The Caste System of Camponotus foreli Emery (Hymenoptera: Formicidae)

by

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ABSTRACT

The caste system of *Camponotus foreli* Emery is described. The two morphological castes (minor, major) detected through biometrical measurements have distinct behavioral tasks. Minor workers are partially specialized as food collectors outside the nest and adipogastric major workers act as food storers in the bottom of the nest. Non-adipogastric major workers (older?) have a defensive function outside the nest. Dufour gland and fat body are differently developed in the two castes.

INTRODUCTION

Differential task allocation is one of the main factors supporting the evolutionary success of ants (Passera, 1987; Wilson, 1987). Disregarding the reproductive division in females (queens and workers), the distribution of tasks in a colony is usually resolved in one of two ways: a) polyethism, a behavioral change during an individual's life or b) polymorphism, the production of morphologically distinct individuals in a single colony. The two possibilities are not mutually exclusive and can coexist in a same species (Wilson, 1976 a; Calabi *et al.* 1983). The caste system, as defined in Wilson (1971), is a key factor in understanding ant evolution. It has been described in many species (Oster & Wilson, 1978) and is usually related to feeding, brood care or colony defense. Data concerning aspects of the caste system in *Camponotus* species can be found in Jaffé & Sánchez (1984), Fowler (1984), Gibson (1989), Walker & Stamps (1986), Wilson (1974), Tashev (1984), Dartigues & Passera (1979) and Ito *et*

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al. (1988).

Our aim in this study is 1) conduct a biometrical and anatomical study of workers in *Camponotus foreli*; and depending on results, 2) ascertain if any caste system is present in this species and 3) provide a functional description at the colony level.

MATERIAL AND METHODS

Camponotus foreli Emery belongs to the most speciose ant genus (Wilson, 1976 b). It is a thermophilous species with diurnal activity pattern correlated with nectar prodution, its main feeding resource (Retana *et al.* 1987). Its distribution is in the western mediterranean and is found on waste land, dry open spaces and steppes (Suñer, 1982). Two nests were excavated (biometry) near Canet de Mar (Barcelona, Spain) (nest #1, June 14, 1986; nest #2, September 2, 1986) at noon (19.30 to 21 h). Three depth levels were defined (L1, L2, L3, 20 cm each one) and workers from each level were collected separately due to possible vertical stratification (see MacKay, 1983). Half an hour before excavation all workers leaving or entering the nest were also collected (L0). Nest #1 populations was of 474 workers vs. 248 in nest #2.

Since *C. foreli* feeds mainly on nectar, a number of workers on *Euphorbia* flowers, and foraging workers -distant from nest openings- were also collected with an entomological aspirator to check for worker specialization as nectar collectors. They were compared with individuals from nest #1 (Kolmogorov-Smirnov test; see Siegel, 1972) though we did not assume that all foraging workers and workers on flowers belonged to a same nest.

Measures of workers were made using a Nikon SMZ at 60x. The following morphological measures were taken: maximum head length (HL), maximum head width (HW), scape length (SL) and maximum pronotum width (PW). Maximum error was 0.0125mm. Frequency distributions were compared with KS test.

Dissections were made in Ringer's solution. The following parameters were evaluated: 1) fat body development, in four categories (1-4) from less to maximum relative abundance; 2) Dufour's gland relative size (1-3). Ovary development was not checked because of the absence of data concerning age and ovary development in this species. Some workers had the fat body with milky appearance (four in nest #1 and three in nest #2); these were excluded from analysis. Kruskal-Wallis tests (Siegel, 1972) were used to determine whether groups with different degrees of development of fat body, Dufor's gland or from distinct nest level differed in the values of morphological variables. Statistical analysis were performed using the NPAR module of SYSTAT (Wilkinson, 1986).

RESULTS

Castes and biometry

Frequency distribution of the morphological variables is clearly bimodal (Fig. 1) with a strong tendency towards dimorphism. Both nests differ in HW frequency distribution (KS test; $p<0.01$).

Nectar-collecting workers (n=130; HW=53.0±11.6; mean±SD) are also smaller (KS test; $p<0.05$) from workers collected outside the nest, but not in flowers (n=109; HW=57.5±15.0) and from nest #1, considered as a whole (n=475; HW=57.9±15.0) (KS test; $p<0.001$). Body measurements usually show a triphasic allometry (Fig. 2).

