Functional Ecology 1990,
4, 531–541

Presence of brood affects caste differentiation in the social wasp, *Polistes exclamans* Viereck (Hymenoptera: Vespidae)

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Abstract. In social insect colonies the sterile individuals that assume the worker role realize their reproductive potential through working and rearing the queen's brood. We have examined the role of the presence of brood in the nest as a determinant of caste in the social wasp *Polistes exclamans* Viereck. We predicted that wasps in colonies where there was no brood would behave like future queens, while wasps in colonies in which brood care was an option would behave like workers. Brood presence was manipulated by removing eggs and larvae or the whole nest from experimental colonies and leaving brood in control colonies. Ability to tolerate cold temperatures was used as an indicator of caste when comparing females emerging in experimental colonies to females emerging in control colonies. Females emerging in experimental colonies survived longer at cold temperatures than those emerging in control colonies. This indicates that females developed characteristics more typical of future queens in response to deprivation of brood. *P. exclamans* is characterized by small colonies whose nests are destroyed frequently. Therefore caste plasticity in adult females of *P. exclamans* is advantageous.

Key-words: Caste determination, nesting cycle, *Polistes exclamans*, production schedules

Introduction

Models of caste systems have analysed the problems of how many castes colonies of social insects should produce (Oster & Wilson, 1978) and when they should produce which castes (Macevicz & Oster, 1976; Oster & Wilson, 1978; Greene, 1984; Walker & Stamps, 1986). Optimization models show that caste number proliferates and specialization accompanied by the surrender of individual reproduction increases since this results in increased efficiency and increased colony productivity (Oster & Wilson, 1978). However, task overlap, unpredictable environmental variation and individual-level selection can act as counterforces inhibiting caste proliferation (Hamilton, 1964a,b; Jeanne, 1986; Franks, 1987).

The preceding factors can also affect the timing of caste production. Macevicz & Oster (1976) have shown that a colony of social insects will maximize its output of reproductives if it produces only workers during the growing season and then, one generation before the end of the season, switches to exclusive production of sexuals (but see Greene, 1984). This model requires that the end of the nesting cycle be predictable with a certain degree of accuracy. In some species, however, factors such as predation and parasite infestations are quite unpredictable and can make it impossible for a colony to predict when the end of the growing season will arrive, making it, in turn, impossible to predict when the switch from workers to reproductives should occur. Under circumstances such as these, the optimum colony response is likely to involve females that are not fixed with regard to caste at emergence.

Here we examine the caste system of such a species: *Polistes exclamans* Viereck, in Houston, Texas. It is a species of social wasps with no morphological castes (Eickwort, 1969; Strassmann *et al.*, 1984). Colonies experience frequent queen turnover and a high degree of failure due to parasitisation, predation and high worker mortality (Strassman, 1981; Strassman & Meyer, 1983; Strassmann, 1985a), making it difficult to predict when the end of the nesting cycle will arrive. Prey availability and foraging opportunities add to the unpredictability, because total precipitation and the number of days with significant amounts of rain fluctuate from year to year for any given month (Strassmann, 1989). Furthermore, because of frequent queen death, workers might end up rearing brood to which they are less related than they are to sisters (Strassmann & Meyer, 1983;

Strassmann, 1985b). This makes it disadvantageous for the individual to be committed to the worker caste at eclosion. In fact, following queen loss, in colonies of *P. annularis* in Austin, Texas, emerging females turn into gynes earlier than they would if the original queen was still present (Strassmann, 1989).

Under circumstances such as the ones described above, *P. exclamans* colonies might benefit from producing individuals whose caste is not determined until adulthood, using a combination of social and environmental cues to determine which role the individual will assume. Such individuals would be capable of responding to unforeseen changes in the social and physical environment. In case the nest is lost at a time when the colony would no longer be able to rebuild it, individuals of flexible caste could become gynes and the colony's reproductive output would not be lost. This kind of strategy would be advantageous for the individual too, since it would not renounce direct reproduction until it could establish whether or not the opportunity for indirect reproduction through sisters would be available.

As in other species of the genus, *P. exclamans* queens, workers and the non-working females (henceforth called gynes) that will mate and overwinter to start new nests in the spring, are distinguished by their behaviour (West Eberhard, 1969; Strassmann & Meyer, 1983), by the relative development of the fat body and ovaries (Eickwort, 1969; Haggard & Gamboa, 1980; Turillazzi *et al.*, 1982; Strassmann *et al.*, 1984), by the ability of gynes to survive longer than workers when exposed to cold temperatures (Strassman *et al.*, 1984; Gervet *et al.*, 1986; C. R. Solís, unpublished observation). Strassmann *et al.* (1984), using Eickwort's (1969) fat body criterion to separate workers from gynes, have shown that in *P. exclamans,* ability to survive prolonged exposure to cold temperatures is a good predictor of caste. C.R. Solís (unpublished observation) has shown that these differences in ability to survive at cold temperatures are not only due to the presence of higher lipid reserves in gynes, but also to differences in metabolism between gynes and workers.

Hypothesis about the role of brood loss in caste determination

We predict that in *P. exclamans* the opportunity to work by raising brood is one of the factors that affects the development of individuals into gynes or workers. If females emerge from a nest in which they have no brood to work for, either because it is absent or because they have lost their nest to predators late in the season, they should become like gynes. Females emerging from nests in which brood is present should become workers, as should females emerging from nests without adult wasps, where work is especially necessary to rear the brood. If our predictions are met, they will indicate that caste can be determined imaginally, allowing individuals or colonies to respond to season length, brood predation or reduction in relatedness towards attended brood.

Materials and methods

To test our hypothesis we simulated, in the laboratory, some of the common events that can prevent *P. exclamans* colonies from reaching the end of the growing season in Houston, Texas. We decided to examine the role of brood loss, nest loss and loss of all adults on caste development. Our assay of caste is ability to survive at cold temperatures. Females are classified as gynes if they survive prolonged exposure to 5 °C and as workers if they do not. We expected that females from broodless colonies would turn into gyne-like females and would show good survival at cold temperatures. We also expected that females from colonies with brood would behave like workers and that their survival at cold temperatures would be poor. To examine the possibility that differential survival to 5 °C could be related to nutritional differences acquired during the experiment, and not to the development of any other gyne-like characters, we measured the lipid reserves of a subsample of each kind of female, before they entered the cold exposure period. If wasps with higher lipid reserves survive better at 5 °C, the only thing that could be concluded would be that survivorship had been enhanced by the availability of more nutrients. However, better survivorship in the absence of nutritional differences would lead us to conclude that differences in metabolism like those of gynes and workers (C.R. Solís, unpublished observation) had been developed. We also compared them in terms of fresh weight.

