Energy investment during the differentiation of sexuals and workers in the Argentine ant Iridomyrmex humilis (Mayr)

Autor(en): **Passera, Luc / Keller, Laurent**

Objekttyp: **Article**

Zeitschrift: **Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society**

Band (Jahr): **60 (1987)**

Heft 3-4

PDF erstellt am: **20.09.2024**

Persistenter Link: https://doi.org/10.5169/seals-402273

Nutzungsbedingungen
Die ETH-Bibliothek ist Anbieterin der digitalisierten Zeitschriften. Sie besitzt keine Urheberrechte an den Inhalten der Zeitschriften. Die Rechte liegen in der Regel bei den Herausgebern.
Die auf der Plattform e-periodica veröffentlichten Dokumente stehen für nicht-kommerzielle Zwecke in Lehre und Forschung sowie für die private Nutzung frei zur Verfügung. Einzelne Dateien oder Ausdrucke aus diesem Angebot können zusammen mit diesen Nutzungsbedingungen und den korrekten Herkunftsbezeichnungen weitergegeben werden.
Das Veröffentlichen von Bildern in Print- und Online-Publikationen ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. Die systematische Speicherung von Teilen des elektronischen Angebots auf anderen Servern bedarf ebenfalls des schriftlichen Einverständnisses der Rechteinhaber.

Haftungsausschluss
Alle Angaben erfolgen ohne Gewähr für Vollständigkeit oder Richtigkeit. Es wird keine Haftung übernommen für Schäden durch die Verwendung von Informationen aus diesem Online-Angebot oder durch das Fehlen von Informationen. Dies gilt auch für Inhalte Dritter, die über dieses Angebot zugänglich sind.

Ein Dienst der *ETH-Bibliothek*
ETH Zürich, Rämistrasse 101, 8092 Zürich, Schweiz, www.library.ethz.ch

http://www.e-periodica.ch

MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT
BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE
60, 249–260, 1987

Energy investment during the differentiation of sexuals and workers in the Argentine ant *Iridomyrmex humilis* (MAYR)[1]

LUC PASSERA & LAURENT KELLER

[2] Laboratoire d'Entomologie, Université Paul-Sabatier, 118 route de Narbonne, 31062 Toulouse (France). U. A. no 333.
[3] Musée Zoologique, Palais de Rumine, CP 448, 1000 Lausanne 17 (Switzerland).

The fresh weight, dry weight, fat content and energy content of larvae, pupae and adults were measured in queens, males, and workers of *Iridomyrmex humilis*. The three forms display several differences in their pattern of development. These differences can be partially explained by differences between the forms, e. g. the development of reproductive organs in queens and the tasks performed by the young workers.

In several studies, authors have assumed that the relative cost of mature winged queens and males can be estimated by their dry weights. However the present results show that between the larval stage and emergence there was a considerable weight loss which was not proportional in winged queens and males. Furthermore, the energy content of individuals was not equal in the two sexes. The extent to which these sources of errors affect the estimation of the relative cost of queens and males is discussed.

INTRODUCTION

Two major questions concerning the biology of social insects are firstly, the relative amount of available resources the society should invest in the production of workers and sexuals and secondly, the relative amount of energy invested in male or female sexuals.

The size of sexuals is almost always larger than workers (BRIAN, 1979), the production of the former representing an important energy investment. For instance in the ant *Plagiolepis pygmaea,* the queen larvae receive up to 6 times more food, weight for weight, than worker larvae (BONAVITA-COUGOURDAN & PASSERA, 1978).

Because the production of sexuals represents a heavy energy investment only mature societies are able to produce winged forms (BRIAN *et al.,* 1967; MARKIN *et al.,* 1973; OSTER & WILSON, 1978; PLATEAUX, 1980).

In ants, there have been several studies on the caloric content of males and queens e. g. in *Tetramorium caespitum* (PEAKIN, 1972), *Lasius flavus* (PEAKIN, 1964, 1985; PEAKIN *et al.,* 1985; NIELSEN *et al.,* 1985) and *Lasius niger* (BOOMSMA & ISAAKS, 1985). Little data is available concerning workers (PORTER & JORGENSEN, 1981; PORTER & TSCHINKEL, 1985; MACKAY, 1985).

---

[1] This paper is dedicated to Dr. HEINRICH KUTTER who was the first to report the presence of the Argentine ant in Switzerland.

The aim of this work was to study the energy content of the different stages of the ant *Iridomyrmex humilis* – a typically polygynous species (see KELLER, 1988) – from larvae to imago in workers, males, and queens. In addition this paper presents data on the relative investment in male and female sexuals.

MATERIAL AND METHODS

Selection of individuals

The larvae, pupae and imago were taken from stock colonies reared in the laboratory under similar conditions to those described in PASSERA *et al.* (1987).

