Flight Capability and Fatty Acid Level in Triacylglycerol of Long-distance Migratory Adults of the Common Cutworm, Spodoptera litura

Authors: Murata, Mika, and Tojo, Sumio

Source: Zoological Science, 21(2) : 181-188

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.21.181

ZOOLOGICAL SCIENCE **21**: 181–188 (2004)

Flight Capability and Fatty Acid Level in Triacylglycerol of Long-distance Migratory Adults of the Common Cutworm, *Spodoptera litura*

Mika Murata[†] and Sumio Tojo[*]

Department of Applied Biological Sciences, Faculty of Agriculture, Saga University, Saga 840-8502, Japan

ABSTRACT—The larvae of *Spodoptera litura* were reared on an artificial diet, and the flight capability, and triacylglycerol (TG) level plus its fatty acid composition in 3-day-old sexually mature and non-fed adults were compared. In males, during 3 hr of tethered flight, the levels of abdominal TG and its fatty acid components did not change. But thereafter the TG and fatty acids, significantly unsaturated fatty acids in TG declined in their levels with the prolongation of flight, unsaturated fatty acids being exhausted preceding saturated fatty acid decline. When males were tested by tethered flight for 20 hr, some could fly for nearly the whole period, and were judged to be able to fly for approximately 24 hr, depending on the level of residual TG. Fatty aids in TG decreased in females similarly to males during tethered flight and some females with fully developed ovaries deposited eggs after 12 hr of flight similarly to non-flown individuals, which supports the long-distance flight capability even in sexually mature females. These results are discussed with regard to the overseas migration of this moth.

Key words: triacylglycerol, flight capability, fatty acid, migration, reproduction

INTRODUCTION

In long-distance migratory insects, triacylglycerol (TG), a neutral lipid which is reserved in the fat body and transported to flight muscles in the hemolymph as diacylglycerol (DG) bound to lipophorin (Chino, 1985; Soulages and Wells, 1994; Ryan and Van der Horst, 2000), has generally been accepted to be utilized as the major flight fuel (Beenakkers *et al*., 1985: Blacklock and Ryan, 1994). However, only a few studies have been reported on the storage and utilization of TG and its fatty acid composition in long-distance migratory insects (Van Handel, 1974; Van der Horst *et al*., 1980; Teo *et al*., 1987; Zongshun and Ouyang, 1995).

Adult moths of the common cutworm *Spodoptera litura*, are regarded to migrate overseas, because males have been caught on weather-forecasting ships on oceans (Asahina and Tsuruoka, 1968), and sudden and coincidental occurrences of these moths have often been recorded in two locations 180 km apart at the time of a typhoon approach to these sites (Murata *et al*., 1998). *Spodopera litura* does not enter diapause in any of its developmental stages (Ishida and Miyashita, 1976), and this supports immigration of the moths overseas to Kyushu, the southernmost mainland of Japan, where the temperature is sometimes less than 0°C in winter but outbreaks of larvae are often recorded. One of the observations inconsistent with their long-distance migration is the early development of ovaries in females who can lay eggs within several days after adult emergence (Okamoto and Okada, 1968).

In this species, activities related to the flight have been examined by tethered flight (Oyama, 1976; Noda and Kamano, 1988) and by actographs (Kawasaki, 1986; Saito, 2000a) to determine the effect of sex and aging, without checking the flight fuel reserves.

In this study, depending on these knowledge, we tried to elucidate how the TG level and its fatty acid composition change during tethered flight in *S. litura* adults of both sexes at the time of high reproductive activity to estimate their flight capability. We demonstrate that fatty acids in TG are the major source of flight energy in the adults, and that even the females with mature ovaries are able to migrate and lay eggs similarly to non-flown females.

