

Carbohydrates as Energy Source during the Flight of Sexu- als of the Ant *Formica lugubris* (Hymenoptera: Formicidae)

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Sexu-als (gynes and males) of the ant *Formica lugubris* Zetterstedt 1838 accumulate large amounts of carbohydrates during the maturation period between emergence and mating flight. The carbohydrate reserves, mostly stored as glycogen, increase by 130% in this period. During the nuptial flight, carbohydrate content decreases by 80% 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 & gynes — maturation period — mating flight — carbohydrate/fat reserve — glycogen — flight energetics.

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Die geflügelten Geschlechtsstiere der Ameise *Formica lugubris* Zetterstedt 1838 (♂♂ & ♀♀) häufen während der Reifungsphase, die sich vom Schlüpfen der Imagines bis zum Hochzeitsflug hinzieht, große Mengen Kohlehydrate an. Diese Reserve — zum größten Teil Glykogen — nimmt während dieser Periode um 130% zu. Während des Hochzeitsfluges verringert sich hingegen der Kohlehydrat-Gehalt in beiden Geschlechtern um 80%. Die Fettreserven unterliegen während des Fluges keinen Veränderungen. Dies zeigt, daß Kohlehydrate während des Hochzeitsfluges die wichtigste Energiequelle darstellen.

Schlüsselwörter: *Formica lugubris* Zetterstedt 1838 — Waldameisen — Geschlechtsstiere — Reifungsphase — Hochzeitsflug — Kohlehydrate — Glykogen — Fettreserve — Flugstoffwechsel.

1 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 apterous 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 ♂♂ die. Thus the nuptial flight is an efficient way of dispersion [Hölldobler & Wilson 1977, Rosengren & Pamilo 1983]. Generally speaking, long-distance sustained fliers, like certain Lepidoptera, use fat whereas short-distance fliers use mainly carbohydrates [Beenackers 1969, Kammer & Heinrich 1978, Beenackers et al 1985].

Little information is presently available on substrates used by the sexual forms of ants during the mating flight. In the leaf-cutting ant *Atta sexdens* (Linnaeus 1758), ♂♂ probably use carbohydrates rather than lipids during flight [Jusum & Quinlan 1978]. In the fire ant *Solenopsis invicta* Buran 1972 biochemical analysis seems to indicate that glycogen is used as the source of energy during the nuptial flight of the ♀♀ [Toom et al 1976].

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

The object of this investigation is to identify the substrates used by gynes and males of *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 *Formica lugubris* were collected in the Swiss Jura Mountains from the supercolony of Marchairuz [Gris & Cherix 1977]. Sexual pupae were collected from a field nest and kept in the laboratory with attendant ♀♀; ♀♀ and ♂♂ 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, ♀♀ and ♂♂ were collected on the ground in an aggregation site situated close to the supercolony [Keller, Cherix, Rosengren, Fortelius, Chautemps, unpublished data].

2.2 Carbohydrate analysis: After collecting, ants were immediately frozen at -79°C with dry ice and taken directly to the laboratory where they were defrosted and dried at 90°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 Handel [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 analyse 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 and post-flight).

2.4 Statistical analysis: % were square-root arc sin transformed to get normal distributions and means were compared with t-test. Means are referred to as not significantly different when $P > 0.05$. Means are listed minus or 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 relatively low for the young ♀♀ ($4.8 \pm 1.1\%$). 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 ♀♀ stored considerable amounts of reserves; the dry weight of the ♀♀ increased from 8.5 ± 0.4 to 10.2 ± 0.7 mg; $t = 6.67$; $P < 0.001$. 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; $t = 3.29$; $P = 0.004$). In contrast, the relative glycogen content increased 410% during this time from $1.6 \pm 0.4\%$ to $8.3 \pm 1.2\%$; ($t = 19.86$; $P < 0.001$). During the flight nearly all of the carbohydrates were utilized; ♀♀ 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.

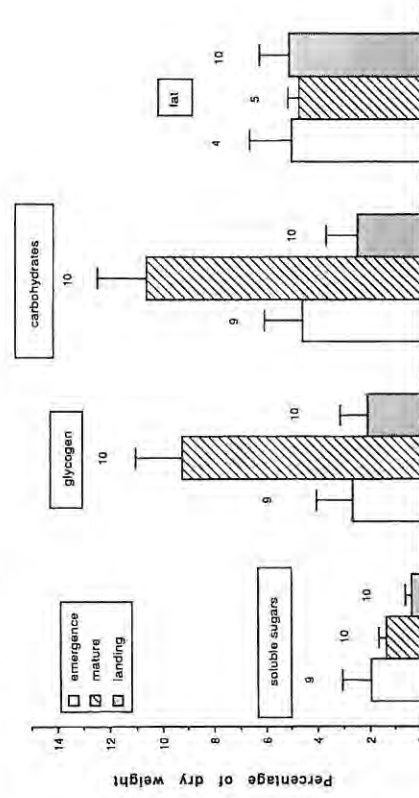


Fig 1: Relative carbohydrate and fat accumulation and utilization before and during the mating flight in gynes of *Formica lugubris* Zetterstedt 1838. Bars show mean \pm SD; the number of individuals is indicated above each bar.

