54$, $r = 0.52$. Die Regressionsgleichung für die einzeln dargestellten Daten großer Kolonien lautet: $y = 0{,}04\ x + 0{,}61$, $r = 0{,}43$.

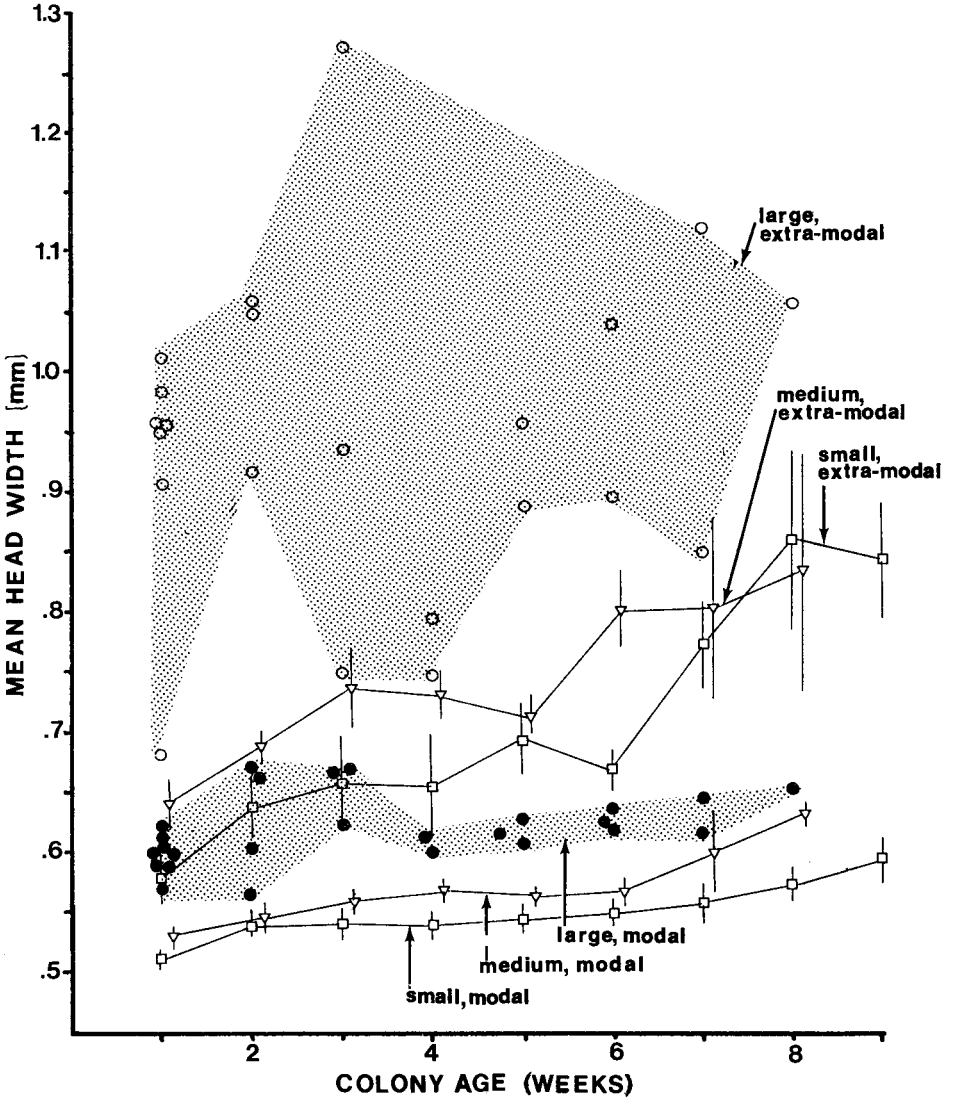

Fig. 3. — Mean head widths of individuals in modal and extra-modal groups. Data were averaged across all small colonies and across all medium colonies each week for both the modal and extra-modal groups. Means of each large colony's modal group and extra-modal group are plotted individually.

Abb. 3. — Mittlere Kopfbreiten von Arbeiterinnen in den modalen und außermodalen Gruppen. Für kleine und mittlere Kolonien wurden wöchentlich alle Werte sowohl der modalen als auch der extramodalen Gruppen gemittelt, von den großen Kolonien sind die Werte der modalen und extramodalen Gruppe jeder Kolonie einzeln eingetragen.

The data from each experimental colony's brood were further analyzed by subdividing worker pupae sizes into two groups. The first includes individuals that measure within two standard deviations on either side of the mean, encompassing the smallest individuals and the mode of the total distribution (modal group). The second is made up of those larger individuals beyond the two standard deviation cut-off (extra-modal group). Data from small, medium, and large colonies are summarized in figure 3.

