Carbohydrates as Energy Source during the Flight of Sexuels of the Ant Formica lugubris (Hymenoptera: Formicidae)

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Carbohydrates in the flight of the ant Formica lugubris Zetterstedt 1838 are stored mostly as glycogen in the fat body. The carbohydrates content decreases by 50% in both sexes. In contrast, fat content remains unchanged during the flight demonstrating that carbohydrates are the main source of energy for the nuptial flight.

Key words: Formica lugubris Zetterstedt 1838 — wood ants — males & females — carbohydrate reserve — glycogen — flight energetics.

Introduction

Flight is the main mode of locomotion among insects, distinguishing them from the other classes of Arthropoda [Pringle 1974]. Ants are characterized by the occurrence of castes which
differ in their mode of movement. Workers are always stouter so they walk. By contrast, the sexuals (gynes and males) are generally winged and they usually fly only at the time of the nuptial flight. After mating, queens lose their wings and engage in colony founding, whereas \\textit{CFO} die. Thus the nuptial flight is an efficient way of dispersion [Hölldobler & Wilson 1977]. Generally speaking, long-distance sustained fliers, like certain Lepidoptera, use fat whereas short-distance fliers use mainly carbohydrates [Beevers 1969, Kammer & Heinrich 1978, Beevers et al. 1985].

Little information is presently available on substrates used by the sexuals during the mating flight. In the leaf-cutting ant \textit{Atta sexdens} (Linnæus 1758), \\textit{CFO} probably use carbohydrates rather than lipids during flight [Jutsus & Quinlen 1978]. In the fire ant \textit{Solenopsis invicta} Burmeister 1872 biochemical analysis seems to indicate that glycogen is used as the source of energy during the nuptial flight of the \textit{CFO} (Toom et al. 1976).

In colonies of ants, there is typically a period of maturation which occurs between the emergence of sexuals from the pupa and the mating flight. During this period, the sexuals store energy: \\textit{CFO} store fat in amounts which are linked to the mode of colony founding, namely independent (without the help of \textit{Q}) or dependent (with the help of \textit{Q}) [Boomsma & Isaks 1985, Passera & Keller 1987, Keller & Passera 1988].

The object of this investigation is to identify the substrates used by gynes and males of \textit{Formica lugubris} (Zetterstedt 1838) during the mating flight and to study the accumulation and breakdown of these substrates from the time of emergence from the pupa until the end of the nuptial flight.

2 Material and methods

2.1 Source of ants: Sexuals of the mound-building ant \textit{Formica lugubris} were collected in the Swiss Jura Mountains from the supercolony of Marchiaura [Gris & Cheria 1977]. Sexual pupae were collected from a field nest and kept in the laboratory with attendant \textit{Q} and \\textit{CFO} were removed as they emerged. The cultures were monitored daily so the newly emerged imagines were less than 24 h old. Mature sexuals were collected on the surface of a nest in the field as they started the nuptial flight. After the nuptial flight, \textit{Q} and \\textit{CFO} were collected on the ground in an aggregation site situated close to the supercolony [Keller, Cheria, Rosengren, Fortelius, Chastemp, unpublished data].

2.2 Carbohydrate analysis: After collecting, ants were immediately frozen at \textdegree{}C with dry ice and taken directly to the laboratory where they were defrosted and dried at 90 \textdegree{}C for 45 min in order to inactivate the enzymes; subsequently ants were stored at room T and analysed for glycogen and sugars according to the procedure reported by Van Hanzel (1985) employing anthrone as the colour reagent. This procedure permitted the determination of the amount of glycogen and free sugars from the same sample. Because of the accuracy of the method, it was possible to analyze ants individually.

2.3 Lipid analysis: Sexuals were killed with ethyl acetate vapour and then subjected to the procedure used by Peakin (1972) and Passera & Keller (1987) using boiling petroleum ether in a Soxhlet apparatus. Once again it was possible to extract ants individually. Sample sizes for carbohydrate and lipid analyses were generally 10 individuals at each stage (emergence, pre-mating flight, post-flight).

2.4 Statistical analysis: 95\% were square-root arcsin transformed to get normal distributions and means were compared with a test. Means are referred to as not significantly different when \textit{P} \textgreater{} 0.05. Means are listed minus plus standard deviation.