Larvae: in order to compare worker, queen and male larvae, we selected large larvae in the final instar. At this stage it is easy to separate them according to sex and caste. Worker larvae are brightly coloured and the size ranges from 1.4 to 1.8 mm. Male larvae have the same shape and colour but are larger (2.0–2.5 mm in length). Queen larvae are on the contrary matt in colour and greater in length than either workers or males (2.7–3.5 mm). All of these larvae were near the prepupal stage.

Prepupae: it is easy to separate worker, male and queen prepupae according to their size. Since the prepupal stage is very short (about 4 days for workers at 28 °C), prepupae were chosen at random.

Pupae: they were selected in the dark eye condition, almost in the middle of their pupal stage.

Imagos at the time of emergence: cultures with pupae were monitored every morning so the newly emerged imagos taken from these units were less than 1 day old.

Imagos at the time of mating: In *I. humilis* there is no nuptial flight and mating occurs within the nest (NEWELL & BARBER, 1913). After emergence, queens were individually transferred into units with males and several hundred workers. After mating, queens rapidly loose their wings. Every morning the units were monitored. Hence 10 newly mated queens which had dealated within the previous 24 hours were collected.

Old imagos: Queens were taken from a stock colony reared in the laboratory since May 1985. So at the time of the experiment (June 1986), they were at least 1 year old. The males which emerged in the laboratory were at least 2 months old. Workers were chosen at random from a mature society.

Experimental procedure

Samples of individuals were sorted and subjected to the following experimental procedure, according to PEAKIN (1972).

- Individuals were weighed (fresh weight) using an electronic microbalance (Mettler ME 30, accurate to +/– 1 μg);
- Specimens were killed with ethyl acetate vapour;
- They were dried for 24 hours at 70 °C and re-weighed (dry weight);
- Fat was extracted over 24 hours using petroleum ether (boiling point 40–60 °C) in a Soxhlet apparatus;

	N	Mean fresh weight (μg)	Mean dry weight (μg)	Mean fat weight (μg)	Fat as a percentage of dry weight	Energy content J per individual	Caloric val. (KJ per g) fresh weight	Caloric val. (KJ per g) dry weight
QUEENS								
Fully grown larvae	11	4406 ± 312	1210 ± 95	300 ± 31	25.62 ± 2.56	28.93 ± 2.17	6.58 ± 0.24	24.08 ± 0.52
Prepupae	11	3942 ± 94	1157 ± 33	269 ± 17	23.05 ± 1.27	27.29 ± 0.83	6.92 ± 0.13	23.58 ± 0.27
Pupae	11	3977 ± 70	975 ± 15	195 ± 15	19.84 ± 1.26	22.14 ± 0.59	5.57 ± 0.15	22.72 ± 0.32
Callows	11	2769 ± 69	680 ± 21	82 ± 11	11.87 ± 1.20	14.45 ± 0.58	5.22 ± 0.17	21.10 ± 0.23
Queens at the time of mating	11	3032 ± 81	1076 ± 54	275 ± 36	24.66 ± 2.0	25.90 ± 1.74	8.46 ± 0.36	23.88 ± 0.41
Old mated queens	11	3393 ± 130	1177 ± 68	405 ± 42	33.85 ± 1.50	30.47 ± 2.12	8.91 ± 0.31	25.77 ± 0.31
MALES								
Fully grown larvae	50	1931 ± 36	609 ± 13	151 ± 5	25.01 ± 0.34	14.54 ± 0.33	7.53 ± 0.05	23.92 ± 0.08
Prepupae	50	1936 ± 44	586 ± 13	121 ± 5	20.63 ± 0.51	13.51 ± 0.33	6.98 ± 0.05	23.06 ± 0.09
Pupae	65	1813 ± 69	502 ± 22	121 ± 6	24.05 ± 0.59	11.93 ± 0.52	6.57 ± 0.09	23.77 ± 0.11
Callows	49	1404 ± 50	410 ± 7	55 ± 3	13.65 ± 0.82	8.68 ± 0.12	6.24 ± 0.20	21.66 ± 0.19
Old males	75	1398 ± 31	417 ± 4	36 ± 2	8.55 ± 0.42	8.58 ± 0.09	6.18 ± 0.13	20.64 ± 0.09
WORKERS								
Fully grown larvae	50	620 ± 3	194 ± 4	49 ± 1	24.84 ± 0.65	4.65 ± 0.09	7.51 ± 0.08	23.96 ± 0.14
Prepupae	100	635 ± 10	164 ± 6	39 ± 4	23.73 ± 1.85	3.89 ± 0.13	7.25 ± 0.18	23.68 ± 0.54
Pupae	100	509 ± 12	138 ± 6	38 ± 4	29.64 ± 1.84	3.38 ± 0.18	6.61 ± 0.21	24.37 ± 0.37
Callows	70	424 ± 10	130 ± 2	31 ± 1	23.51 ± 0.63	3.08 ± 0.06	7.27 ± 0.08	23.66 ± 0.13
Old workers	900	410 ± 5	119 ± 1	17 ± 1	14.54 ± 0.77	2.60 ± 0.03	6.34 ± 0.11	21.79 ± 0.16

Tab. 1. Variation in body composition and energy content during the course of development in queens, males and workers of the Argentine Ant.