Collection dates and colony characteristics

We made three collections of *P. exclamans*' colonies, one in 1985 and two in 1986. In 1985, we collected 24 nests from 13 to 16 July. In 1986, we collected 41 nests from 23 to 31 July (1986a), and 24 nests from 26 August to 1 September (1986b). The colonies were collected during the late afternoon and early evening (for techniques see Strassmann, 1979), and kept in plastic bags in a cooler with ice to assure survival while on the way to the laboratory. They were kept in the cooler for 2–3 h.

Colonies were assigned by random draw without replacement (Freund, 1979) to one of the following treatments to simulate nest infestation by parasites or predation events:

1 Removal of larvae and eggs, which left adult females and pupae with a nest.

2 Removal of the whole nest, leaving only adult females present at the time of collection.

3 Controls, adult females with intact nest.

For the 1986 experiments, a fourth treatment was added: removal of the adults present on the colony, leaving females emerging from pupae in the nest with the intact brood but no previous adults. Treatment 1 simulated loss of brood due to parasites and ant raids. Treatment 2 simulated nest loss due to predation by vertebrates. Treatment 3 represented a nest under natural conditions at that time of the year; and treatment 4 simulated nest orphanage due to predation on workers away from the nest. All these events have been observed in the field (Strassmann, 1981; C.R. Solís, unpublished observation).

All females present at the time of collection were marked on the thorax with a dot of Testor's PLA® enamel, using different colours for different treatments. This allowed us to distinguish females that eclosed after the colonies were collected and treated from those present at collection. Females that eclosed before colony collection will be referred to as field-eclosed females, while females that eclosed during the experimental period will be referred to as laboratory-eclosed females.

Our hypothesis requires that colonies do not differ among treatments for any other factors that could affect opportunity to work, so that observed differences could be attributed to treatment alone. Such factors include: number of nestmates; number of larvae per female; number of empty cells; and number of parasitized cells. Therefore, nests of each collection were compared between treatments to ensure that the degree of colony development and factors that affect opportunity to work were not significantly different.

For all the colonies, nests did not differ significantly among groups for any of the factors that could have affected opportunity to work before the colonies were collected ($P > 0{\cdot}10$, Kruskal–Wallis test; Fig. 1). Therefore we can say that observed differences in response to treatments are not the result of any of these factors. The collected colonies did not differ significantly between the three experimental dates either ($P > 0{\cdot}10$, Kruskal–Wallis test).

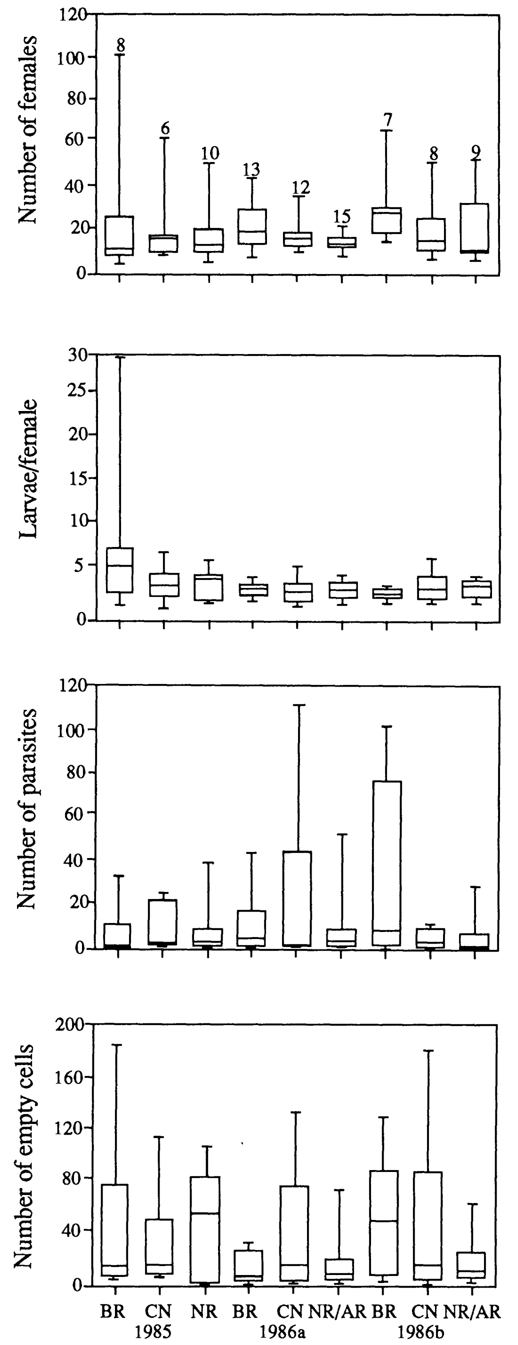

Fig. 1. Percentile distribution and range of the characteristics of the colonies used in the experiments. CN, control nests; BR, brood-removed nests; NR/AR, nest removed/adults removed nests. The error bars indicate ±1 SE; the numbers indicate sample size.

Rearing conditions and laboratory manipulations

Colonies were placed in plexiglass and wire screen cages (15 × 15 × 15 cm) and kept under a midsummer light cycle (light:dark = 14:10) for 16 days. The mean maximum temperature in the rearing room varied between 28·2 and 29·7 °C. The mean minimum temperature fluctuated between 23·2 and 24·5 °C. The wasps were fed *ad libitum* from an artificial diet of 40 g sucrose, 40 g dextrose, 1 g dried yeast and 40 g protein (egg albumin in 1985; casein in 1986) in 400 ml of water. In addition, water was constantly available as was coloured construction paper for nest building. At the end of the treatment periods, the nests were examined to determine whether or not further construction and egg laying had taken place during the treatment. The colonies were never disturbed during the 16-day treatment period and females emerging from the pupae remained with the rest of the individuals present on the nest.

