WORKER MORTALITY AND THE EVOLUTION OF CASTES IN THE SOCIAL WASP *POLISTES EXCLAMANS*

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SUMMARY

Workers of the primitively social wasp, *Polistes exclamans*, had very short average lifespans, averaging 14 days (S.D. = 11, N = 497) in 1977, 17 days (S.D. = 14, N = 503) in 1978 and 14 days (S.D. = 10, N = 222) in 1979; the oldest worker observed on a natural colony was 102 days old. Colony of origin explained more of the variance in worker longevity than did any other variable. Worker longevity decreased over the season, accompanied by an increase in larval development times and an increase in colony failure rates. In 1978 workers emerging in the presence of greater numbers of other workers lived longer which indicates that they may have performed risky tasks less often when many other females were present. Compared to 1977 and 1979, 1978 was characterized by greater numbers of workers per colony, shorter larva development times, longer average lifespans for workers, much higher probabilities of nest survival and greater average production of reproductives per colony.

RESUME

Le taux de mortalité des ouvrières et l'évolution des castes chez la guêpe sociale Polistes exclamans

La durée de vie des ouvrières appartenant à l'espèce *Polistes exclamans* fut en moyenne de 14 jours (déviation standard égale à 11 pour 497 individus) en 1977, de 17 jours (déviation standard égale à 14 pour 503 individus) et de 14 jours (déviation standard égale à 10 pour 222 individus) en 1979. L'ouvrière la plus vieille que nous ayons observée avait 102 jours. La variance de longévité a été due à la colonie d'origine plutôt qu'à n'importe quelle autre variable. La diminution saisonnière de la longévité d'une ouvrière s'accompagne d'un accroissement de la durée du développement larvaire et d'un accroissement du nombre des colonies abortives. Ces observations suggèrent que la disponibilité de proies décroît tard dans la saison. En 1978, les ouvrières apparues en présence d'un grand nombre d'autres ouvrières vécurent plus longtemps. L'année 1978 comparée à celles de 1977 et de 1979 a été caractérisée par un plus grand nombre d'ouvrières par colonie, des durées du développement larvaire raccourcies et une durée de vie moyenne plus longue pour les ouvrières, des probabilités plus grandes pour la survie des nids et une plus grande moyenne de production de « reproductrices » par colonie.

INTRODUCTION

Among social insects, worker longevity has been studied most extensively in the highly social bees, wasps and ants (BRIAN, 1965 ; WILSON, 1971 p. 428 ; MICHENER, 1974 ; OSTER and WILSON, 1978). These species are characterized by large colonies, multiple castes and workers that are unlikely or unable to become queens. Different castes of highly social insects often perform different functions, spending varying amounts of time within and outside the nest, and have different survivorship curves (WILSON, 1971). However longevity has not been thoroughly investigated in social insects which lack morphological castes. Such species may be most interesting because small colony sizes mean that individual workers are much more critical to colony survival and because workers regularly become queens under certain circumstances (STRASSMANN and MEYER, 1983 ; LITTE, 1979).

The most pronounced dichotomy in behavior and longevity is usually between workers and the queen. The queen typically remains on the nest where she lays eggs, tends brood, and is aggressive towards other females. Workers not only defend the nest against predators and care for brood, but they also leave the nest to forage for paper, nectar and prey. While they are off the nest workers are most vulnerable to predators, particularly if they are weighted down by prey on a return trip to the nest. Worker life lengths are usually much shorter than queen life lengths (WILSON, 1971).

Variability in longevity among workers may indicate that there are differences in the type or frequency of work each performs. Individuals thet remain on the nest and avoid risky foraging trips may increase the probability that they will become egg layers because the oldest remaining female replaces an original queen that has died (STRASSMANN and MEYER, 1983). However colonies with workers that forage frequently will produce more reproductives and be less likely to fail through death of all workers.