Admitting that precise limits among castes are arbitrary - we take the limit as the minimum between modal peaks - we consider HW 60 (=1.5mm) as a top for minor workers (77% in nest #1, 84% in nest #2); major workers account for 23% in nest #1 and 16% in nest #2.

Castes and anatomy

Some workers (Buscher *et al.*, 1985; Jaffé & Sánchez, 1984) define three or four castes in *Camponotus* (minor, media, major, soldier) along the size continuum and compare differences among them. We based the groups on internal anatomy (fat body, Dufour's gland) and compared the four morphological variables according to these groups. Relative abundance of fat body is strongly correlated with size (Table 1 A,B) with larger workers most adipogastric (HW 90.6). Dufour's gland also shows a similar tendency in both nests, though less marked (Table 2 A, B).

Castes and vertical stratification

Workers of different size were not uniformly distributed (Table 3 A,B) and larger workers were found deep inside the nest (levels 2, 3) rather than in level 1 or outside (L0).

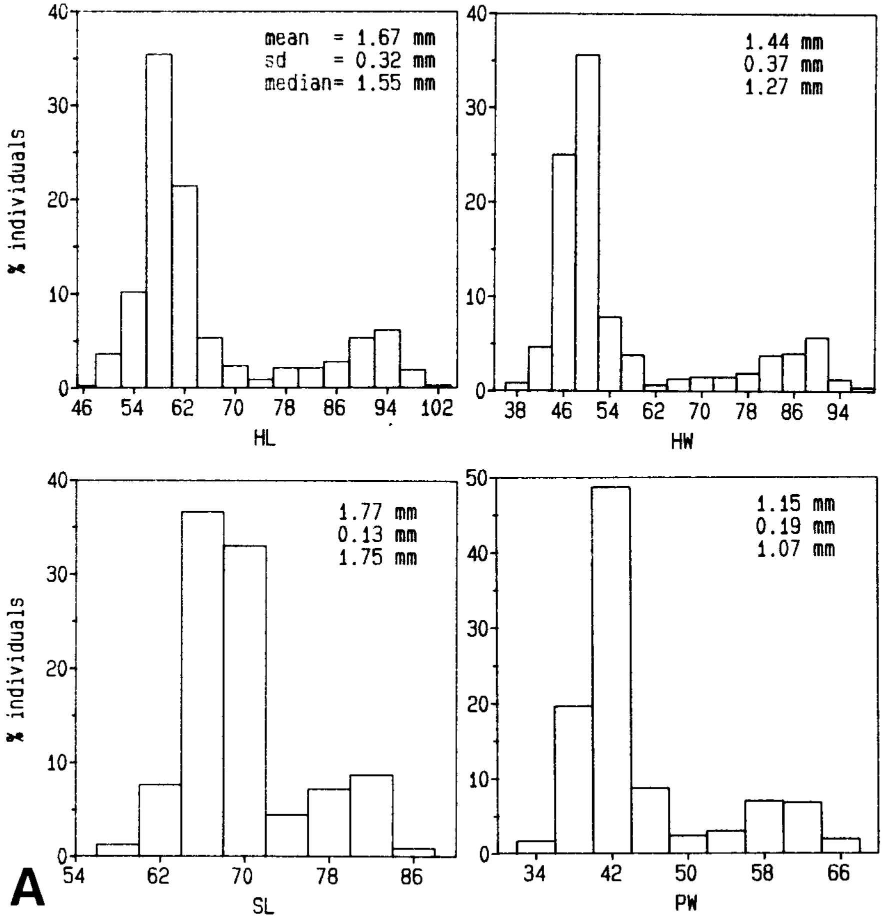

Fig. 1A

Fig. 1. Frequency distributions of four morphological variables in two *Camponotus foreli* Emery colonies from Canet de Mar (Barcelona, Spain). HW: maximum head width; HL: maximum head

DISCUSSION

Camponotus foreli is a polimorphic species (sensu Wilson, 1953). Morphological allometric differences can be detected among individuals at the extremes of the size range in a mature colony. Similar studies (Baroni Urbani, 1974; Benois, 1969 in