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, ♂♂ 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 $76 \pm 12\%$ of their carbohydrates ($68 \pm 23\%$ sugar and $77 \pm 11\%$ glycogen). These data are very similar to those observed for the ♀♀, 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).

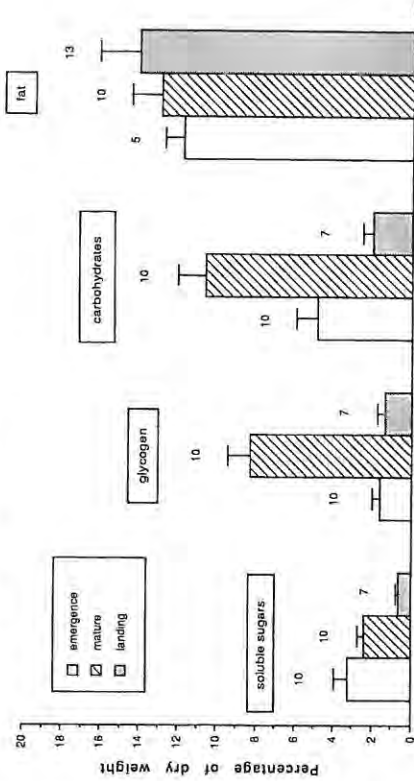


Fig. 2: Relative carbohydrate and fat accumulation and utilization before and during the mating flight in males of *Formica lugubris* Zetterstedt, 1838. Bars show mean \pm SD; the number of individuals is indicated above each bar.

3.3 Fat content in gynes

At the time of emergence, the fat/dry weight ratio of ♀♀ was $11.8 \pm 1.0\%$ (Fig. 1). Between emergence and mating, fat content increased only slightly to $12.9 \pm 1.6\%$ ($t = 1.42$, $P = 0.18$ NS). ♀♀ collected after the mating flight contained a % of fat ($14.1 \pm 2.0\%$) 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 ♀♀, there is no increase in fats between the time of emergence ($5.0 \pm 1.7\%$) and the time of pre-flight ($4.8 \pm 0.4\%$; $t = 0.26$, $P = 0.80$ NS). During the mating flight, there was no reduction in the quantity of fat. After landing, the % of fat was $5.1 \pm 1.2\%$ ($t = 0.58$, $P = 0.58$ NS), thus showing that the ♂♂ as the ♀♀ do not use fats to fuel their flight.

4 Discussion

Comparison of the relative carbohydrate and fat contents in sexuals of *F. 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 ♀♀ and ♂♂, respectively; sexuals 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 89–95% in ♂♂ [Jutsum & Quinlan 1978]. In the fire ant *Solenopsis invicta*, Toom et al [1976] found a lower value (approximately 60%) for the consumption of glycogen by ♀♀ 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 underevaluation of the actual amount of glycogen breakdown during flight.

Our data show that ♀♀ as well as ♂♂ 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 ♂♂. Carbohydrate reserves increased as much as 120% and 132% for ♀♀ and ♂♂, respectively. During the time of maturation, ♀♀ as well as ♂♂ of this species did not accumulate fat. This may be explained by the following 2 causes. Firstly, neither ♀♀ nor ♂♂ use fat as a source of energy for the nuptial flight. Secondly, neither ♀♀ nor ♂♂ of *F. lugubris* need fat after the mating flight. ♂♂ probably do not live more than 1 d after mating (unpublished data), whereas ♀♀ join a conspecific nest or parasitize a nest of *Serripiformica* Forel 1913 [Kutter 1977]. In ant species in which ♀♀ found colonies independently, ♀♀ 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 claustral in higher ants [Keller & Passera 1988].