As a result of the treatments, six different kinds of females were available at the end of the experimental period: **i** Field-eclosed females without brood but with a nest; **ii** Laboratory-eclosed females without brood but with a nest. **iii** Field-eclosed females without brood and without a nest. **iv** Field-eclosed females with a nest and with brood. **v** Laboratory-eclosed females with a nest, with brood and field-eclosed females. **vi** Laboratory-eclosed females with brood and a nest, but without field-eclosed adults (for 1986).

Assay for caste

After 16 days in the rearing room, all adults were collected and put in groups of three in petri dishes (1985, dish diameter = 50 mm; 1986, dish diameter = 100 mm) containing wet filter paper. The dish was wrapped in black plastic and put in an incubator at 5 °C, in total darkness. Each dish contained only females from the same nest and of the same kind (i.e. i–vi). Mortality was assayed by drawing independent samples without replacement every 3 days. Only wasps capable of co-ordinated movement (i.e. capable of walking with movement of all six legs and without 'twitching') were considered to be alive. Wasps of doubtful health were left in unwrapped petri dishes at room temperature and checked again the next day. Only in two cases out of over 1300 wasps assayed were wasps alive when they were initially scored as dead. The sampling schemes for 1985 and 1986 were different. In 1985 we continued to open petri dishes until we had a sample of about 10 live wasps of each treatment. The sampling period lasted 9 days. In 1986 we opened the same number of petri dishes at each date. However if a surplus of one treatment was available, more were sampled. The sampling period in 1986 lasted 24 days. Ratios of live/total (live + dead) were determined for each date.

Reserve lipids and weight determination

A subsample of each kind of female (i–vi) was drawn at the end of the treatment period of the 1986b experiment to determine the levels of reserve lipids (triacylglycerols and fatty acids) and fresh weight. The lipids were extracted using a modified Folch, Lees & Sloane-Stanley (1957) procedure. After the wasp was weighed on an analytical balance (H5, Mettler Instrument Corp., Hightstown, New Jersey, USA), it was put in a test tube with butylated-hydroxy-toluene(BHT) in an ice bed. The wasp was ground in 3 ml of chloroform:methanol (1:2 v/v) using a motorized tissue homogenizer (Tekmar Tissuemizer, Tekmar Co., Cincinnati, Ohio, USA) for 1 min. The homogenizer probe was washed into the homogenate with 2 ml of the same chloroform:methanol solution. The fat was extracted for 1 h under rotation at 4 °C. After filtering the supernatant the homogenate was washed and re-extracted in chloroform:methanol for 12 min. The extracts were combined and washed with 1 ml chloroform and 3 ml of water. After removing the organic phase, the aqueous phase was washed again with 1 ml of chloroform, which was combined with the organic phase. The organic phase was washed with 2 ml of 0·2 M KCl:methanol (1:1 v/v). The organic fraction was pipetted into a vial and evaporated under an atmosphere of nitrogen at 35 °C. The lipid extract was resuspended in 1 ml of hexane and stored in a nitrogen atmosphere at −70 °C in teflon-lined vials after adding BHT to preserve the sample. All chemicals used were of chromatographic grade.

The lipid classes were separated by high performance thin layer chromatography using the two-solvent system of Kupke & Zeugner (1978). After charring the plate with phosphomolibdic acid, the amount of each lipid class was established by computerized video densitometry (C.R. Solís, unpublished observation) and standardized with internal lipid standards (Supelco 18-4A). Amounts of reserve lipids are reported as microgram lipids per milligram wasp fresh weight.

Statistical analysis

For the statistical analysis of survival, data were analysed in three grouping schemes:

1 Tables of experimental group by mortality by time at 5 °C.
2 Tables of age (field-eclosed or laboratory-eclosed) (i.e. old or young wasps) by mortality by time at 5 °C.
3 Tables of predicted caste by mortality by time at 5 °C.

Samples of two consecutive days were combined for the analysis of the two 1986 experiments to increase sample size per date. The data were analysed using a three-way comparison of categorical data based on a log linear model (Sokal & Rohlf, 1981; Rohlf, 1984). Mortality curves were analysed using two kinds of tests:

1 Differences in the degree of dependence for the time spent at 5 °C and mortality tables, between experimental groups.
2 Independence of mortality from experimental group and time spent at 5 °C.

Williams correction for G was used because some of the tables contained small sample sizes (Sokal & Rohlf, 1981). Only tests with $P < 0{\cdot}005$ were considered to be significant to compensate for effects of multiple testing inherent to the model (Sokal & Rohlf, 1981). To be able to establish the role of each of the factors examined by the model, it is first necessary to discard the existence of significant three-way interaction between experimental group, mortality and time spent at 5 °C (Sokal & Rohlf, 1981). If three-way interaction between these factors were to be significant, then it would not be possible to unravel the effect of each factor and further testing would not make sense (Sokal & Rohlf, 1981).

The reserve lipids and fresh weight data were compared between the experimental groups and between predicted castes using a Kruskal–Wallis test (Sokal & Rohlf, 1981).

Results

The mortality curves of the six kinds of females show that, by the end of the cold exposure period, those females that had no opportunity to take care of larvae or that had lost their nest survived better at 5 °C than those that worked taking care of larvae (Table 1). Analyses of the data organized by experimental group (i-vi) show that mortality was dependent upon experimental group and time spent at 5 °C ($P < 0{\cdot}005$). The degree of dependence between mortality and time spent at 5 °C was significantly different for each of the six kinds of females (five kinds of females in 1985; $P < 0{\cdot}005$).

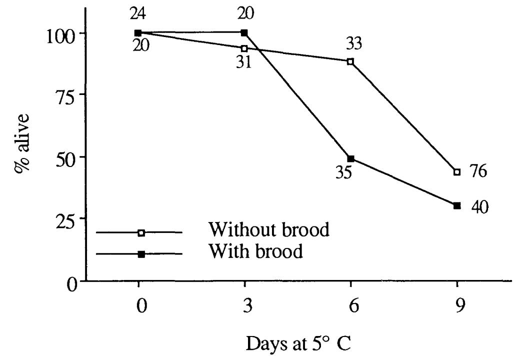

Fig. 2. Survivorship curves of wasps in broodless colonies (predicted gynes) and with brood colonies (predicted workers) in the 1985 experiment. Mortality is significantly dependent on predicted caste and time spent at 5 °C ($P < 0{\cdot}005$). The degree of dependence between mortality and time spent at 5 °C is significantly different for predicted gynes and predicted workers ($P < 0{\cdot}005$). The numbers indicate sample size.