MATERIALS AND METHODS

Insects

Spodoptera litura eggs were kindly supplied by Sumitomo Chemical Co. Ltd. Their progenies were reared at 25°C under a 16 hr L-8 hr D photo-regime for several generations on an artificial diet

---

[*] Corresponding author: Tel. +81-952-28-8747;
FAX. +81-952-28-8747.
E-mail: tojos@cc.saga-u.ac.jp

[†] Present address: Department of Biology, Faculty of Science and Engineering, Konan University, Kobe, 658-8501, Japan

composed mostly of kidney beans, wheat germ and yeast powder (Okamoto and Okada, 1968). The larvae for the experiments were reared on the artificial diet under the same conditions used for the stock culture. After the ecdysis to the sixth (last) larval stadium, 50 larvae were transferred in a cage (23 cm×33 cm, 6 cm h) and reared to adults. Adult emergence was checked every 8 hr and, to avoid wasting the flight energy source, each adult was maintained in a test tube (1.2 cm i.d., 10.5 cm h) containing a segment of filter paper moistened with water, which was exchanged every other day, until the flight experiment.

Tethered flight

Each 3-day-old moth (72–80 hr after emergence) was anesthetized under carbon dioxide, and the scales on the back of thorax were removed using a small brush. The animal was then anesthetized again, and a polyethylene tube (d. 2.5 mm) with a pin inserted from the other end (pinhead inside the tube and tip outside) was adhered to the back of the thorax where the scales had been removed, with the aid of manicure mixed with small glass beads. After drying the adhered portion under carbon dioxide flow, the adult was suspended just below by piercing a Styrofoam plate with the tip of the pin. After recovery from anesthesia, the animal was allowed to fly. The flights of ten moths were measured for each set of experiments and recorded for 2 s every 30 s during 15 to 20 hr by a video camera. The flying times of each moth were counted by eye from the video film taken every 30 s, and the values in seconds were multiplied by 0.25 to obtain the total flight duration in minutes. If an adult did not start flying during the first 30 min, the leg was briefly touched with a small brush to insist on the flying. After flight, the abdomen was excised from the moth, frozen at –20°C, lyophilized within a week and stored at –20°C for lipid analysis. During the period of storage and lyophilization, slight changes in the lipid quantity and quality occurred, but were not to a degree which would cause significant effects on the interpretation of the results (data not shown). When a moth did not initiate flying during the course of flight experiment, even after the brief touch, it was removed from the set and frozen as a non-flyer. For non-flying controls, 0-, 3-, 7- and 10-day-old moths maintained in test tubes with water were treated similarly to the flown moths. To investigate the possible transport of lipid to the ovaries from other parts of the body, abdomens (including ovaries) or ovaries were taken from 0- and 3-day-old non-flown females and examined for TG levels.

Lipid analysis

Extraction of total lipid, TG separation and its fatty acid composition analysis were performed as described in a previous paper (Itoyama *et al.*, 1999). Briefly, the lyophilized abdomens or ovaries were weighed, and the total lipid was extracted with chloroform-methanol (2:1, v/v) according to Folch *et al.* (1957). The concentrated extract was fractionated by thin-layer chromatography on a silica gel G plate (Whatman K5, 20 cm×20 cm) in petroleum ether-diethylether-acetic acid (82:18:1, v/v/v) as the solvent system and the TG fraction was cut from the plate. The fatty acids in the fractions were converted to their methyl esters, and their fatty acid compositions were analyzed by gas-liquid chromatography (GLC, Shimazu GC-14B, Kyoto, Japan) on a fused silica capillary column (HR-SS-10, i.d. 0.25 mm×25 m, Shinwa Chemical Industries Ltd.), using helium as the carrier gas. The oven temperature for analysis was fixed at 170°C. The amount of TG was represented as the total µmoles of fatty acids recovered in the fraction per gram of dry weight of insects (µmol/g d.w.). The values were corrected by comparison to the recovery of pentadecanoic acid as an internal standard.

Statistical analyses in this article were performed with Stat View 4.0 (SAS Institute, 1990).

RESULTS

Changes in TG levels and their fatty acid compositions during tethered flight in males

The TG fatty acid level per g dry weight in the abdomen of 3-day-old males was 850 µmol on average, and significantly declined with prolongation of tethered flight (r=–0.723, P<0.0001), to 409 µmol after 15 hr of flight, and 114 µmol after flight longer than 18 hr (Fig. 1). In contrast, in non-flown moths maintained without food, the TG fatty acid level