The social wasp, *Polistes exclamans*, was chosen for this study because its colonies are small and abundant in central Texas, because death of all workers accounts for the demise of 13 % to 76 % of all colonies depending on the year, and because workers have several behavioral and reproductive options available to them which may influence their probability of dying at a given age (STRASSMANN, 1981 a ; 1981 b ; 1981 c ; STRASSMANN and MEYER, 1983 ; STRASSMANN *et al.*, 1984). Workers may help on the main nest or a satellite nest, or they may become queen of either type of nest. Satellite nests are new nests started by the queen or a worker from about 30 % of *P. exclamans* nests ; they are near the main nest and are joined by additional workers which help to rear the brood. Original queens disappear from over half of all nests and are replaced by mated workers (STRASSMANN, 1981 a).

METHODS

Worker longevity was measured on naturally occurring colonies at Brackenridge Field Station (BFL) of the University of Texas at Austin, Texas. All wasps were marked with enamel on the day each nest was discovered, and subsequent emergences were marked between midnight and 0700 h about every third day. Life length was calculated as beginning the day the wasp was marked and ending the last day the wasp was seen. Therefore actual life length was 0 to 4 days longer than estimated longevity.

In all 2238 wasps were marked: 1018 from 27 nests in July, August and September, 1977; 843 wasps from 58 nests in May through August, 1978; and 377 wasps from 2 nests in May through August, 1979. The following categories of marked wasps were excluded from the analyses presented here: (1) queens; (2) wasps whose nests were destroyed during their lifetime; (3) wasps that were marked on the first day the nest was discovered (because these wasps were of unknown ages at this time); (4) wasps which were still alive when the nest ceased to be censused in autumn (because they are mainly future queens that do not forage); and (5) males. The remaining sample was 1222 wasps: 497 wasps on 26 nests in 1977, 503 wasps on 34 nests in 1978, and 222 wasps on 2 nests in 1979. For analyses which focus on colonies only those with at least 4 wasps of known life length were used. This reduced the sample to 1089 wasps: 430 in 1977, 437 in 1978 and 222 in 1979.

The impact of nest of origin, number of females on the nest at the date of emergence and at the date of death, and dates of emergence and death on individual life length was examined using analysis of variance after normalizing the data using a log transform of all variables except nest of origin (SOKAL and ROHLF, 1982). The proportion of surviving wasps was calculated for 3 day age intervals from 0-80 days and analyzed using the survival function of the Statistical Package for the Social Sciences (SPSS; HULL and NIE, 1981). Hazards rates (or age-specific mortality rates) defined as the probability per unit time that an individual who has survived to the beginning of an inteval will die during that interval were calculated. Hazard rates are a measure of the slope of the survivorship curve with the advantage that they are easier to see when plotted than slope changes in survivorship curves over time, and standard errors can be calculated (HULL and NIE, 1981). For example hazard rates would increase sharply among senescing individuals at an age greater than that reached by most individuals.

RESULTS

P. exclamans workers lived an average of 14 days (S.D. = 11, N = 497) in 1977, 17 days (S.D. = 14, N = 503) in 1978 and 14 days (S.D. = 10, N = 222) in 1979. Counting only days since initiation of spring nests (not including time spent hibernating) queens survived an average of 118 days in 1978 (N = 33) and 108 days in 1979 (N = 27). Queens lived 6.9 times as long as workers in 1978 and 7.7 times as long as workers in 1979.

Analysis of variance of life length of workers by colony with the covariates of date emerged and number of females on the nest at that time revealed that colony of origin is the most important predictor of life length *(table I)*. The same was true with the covariates of date died and number of females on the nest at that time. In 1979 colony of origin did not have

Table I. — ANOVA and regression on the effects of nest of origin, date emerged, females at emergence date, date died, and females at that date on life length. Alle variables except nest are log transformed. Sample sizes are 430 wasps in 1977, 437 in 1978 and 222 in 1979.

Tableau I. — ANOVA et relation de régression pour les effets, sur la durée de vie, du nid d'origine, de la date d'émergence, des femelles présentes à la date d'émergence, de la date de mort et des femelles présentes à cette date. Toutes les variables sauf celle du nid sont exprimées logarithmiquement. L'échantillon était de 430 guêpes en 1977, 437 en 1978 et 222 en 1979.