In 1986, wasps emerging in colonies with no adults but with larvae showed the poorest survival by the end of the cold exposure period.

Survivorship of predicted castes

The results show that when the data are grouped by predicted caste, predicted gynes survived better at 5 °C ($P < 0{\cdot}005$). Also, the degree of dependence between mortality and time spent at 5 °C was significantly different for the predicted castes ($P < 0{\cdot}005$) as can be observed on the mortality curves (Figs. 2 and 3).

The effect of date

When the 1986 data are compared, a general increase in survival by the end of the cold exposure period in those individuals collected later in 1986 was observed (Table 1, Fig. 4). This increase is slight but significant when predicted gynes of the 1986a and 1986b experiments are compared, but is more apparent when predicted workers of both experiments are compared (Fig. 4). Mortality was dependent on time of the year for both predicted castes ($P < 0{\cdot}005$). The degree of dependence between mortality and time spent at 5 °C was also significantly different for the two dates.

The effect of age

In the 1985 and 1986a experiments, laboratory-eclosed wasps of the brood-removed group showed better survival than field-eclosed wasps of

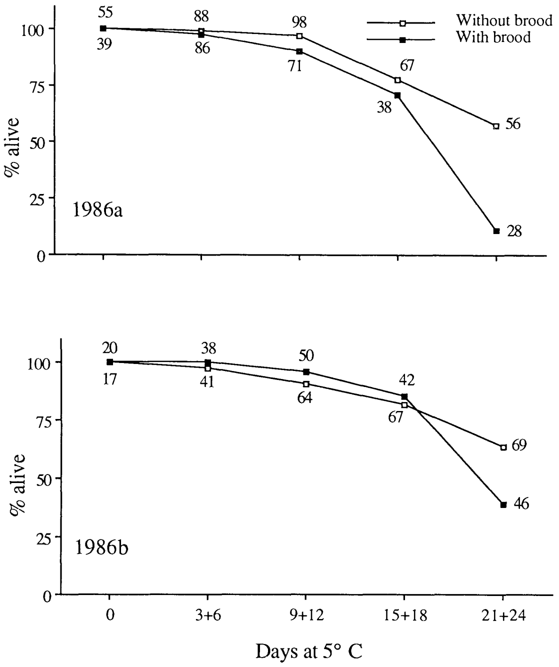

Fig. 3. Survivorship curves of wasps in broodless colonies (predicted gynes) and with brood colonies (predicted workers) in the 1986a and 1986b experiments. Mortality is significantly dependent on predicted caste and time spent at 5 °C ($P < 0{\cdot}005$). The degree of dependence between mortality and time spent at 5 °C is significantly different for predicted gynes and predicted workers ($P < 0{\cdot}005$). The numbers indicate sample size.

the same group. Laboratory-eclosed wasps in nests where brood care was an option showed reduced survival when compared to field-eclosed wasps of the same group (Table 1). In experiment 1986b, however, laboratory-eclosed wasps from the brood-removed group and from the control group, showed higher survival than field-eclosed wasps in their respective groups. Analyses of data grouped by age show that mortality was dependent upon age and time spent at 5 °C ($P < 0{\cdot}005$). The degree by which cold exposure affected mortality for the two age groups (laboratory-eclosed and field-eclosed) was also significantly different ($P < 0{\cdot}005$). No three-way interaction was detected between group, mortality and time spent at 5 °C, for any of the three kinds of comparisons run on the data.

Lipid reserves

The analyses of the reserve lipids and weight data of the 1986b wasps show that females from experimental colonies had not accumulated significantly higher levels of reserve lipids than controls ($P > 0{\cdot}6$) (Figs. 5 and 6) and that females from experimental groups were not heavier than controls ($P > 0{\cdot}7$). Analysis of the same parameters by predicted caste also failed to reveal any significant differences in reserve lipids ($P > 0{\cdot}8$) or fresh weight ($P > 0{\cdot}4$) between predicted gynes and predicted workers. No egg laying or nest construction took place in the experimental nests during the treatment period.

In summary, treatment, age and date effects are involved in the response of the different groups to deprivation of opportunity to work in terms of brood care and nest care. These differences cannot be attributed to a nutritional advantage acquired during the period during which the wasps were exposed to the treatments.

Discussion

We have shown that females of *P. exclamans* emerging during middle and late summer can respond to brood loss, nest loss and nest orphanage. More importantly, we show that depending on the presence of brood offered by the nest at the

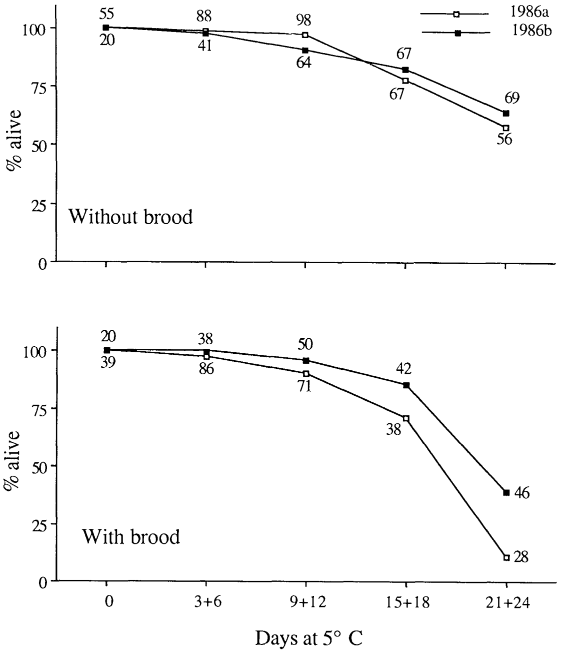

Fig. 4. Comparison of the survivorship curves within predicted castes in the 1986a and 1986b experiments. Mortality is significantly dependent on time of the year (1986a = early summer; 1986b = late summer) and time spent at 5 °C ($P < 0{\cdot}005$) for both predicted castes. The degree of dependence between mortality and time spent at 5 °C is significantly different for early and late summer for both predicted castes ($P < 0{\cdot}005$). The numbers indicate sample size.