These data clearly demonstrate that in *F. 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 triatome bug *Rhodnius* [Ward et al 1982], and in Lepidoptera, e.g. *Heliothis zea* (Boddie 1955) [Van Handel 1974]. In *Locusta migratoria* Reiche & Farmaire 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 [Beenakers 1969, Bailey 1975, Brandt & Huber 1979, Bisht 1983, Beenakers 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. *Plagiolepis pygmaea* Latreille 1798 [Passera 1962], *Acantholepis frauenfeldti* Mayr [Tohme & Tohme 1975] and *Leptothorax* (Mayr 1885) spp [Plateaux 1978]. Secondly, some observations performed in the field confirm that winged ants fly a rather short distance. In *Pheidole sitarches*, [Wilson 1957] showed that ♂♂ performing swarms had emerged from nests within 13 m of the swarms. Chapman [1969] noted that winged sexuals of *Formica submuda* captured at a 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

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 1976]. When the distances covered are rather large, e.g. in *Solenopsis invicta* [Banks et al 1973], where ♀♀ may disperse up to 20 km, or in *Atta* species [Fowler et al 1986], where ♀♀ are known to fly 10 km, the flight is likely to be more passive than 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 ♀♀ is well established. These data identify another important aspect of maturation which applies equally to ♀♀ and ♂♂, that is, the accumulation of large quantities of carbohydrate to provide energy for the mating flight. The estimation of the total energy investment in the rearing of ♀♀ and ♂♂ in social Hymenoptera is of special interest because it is a parameter connected to kin selection theory [Trivers & Hare 1976].

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Unter Bionik versteht man ein Durchforsten der belebten Welt mit der Absicht, Anregungen für eigenständig-technisches Weiterarbeiten zu bekommen. Bionik ist damit eine technische Disziplin, die sich der Biologie als Basis bedient. Im Gegensatz dazu steht Biotechnik, eine biologische Disziplin, die Konstruktionen und Phänomene der Natur mit den Analysen — und Deskriptionsmöglichkeiten der technischen Physik erforscht. Biotechnik sollte nicht verwechselt werden mit Biotechnologie, Bakterienzucht etc, ein aufblühender und zukunftsreicher Wissenschaftszweig mit dem wichtigen Ableger „Molekulargenetik“. Nach einer Einführung über Bionik als methodisches Prinzip und die Vorgangswesen in dieser Disziplin diskutiert der Verfasser die folgenden Schwerpunkte: Aspekte bionischer Methodik — Grundeigenschaft lebender System — allgemeine Bioenergetik/Energebionik — spezielle Energeto-Bionik — Strukturionik — Bionik organischer Lebensvorgänge/physiologische Bionik — Chronobiologie/Bionik oszillierender Prozesse — allgemeine Neurobionik — Bionik und Biotechnologie. Im Vorwort warnt er vor einer unkritischen Übernahme „nichtsausgeschöpfter Patentschriften“ in der Natur, die häufig nur zur Enttäuschung bei Realisationsversuchen und damit zur Diskreditierung der Methode führe. In der Darstellung allerdings bringt er soviel Aspekte ein, die nach meinem Gefühl klassischer Physiologie und Biochemie sind, daß gerade diese Gefahr auftritt (Stichworte: Glykogen als Energiespeicher; biologische Vorgänge der Wärmeregulation; ionaler Ladungsträgertransport durch Membranen; Mustererkennung und Speicherung durch das zentrale Nervensystem. Auf der anderen Seite sind so wichtige und „typische bionische“ Ansätze beschrieben wie Energiewandlungen, biologische Formgebung, Biophysik biologischer Materialien (nicht jede physikalische Diskription ist auch ein biologischer Ansatz), biologische Auswertung des Bernoulli-Prinzips, Formoptimierung bei der Verzweigung im Blutgefäßsystem, Kraftverstärker und künstliche Gliedmaßen, Biomechanik des Vogelflugs und der davon abgeleitete Windkonzentrator, sensorische elektrostimulatorische Prothesen. Auf die Aspekte künstlichen Organersatzes legt der Autor als Humanphysiologe und Spezialist für biomedizinische Technik besonders Gewicht. Das kleine, sorgfältig geschriebene Buch enthält nur zu etwa einem Drittel wirklich das, was man unter Bionik versteht. Zwei Drittel sind Bionik im eingangs definierten Sinn beziehungsweise klassische Physiologie. Das macht aber nichts, der Verfasser definiert sich seinen Bezugskreis eben so. Bedauerlich finde ich, daß der Verfasser das, was die Bionik momentan, in unserer Zeit, so wichtig macht, so wenig oder gar nicht betont und an Beispielen dokumentiert: die ungeheurer zukunftsweisende Potenz dieses aufblühenden Fachgebiets. Das Ganze liest sich deshalb trocken; der Verfasser versucht geradezu verbissen, alles nicht vollständig Gesicherte wegzulassen. Typisch bionische Ansätze, die zu abschließenden Lösungen geführt haben, sind zur Zeit eben noch selten. Vieles ist im Fluß, gerade in der „Materialbionik“; im nächsten Jahrzehnt werden sich die Ergebnisse überstürzen. Es wäre schön gewesen, wären die Wege dahin skizziert worden. Man schreibt Bücher ja nicht für die Vergangenheit, sondern will, hat man ein Anliegen für sein Fachgebiet, in die Zukunft wirken.

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