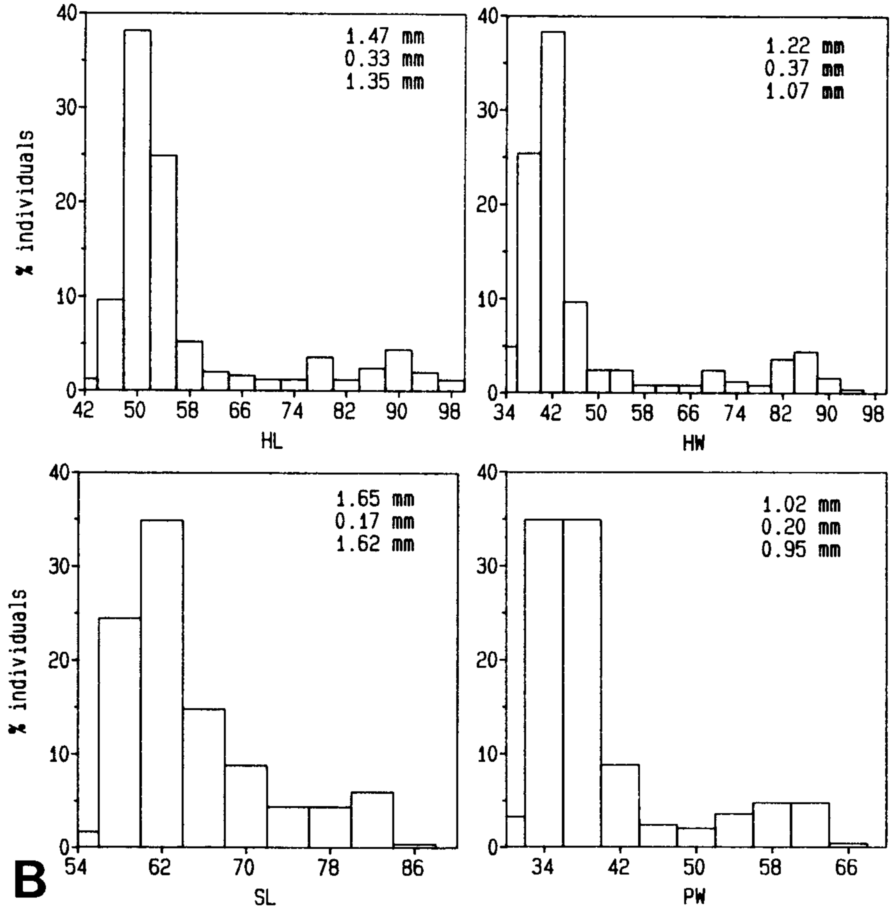

Fig. 1B (nest #2)

length; SL: scape length; PW: pronotum width. Micrometric units (unit 0.025mm). Data are grouped in 0.1mm classes. Data from the two nests have not been pooled since they represent different moments during colony development.

Passera, 1987; Buscher *et al.*, 1985; Suñer, 1982; Wilson, 1953; Weyrauch, 1933) have shown a bimodality in *Camponotus*. Three castes (minor, media and major) are usually defined, with the media as the individuals near the through between the curves in the bimodal distribution. In *C. foreli* this caste seems to be disappearing.