Table 1. Survivor percentage (sample size) of wasps of each treatment in experiments 1985, 1986a, 1986b.

Treatment	Days at 5 °C				
1985	0	3	6	9	
Brood removed					
Laboratory-eclosed	100·0 (5)	90·9 (11)	100·0 (13)	45·4 (22)	
Field-eclosed	100·0 (14)	90·0 (10)	79·6 (10)	22·2 (45)	
Nest removed					
Field-eclosed	100·0 (5)	100·0 (10)	90·0 (10)	55·5 (45)	
Control					
Laboratory-eclosed	100·0 (13)	100·0 (10)	38·0 (21)	20·0 (15)	
Field-eclosed	100·0 (7)	100·0 (10)	64·2 (14)	36·0 (25)	
1986a	0	3 + 6	9 + 12	15 + 18	21 +24
Brood removed					
Laboratory-eclosed	100·0 (17)	100·0 (27)	96·7 (31)	77·7 (9)	66·6 (3)
Field-eclosed	100·0 (19)	96·9 (33)	94·1 (34)	80·0 (40)	40·0 (30)
Nest removed					
Field-eclosed	100·0 (19)	100·0 (27)	100·0 (33)	72·2 (18)	78·2 (23)
Adults removed					
Laboratory-eclosed	100·0 (10)	96·5 (29)	85·7 (21)	60·0 (5)	0·0 (3)
Control					
Laboratory-eclosed	100·0 (12)	100·0 (27)	93·7 (16)	61·5 (13)	0·0 (8)
Field-eclosed	100·0 (17)	93·6 (30)	91·1 (34)	80·0 (20)	17·6 (17)
1986b	0	3 + 6	9 + 12	15 + 18	21 + 24
Brood removed					
Laboratory-eclosed	100·0 (5)	100·0 (8)	90·0 (20)	62·5 (16)	87·5 (16)
Field-eclosed	100·0 (7)	93·7 (16)	90·4 (21)	88·0 (25)	56·6 (30)
Nest removed					
Field-eclosed	100·0 (8)	100·0 (17)	91·3 (23)	88·4 (26)	56·5 (23)
Adults removed					
Laboratory-eclosed	100·0 (7)	100·0 (14)	95·6 (23)	94·1 (5)	20·0 (15)
Control					
Laboratory-eclosed	100·0 (4)	100·0 (10)	100·0 (6)	NA	66·6 (3)
Field-eclosed	100·0 (6)	100·0 (14)	95·2 (21)	80·0 (25)	46·6 (28)

NA = not available during this period.

time of eclosion, females will acquire gyne or worker characters. Hence not only is caste determined imaginally but it can also be molded after the eclosion of the adult female by factors other than the physical environment. Furthermore, while nutritional state can be a factor that differentiates castes, it is not necessarily involved in this response. As a result of the treatments, wasps in broodless and nestless colonies developed two of the characteristics found in gynes, while wasps in orphaned colonies and controls did to a lesser degree. First, they show increased survivorship at cold temperatures. Second, the fact that wasps in treatments that precluded them from raising brood did not develop higher lipid reserves than wasps that raised brood, suggests that wasps in broodless colonies had a different metabolism (C.R. Solís, unpublished observation) from controls allowing them to survive longer with the same amount of lipid reserves. The absence of differences in lipid amounts is especially important since it shows that wasps in broodless groups did not survive better just because they were able to accumulate nutrients that they were not passing on to larvae.

The data show that caste determination is not only affected by the presence of brood in the colony, but also by time of year and by age of individual. This is reflected in the change in mortality between 1986a and 1986b and the differences in mortality between age groups exposed to the same treatment at the same time of the year. The differences in mortality associated with date are possibly caused by changes in the physiology of individuals triggered by day length, differences

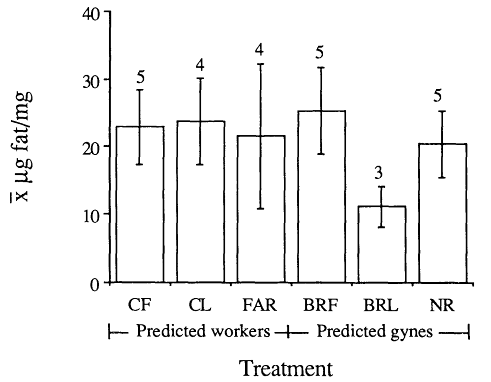

Fig. 5. Mean amount of reserve lipids (±SE) of wasps coming out of the treatment period in experiment 1986b. CF, controls field eclosed; CL, controls laboratory eclosed; FAR, field-eclosed adults removed; BRF, brood-removed field-eclosed wasps; BRL, brood-removed laboratory-eclosed wasps; NR, nest-removed field-eclosed wasps. The numbers indicate sample size.

between the night and day temperatures or dietary factors experienced in the field as the season progresses towards the winter. These differences, however, cannot be attributed to differences in the nest environment between nests used in the 1986a and 1986b experiments. It is more likely that they reflect changes in reproductive strategies to allow responses to changing environmental factors such as increased predation pressures and food availability. As the probability of nest and brood loss increases in time (Strassmann, 1981) adults of undetermined caste could change their behaviour in preparation for an eventual colony catastrophe. This could further explain the change in response of the field-eclosed and laboratory-eclosed wasps in the experiments performed in mid summer (1985 and 1986a) and late summer (1986b). Increased parasite and predation pressures could lead the colonies to produce females that are ready to overwinter in case of nest loss before the end of the growing season. Therefore both the social and the physical environment are involved in caste differentiation.

When the mortality curves for 1985 and 1986a are compared, the same patterns are apparent. It must be remembered, though, that different experimental designs were used in both years. The dishes used in 1985 were smaller than those used in 1986. Furthermore, the protein component of the diet was different.