Year	Variable	d.f.	$R^2 \times 100$ (% of variance explained)	F	Regression b ± S.E.
1977	Nest	10	8.8	4.1***	
Covariates :		2	1.9	4.4*	
	Date emerged	1	1.5	7.1**	— 1.53 ± 0.57
	♯ Females on nest at emergence date	1	0.0	0.1	0.06 ± 0.19
1978	Nest	12	13.9	6.1***	
Covariates :		2	5.9	15.6***	
	Date emerged	1	3.7	29.9***	— 3.43 ± 0.63
	♯ Females on nest at emergence date	1	2.3	12.2***	0.57 ± 0.16
1979	Nest	1	0.2	0.5	
Covariates :		2	4.7	5.5**	
	Date emerged	1	0.4	0.9	— 1 39 ± 1.47
	♯ Females on nest at emergence date	1	0.2	0.5	— 0.15 ± 0.21
1977	Nest	10	8.8	4.7***	
Covariates :		2	13.6	37.2***	
	Date died	1	4.4	23.9***	3.76 ± 0.77
	♯ Females on nest at death date	1	0.1	0.8	— 0.14 ± 0.18
1978	Nest	12	13.9	6.3***	
Covariates :		2	8.4	22.7***	
	Date died	1	5.5	29.7***	2.99 ± 0.55
	♯ Females on nest at death date	1	0.1	0.9	— 0.14 ± 0.15
1979	Nest	1	0.2	0.5	
Covariates :		2	6.9	8.2	
	Date died	1	2.3	5.5*	3.85 ± 1.64
	♯ Females on nest at death date	1	0.2	0.4	— 0.15 ± 0.24

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

a significant effect on life length, but only 2 colonies were studied. Females emerging later in the season tended to have shorter lives in 1977 and 1978 but not in 1979 *(table I)*. In 1978 females lived longer than average if they emerged when there were greater numbers of other females on the nest. Date of death was a significant covariate in all 3 years. No independent variable explained more than 15 % of the variance in life length. Maximum

longevity recorded for a worker was 84 days in 1977, 102 days in 1978 and 66 days in 1979.

Analysis of survivorship curves differs from that of average lifespan discussed above in that the emphasis is on the probability of dying at each age. Probability of dying did not change markedly with age of wasp in 1977 or 1978 *(fig. 1)*. In 1979 probability of dying increased with age. Comparing survivorship curves within years the only significant difference was that in July 1978 survivorship was greater than in August 1978 (July 1978 mean score = 47.1, N = 124 ; August 1978 mean score = — 22.3, N = 220 ; Lee-Desu Statistic = 9.7, degrees of freedom = 1, $p < 0.01$).

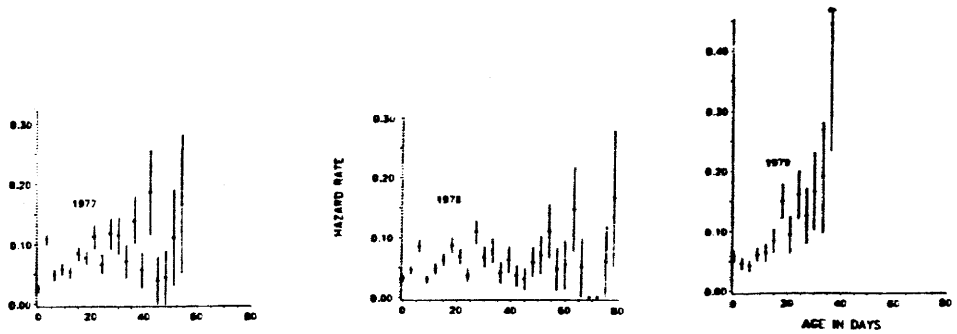

Fig. 1. — Means and standard errors of hazard rates which are the probability that an individual surviving to the beginning of each 3 day interval will die during the interval are given for each year. Sample sizes are 430 wasps in 1977, 437 wasps in 1978 and 222 wasps in 1979.

Fig. 1. — Probabilités moyennes et erreurs standards pour qu'un individu ayant survécu jusqu'au début de chaque intervalle de trois jours meure pendant cette durée, exprimées pour chaque année. Les échantillons sont de 430 guêpes en 1977, 437 en 1978 et 222 en 1979.