- After re-drying for 24 hours the extracted individuals were weighed again in order to obtain the lean weight and the fat content by difference;
- The caloric value was calculated from the data on the assumption that 1 g of fat is equivalent to 39.33 KJ and the lean dry material (carbohydrates + proteins) has a caloric value of 18.83 KJ per g (PEAKIN, 1972; BARONI-URBANI *et al.*, 1978).

For each treatment the number of specimens was as follows:

Workers:
- larvae: each sample contained 5 individuals; 10 replicates;
- prepupae and pupae: each sample contained 10 individuals; 10 replicates;
- young imagos: each sample contained 7 individuals; 10 replicates;
- old imagos; each sample contained 100 individuals; 9 replicates.

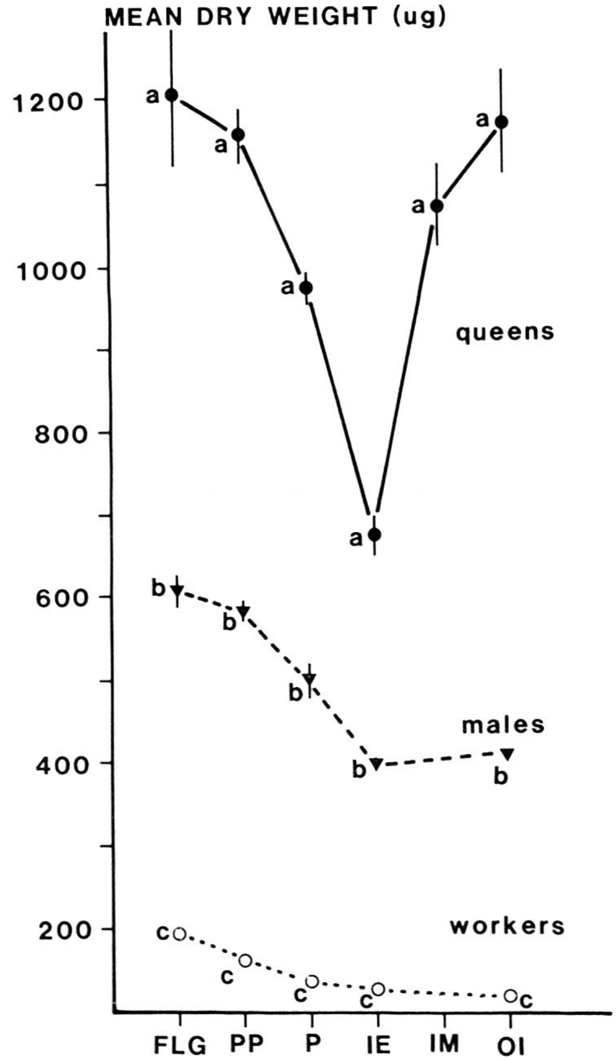

Fig. 1. Mean dry weight (μg) of queens, males and workers. FGL = Full grown larvae; PP = Prepupae; P = Pupae; IE = Imagos at the time of emergence; IM = Imagos at the time of mating; OI = Old imagos. Means followed by different lower case letters are significantly different ($P < 0.05$, Duncan's Multiple Range Test). Bars were drawn when they were large enough to be visible = ± 1 SE about mean.

Queens:
- each sample contained 1 individual; 10 replicates for each stage.

Males:
- larvae and prepupae: each sample contained 5 individuals; 10 replicates;
- pupae: each sample contained 5 or 10 individuals; 10 replicates;
- young imagos: each sample contained 5 indiviuals; 10 replicates;
- old imagos: each sample contained 5 individuals; 15 replicates.

RESULTS

The data are pooled and summarized inTab. 1.

Dry weight

Fig. 1 shows that between the stage of the fully grown larva and emergence, the dry weight of the three forms (queens, males and workers) decreased. This is because pupae do not receive any food. At the fully grown larval stage, queens were twice the weight of males an 6.2 times heavier than workers. At the time of emergence these ratios were 7.7 and 5.2, respectively, so more waste material appears to be extruded in the meconium in queens than in males or workers.