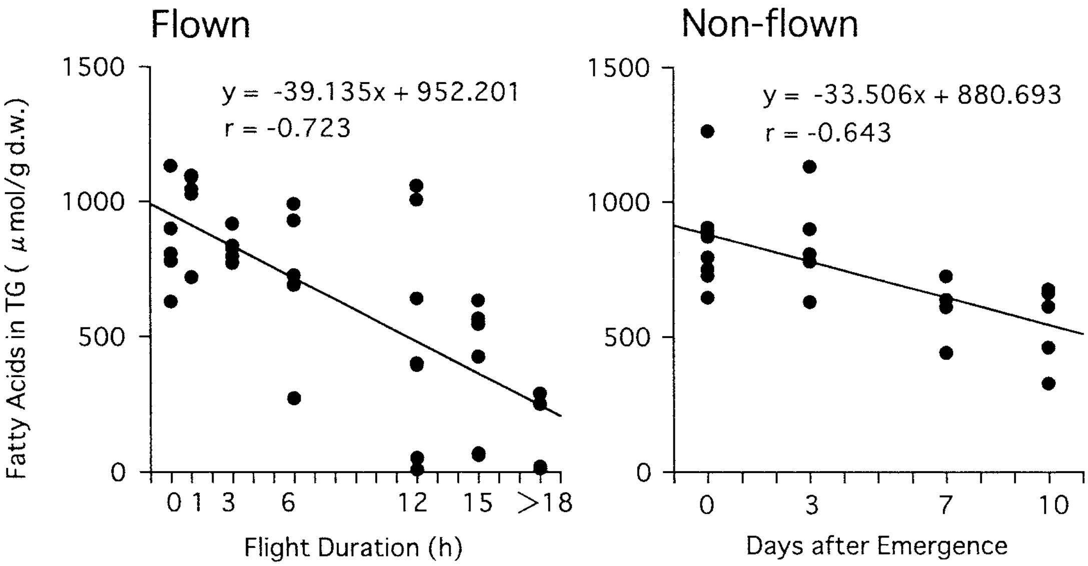

Fig. 1. Changes in the triacylglycerol (TG) level in the abdomens of flown and non-flown *S. litura* males. Closed circles represent values for individuals (n=5–8). Flown: adults which had been kept separately in tubes (1.5×10.5 cm) for 3 days without food were used for tethered flight for a maximum period of 15–20 hr; Non-flown: adults were maintained similarly to the flown adults until the stage shown in the abscissa. The corresponding regressions are given in the figures (P<0.0001, n=38 for flown males and P=0.0012, n=22 for non-flown males).

declined far more slowly but still significantly (*P*=0.0012), and 549 µmol still remained in the abdomen even at 10 days after emergence (Fig. 1). Hourly loss of TG fatty acid per g dry weight was 39 µmol in the flown males, but was only 1.4 µmol in the non-flown ones, i.e., 28-times more TG fatty acid consumption during flight than when at rest.

Table 1. Changes in fatty acid quantity (µmol / g. d. w.) of TG in the abdomen of *S. litura* males during tethered flight[1,2]

Duration of tethered flight (hr)	Fatty acid[3] 18:3	18:2	18:1	16:1	N
0	14.8 (1.00) a	101.6 (1.00) a	244.3 (1.00) a	84.1 (1.00) a	5
3	11.8 (0.80) a	92.4 (0.91) a	225.3 (0.92) a	62.3 (0.74) ab	5
6	6.6 (0.45) b	69.3 (0.68) ab	177.1 (0.72) ab	39.2 (0.46) bc	6
12	3.3 (0.22) bc	39.5 (0.39) bc	121.7 (0.50) bc	26.9 (0.32) cd	6
15	2.9 (0.20) c	27.0 (0.26) cd	81.2 (0.33) cd	18.6 (0.22) cd	7
>18	0.0 (0.00) c	3.1 (0.04) d	11.4 (0.04) d	8.7 (0.10) d	4
P (ANOVA)	<0.001	<0.001	<0.001	<0.001	

Duration of tethered flight (hr)	Fatty acid[3] 18:0	16:0	14:0	12:0	N
0	10.1 (1.00)	380.5 (1.00) a	6.4 (1.00)	2.2 (1.00)	5
3	12.2 (1.08)	409.9 (1.25) a	8.1 (1.26)	10.0 (4.53)	5
6	12.8 (1.26)	390.0 (1.02) a	8.4 (1.31)	3.2 (1.45)	6
12	8.7 (0.86)	294.7 (0.77) a	8.5 (1.33)	13.1 (5.95)	6
15	7.9 (0.78)	251.6 (0.66) ab	8.6 (1.34)	11.1 (5.04)	7
>18	4.7 (0.45)	84.5 (0.22) b	9.7 (1.51)	8.5 (3.86)	4
P (ANOVA)	0.134	0.028	0.978	0.345	

[1] Males were kept with water for three days after adult emergence, and flown using tethered flight for 15–20 hr.