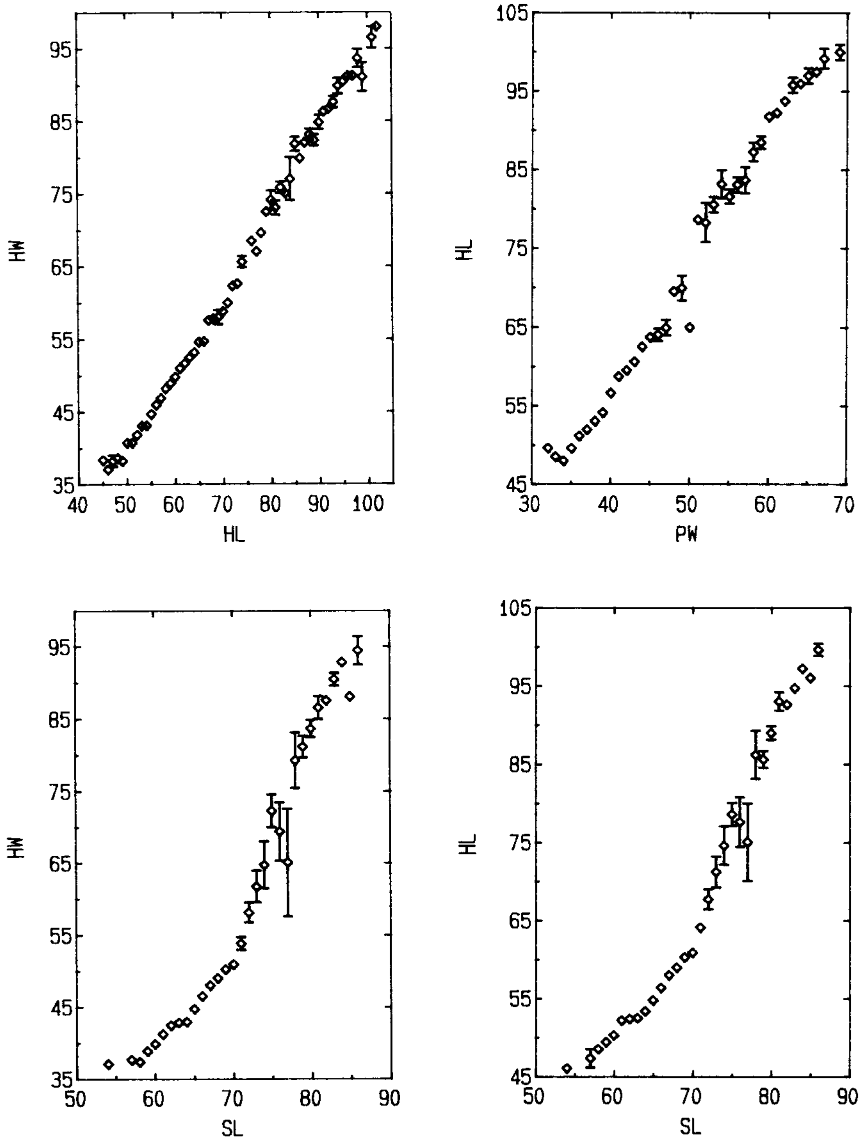

Fig. 2. Allometric relations among four morphological variables in workers of *Camponotus foreli* Emery (n=722) from Canet de Mar (Barcelona, Spain). Abreviations as in Fig. 1. Data from nest #1 and nest #2 have been pooled. A triphasic allometry can be detected in all cases.

Different allometric phases are typical in *Camponotus* (Baroni Urbani, 1974). The middle segment of the regression line in

Table 1. Relation between size and fat body development in workers of *Camponotus foreli* from Canet de Mar (Barcelona, Spain). A: nest #1; B: nest #2. HL: head length; HW: head width; SL: scape length; PW: pronotum width. Values are means±SD in micrometric units; unit 0.025mm. Relative fat body size has been grouped in four categories (1-4) from less to mostly developed. Parentheses indicate the number of workers in each category. Groups differences are significantly different ($p<0.01$) (H, Kruskal-Wallis test, 3 d.f.). Data of both nests have not been pooled since they represent different moments during colony development.

A

	Categories of fat body development				
Mean(SD)	1(216)	2(122)	3(62)	4(44)	H
HL	63.8 (10.2)	64.2 (11.7)	66.8 (11.7)	90.6 (7.8)	93.5
HW	54.1 (11.6)	54.8 (13.0)	57.4 (13.4)	84.9 (9.4)	91.9
SL	69.9 (4.2)	69.9 (4.8)	71.0 (4.8)	80.7 (3.5)	95.5
PW	44.6 (6.0)	44.8 (6.6)	44.8 (8.2)	59.7 (5.4)	89.3

B

	Categories of fat body development				
Mean(SD)	1(74)	2(114)	3(35)	4(22)	H
HL	52.0 (5.0)	55.0 (6.6)	65.6 (14.2)	90.5 (5.0)	96.5
HW	41.7 (5.2)	44.8 (7.1)	56.1 (16.6)	85.5 (5.8)	96.5
SL	62.5 (3.7)	64.8 (4.4)	70.3 (6.5)	80.4 (3.5)	92.8
PW	37.0 (3.6)	39.0 (8.9)	45.6 (8.9)	60.3 (3.5)	95.7

C. foreli, corresponding to the media, shows higher standard errors than first and third segments. Wilson (1953) saw this as a characteristic of un unstable size class and a step towards complete dimorphism.