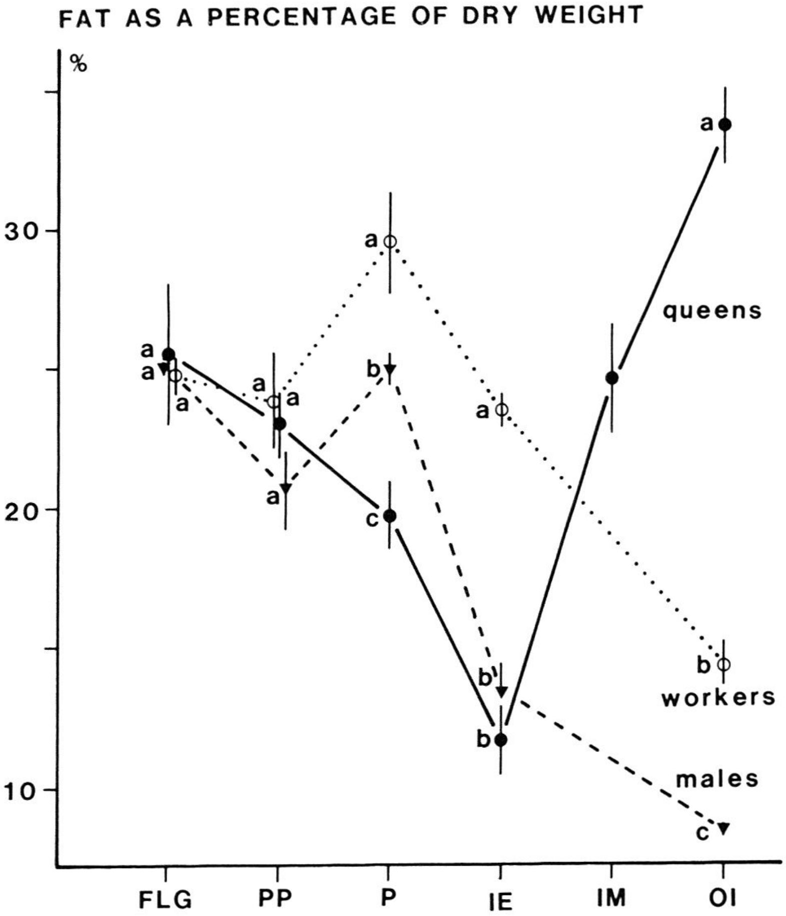

Fig. 2. Fat as a percentage of dry weight; for symbols see Fig. 1.

After emergence the weight of the queens increased greatly whereas male dry weight increased only slightly and worker dry weight decreased slightly. At the time of old imagos queens were 2.8 times heavier than males and 9.9 times heavier than workers.

Fat content

The fat content of individuals is a good measure of energy reserve (Peakin, 1972; Nielsen *et al.*, 1985). Fig. 2 shows that at the end of the larval stage, queens, males and workers had a similar ratio of fat/dry weight, 25.6%, 25.0% and 24.8% respectively. This ratio slightly decreased in the prepupal stage for the three forms.

In the pupal stage the ratio fat/dry weight decreased in queens, whereas it increased in males and workers. At this time, the ratio was significantly higher in workers than in males and queens.

Between the pupal stage and the callows, the ratio fat/dry weight decreased in all three forms. Queens and males had a similar ratio of ca. 12% fat, whereas workers had a ratio twice this value.

After emergence the ratio of fat to dry weight decreased further in males and workers, whereas it strongly increased in queens.

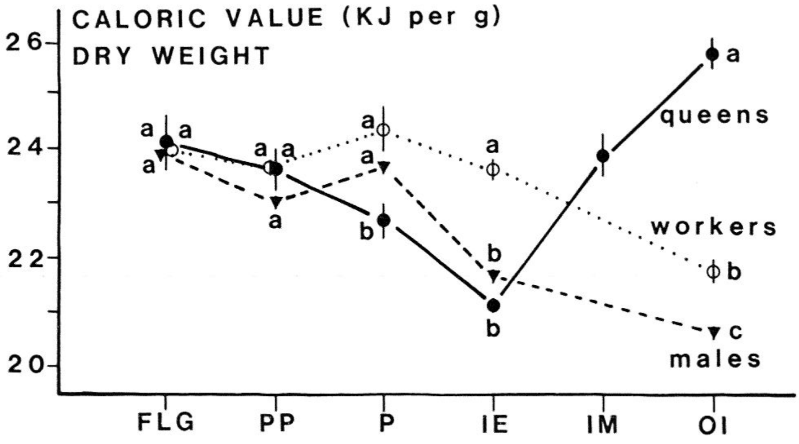

Fig. 3. Caloric value (KJ per g dry weight); for symbols see Fig. 1.

Energy content per g

The curves of energy content per g in the three forms have exactly the same pattern as the curves of fat/dry weight ratio (Fig. 3). This is because the energy content/g is directly dependent on the relative content of fat which contains more energy per g than proteins and carbohydrates.

