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Size and fat content of gynes in relation to the mode of colony founding in ants (Hymenoptera; Formicidae)

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Summary. In ants, there are two main processes of colony founding, the independent and the dependent modes. In the first case young queens start colony founding without the help of workers, whereas in the second case they are accompanied by workers. To determine the relation between the mode of colony founding and the physiology of queens, we collected mature gynes of 24 ant species. Mature gynes of species utilizing independent colony founding had a far higher relative fat content than gynes of species employing dependent colony founding. These fat reserves are stored during the period of maturation, i.e. between the time of emergence and mating, and serve as fuel during the time of colony founding to nurture the queen and the brood. Gynes of species founding independently but non claustrally were found to have a relative fat content intermediate between the values found for gynes founding independently and those founding dependently. This suggests that such gynes rely partially on their fat reserves and partially on the energy provided by the prey they collect to nurture themselves and the first brood during the time of colony founding. Study of the fat content of mature gynes of all species has shown that it gives a good indication of the mode of colony founding.

Key words: Reproductive strategies – Colony founding – Ant – Fat content

The existence of a well-developed size dimorphism between queens and workers is a striking feature of most social insects (see Wilson 1971; Passera 1984). In ants, the size of sexuals is almost always larger than that of workers and their production requires an important investment of energy on the part of the colony. An important factor which may possibly influence the relative cost of sexuals is the way queens start colonies. There are two main strategies of colony founding, namely the independent and dependent modes (Hölldobler and Wilson 1977). After the nuptial flight and mating, queens may start colony founding without the help of workers. This is the independent mode of colony founding, which is generally claustral in ants, i.e., after the nuptial flight, the newly mated queen confines herself in a cell and rears the first brood in isolation. However, in some species newly mated queens leave the nest during colony founding to forage (the independent but non claustral mode of colony founding). In species employing independent and claustral colony founding, the queens rely on their fat reserves and the energy provided by the histolysis of the flight-muscles (Janet 1907) to nurture themselves and their first brood during the founding stage. The other (dependent) method of colony founding is when queens need the help of workers to start new colonies. This phenomenon occurs in the case of parasitism (i.e., newly mated queens parasitize the nest of another species) and in the case of nest-budding, a process in which one or several queens move out of the nest accompanied by workers and establish a new colony. Nest-budding occurs mostly in species where mating takes place within or nearby the nest, or when newly mated queens are accepted into their parental nest or another nest of the same species.

Study of the physiological status of gynes of the Argentine ant *Iridomyrmex humilis*, a species utilizing dependent colony founding, showed that mature gynes had a very low relative content of fat (g fat/g dry weight) in comparison to species employing independent colony founding (Keller and Passera 1988). Gynes of *I. humilis* also differed from species utilizing independent colony founding in their physiological development (i.e., increase in weight and energy content). This raises the question of whether the mode of colony founding may possibly be an important factor associated with physiology of queens. To investigate this question, we collected mature gynes of 24 ant species and compared their weight and fat content.

Materials and methods

Source of mature and immature gynes

Gynes were collected during summer and autumn of 1987 in Switzerland (CH) and France (F) (see Table 1). To ensure that they were mature, all gynes were collected either from their nest just before the nuptial flight or on the ground just after the nuptial flight. Gynes at the time of emergence were obtained by collecting pupae and workers and then holding them in the laboratory until emergence of the adults. The units were monitored daily and ten winged queens less than 24 h old were weighed and their fat and energy content determined (see below).

Mode of colony founding of the studied species

Although the biology of many European ant species has been well-studied, surprisingly little is known about the