Caste structure in ant societies is not a fixed characteristic and can change with colony size or age (Wilson, 1983) or shift in response to external pressures such as predation or competition

Table 2. Relation between size and Dufour's gland size in workers of *Camponotus foreli* from Canet de Mar (Barcelona, Spain). A: nest #1, B: nest #2. HL: head length; HW: head width; SL: scape length; PW: pronotum width. Values are means±SD in micrometric units; unit 0.025mm. Relative size of Dufour's gland was grouped in three categories (1-3) from less to mostly developed. Parentheses indicate the number of workers in each category. Groups differences are significant ($p<0.01$) (H, Kruskal-Wallis test, 2 d.f.). Data from both nests have not been pooled since they represent different moments during colony development.

A	Categories of Dufour's gland development			
Mean(SD)	1(223)	2(129)	3(78)	H
HL	65.1 (11.8)	67.8 (13.6)	72.4 (15.5)	16.6
HW	55.8 (13.3)	58.7 (15.3)	64.1 (17.8)	13.4
SL	70.3 (4.9)	71.7 (5.4)	73.5 (6.3)	17.6
PW	45.0 (7.4)	46.6 (7.7)	49.4 (9.0)	11.0

B	Categories of Dufour's gland development			
Mean(SD)	1(154)	2(45)	3(46)	H
HL	55.3 (8.9)	64.6 (16.4)	63.8 (16.8)	14.1
HW	45.2 (10.0)	55.4 (18.7)	55.2 (19.3)	14.8
SL	64.6 (5.1)	69.4 (8.0)	68.5 (7.8)	15.1
PW	39.1 (5.9)	45.1 (10.1)	44.1 (9.7)	16.7

(Bernstein, 1979; Davidson, 1978; Herbers, 1980). Different caste proportions in the two nests of *C. foreli* can be interpreted as age related. Major workers have been shown to become more abundant during colony growth in *C. novaeboracensis* (Gibson, 1989), *C. pennsylvanicus* (Fowler, 1986) and *C. ferrugineus* (Ito *et al.*, 1988).

Table 3. Relation between size and vertical stratification (levels) in workers of *Camponotus foreli* from Canet de Mar (Barcelona, Spain). A: nest #1, B: nest #2. HL: head length; HW: head width; SL: scape length; PW: pronotum width. Values are means±SD in micrometric units; unit 0.025mm. Level 0: outside workers; level 1 to 3, 20 cm, 40 cm, 60 cm. Parentheses indicate the number of workers in each category. Groups differences are significant ($p<0.01$) (H, Kruskal-Wallis test, 3 and 2 d.f.) but for HW ($p=0.07$) and PW ($p=0.05$) in nest #1.

A

	Level				
Mean(SD)	0(30)	1(172)	2(169)	3(100)	H
HL	63.3 (10.6)	64.8 (11.5)	69.6 (14.3)	66.8 (13.5)	14.6
HW	54.8 (11.5)	55.7 (12.9)	60.7 (16.5)	57.4 (15.3)	7.0
SL	69.8 (4.0)	69.7 (4.4)	72.6 (5.9)	71.2 (5.7)	23.7
PW	45.0 (6.0	44.9 (7.3)	47.6 (8.4)	45.8 (7.9)	7.5

B

	Level			
Mean(SD)	0(26)	1(97)	2(127)	H
HL	52.0 (8.1)	54.3 (9.3)	63.7 (15.0)	58.5
HW	41.6 (9.3)	44.0 (9.9)	54.6 (17.1)	68.5
SL	60.8 (3.0)	63.8 (5.4)	69.3 (6.9)	69.3
PW	36.6 (5.0)	38.5 (5.8)	44.4 (9.1)	59.0

As defined here, function and behavior of the two worker castes are different. The lipid reserves and metabolic water can be distributed through trophallaxis to all colony members. The largest workers (majors) of *C. foreli* accumulate a large fat body (adipogastry) with an opaque gaster, inflated, as in *C. thoracicus* and *C. mozabensis* (Délye, 1968) in the Sahara, *C. fraxinicola* in Florida (Wilson, 1974) or *C. micans* in Morocco (per. obs.).