Energy content per individual

Energy content per individual (Fig. 4) is equal to the dry weight × the energy content/g of the individuals. Since the dry weight of the animal varies more during the development of the individuals than the energy content/g, the

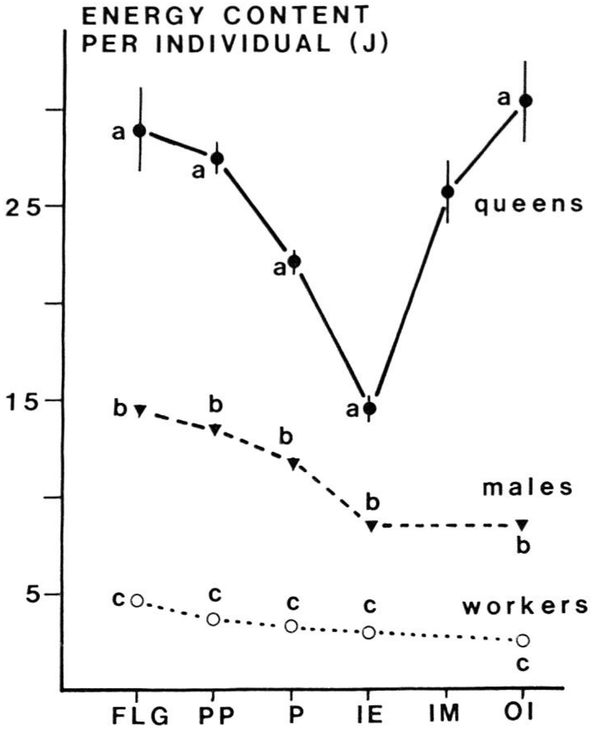

Fig. 4. Energy content per individual; for symbols see Fig. 1.

variations of energy content of all stages of the three forms follow a similar pattern as the variation of their dry weight.

DISCUSSION

The three forms (queens, males, workers) display some differences in their development. Between the fully grown larval stage and the time of emergence, queens loose 43.8% of their dry weight, whereas males and workers loose only 35% and 33% respectively. Between the prepupal and pupal stage there is a striking difference in fat content: the ratio of fat/dry weight increases for males and workers, whereas it decreases for queens. A reasonable explanation for this is that fat is metabolized by queens in order to provide energy for building the reproductive organs.

Workers

Workers have the highest fat content at the time of emergence. It is likely that these reserves, stored before emergence, allow the callows to act quickly as nurses, or perform other domestic functions. It is well known that the interior ants which are younger than the foragers are also better at laying eggs. Fat body is involved in the synthesis of vitellogenins, the major component of the yolk proteins and thus favours vitellogenesis (KUNKEL & NORDIN, 1985). Similar differences in fat content between young workers and old workers have also been reported in other ant species. In *Messor sancta* fat constitutes 14% of the dry weight of young interior workers whereas it constitutes only 7% of the dry weight of old foragers (PASSERA, unpublished data). In *Pogonomyrmex owyheei* (PORTER &

JORGENSEN, 1981) and in *P. subnitidus* and in *P. rugosus* (MACKAY, 1985) interior workers were also found to have a higher ratio fat/dry weight than exterior workers.

Queens

The ratio of fat/dry weight of queens of *I. humilis* decreased between the pupal stage and the emergence (20% and 12% respectively). In *Tetramorium caespitum,* the ratio fat/dry weight is slightly higher at the pupal stage and at the emergence (27% and 28% respectively) (PEAKIN, 1972). In *Lasius flavus,* the amount of fat was also higher at the time of emergence (22%) (NIELSEN *et al.*, 1985). In mature queens, the difference is still more striking with a 51% ratio in *T. caespitum,* a 60% ratio in *L. flavus,* whereas this ratio is only 25% in *I. humilis*. The first explanation should be phylogenetic differences since *I. humilis* is a Dolichoderine, *Lasius* a Formicine and *Tetramorium* a Myrmicine. Without do denying possible physiological parameters according to the subfamily we prefer the following hypothesis: this difference in the accumulation of fat probably results from the different mode of colony founding that these species display (see KELLER & PASSERA; 1987). *L. flavus* and *T. caespitum* are monogynous species and have an independent mode of colony founding: queens found new colonies without the help of workers and store a high amount of energy in order to feed the larvae. In contrast, *I. humilis* is a polygynous species and has a dependant mode of colony founding: the foundation of new colonies occurs by budding, a process in which one or several queens move out of the nest, accompanied by workers and establish a new colony. Therefore, queens do not need to accumulate a high amount of fat reserves.

Males

In *I. humilis,* the ratio of fat/dry weight is 24%, 14% and 9% for pupae, imago at the time of emergence and old adults, respectively. These values are very similar to those found in *T. caespitum* (29%, 14% and 9% respectively) (PEAKIN, 1972). In *L. niger,* the energy content of male pupae and adults is 23 J/mg and 18 J/mg respectively (BOOMSMA & ISAAKS; 1985) which is slightly lower than in the Argentine ant (24 J/mg for pupae and 21 J/mg for old males). However, these differences may have resulted from the different methods used for calculating the energy content in these species (see BOOMSMA & ISAAKS, 1985).