3 Results

3.1 Carbohydrate content in gynes

The results are summarized in Fig 1. At the time of emergence, carbohydrate content, expressed as a \% of dry weight, was related to the number of \textit{Q} (4.8 \pm 1.1\%). Soluble sugars represented most (67 \pm 2\%) of the carbohydrates, whereas glycogen accounted for 33 \pm 2\%. Between the time of emergence and the mating flight, the \textit{Q} stored considerable amounts of reserves; the dry weight of the \textit{Q} increased from 8.5 \pm 0.4 to 10.2 \pm 0.7 mg; \textit{t} = 6.67; \textit{P} \textless{} 0.001. The amount of carbohydrates increased substantially reaching 10.6 \pm 1.4\% an increase of 120\%. It is worthwhile to mention that the relative quantity of free sugars decreased during the time of maturation (3.2 \pm 0.7\% at emergence and 2.4 \pm 0.3\% at pre-flight; \textit{t} = 3.29; \textit{P} = 0.004). In contrast, the relative glycogen content increased 410\% during this time from 1.6 \pm 0.4\% to 8.3 \pm 1.2\% (\textit{t} = 19.86; \textit{P} \textless{} 0.001). During the flight nearly all of the carbohydrates were utilized; \textit{Q} contained only 2.0 \pm 0.5\% of carbohydrates after landing, having consumed 81 \pm 6\% of the carbohydrate reserve. Both soluble sugars and glycogen were used during the flight with a slight preference for glycogen: 83 \pm 6\% of the glycogen and 72 \pm 6\% of the soluble sugars were utilized.

\begin{figure}[h]
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\includegraphics[width=\textwidth]{fig1.png}
\caption{Relative carbohydrate and fat accumulation and utilization before and during the mating flight in gynes of \textit{Formica lugubris} Zetterstedt 1838. Bars show mean \pm SD; the number of individuals is indicated above each bar.}
\end{figure}

3.2 Carbohydrate content in males

The results are summarized in Fig 2. They are similar to those found for gynes. At the time of emergence the amount of carbohydrates as a percentage of dry weight was low: 4.6 \pm 1.5\%, but in contrast to gynes glycogen exceeded sugars (57 \pm 18\%). During the maturation period, \textit{CFO} stored carbohydrates mainly as glycogen. At the time of mating, carbohydrates reached 10.6 \pm 1.9\% of dry weight of which 87 \pm 3\% was glycogen. During the mating flight the
utilized 76 ± 12% of their carbohydrates (68 ± 23% sugar and 77 ± 11% glycogen). These data are very similar to those observed for the Q0, and there is not significant difference between the sexes (t = 0.84, P = 0.58; t = 0.06, P = 0.95; t = 1.34, P = 0.20 for carbohydrates, free sugars and glycogen, respectively).

3.3 Fat content in gynes

At the time of emergence, the fat/dry weight ratio of Q0 was 11.8 ± 1.0% (Fig 1). Between emergence and mating, fat content increased only slightly to 12.9 ± 1.6% (t = 1.42, P = 0.18 NS). Q0 collected after the mating flight contained a % of fat (14.1 ± 2.0%) which was not statistically different from the % before flying (t = 1.60, P = 0.12 NS), showing that fats are not used as a fuel during the nuptial flight.

3.4 Fat content in males

As in the Q0, there is no increase in fats between the time of emergence (5.0 ± 1.7%) and the time of pre-flight (4.8 ± 0.4%; t = 0.26, P = 0.80 NS). During the mating flight, there was no reduction in the quantity of fat. After landing, the % of fat was 5.1 ± 1.2% (t = 0.58, P = 0.58 NS), thus showing that the COF as the Q0 do not use fats to fuel their flight.

4 Discussion

Comparison of the relative carbohydrate and fat contents in sexuals of Formica lugubris before and after the mating flight shows that they use carbohydrates as the main source of energy for the nuptial flight. The fat content remained unchanged in both sexes after the mating flight, whereas the breakdown of carbohydrates was substantial for individuals of both sexes. Nevertheless, it is important to note that the breakdown is not complete since relative carbohydrate content decreased 81% and 77% for Q0 and COF, respectively; sugars contained about 20% of the initial quantity of carbohydrates after flight. This may permit sexuals to fly again after mating as we have observed on several occasions (unpublished observations). In the case of Atta sexdens, the breakdown of carbohydrates is more complete where it reaches 69–95% in COF (Jutsum & Quinlan 1978). In the fire ant Solenopsis invicta, Toorn et al. (1976) found a lower value (approximately 60%) for the consumption of glycogen by Q0 during the nuptial flight; however, the analysis was not done precisely at the time of landing but within 2 h following nuptial flights. The concentration of this polysaccharide increased markedly during the following 12 h suggesting an overevaluation of the actual amount of glycogen breakdown during flight.