Comparing the same month in different years, workers lived shorter lives in July 1977 than they did in July 1978 (July 1977 mean score = — 20.3, N = 173 ; July 1978 mean score = 33.8, N = 104, Lee-Desu Statistic = 7.4, degrees of freedom = 1, $p < 0.01$). July 1977 was also often very dry and hot, factors which may have caused the reduction in prey availability. There were no significant differences between years for survivorship of workers emerging in August. Overall survivorship was greater in 1978 than in 1977 (1977 mean score = — 45, N = 497 ; 1978 mean score = 44, N = 503 ; Lee-Desu Statistic = 6.0 degrees of freedom = 2, $p < 0.02$), and did not differ between 1977 and 1979 or between 1978 and 1979.

Survivorship curves for individual nests were highly variable *(table II)*. In 1977 11 of the 55 comparisons in survivorship curves between pairs of

nests (11 total nests) were significant *(table II)*. In 1978 21 of 45 comparisons were significant ; in 1978 there was greater variability in survivorship curves between nests than in 1977. Neither numbers of wasps on the nest nor numbers that had their lifespan measured influenced the shape of the survivorship curve significantly *(table II)*.

Forty-two nests (21 in 1977 and 21 in 1978) with at least 4 females of known life length were available for analysis of longevity vs. number of cells in the nest, whether or not the nest was a satellite nest, and presence of two parasites, a chalcid wasp, *Elasmus polistis* and a pyralid moth, *Chalcœla iphitalis*. Average life lengths of workers per nest did not vary significantly among original nests, their satellites, and independent nests that never had satellites. Numbers of cells in the nests did not vary significantly with average life length of workers. Numbers of nest cells infested with the wasp parasite *Elasmus polistis* was greater on nests whose females lived longer on average ($r = 0.46$, $p < 0.02$) and explained 21 % of the variance in average worker life length in 1977 but was not significant in 1978 ($r = -0.04$, $p > 0.4$). In this population in 1977 *E. polistis* killed 8 % of all pupæ while in 1978 it killed 18 % of all *P. exclamans* pupæ (STRASSMANN, 1981 c). *C. iphitalis* killed over 19 % of all pupæ in both years but its presence had no effect on worker longevity.

Nests that subsequently failed because they lost all workers in 1977 averaged 13 workers (S.D. = 11, N = 14) in July compared to successful nests that had 21 workers (S.D. = 18, N = 25) at the same time, but these differences were not significant (Mann Whitney U = 134, $p > 0.2$). Nests with fewer workers in July in 1978 were more likely to fail because of the loss of all workers (Mann Whitney U = 15, $p < 0.01$ N = 5,41).

Workers lived longer in years when nests were generally more successful. In 1977 and 1979, less than 8 % of all colonies of *P. exclamans* in the population studied in this paper survived to produce any reproductives while in 1978 58 % of all colonies survived and produced reproductives *(table III)*. Numbers of reproductives produced by successful colonies averaged under 20 in 1977 and 1979, and over 45 in 1978 which was also the year with highest colony survival, and longest overall worker longevity *(table III)*. The successful year (1978) was hotter and wetter than 1977 which was hot and dry, and 1979 which was cool and dry *(table III)*.

DISCUSSION

The lives of workers of *P. exclamans* are short on average and highly variable in length. Queens live over 6 times longer than workers do on average illustrating the great differences between these two behavioral castes. High levels of variability in worker longevity may result from variation

Tabe II. — Lee-Desu statistics comparing survivorship curves between nests. Nests are arranged in order of increasing number of females present on the nest at any one time. Only nests with at last 10 females of know lifespan are included. A minus sign before the Lee-Desu statistic indicates the nest in the column has shorter life lengths than the nest in that row.

Tableau II. — Statistique Lee-Desu comparant les courbes du nombre croissant de femelles présentes à chaque moment. Seuls sont indiqués les nids ayant au moins 10 femelles de longévités connues. Un signe négatif devant l'index Lee-Desu indique que le nid dans la colonne a une durée de vie plus courte que celle du nid dans la rangée.