This comparison of out data with the *Tetramorium* and *Lasius* species shows that unlike the case with queens, there is no important difference in the physiological development of males between *Tetramorium* or *Lasius* species and the Argentine ant. This suggests that the difference between the fat contents of queens of *I. humilis* and those of *T. caespitum* and *L. niger* is due more to the differences in the mode of colony founding than phylogenetic differences.

Relative cost of sexuals and workers in ants

TRIVERS & HARE (1976) proposed that in social Hymenoptera, a queen and her daughter workers can be in conflict over the relative amount invested in both sexes. Their arguments were based on kin selection (HAMILTON, 1964a, b) and FISCHER (1958) sex ratio theories. These genetical theories were further extended by several authors (OSTER *et al., 1977;* OSTER & WILSON, 1978; CHARNOV, 1978;

MACNAIR, 1978; BENFORD, 1978; CRAIG, 1980; BULMER, 1981, 1983; IWASA, 1981; ORLOVE, 1981; PAMILO, 1981), but criticisms have been raised by ALEXANDER & SHERMAN (1977) who argued that local mate competition is a more harmonious explanation for the asymmetrical sexual investment in many social insects. Several studies have attempted to test both theories (see NONACS, 1986). However, since little data is available on the energy content of males and females, it is generally assumed that the relative energy content of queens and males is equal to their ratio of dry weight. However, this estimation presents several sources of errors:

– Firstly, it does not take into account the cost of respiration (JENSEN, 1978). Since the specific metabolic rate of larvae, pupae and adults is generally higher for males than for queens, the relative cost of males is therefore underestimated (MACKAY, 1985; BOOMSMA & ISAAKS, 1985). The ratio of metabolic rate for males/queens is proportional to that of sexual dimorphism. It may range between 1.15 to 1.6 according to the species (BOOMSMA & ISAAKS, 1985).

– Secondly, since queen dry weight increases between the time of emergence and the time of mating, the relative cost of queens should be calculated exclusively with mature winged queens. The increase of dry weight amounts to 146% in the Argentine ant and may reach almost 400% in other ant species (BOOMSMA & ISAAKS, 1985; NIELSEN *et al.*, 1985). From this it is clear that if the relative cost of queens is estimated from immature winged queens, it can be greatly underestimated.

Worker and male dry weights change only slightly after emergence: males are 4% heavier and workers 8% lighter several weeks after emergence. Since the physiology of males changes only slightly with age (Tab. 1), their physiological status is approximately identical at the time of mating and when they are old. The data recorded on old males can thus be used to estimate their relative cost. Since workers act as nurses soon after emergence, they can be considered as functional at the time of emergence and their relative cost can be estimated with the data obtained at this time.

– Thirdly, the assumption that the energetic cost of mature winged queens and males is proportional to their dry weight is incorrect. There is an important loss of dry weight (LDW) between the fully grown larval stage and emergence (Tab. 1). Therefore, LDW should be added to the final dry weight of queens, males and workers in order to estimate their relative cost. Tab. 1 shows that LDW amounts to 78% of queen dry weight at the time of emergence, whereas it amounts to only 52% and 49% of male and worker dry weight, respectively. When LDW is expressed as a function of the dry weight of mature winged queens and mature males of *I. humilis,* the values are 49% and 50% respectively. Since the dry weight of mature winged queens, mature males and workers at the time of emergence are used for estimating the relative cost of the three forms and, because LDW amounts to ca. 50% of these three values, the correction of the dry weight of the three forms with the LDW will not influence their ratio in this species. However, for other ant species LDW may not always be proportional to the dry weight of mature individuals. This may be particularly true for ant species with a similar mode of colony founding as *L. niger* and *L. flavus,* in which queen weight increases ca. 400% between emergence and the time of the mating (BOOMSMA & ISAAKS, 1985; NIELSEN *et al.*, 1985), whereas it increases only 146% in the Argentine ant. Hence if one assumes that LDW also amounts to 78% of the queen dry weight at the time of emergence it will represent only 22% of the dry weight of mature winged queens.

Thus for these species, LDW amounts to 20% of the dry weight of mature winged queens, whereas it amounts to 50% of the weight of mature males and workers. Consequently the estimation of the relative cost of queens by the ratio of the dry weight of mature individuals may be overestimated by as much as 25%, and possibly more in other species.

– Finally, the assumption that the energetic cost of one individual is proportional to its dry weight is not true since not all individuals have the same physiological composition. For instance, Tab. 1 shows that mature winged queens have a higher specific energy content than old males. This difference in the relative energy content is due to the higher relative amount of fat in queens. Therefore, the amount of the total energy content of individuals gives a better estimation of their relative energetic cost. In the Argentine ant, the use of dry weight instead of the energetic content underestimates the relative cost of queens by 14%. In species with an independent mode of colony founding, in which the amount of fat may reach 51% of the dry weight in mature queens (PEAKIN, 1972), the error may be still higher (ca. 30%).