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Table 1. Origin of gynes

Species	N	Location where samples where collected
1 Camponotus ligniperda	10	close to Marchairuz in the Jura Mountains, CH
2 Camponotus herculaneus	10	close to Marchairuz in the Jura Mountains, CH
3 Camponotus truncatus	3	northern Italy near the Lake Garda
4 Lasius flavus	10	near Lausanne, CH
5 Lasius niger	10	near Lausanne, CH
6 Lasius emarginatus	10	near Lausanne, CH
7 Lasius alienus	10	near Lausanne, CH
8 Tetramorium caespitum	10	in the Alps close to Pont-De-Nant near Bex, CH
9 Aphaenogaster subterranea	10	in the Alps near Briançon, F
10 Diplorhoptrum fugax	10	on the Campus of the University of Paul Sabatier, F
11 Formica gagates	10	in the Alps near Briançon, F
12 Formica fusca	4	in the Alps near Briançon, F
13 Formica lemani	10	in the Alps close to Pont-De-Nant near Bex, CH
14 Leptothorax nylanderi[a]	10	Fontaineblaux near Paris, F
15 Manica rubida	10	in the Alps near Briançon, F
16 Formica lugubris	10	from the supercolony in the Jura mountains, CH (see Gris and Cherix 1977)
17 Formica pratensis	10	from the Bois de Chêne, near Nyon, CH
18 Formica rufa	10	from the Bois de Chêne, near Nyon, CH
19 Formica polyctena	10	near Lausanne, CH
20. Cataglyphis cursor	10	St. Hyppolyte, F
21 Lasius fuliginosus	3	in the Alps near lake Tanney, CH
22 Myrmica scabrinodis	10	on the Campus of the University of Paul Sabatier, Toulouse F
23 Myrmica rugulosa	3	Donneloye near Yverdon, CH
24 Iridomyrmex humilis[b]	10	Port Leucate, near Narbonne, F

[a] Gynes of *Leptothorax nylanderi* were kindly furnished by Luc Plateaux who reared them in the laboratory from colonies which had been collected in forest of Fontainebleau near Paris; they were collected just after a nuptial flight in laboratory in April 1987. After the nuptial flight these gynes were maintained for 6 months under experimental conditions of hibernation; similar exposure of gynes of other species showed that they only lose a little weight and fat content (Keller, unpublished data)

[b] Gynes of *Iridomyrmex humilis* were reared under similar conditions to those described in Passera et al. (1988a) and Keller and Passera (1989) and collected just after mating which occured in the laboratory (see Passera et al. 1988b)

mode of colony founding. We give here the information we have found in the literature and unpublished observations (Table 2).

Determination of fat content

Queens were killed with ethyl acetate vapour and then subjected to the same experimental procedure as used by Peakin (1972). It is as follows: 1) Fresh weight was individually determined. 2) Queens were dried for 24 h at 70° C and the dry weight was determined. 3) Fat was extracted with petroleum ether (boiling point 40–60° C) for 24 h and then the queens were dried again for 24 h and weighed. All weights were determined to the nearest 10^{-6} g.

Table 2. Mode of colony founding of the species

Species	Mode of colony founding	
Camponotus ligniperda	I	Hölldobler 1962
Camponotus herculaneus	I	Hölldobler 1962
Camponotus truncatus	I	Keller unpublished
Lasius flavus	I	Kutter 1977; Dumpert 1978
Lasius niger	I	Kutter 1977; Dumpert 1978
Lasius emarginatus	I	Kutter 1977; Dumpert 1978
Lasius alienus	I	Kutter 1977; Dumpert 1978
Tetramorium caespitum	I	Poldi 1963
Aphaenogaster subterranea	I	Buschinger 1973; Poldi pers. com.
Diplorhoptrum fugax	I	Buschinger 1974; Lachaud 1981; Poldi pers. com.
Formica gagates	I	Hölldobler 1950
Formica fusca	I	Kutter 1977; Pamilo et al. 1978, 1979
Formica lemani	I	Kutter 1977; Keller unpublished
Leptothorax nylanderi	I(nc)	Buschinger 1969; Plateaux pers. com.
Manica rubida	I(nc)	Le Masne and Bonavita 1969
Formica lugubris	D, D(p)	Kutter 1977
Formica pratensis	D, D(p)	Kutter 1977
Formica rufa	D, D(p)	Kutter 1977
Formica polyctena	D, D	Kutter 1977
Cataglyphis cursor	D	Lenoir et al. 1988
Lasius fuliginosus	D(p)	Kutter 1977; Collingwood 1979
Myrmica scabrinodis	I(nc), D	Elmes pers. com.
Myrmica rugulosa	I(nc), D	Elmes pers. com.
Iridomyrmex humilis	D	Newell and Barber 1913; Keller 1988; Keller and Passera 1988

I: independent colony founding, *I(nc)*: independent but non claustral colony founding, *D*: dependent colony founding, *D(p)*: parasitic colony founding

Results

Mature gynes

Variation among species of fat content/gynes was significantly related to dry weight of these gynes and to the mode of colony founding (ANCOVA test, both $P<0.001$; ln-transformation of fat content). In this analysis, these two factors accounted for nearly all of the variance (97.1%) in the fat content of gynes. There was a slight but significant interaction between both factors ($P=0.036$); we therefore estimated the regression lines independently for gynes utilizing independent and those employing dependent colony founding (Fig. 1). The equations of the two regression lines were as follows:

$ln\mathrm{F}=0.913\ \mathrm{lnW}-0.407$ for species utilizing independent colony founding ($r^2=0.99$)

$ln\mathrm{F}=0.682\ \mathrm{lnW}-1.215$ for species utilizing dependent colony founding ($r^2=0.82$).