For the individuals of the colony, the brood represents a most valuable resource, especially for those individuals that have given up reproduction and are reproducing indirectly by raising siblings which will in turn reproduce themselves or help them raise more siblings (Hamilton, 1964a,b). In *P. exclamans*, where brood loss becomes highly probable as the season progresses (Strassmann, 1981) and queen turnover is frequent (Strassmann & Meyer, 1983; Strassmann, 1985b), individual level selection should work against caste overspecialization and total renunciation to self reproduction (Jeanne, 1986). Several kinds of proximate cues could be involved in the response to brood presence or absence. They could range from the physical absence of the larvae to chemical factors produced by them. Ovarian development is triggered by behavioural cues in females of the burying beetle *Nicrophorus tomentosus* (Scott & Traniello, 1987). In the vespines, colonies do not survive satisfactorily in the absence of larvae, as there is a nutritional interdependence between adults and larvae (Spradberry, 1973). In the honeybees, larval secretion of pheromones keeps workers from developing their ovaries. Here, however, following brood loss, workers develop ovaries in half the time it takes when the brood is present but the queen is not, allowing colonies to respond quickly to queen loss (Winston, 1987). It must be remembered, however, that in these two groups, workers and queens show a higher degree of differentiation than is apparent in *Polistes*. The presence of a low volatility pheromone can be ruled out though, since we observed the same directional change in wasps without a nest than in wasps with a nest and without brood. The presence of a high volatility pheromone produced by the larvae can, however, not be ruled out. Whether the mechanism involved in the response to brood loss is physical, behavioural or chemical, the

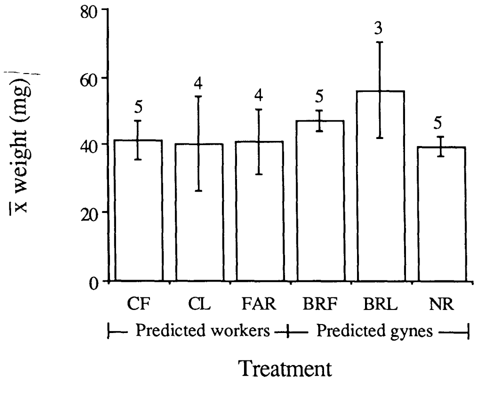

Fig. 6. Mean fresh weight (±SE) of wasps coming out of the treatment period in experiment 1986b. For key see Fig. 5. The numbers indicate sample size.

selective advantage is still the same. The individuals are not locked out of reproductive opportunities when a catastrophe of this kind occurs.

The production of females whose caste remains undetermined until after the time of adult eclosion is in sharp contrast with what is observed in highly social species, both monomorphic and polymorphic, in which caste is pre-imaginally determined, sometimes very early in development (de Wilde & Beetsma, 1982; Wheeler, 1986). For example, in the ant *Pheidole pallidula*, caste is determined at oviposition, influenced by the ecdysteroid levels experienced by the queen and by queen weight (Suzzoni & Passera, 1984; Suzzoni, Passera & Strambi, 1980). In *Nasutitermes exitiosus* caste is also determined at the time of oviposition, presumably by maternal influence (Watson & Abbey, 1987). In *Pheidole bicarinata* colonies, soldier determination occurs during the larval stage, controlled by a pheromone released by adult soldiers (Wheeler & Nijhout, 1983). In honey-bees (*Apis mellifera*) and stingless bees (*Trigona* and *Melipona*), gyne determination occurs during the larval stage, as gyne larvae are fed different foods from worker larvae (Ascencot & Lensky, 1976, 1988; Dietz, Herman & Blum, 1979; Jaisson, 1982; Brouwers, 1984). While the latter species can potentially respond to the environment by altering colony caste ratios and brood production, their responses are lagged with respect to the stimuli. The lagged response can disrupt the colony cycle leading to colony death. Seeley & Visscher (1985) showed that the timing of honey-bee colony cycles is critical. When colonies are disrupted, swarming occurs later than it should, often resulting in colonies that starve over the winter (Seeley & Visscher, 1985) (but see Winston, 1987, above).

In contrast, *P. exclamans* colonies can respond to social and environmental contingencies much more quickly. This kind of strategy may be advantageous for all members of the colony since they do not depend on having to produce a special kind of reproductive female in a case where nest loss is highly probable. Further, individuals can benefit from not being committed to a particular caste since there is the possibility that they might emerge in a colony where they could only work by rearing a brood of females towards which they are not closely related (Strassmann & Meyer, 1983; Strassmann, 1985b). Greene (1984) and Gervet *et al.* (1986) discuss alternative strategies used by vespine wasps and the polistine wasp *P. gallicus*, also a temperate species, to deal with the same kind of unpredictability factors involved in the determination of the end of the nesting cycle. Both show that the species they examined produce mixed broods of gynes and workers, starting sometimes very early in the season. This allows them to have some reproductive output in case the queen dies or the nest is destroyed before the end of the season. This kind of caste flexibility has not been shown to exist in all primitively social insects. In the tropical wasp *Ropalidia marginata* nests can be started at any time of the year (Gadagkar *et al.*, 1982), so that nest rebuilding possibilities are not constrained and members of the colony do not lose out if the nest does not produce reproductives at a given time. In this species only 50% of eclosing females are capable of building nests and of laying eggs (Gadagkar *et al.*, 1988).

Previous research has shown that several factors can influence caste differentiation in *Polistes*, but has mainly focused on caste differentiation among foundresses or how workers become egg layers during the current season. In the adult *P. exclamans*, when the queen disappears or dies, one of the other females will become a queen, often within hours (Strassmann & Meyer, 1983). The female replacing the queen is usually the oldest forager, suggesting that even well into adulthood caste is not fixed (Strassmann & Meyer, 1983).