Relative cost of sexuals and workers in the Argentine ant

As discussed above, a better estimation of the relative cost of queens, males and workers is given by the energy content of mature individuals, plus the loss of energy between the fully grown larval stage and emergence. Since the three forms were selected when they were mature, the only source of error is the difference between the relative respiration rate between queens, males and workers. The difference between specific metabolic rate of queens and males is proportional to the sexual dimorphism (1.15 to 1.60 times higher in males than in queens, BOOMSMA & ISAAKS, 1985). Since in the Argentine ant, as in most other polygynous ant species sexual dimorphism is small (BERNARD, 1952, a lower specific respiratory rate of 1.35 in queens than in males seems a reasonable approximation. With such a pattern, the relative cost of males should be increased by 15–20%. Thus the relative cost of a mature queen can be estimated to amount to 2.3–2.5 times the cost of a mature male. Since no data exists on the specific respiratory rate of worker larvae, it is not possible to estimate their relative cost of respiration. However, because of their small size, workers probably have a specific respiratory rate which is closer to that of males than to queens. By using a similar specific respiratory rate for males and workers the relative cost of queens/workers and males/workers can be estimated at ca. 7.5 and 3.1, respectively.

ACKNOWLEDGEMENTS

We are grateful to Dr. Edward Vargo for its helpful comments on the text. Thanks are also due to Dr. D. Stone and Dr. S. Goss for improving the English. This study was supported by a grant of the University of Lausanne.

RESUME

Le poids frais, le poids sec, le pourcentage de corps gras et le contenu énergétique des larves, nymphes et adultes ont été mesurés chez les reines, les mâles et les ouvrières de la fourmi d'Argentine.

Ces trois formes montrent plusieurs différences dans leur développement. Ces différences s'expliquent en partie par des variations spécifiques comme par exemple l'édification des organes de la reproduction chez les reines ou les tâches accomplies après l'émergence par les ouvrières.

Dans différents travaux, plusieurs auteurs ont postulé que le coût relatif de l'investissement pour obtenir des reines et des mâles aptes à la fécondation peut être estimé à partir du calcul de leur poids sec. Mais notre travail montre qu'entre la larve du dernier stade et l'émergence il y a une sévère perte de poids qui n'est pas proportionnelle chez les reines et chez les mâles. De plus le contenu énergétique spécifique n'est pas égal dans les deux sexes. L'importance de ces sources d'erreurs dans l'estimation du coût de l'investissement pour fabriquer les reines et les mâles est discutée.

BIBLIOGRAPHY

Alexander, R. D. & Sherman, P. W. 1977. Local mate competition and parental investment in social insects. – *Science N. Y., 196:* 494–500.

Baroni-Urbani, C., Josens, G. & Peakin, G. 1978. Empirical data and demographic parameters. *In: Brian, M. V. (ed.), Production Ecology of Ants and Termites,* pp. 5–44, Cambridge University Press.

Benford, F. A. 1978. Fisher's theory of sex ratios applied to the social Hymenoptera. – *J. Theor. Biol., 72:* 701–727.

Bernard, F. 1952. Le polymorphisme social et son déterminisme chez les Fourmis. – *Coll. int. C.N.R.S., 34: Structure et Physiologie des Sociétés Animales,* pp. 123–140.

Bonavita-Cougourdan, A. & Passera, L. 1978. Etude comparative au moyen d'or radioactif de l'alimentation des larves d'ouvrières et des larves de reine chez la fourmi *Plagiolepis pygmaea* Latr. – *Insectes soc., 25:* 275–287.

Boomsma, J. J. & Isaaks, J. A. 1985. Energy investment and respiration in queens and males of *Lasius niger* (Hymenoptera: Formicidae). – *Behav. Ecol. Sociobiol., 18:* 19–27.

Brian, M. V. 1979. Caste differentiation and division of labor. *In: Hermann, H. R. (ed.), Social Insects, 1:* 122–222, Acad. Press, New York.

Brian, M. V., Elmes, G. & Kelly, A. 1967. Populations of the ant *Tetramorium caespitum* Latreille. – *J. Anim. Ecol., 36:* 337–342.

Bulmer, M. G. 1981. Worker-queen conflict in annual social Hymenoptera. – *J. Theor. Biol., 93:* 239–251.

Bulmer, M. G. 1963. Sex ratio evolution in social Hymenoptera under worker control with behavioral dominance. –*Am. Nat., 121:* 899–902.

Charnov, E. L. 1978. Sex ratio selection in eusocial Hymenoptera. –*Nat., 112:* 317–326.