For both regressions, the slopes were significantly lower than a theoretical slope of 1 (t-test; $P<0.001$) thus indicating that the relative fat content (*F*/*W*) of gynes decreases

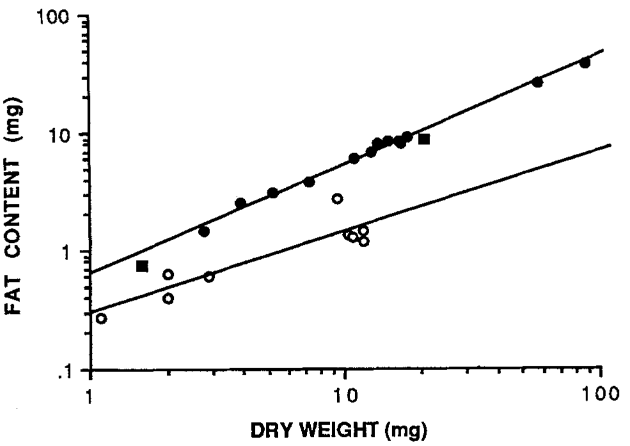

Fig. 1. Fat content of gynes as a function of their dry weight and mode of colony founding. ● independent; o dependent; ■ independent (nc)

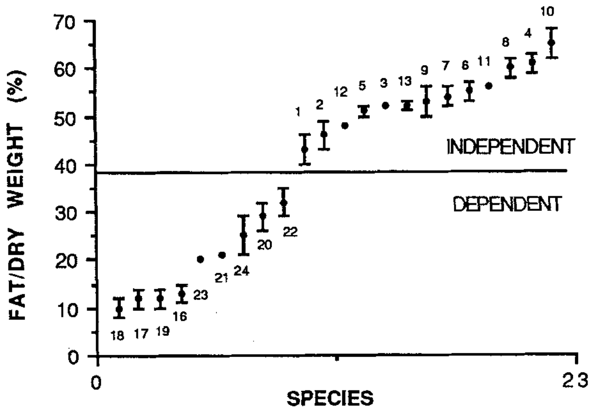

Fig. 2. Mean relative fat content of gynes in relation to their mode of colony founding. Numbers indicate the species as referred to in Table 1, SD is given when more than 4 individuals per species.

with increasing dry weight both for species employing independent and dependent colony founding. For exemple, in species employing independent colony founding, the lower value of relative fat content of gynes was found in the species with the largest gynes (*Camponotus ligniperda*; fat/dry weight: 43%) and the highest value was found in one of the species with the smallest gynes (*Diplorhoptrum fugax*; fat/dry weight: 65%).

There was no overlap in the values of the relative fat content between gynes founding independently and those founding dependently (min. of 43% in species with independent colony founding and max. of 32% in those with a dependent colony founding) (Fig. 2).

Gynes of the two species with independent but non claustral colony founding (*Manica rubida* and *Leptothorax nylanderi*) had relative fat contents (43% and 46%, respectively) intermediate between the values of species with independent and dependent colony founding (Fig. 1).

Maturation

In order to investigate the possible differences in the processes of maturation of gynes between species utilizing independent and dependent colony founding, we studied the increase of weight and fat and energy content of gynes from the time of emergence to the time of mating in eight species, of which three utilize independent and claustral colony founding, one utilizes independent but non claustral colony founding, and five utilize dependent colony founding.

At the time of emergence the relative fat content was slightly lower in gynes founding dependently than in those founding independently (Table 3). Between the time of emergence and the time of mating, the mean increase of dry weight was far higher for gynes utilizing independent and claustral colony founding than for those utilizing dependent colony founding (172% and 31% respectively). It is worthwhile mentioning that the increase in dry weight was higher for all gynes founding independently than for those founding dependently. Similarly, the increase in the relative fat content was far higher in species founding independently (295% and 48% for gynes founding independently and dependently, respectively). t-tests showed that the increase in fat content was significantly higher in all species founding independently than in those founding dependently ($P < 0.001$ for all comparisons).