Food accumulation via major worker repletes is the usual form in *Camponotus* (Jaffé & Sánchez, 1984 and refs.; per. obs.).It is interesting to note that maxillary glands, secreting enzymes for sugar and glucogen processing, are size-correlated in *C. sericeiventris* (Buscher *et al.*, 1985).

The existence of adipogastric workers, not to be confused with repletes, which accumulate liquid food (Wilson, 1971), have been known from more than a century, but seldom reported. Emery (1898) mentions *C. fedtschenkoi* and *C. atlantis* with adipogastric workers. This phenomenon appears in some *Camponotus* species from highly fluctuating environments. In contrast, it is worth mentioning the absence of replete workers and a mere 10% of workers with a slight fat body development in *C. detritus* that inhabits the Namib, a desert with a stable climate the year round (Curtis, 1985). An hypothetical relationship of nocturnal activity with adipogastry (Wheeler, 1928) is not confirmed in *C. foreli*, a strictly diurnal species (Retana *et al.*, 1987).

Nest stratification has been described in other ant species but is usually related with worker age and behavioral profile (Billen, 1984; MacKay, 1983) and not with adipogastry. In three *Pogonomyrmex* species, workers with highest fat content are also found in the bottom of the nest, but due to the absence of trophallaxis in this granivorous genus, the situation is not the same as in *C. foreli*.

Non-adipogastric major workers in *C. foreli* have an offensive function when confronted with nests of *Cataglyphis iberica* Emery (Cerdá, 1989; per. obs.) and a defensive function against predator spiders (per. obs.). Since division of labor with age seems to be a fairly general phenomenon in *Camponotus* (Calabi, 1988) we can not exclude a certain degree of behavioral flexibility in *C. foreli*. We could then support the reasoning of MacKay (1983) and assume that these major workers are old ones that have passed through an adipogastric state and, when emptied, shift their behavior to outside tasks. A defensive function for older workers has been described or proposed in other *Camponotus* species (Busher *et al.*, 1985; Fowler, 1986; Jaffé & Sánchez, 1984; Lamon & Topoff, 1981).

Dufour's gland secretions are the most complex secretions described in arthropods and are composed of hydrocarbons and long chain aliphatic compounds (Blum & Hermann, 1978). Their function as alarm pheromones has been suggested in the Formicinae (Ali *et al.*, 1987; Fowler & Crestana, 1987). The higher development of this gland in major workers of *C. foreli*, also with much fat body, suggests such workers function as nurses, as was found in *Lasius niger* (Lenoir, 1979). More behavioral observations and tests are needed to ascertain this point.

Other marked differences exist between minors and majors in the type of food they collect. Nectar collectors belong to the minor caste (HW 53.08; SD 11.68, n=132). Although *Euphorbia* nectaries are not concealed, it is to be expected that the smaller workers have easier access to floral nectaries. It has been suggested that floral morphology, specially oclusive structures, limits the access of ants to nectaries (Herrera *et al.*, 1984). Nectar collection in *C. sericeiventris* is restricted to minor workers (Busher *et al.*, 1985). In our study site *C. foreli* gathers nectar from a minimum of eight species (Retana et al., 1987). Major and minor in *C. foreli* have also a distinct profile of prey recovery: in field experiences in which foragers are offered prey, majors take a 77% of arthropod corpses (n=71 tested items), but minor workers accept a mere 13% (n=83) (per. obs.).

To summarize, in *C. foreli* there are two morphological castes that are functionally segregated: minor workers being partially specialized as food collectors outside the nest and major workers (adipogastric) as food storers in the bottom of the nest.

An age related polyethism could add a behavioral flexibility as was suggested by the observed aggressive behavior of majors (oldest workers?). A study of ovarian development and an eventual minor worker poliethism could confirm these results. It would be interesting to check the annual phenology of adipogastric workers, with an hypothetical maximum at the end of the season (summer) after the eclosion of all callow workers, and a minimum in spring, after hibernation; also, to compare the proportion of adipogastric workers in colonies from habitats differing in its primary production.

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