1977 Nest Identification Number	27	8	41[t]	9	80	51[t]	93[t]	53	74	77	18
Number of females that had their lifelengths measured	19	51	17	29	16	23	24	21	13	12	204
Maximum # of females present on the nest at one time	30	28	29	30	30	35	36	39	39	39	88
27	—	3.4	1.3	—2.6	—0.1	—2.3	—1.8	0.6	—0.1	—0.5	—6.5*
8		—	12.4***	—0.0	1.1	—0.1	0.3	5.9*	2.3	0.7	—1.3
41			—	—6.6*	—5.3*	—7.4**	—6.5*	—0.3	—2.4	—3.4	—16.4***
9				—	3.2	0.1	—0.0	2.7	0.7	0.8	0.7
80					—	—3.3	—0.2	1.5	0.0	—0.0	—4.6*
51						—	0.0	2.9	0.6	0.7	—0.8
93							—	3.9*	1.6	0.4	—1.4
53								—	1.2	—1.6	—10.7**
74									—	—0.1	—3.4
77										—	—1.7
18											—

1978 Nest Identification Number	9	41	13°	57	29	20	40	77	22	14°
Number of females that had their lifelengths measured	26	14	38	36	24	32	16	52	58	87
Maximum # of females present on the nest at one time	20	25	30	45	65	74	84	90	120	140
9	—	—13.2***	0.6	—1.2	—8.3**	—3.8*	—2.8	—6.2*	—0.9	—4.6*
41		—	16.8***	13.3***	3.7	9.1**	2.4	6.8**	12.4***	9.3**
13			—	—4.1*	—13.6***	—7.6**	—0.7	—13.0***	—4.1*	—13.9***
57				—	—4.4*	—1.0	—0.0	—3.0	0.1	—2.1
29					—	0.7	1.0	1.5	7.7*	1.7
20						—	0.1	—0.4	1.8	—0.0
40							—	—0.8	0.0	—0.6
77								—	5.3*	0.3
22									—	—4.0*
14										—

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ [t] nets that ultimately lost all workers • original nests * satellite nests

Table III. — Temperature, rainfall, larval development times, worker longevity, nest survivorship and reproductive production for *P. exclamans* at BFL, 1977-1979.

Tableau III. — Température, pluviosité, durées de développement larvaire, longévité des ouvrières, survie des nids et production des reproducteurs chez *P. exclamans* à BFL, 1977-1979.

	June MDT* (°C)	July MDT* (°C)	June rain-fall cm	July rain-fall cm	larval devolpment time in July in days			number of workers per nest in mid July			workers longevity in July in days			probability of nest survival	number of reproductives produced per successful nest		
					$\overline{X}$	*S.D.*	*N*	$\overline{X}$	*S.D.*	*N*	$\overline{X}$	*S.D.*	*N*		$\overline{X}$	*S.D.*	*N*
1977	27.9	29.5	3.0	0.5				18.3	16.3	39	15.6	13.6	171	7 %	12.6	10.0	17
1978	27.9	30.2	7.6	3.0	15.7	4.8	170	24.0	21.5	46	20.8	16.2	104	58 %	47.7	54.7	25
1979	26.6	28.4	2.0	26.8	21.8	5.1	150				13.6	8.7	108	5 %	30.4	39.9	18

* MDT = mean daily temperature

Table IV. — Worker longevities for eusocial wasps and bees.

Tableau IV. — Longévité des ouvrières chez les guêpes et les abeilles eusociales.