Craig, R. 1980. Sex investment ratios in social Hymenoptera. –*Am. Nat., 116:* 311–323.

Fisher, R. A. 1958. *The genetical theory of natural selection.* 2nd revised edn. Dover, New York, 291 pp.

Hamilton, W. D. 1964a. The genetical evolution of social behavior. I. – *J. Theor. Biol., 7:* 1–16.

Hamilton, W. D. 1964b. The genetical evolution of social behavior. II. – *J. Theor. Biol., 7:* 17–52.

Iwasa, Y. 1981. Role of sex ratio in the evolution of eusociality in haplodiploid social insects. – *J. Theor. Biol., 93:* 125–142.

Jensen, T. F. 1978. An energy budget for a field population of *Formica pratensis* Retz. (Hymenoptera, Formicidae). –*Natura Jutlandica, 20:* 203–226.

Keller, L. 1988. Evolutionary implications of polygyny in the Argentine ant, *Iridomyrmex humilis* (Mayr) (Hymenoptera: Formicidae): an experimental study. *Anim. Behav. 39:* 159–165.

Keller, L. & Passera, L. 1987. Energy investment in virgin queens of the Argentine ant, *Iridomyrmex humilis* (Mayr), in relation to the mode of colony founding in ants (Hymenoptera: Formicidae). – *Int. J. Invert. Repr. Develop.* (in press).

Kunkel, J. G. & Nordin, J. H. 1985. Yolk proteins. *In: G. A. Kerkut & L. I. Gilbert (eds.) Comprehensive insect physiology, biochemistry and pharmacology, 1:* 83–111.

Macnair, M. R. 1978. An ESS for the sex ratio in animals, with particular reference to the social Hymenoptera. – *J. Theor. Biol. 70:* 449–459.

Markin, G. P., Dillier, J. H. & Collins, H. L. 1973. Growth and development of colonies of the red imported fire ant *Solenopsis invicta.* –*Ann. entomol. Soc. Amer., 66:* 803–808.

Newell, W. & Barber, T. C. 1913. The Argentine ant. –*USDA Bureau of Entomology Bull., 122:* 98 pp.

Nielsen, M., Skyberg, N. & Peakin, G. 1985. Respiration in the sexuals of the ant *Lasius flavus.* –*Physiol. Entomol., 10:* 199–204.

Mackay, W. P. 1985. A comparison of the energy budget of three species of *Pogonomyrmex* harvester ants (Hymenoptera, Formicidae). – *Oecologia, 66:* 484–496.

Nonacs, P. 1986. Ant reproductive strategies and sex allocation theory. – *Quart. Rev. Biol., 61:* 1–21.

Orlove, M. J. 1981. A model of the sex ratio in flying ants with an unexpected equilibrium and an expected ESS. – *J. Theor. Biol., 93:* 523–532.

Oster, G., Eshel, I. & Cohen, D. 1977. Worker-queen conflict and the evolution of social insects. – *Theoret. Pop. Biol., 12:* 49–85.

Oster, G. F. & Wilson, E. O. 1978. *Caste and Ecology in the Social Insects.* Princeton Univ. Press, Princeton, New Jersey, 354 pp.

Pamillo, P. 1981. Genetic organization of *Formica sanguinea* populations. – *Behav. Ecol. Sociobiol., 9:* 45–50

Passera, L., Keller, L. & Suzzoni, J.P. 1987. The control of the brood male differentiation in the Argentine ant *Iridomyrmex humilis* (Mayr). – *Insectes soc.* (In press).

Peakin, G. J. 1972. Aspects of productivity in *Tetramorium caespitum* L. – *Ekologia Polska, 20:* 55–63.

Peakin, G. J. 1985. The growth and development of the overwintering larvae in the ant *Lasius flavus* (Hymenoptera, Formicidae). – *J. Zool. Lond. (A). 205:* 179–189.

Peakin, G., Nielsen, M., Skyberg, N. & Pedersen, J. 1985. Respiration in the larvae of the ants *Myrmica scabrinodis* and *Lasius flavus.* – *Physiol. Entomol., 10:* 205–214.

Plateaux, L. 1980. Dynamique des sociétés de la fourmi *Leptothorax nylanderi* (Förster). – *Biol. Ecol. méditerranéenne, 7:* 195–196.

Porter, S. D. & Jorgensen, C. D. 1981. Foragers of the harvester ant, *Pogonomyrmex owyheei:* a disposable caste? – *Behav. Ecol. Sociobiol. 9:* 247–256.

Porter, S. D. & Tschinkel, W. R. 1985. Fire ant polymorphism: the ergonomics of brood production. – *Behav. Ecol. Sociobiol., 16:* 323–336.

Trivers, R. L. & Hare, H. 1976. Haplodiploidy and the evolution of the social insects. – *Science N. Y., 191:* 249–263.

(received October 1, 1987)