Evidence from other species, both physiological and demographic, also supports the notion that caste is determined imaginally in *Polistes* or, at least, that it can be modified in the adult female. When *P. gallicus* females join groups to found a colony, a dominance hierarchy is formed among the foundresses (Pardi, 1948). The most dominant female becomes the queen, while the rest become workers (Pardi, 1948). While dominance is correlated with corpora allata volume (Röseler, Röseler & Strambi, 1980; Turillazi *et al.*, 1982; Röseler *et al.*, 1984; Röseler, 1985) the volume of the corpora allata *per se* appears to be determined by when individuals emerge from hibernation, with earlier emerging individuals showing larger corpora allata (Röseler, Röseler & Strambi, 1986). Demographic data on *P. annularis* in Austin, Texas, contribute further support to this. Strassmann (1989) has shown that *P. annularis* colonies in that area exhibit a great degree of variability in switching from production of workers to sexuals, both between and within years. This variability can be partly explained as a response of individual colonies to variable rain and food availability (Strassmann, 1989).

In more temperate species the role of the environment has been established in caste determination in *Polistes,* suggesting that caste determination is mediated, partly, by physical factors.

P. metricus produce diapausing females by July. However, photoperiod and thermoperiod, and juvenile hormone applications can break diapause in gynes, inducing ovarian development (Bohm, 1972). *P. foederatus* larvae that would normally become workers develop gyne-like fat bodies when exposed to cold nights (Turillazzi & Conte, 1980; 1981). The previous examples show that both the physical as well as the colonies social environment can affect and modify caste in *Polistes*. Our data demonstrate that social factors can also affect caste. They show the presence or absence of brood by itself can also induce physiological changes that lead to caste differentiation in *Polistes*.

While division of labour accompanied by morphological specialization might in theory yield high returns per unit invested, environmental factors can put constraints on extreme commitment to one caste by colony members. Our data show that *P. exclamans* follows another strategy to cope with environmental unpredictability; the production of individuals that are not commited to a specific caste. With these experiments we have shown that colonies produce individuals of undetermined caste that can respond to reproductive opportunities and that caste in this species is not only determined by physical or nutritional factors.

Acknowledgments

We are indebted to Dina Montúfar-Solís for her help in the field, with the experimental set-up, her comments on the manuscript and for her constant support. We thank Colin R. Hughes, Robert G. Knox, David Queller and anonymous referees for comments on the manuscript. We thank John G. Baust, for sharing his laboratory facilities in 1985 and Robert Rojas for help and guidance in the laboratory in 1985. We are indebted to Jan S. Pyrek and Linda Riggan for their guidance on lipid analysis. We thank Edwin G. Bryant for advice on the statistical analyses of the data. The research was partially supported by NSF BSR 86-05026 to JES and a Sigma Xi Grant in Aid of Research to CRS. Rice University kindly supplied part of the computing resources through the Institute of Computer Sciences and Applications.

References

Ascencot, M. & Lensky, Y. (1976) The effect of sugars and juvenile hormone on the differentiation of the female honey bee larvae (*Apis mellifera*) to queens. *Life Sciences,* **18,** 693–700.

Ascencot, M. & Lensky, Y. (1988) The effect of soluble sugars in stored royal jelly on the differentiation of female honey bee (*Apis mellifera* L.) larvae to queens. *Insect Biochemistry,* **18,** 127–133.

Bohm, M.K. (1972) Effects of environment and juvenile hormone on ovaries of the wasp, *Polistes metricus. Journal of Insect Physiology,* **18,** 1875–1883.

Brouwers, E.V.M. (1984) Glucose/fructose ratio in the food of honey bee larvae during caste determination. *Journal of Apicultural Research,* **23,** 94–101.

Dietz, A., Herman, H.R. & Blum, M.S. (1979) The role of exogenous JH I, JH III and anti-JH (precocene II) on queen induction of 4.5-day-old worker honey bee larvae. *Journal of Insect Physiology,* **25,** 503–512.

Eickwort, K. (1969) Separation of castes of *Polistes exclamans* and notes on its biology (Hym.:Vespidae). *Insectes Sociaux,* **16,** 67–72.

Folch, J., Lees, M. & Sloane-Stanley, G.H. (1957) A simple method for the isolation and purification of total lipids from animal tissue. *Journal of Biological Chemistry,* **226,** 497–509.

Franks, N.R. (1987) The organization of working teams in social insects. *Trends in Ecology and Evolution,* **2,** 72–75.

Freund, J.E. (1979) *Modern Elementary Statistics,* 5th edn. Prentice Hall, Inc., Englewood Cliffs, New Jersey.

Gadagkar, R., Gadgil, M., Joshi, N.V. & Mahabal, A.S. (1982) Observations on the natural history and population ecology of the social wasp *Ropalidia marginata* (Lep.) from peninsular India (Hymenoptera: Vespidae). *Proceedings of the Indian Academy of Sciences. Animal Sciences,* **91,** 539–552.

Gadagkar, R., Vinutha, C., Shanubhogue, A. & Gore, A.P. (1988) Pre-imaginal biasing of caste in a primitively eusocial insect. *Proceedings of the Royal Society of London, Series B,* **233,** 175–189.

Gervet, J., Pratte, M., Semenoff, S. & Gabouriaut, D. (1986) Pattern of offspring production in colonies of paper wasps (*Polistes gallicus* L.). II. Demographic data hypothesis concerning fitness implications. *Insectes Sociaux,* **33,** 375–387.

Greene, A. (1984) Production schedules of vespine wasps: an empirical test of the bang-bang optimization model. *Journal of the Kansas Entomological Society,* **57,** 545–568.

Haggard, C.M. & Gamboa, G.J. (1980) Seasonal variation in body size and reproductive condition of a paper wasp, *Polistes metricus* (Hymenoptera: Vespidae). *Canadian Entomologist,* **112,** 239–248.

Hamilton, W.D. (1964a) The genetical theory of social behavior. I. *Journal of Theoretical Biology,* **7,** 1–16.

Hamilton, W.D. (1964b) The genetical theory of social behaviour. II. *Journal of Theoretical Biology,* **7,** 17–52.

Jaisson, P. (1982) The trophogenic grounds of caste determination in *Melipona* and *Trigona* (Hymenoptera: Apidae). In *Social Insects in the Tropics: Proceedings of The First International Symposium,* vol. 1 (ed. P. Jaisson), pp. 31–40. University of Paris XIII Press, Paris.

Jeanne, R.L. (1986) The evolution of the organization of work in social insects. *Monitore zoologico italiano (NS),* **20,** 119–133.