The mean head width of pupae in both the modal and extra-modal groups of small and medium colonies increased fairly regularly with time. The increase in mean head width was greater in the extra-modal groups because these pupae were of increasingly larger sizes, whereas, in the modal group, there were greater numbers of pupae being produced within a smaller size range. Not every small and medium colony produced individuals in the extra-modal group every week. All large colonies produced more and larger pupae in all broods than did small and medium colonies. The average number of pupae in the extra-modal group ranges from 0.3 to 4.4 pupae/small colony and 1.4 to 21.0 pupae/medium colony. In large colonies, the average numbers ranged from 3.5 to 129.5 pupae/colony. Few ants as large as those in the extra-modal group from large colonies appeared in small and medium colonies during the course of the experiment. The largest ants ever produced from small colonies measured 0.79 mm and from medium colonies, 0.94 mm.

Queens in newly founded colonies produced an increasing range of worker sizes on a different schedule than newly mated queens adopted into experimental colonies. The mean head width of individuals in incipient colonies surpassed that of pupae produced by small and medium experimental colonies by the fifth week of the experiment. By the seventh week, incipient colonies produced individuals comparable in mean size to those produced by large experimental colonies.

In summary, incipient colonies' initial broods are comprised entirely of minims while the initial broods of experimental colonies are composed exclusively of larger workers. Experimental colony size has a marked effect on the mean size and mean number of pupae produced, and each of these increases as the queen and the colony ages. Fire ant colonies typically produce a preponderance of small workers, causing the size distribution to be positively skewed.

DISCUSSION

Incipient fire ant colonies increased in size at a high rate during the 7 months they were monitored. This conforms to data from other social insect colonies where colony size generally increases exponentially in its initial growth phase (WILSON, 1971) and eventually tapers off to some asymptotic limit. A typical fire ant colony over three years old contains

100,000 to 150,000 workers but sizes of about 230,000 ants have been reported (LOFGREN *et al.*, 1975).

BRIAN (1957), and PASSERA (1972) both showed that an increase in the worker force increases a queen's oviposition rate. Similarly, in the present study, the mean number of pupae in the first brood of a newly mated fire ant queen in experimentally controlled colonies of 3 different static sizes was correlated to colony size. However, in contrast to Brian's finding, the mean number of pupae increased with time in all experimental colonies even though colony size was not increasing.

Obviously, the number of eggs laid by a queen can't be assumed to be a simple multiple of the number of workers but is probably an additive function of both colony size and queen age. A queen's oviposition rate must level off, otherwise colonies would grow indefinitely. In honeybee colonies of around 20,000 workers, the queen maintains an oviposition rate of a thousand or more eggs a day (WILSON, 1971) which is needed to defray the costs of mortality and production of reproductives. The physical constraints of a queen's reproductive system probably sets this limit.

Species of social insects are characterized not only by the kinds of castes they produce, but also, by the ratios of individuals belonging to each caste within single colonies (WILSON, 1968). Mature fire ant colonies display a skewed distribution of worker sizes where the mode falls within the small size range, the mean in the medium size range, and less than 20 % of the population constitutes the wide upper range of large sizes. In their initial stages, fire ant colonies are made up of minims and then ants of small sizes. As they grow, colonies accumulate increasingly larger ants gradually. By 7 months of age, incipient laboratory colonies produce ants measuring over 1.15 mm in head width, although in small proportions (less than 1 %). Field colonies of that age accumulated slightly larger (3 %) proportions of " majors " (MARKIN *et al.*, 1973 ; HORTON and HAYES, 1974). Observations of other Hymenopteran species found that smaller field colonies display a smaller mean size of workers than larger colonies (GRAY, 1971 ; BRIAN, 1957 ; ARCHER, 1972 ; LEUTERT, 1963) and worker size increases throughout a season (PASSERA, 1977 ; PETERSEN-BRAUN, 1977 ; GRAY, 1971).

All the initial broods of experimental colonies included only worker pupae that were larger than minims. The absence of minims suggests that either the queen's first minim-biased offspring were cannibalized or that the larvae developed into larger workers. The fact that the first pupae in some experimental colonies emerged within the same developmental time as did minims in incipient laboratory colonies suggests that the latter explanation is possible. The mean head width of the first worker pupae in experimental colonies was correlated to colony size and subsequent broods included individuals of even larger dimensions, consequently increasing mean head width over time. During the experiment the mean head width of

workers in incipient colonies surpassed that of pupae in broods of small and medium colonies. BRIAN (1953) showed that an increase in the number of nurse workers increases worker progeny size. Individuals being produced by the experimental colonies were continually being removed, so there was no influx of young workers, those typically found nursing the queen and her brood. This lack of callows apparently didn't limit the potential for large colonies to produce large workers along with reproductives. However, the effect may have accounted for the fact that incipient colonies rapidly surpassed small and medium colonies in mean worker size.