The only species with independent but non claustral

Table 3. Physiological status (mean ± SD) of gynes at emergence and mating

Species employing	N	Dry weight (mg) (emergence)	Dry weight (mg) (time of mating)	Increase (%)	Fat content (%) (emergence)	Fat content (%) (mating time)	Increase (%)
Independent colony founding							
Lasius flavus	10	3.8 ±0.2	13.5±0.3	255±25	11±4	61±2	455±62
Lasius niger	10	6.3 ±0.6	16.4±0.7	160±33	22±2	51±1	132±24
Tetramorium caespitum	10	2.6 ±0.2	5.2±0.5	100±33	15±4	60±2	300±95
Mean		4.2 ±1.9	11.7±5.8	172	16±6	57±6	295
Independent but non claustral colony founding							
Manica rubida	10	6.3 ±0.1	10.9±0.4	73±9	10±1	43±2	330±58
Dependent colony founding							
Formica lugubris	10	8.5 ±0.4	10.2±0.7	20±13	12±1	13±2	8±24
Formica pratensis	10	9.6 ±0.7	11.9±1.9	24±27	8±3	12±2	50±63
Formica rufa	10	9.4 ±0.5	11.8±0.7	26±16	8±3	10±2	25±53
Formica polyctena	10	8.5 ±0.6	10.7±0.8	26±18	8±2	12±2	50±50
Iridomyrmex humilis	10	0.68±0.0	1.1±0.1	62±20	12±2	25±4	108±58
Mean		7.3 ±3.8	9.1±4.6	31	10±2	14±6	48

colony founding (*M. rubida*) which was studied at the time of emergence and nuptial flight exhibited an increase in weight and fat content which was intermediate between those found in species with independent and those found in species with dependent colony founding (Table 3).

Discussion

The results of the present study show that gynes founding independently accumulate strikingly high amounts of fat between the time of emergence and the time of mating, whereas gynes founding dependently accumulate only small amounts of fat. To date, relative fat content of mature gynes of ants was known only in *Tetramorium caespitum* (51%, Peakin 1972), *Lasius niger* (44%, Boomsma and Isaaks 1985) and *Lasius flavus* (60%, Nielsen et al. 1985). These values are slightly lower than those found in our study for the same species, but this difference may be partly due to the fact that in the three above studies, gynes were collected within the nest before nuptial flight and were therefore probably not totally mature.

There was a negative relationship between the relative fat content and dry weight both for gynes founding independently and dependently. There are three possible explanations for the lower relative fat content of larger gynes. (i) Accumulation of fat is limited by physiological contraints linked to allometric growth in insects (e.g. relative mass of the wing muscles and cuticule could be higher in larger animals therefore resulting in a negative correlation between fat content and body mass). In vertebrates, comparative studies have shown that skin and skeleton considered together as well as skeletal muscles tend to occupy a constant fraction of body size (Calder 1984). Unfortunately, up to now, only little attention has been devoted to proportional structuring in arthropods in relation with their body size and it is therefore not known if there is a relationship between relative weight of muscles and/or cuticule and body size. (ii) Several studies have shown that in insects (Kayser and Heusner 1964; Zotin and Konoplev 1978; Bartholomew and Casey 1977), spiders (Greenstone and Benett 1980), and many other poikilotherms and homeotherms (see Peters 1983) specific oxygen consumption is negatively correlated to body mass. Large queens may therefore need a lower amount of energy (in proportion to their weight) for their own metabolism. However, in ants, Nielsen (1986) failed to find a correlation between dry mass and specific respiratory rate in workers thus raising the question of whether larger queens really have a lower specific respiratory rate than smaller ones. (iii) Larger species often produce lower numbers of workers than smaller ones during colony founding (Keller unpublished data) and therefore need less fat reserves to rear them. However, the reverse may also be true, i.e., as a result of their lower relative fat reserve, larger species may produce fewer offspring. These three explanations are not mutually exclusive and further experiments are necessary to determine their relative importance.

The lower coefficient of determination between *ln* of fat and *ln* of dry weight of gynes founding in dependently than in those founding dependently suggest that there is a higher inter-specific variability in the fat content in gynes founding dependently. This higher variability may indicate that some differences in the biology of species with dependent colony founding (e.g., length of time spent out of the nest for mating) could influence the relative fat content of gynes.

The intermediate value (in comparison with species employing independent and those utilizing dependent colony founding) of relative fat content of the two studied species which reproduce via independent but non claustral colony founding suggests that gynes of these species rely partially on their fat reserves and partially on the energy provided by the prey they collect during the time of colony founding.

Finally, it is worthwhile mentioning that there was no overlap in the values of the relative fat content between gynes founding independently and those founding dependently. The study of the fat content of mature gynes of any ant species may thus give a good indication of the mode of colony founding.

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