Kupke, I.R. & Zeugner, S. (1978) Quantitative high-performance thin-layer chromatography of lipids in plasma and liver homogenates after direct application of 0·5-μl samples to the silica gel layer. *Journal of Chromatography,* **146,** 261–271.

Macevicz, S. & Oster, G.F. (1976) Modeling social insect populations II: Optimal reproductive strategies in annual eusocial colonies. *Behavioral Ecology and Sociobiology,* **1,** 265–282.

Oster, G.F. & Wilson, E.O. (1978) *Caste and Ecology in the Social Insects.* Princeton University Press, Princeton.

Pardi, L. (1948) Beobachtungen über das interindividuelle Verhalten bei *Polistes gallicus. Behavior,* **1,** 138–172.

Rohlf, F.J. (1984) *BIOM, A Package of Statistical Programs to Accompany the Text Biometry.* State University of New York, New York.

Röseler, P.-F. (1985) Endocrine basis of dominance and reproduction in polistine wasps. *Fortschritte für Zoologie,* **31,** 259–272.

Röseler, P.-F., Röseler, I. & Strambi, A. (1980) The activity of the corpora allata in dominant and subordinate females of the wasp *Polistes gallicus. Insectes Sociaux,* **27,** 97–107.

Röseler, P.-F., Röseler, I., Strambi, A. & Augier, R. (1984) Influence of insect hormones on the establishment of dominance hierarchies among foundresses of the paper wasp, *Polistes gallicus. Behavioral Ecology and Sociobiology,* **15,** 133–142.

Röseler, P.-F., Röseler, I. & Strambi, A. (1986) Studies of the dominance hierarchy in the paper wasp, *Polistes gallicus* (L.) (Hymenoptera Vespidae). *Monitore zoologico italiano (NS),* **20,** 283–290.

Scott, M.P. & Traniello, J.F.A. (1987) Behavioural cues trigger ovarian development in the burying beetle, *Nicrophorus tomentosus. Journal of Insect Physiology,* **33,** 693–696.

Seeley, T.D. & Visscher, P.K. (1985) Survival of honey bees in cold climates: the critical timing of colony growth and reproduction. *Ecological Entomology,* **10,** 81–88.

Sokal, R.R. & Rohlf, J.F. (1981) *Biometry,* 2nd edn. Freeman, San Francisco.

Spradberry, J.P. (1973) *Wasps, an Account of the Biology and Natural History of Social and Solitary Wasps.* University of Washington Press, Seattle, Washington.

Strassmann, J.E. (1979) Honey caches help female paper wasps (*Polistes annularis*) survive Texas winters. *Science,* **204,** 207–209.

Strassmann, J.E. (1981) Parasitoids, predators, and group size in the paper wasp, *Polistes exclamans. Ecology,* **62,** 1225–1233.

Strassmann, J.E. (1985a) Worker longevity and the evolution of caste in the social wasp *Polistes exclamans. Insectes Sociaux,* **32,** 275–285.

Strassmann, J.E. (1985b) Relatedness of workers to brood in the social wasp, *Polistes exclamans. Zeitschrift für Tierpsychologie,* **69,** 141–148.

Strassmann, J.E. (1989) Early termination of brood rearing in the social wasp, *Polistes annularis* (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society,* **62,** 353–362.

Strassmann, J.E. & Meyer, D.C. (1983) Geronotocracy in the social wasp, *Polistes annularis* (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society,* **62,** 353–362.

Strassmann, J.E., Lee, R.E., Jr, Rojas, R.R. & Baust, J.G. (1984) Caste and sex differences in cold-hardiness in the social wasps *Polistes annularis* and *P. exclamans* (Hymenoptera: Vespidae). *Insectes Sociaux,* **31,** 291–301.

Suzzoni, J.P. & Passera, L. (1984) La ponte d'oeufs préorintés par la fourmi *Pheidole pallidula* (Nyl.): caractéristiques biologiques des reines a la fin de l'hibernation. *Insectes Sociaux,* **31,** 155–170.

Suzzoni, J.P., Passera, L. & Strambi, A. (1980) Ecdysteroid titre and caste determination in the ant, *Pheidole pallidula* (Nyl.) (Hymenoptera: Formicidae). *Experientia,* **36,** 1228–1229.

Turillazzi, S. & Conte, A. (1980) Influence of temperature on caste differentiation in *Polistes foederatus* (Kohl) (Hymenoptera Vespidae). *Monitore zoologica italiano (NS),* **14,** 116.

Turillazzi, S. & Conte, A. (1981) Temperature and caste differentiation in laboratory colonies of *Polistes foederatus* (Kohl) (Hymenoptera Vespidae). *Monitore zoologica italiano (NS),* **15,** 275–291.

Turillazzi, S., Marino Piccioli, M.T., Hervatin, L. & Pardi, L. (1982) Reproductive capacity of single foundress and associated foundress females of *Polistes gallicus* (L.) (Hymenoptera: Vespidae). *Monitore zoologica italiano (NS),* **16,** 75–88.

Walker, J. & Stamps, J. (1986) A test of optimal caste ratio theory using the ant *Camponotus (Colobopsis) impressus. Ecology,* **67,** 1052–1062.

Watson, J.A.L. & Abbey, H.M. (1987) Maternal determination of reproductive vs sterile castes in *Nasutitermes exitiosus* (Hill) (Isoptera: Termitidae). *Insectes Sociaux,* **34,** 291–297.

West Eberhard, M.J. (1969) The social behavior of polistine wasps. *Miscellaneous Publications Museum of Zoology, University of Michigan,* **140,** 1–100.

Wheeler, D.E. (1986) Developmental and physiological determinants of caste in social Hymentoptera: evolutionary implications. *American Naturalist,* **128,** 13–34.

Wheeler, D.E. & Nijhout, H.F. (1983) Soldier determination in *Pheidole bicarinata:* inhibition by adult soldiers. *Journal of Insect Physiology,* **30,** 127–135.

de Wilde, J. & Beetsma, J. (1982) The physiology of caste development in social insects. *Advances in Insect Physiology,* **16,** 167–246.

Winston, M.L. (1987) *The Biology of the Honey Bee.* Harvard University Press, Cambridge, Massachusetts.

Received 15 May 1989; revised 23 October 1989; accepted 21 December 1989