Our data show that Q0 as well as COF accumulate glycogen during the period of maturation between emergence and the nuptial flight. During this time, winged sexuals remain for a time in the nest where they are fed by nurse Q0. Carbohydrates reserves increased as much as 120% and 132% for Q0 and COF, respectively. During the time of maturation, Q0 as well as COF of this species did not accumulate fat. This may be explained by the following 2 causes. Firstly, neither Q0 nor COF use fat as a source of energy for the nuptial flight. Secondly, neither Q0 nor COF of E. lugubris need fat after the mating flight. COF probably do not live more than 1 d after mating (unpublished data), whereas Q0 join a conspecific nest or parasitize a nest of Strumigenys Foei 1913 (Kutter 1977). In ant species in which Q0 found colonies independently, Q0 accumulate large amounts of fat. For example, in Lasius flavus (Fabricius 1781), fat content constitutes 22% of the dry weight at the time of emergence and increases to 60% at the time of the nuptial flight (Nielsen et al. 1985). Similarly these values are 24 and 51%, respectively, in Tetramorium caespitum (Linnaeus 1758) (Peakin 1972). This fat is used as energy for rearing the first brood during the founding stage which is often caustal in higher ants (Keller & Passera 1988).

These data clearly demonstrate that in E. lugubris carbohydrates are the main source of energy for the nuptial flight. Generally in other insects, species able to fly long-range use lipids as energy during the flight. Such examples are found in Hemiptera, e.g. the trisome bug Rhodnius (Ward et al. 1982), and in Lepidoptera, e.g. Heliothis zea (Boddie 1955) [Van Hande 1974]. In Locusta migratoria Reiche & Farnaire 1850, which also undergoes long flights, the major source of energy is carbohydrates at the beginning of the flight but after the first few minutes individuals start to use fat as the main source of energy [Jutsum & Goldworthy 1976]. By contrast, insect species which perform only short-range flights use mainly carbohydrates as substrate; this is the case in Diptera and Hymenoptera (Beekers 1969, Bailey 1975, Brande & Huber 1979, Bish 1983, Beekers et al. 1985). However, some Diptera, e.g. mosquitoes although they are strong flyers, use only carbohydrates for flight [Nayar & Van Handel 1971]. In ants little information is presently available concerning how far sexuals fly during the mating flight. However, several lines of evidence suggest that it is rather short-range. Firstly, several species are able to perform mating flights in laboratory cages, e.g. Plagiopelte pygmaea Latreille 1798 (Passera 1962), Acanthoscelides femoralis Mayr (Tome & Thomas 1973, and Leptothorax Mayr, 1885) e.g. (Gratux 1978). Secondly, some observations performed in the field confirm that winged ants fly a rather short distance. In Pheidole aridicrus, (Wilson 1957) showed that COF performing swarms had emerged from nests within 13 m of the swarms. Chapman (1969) noted that winged sexuals of Formica sparsa captured at swarming site are able to fly up to 760 m in order to return to the swarming site in less than 20 min. In another
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Formica species (F. montana) fly directly to nests containing females, distances of less than 50 m [Kannowski & Johnson 1969]. Flights do not exceed a few 100 m in Pogonomyrmex species (Hölldobler 1974). When the distances covered are rather large, e.g. in Solenopsis invicta (Banks et al. 1973), where QQ can disperse up to 20 km, in Attta species (Fowler et al. 1986), where QQ are known to fly 10 km, the flight is likely to be more passive or active. Such passive flight by sexuals has also been observed for other ant species: Wheeler [1905] mentioned sexuals being carried by air currents to the summit of Mount Washington in New Hampshire. It is likely that such flights require small amounts of energy. Thus it appears that ant sexuals are probably only short-range flyers and this is in agreement with the data on Formica lugubris which indicate that they use only carbohydrates as an energy substrate. Furthermore, the data indicate that the breakdown of carbohydrates is nearly complete after the nuptial flight, suggesting that the range of the flight is limited by the content of glycogen. The study of glycogen content of sexuals of ants could be a powerful tool to assess the length of flight they are able to perform.

The importance of the maturation period as a preparation for colony foundation by QQ is well established. These data identify another important aspect of maturation which applies equally to QQ and QQ, that is, the accumulation of large quantities of carbohydrates to provide energy for the mating flight. The estimation of the total energy investment in the rearing of QQ and QQ in social Hymenoptera is of special interest because it is a parameter connected to kin selection theory [Trivers & Hare 1976].

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References


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