While the final determining factor of an insect's developmental schedule is physiological (WIGGLESWORTH, 1961 ; BRIAN, 1974) the path along which that development progresses ultimately may depend on the treatment the larva receives in its early stages. BRIAN and BRIAN (1951) propose that as a colony grows there is an increase in the worker to larva ratio, which affords better larval care and, therefore, potentiates emergence of larger workers. In the present study, where experimental colony size remained constant, pupal production nevertheless increased in both numbers and mean size. A colony that has grown beyond the critical incipient stages may trade numerical strength for the benefits gained by producing larger individuals for its worker force. While caste polyethism is not as distinct in *S. invicta* as in genera such as *Pogonomyrmex, Atta, Pheidole,* and *Œcophylla,* larger workers are capable of carrying larger objects. In order to complete the final analysis of the adaptive significance of worker size variation in *Solenopsis invicta,* studies of standing age distributions within the worker caste and of temporal polyethism are necessary.

References

ARCHER M.E., 1972. — The significance of worker size in the seasonal development of the wasps *Vespula vulgaris* (L.) and *Vespula germanica* (F.). *J. Entomol. Ser. A. Gen. Entomol., 46,* 175-183.

BRIAN M.V., 1953. — Brood-rearing in relation to worker number in the ant Myrmica. *Physiol. Zool., 26,* 355-366.

BRIAN M.V., 1957. — The growth and development of colonies of the ant Myrmica. *Ins. Soc., 4,* 177-190.

BRIAN M.V., 1974. — Caste differentiation in *Myrmica rubra:* The role of hormones. *J. Ins. Physiol., 20,* 1351-1365.

BRIAN M.V., BRIAN A.D., 1951. — Insolation and ant population in the west of Scotland. *Trans. R. Entomol. Soc. Lond., 102,* 303-330.

BUSCHINGER A., WINTER U., 1975. — Der Polymorphismus der Sklavenhaltenden Ameise *Harpagoxenus sublævis* (Nyl.). *Ins. Soc., 22,* 333-362.

COLE D., JONES L., 1948. — A study of the weaver ant *Œcophylla smaragdina* (Fab.). *Am. Midl. Nat., 39,* 641-651.

GOETSCH W., 1937. — Die Entstehung der « Soldaten » im Ameisenstaat. *Naturwiss., 25,* 803-808.

GRAY B., 1971. — A morphometric study of the ant species, *Myrmecia dispar* (CLARK) (Hymenoptera: Formicidæ). *Ins. Soc., 18,* 95-110.

GREGG R.E., 1942. — The origin of castes of ants with special reference to *Pheidole morrisi* Forel. *Ecol., 23,* 295-308.

GREEN H.B., 1967. — The imported fire ant in the southeastern United States. *Bull. Miss. State Univ. Agric. Exp. Station,* N° 737.

HORTON P.M., HAYES S.B., 1974. — Occurrence of brood stages and adult castes in field colonies of the red imported fire ant in South Carolina. *Environ. Entomol., 3,* 656-658.

KHAN A.R., GREEN H.B., BRAZZEL J.R., 1967. — Laboratory rearing of the imported fire ant. *J. Econ. Entomol., 60,* 915-917.

LEUTERT W., 1962. — Beitrag zur Kenntnis des Polymorphismus bei *Campanotus ligniperda. Latr. Mitt. Schweiz. Entomol. Gesellsch, 35,* 146-154.

LOFGREN C.S., BANKS W.A., GLANCY B.M., 1975. — Biology and control of imported fire ants. *Ann. Rev. Entomol., 20,* 1-30.

MARKIN G.P., COLLINS H.L., DILLIER J.H., 1972. — Colony founding by queens of the red imported fire ant, *Solenopsis invicta. Ann. Entomol. Soc. Am., 65,* 1053-1058.

MARKIN G.P., DILLIER J.H. COLLINS H.L., 1973. — Growth and development of colonies of the red imported fire ant, *Solenopsis invicta. Ann. Entomol. Soc. Am., 66,* 803-808.

PASSERA L., 1972. — Etude de quelques facteurs réglant la fécondité des reines de *Plagiolepis pygmæ* Latr. (Hym. Formicidæ). *Ins. Soc., 19,* 369-388.

PASSERA L., 1974. — Différentiation des soldats chez la fourmi *Pheidole pallidula* (Nyl.) *(Formicidæ, Myrmicinæ). Ins. Soc., 21,* 71-86.

PASSERA L., 1977. — Production des soldats dans les sociétés sortant d'hibernation chez la fourmi *Pheidole pallidula* (Nyl.) *(Formicidæ. Myrmicinæ). Ins. soc., 24,* 131-146.

PETERSEN-BRAUN M., 1977. — Untersuchungen zur sozialen Organisation der Pharaoameise *Monomorium pharoanis L. (Hymenoptera, Formicidæ)* II. Die Kastendeterminierung. *Ins. Soc., 24,* 303-318..

WIGGLESWORTH V.B., 1961. — *Insect polymorphism - A tentative synthesis.* From Symposia of the Royal Entomol. Soc. of London : N° 1, " Insect Polymorphism ", ed. J.S. Kennedy, pp. 103-114.

WILSON E.O., 1968. — The ergonomics of caste in the social insects. *Am. Nat., 102,* 41-66.

WILSON E.O., 1971. — *"The Insect Societies"*. Harvard Univ. Press. Cambridge, Mass. 548 p.