Species	Months of study	Number of females sampled	Number of nests sampled	Lifelength ± S.D. (days)	Longest lifelength (days)	Location	Reference
WASPS (Vespidae)							
Polistes gallicus	June-Aug.	341	4	19.2	73	Italy	Pardi, 1948
Polistes gallicus	1-15 June			31.4	73	Italy	Pardi, 1948
Polistes gallicus	16-30 June			24.2	65[b]	Italy	Pardi, 1948
Polistes gallicus	1-15 July			26.1	45[b]	Italy	Pardi, 1948
Polistes gallicus	16-31 July			20.2	45[b]	Italy	Pardi, 1948
Polistes gallicus	1-15 Aug.			11.7	35[b]	Italy	Pardi, 1948
P. chinensis antennalis	June-Aug.	122	2	37.8	100	Japan	Miyano, 1980
P. fuscatus	June-Aug.	32	1	22.8 ± 10.7	30	Michigan	West Eberhard, 1969
Mischocytarrus drewseni		148	1 ?	31 ± 16.9	97	Brazil	Jeanne, 1972
M. flavitarsis (1977)	June-July	71		45.7	125	Arizona	Litte, 1979
M. flavitarsis (1978)	June-July	35		31.9		Arizona	Litte, 1979
Vespula vulgaris	Aug.-Sept.	129	1	10.3 ± 0.6[a]	37	England	Archer, 1981
Vespula vulgaris	June			12.4	26	England	Spradbery, 1963 Spradbery, 1973
Vespula vulgaris	July			13.6	27	England	Potter in Spradbery, 1973
Vespula vulgaris	Aug.			22.3	37	England	Potter in Spradbery, 1973
Vespula vulgaris	Aug.			11.6	33	England	Roland, 1969 in Spradbery, 1973
Vespula vulgaris	Sept.			17.4	29	England	Potter in Spradbery, 1973
Vespa orientalis				36.1	64	Israel	Ishay et al. 67 in Spradbery, 1973
Vespa crabro	May-Sept.			19.5	41	France	Janet in Spradbery, 1973
BEES (Apidae)							
Bombus humilis		48	1	25		England	Brian, 1965
Bombus agrorum	July-Aug.	39	1	18	65	England	A.D. Brian, 1952
Apis mellifera	summer	47	1	33.6	40	England	Ribbands, 1952
Apis mellifera	summer	13	1	32.1	55	England	Rosch, 1925 in Ribbands, 1953

a. this is a standard error; b. these are taken from bar graphs

in worker foraging rates since foraging rate is negatively correlated with longevity in this population (STRASSMAN *et al.*, 1984). Average worker longevity may decrease over the season because prey becomes less available as the season progresses. A decrease in prey availability is also suggested by the increase in larval development times over the season (STRASSMANN and ORGREN, 1983) and the increase in the probability of a nest failing due to loss of all workers (STRASSMANN, 1981 c).

The death of a worker does not mean that the brood she tended also dies since brood care is shared. Average worker longevity is less than half the time an egg takes to develop into an adult. Workers may take more risks than solitary wasps or lone foundresses by foraging more often, taking prey which is risky to harvest, foraging in areas where predators lurk, or brinding back large loads at a time.

Since a worker's natal colony constitutes her social, ecological and genetic environment, it is not surprising that colony of origin explains more of the variance in longevity than does any other factor. Workers on a nest share number of nestmates, the queen, the nest with its specific needs for protection from parasites, predators and the weather and they share phenotypic traits because they are related. Numbers of females on the nest had a significant impact on worker longevity only in 1978 when benign conditions meant that colony failure due to the loss of all workers was rare. Under these circumstances workers may have curtailed their foraging in an attempt to increase the probability that they would become the next queen. Presence of *E. polistis* in the nest increased longevity, perhaps because it decreased numbers of larvæ needing to be fed. *C. iphitalis*, nest size (number of cells) and satellite status had no impact on longevity.

Average worker life lengths of *P. exclamans* are among the shortest reported for social bees and wasps ; only *Vespula vulgaris* has similarly short worker lifespans (SPRADBERY, 1973 ; *(table IV)*. All studies on *Polistes* except *P. gallicus* in August report average lifespans for workers of 19-39 days. *P. exclamans* is the only subtropical species for which there are data on longevity except for *Mischocyttarus flavitarsis* and that species had life lengths averaging over 30 days *(table IV)*. It appears that the more primitively eusocial species generally exhibit the longest maximum lifespans, while highly eusocial genera such as *Vespula*, *Vespa* and *Apis* have shorter maximum longevities. This may be the result of a greater flexibility in castes in the more primitively social species where workers can become mated, fully functional queens, and therefore do not senesce.

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