[2] Values in parenthesis are the ratios of the quantity of respective fatty acid against that of 3-day-old non-flown control.

[3] 18:3, linolenic acid; 18:2, linoleic acid; 18:1, oleic acid; 16:1, palmitoleic acid; 18:0, stearic acid; 16:00, palmic acid; 14:00, miristic acid; 12:0, lauric acid.

Different letters mean significant difference (Fisher's PLSD, *P*<0.05).

Table 2. Changes in fatty acid quantity (µmol / g. d. w.) of TG in the abdomen of *S. litura* males under non-flown condition[1,2]

Duration of starvation (day)	Fatty acid[3] 18:3	18:2	18:1	16:1	N
0	13.2 (0.81) a	89.9 (0.88) a	241.8 (0.99) a	54.0 (0.64) b	8
3	14.8 (1.00) a	101.6 (1.00) a	244.3 (1.00) a	84.1 (1.00) a	5
7	6.5 (0.43) b	52.6 (0.52) b	157.9 (0.65) b	42.2 (0.50) b	4
10	5.9 (0.39) b	62.8 (0.62) b	130.5 (0.53) b	46.9 (0.55) b	5
P (ANOVA)	0.003	0.002	0.003	<0.001	

Duration of starvation (day)	Fatty acid[3] 18:0	16:0	14:0	12:0	N
0	21.2 (2.11) a	412.5 (1.80)	7.4 (1.16)	11.6 (5.27)	8
3	10.1 (1.00) b	380.5 (1.00)	6.4 (1.00)	2.2 (1.00)	5
7	8.1 (0.80) b	327.0 (0.86)	6.9 (1.08)	2.7 (1.23)	4
10	5.1 (0.50) b	285.0 (0.75)	7.0 (1.09)	5.0 (2.28)	5
P (ANOVA)	0.005	0.113	0.914	0.312	

[1] Males were kept only with water for the days after adult emergence as given in the left column without flight.

[2] Values in parenthesis are the ratios of the quantity of respective fatty acid against that of 3-day-old male.

Different letters mean significant difference (Fisher's PLSD, *P*<0.05).

Fatty acid levels in abdominal TG in 3-day-old flown male moths were shown in Table 1. Comparisons were also done in the non-flown males kept without food for a further 7 days (Table 2), where relative quantities of each fatty acid per g dry weight are represented as ratios to the value in 3-day-old males; to make comparison easier with the flown ones of this age. In the abdominal TG of flown and non-flown males (Tables 1 and 2), palmitic (C16:0) and oleic (C18:1) acids were the predominant fatty acids, followed by palmitoleic (C16:1) and linoleic (C18:2) acids, with minor components of linolenic (C18:3), stearic (C18:0), miristic (C14:0) and lauric (C 12:0) acids. During 3 hr of tethered flight, the levels of all fatty acids in abdominal TG did not significantly change, and so TG fatty acid level was regarded not to decrease during this period, although the correlation between TG level and flight duration was calculated in Fig. 1 assuming continuous consumption of TG during flight. But thereafter all of the four unsaturated fatty acids significantly decreased with prolongation of flight (ANOVA, linolenic acid: $P<0.0001$; linoleic acid: $P<0.0001$; oleic acid: $P=0.0001$; palmitoleic acid: $P<0.0001$). The level of a predominant saturated fatty acid, palmitic acid decreased rapidly as flight duration exceeded 15 hr, although the level did not significantly change when the moths flied less than 15 hr (ANOVA, $P=0.0276$) (Table 1). On the other hand, the levels of other three saturated fatty acid did not significantly change with flight duration (ANOVA, stearic acid (C 18:0): $P=0.1336$; miristic acid (C 14:0): $P=0.9777$; lauric acid (C 12:0): $P=0.3445$) (Table 1).

In the abdominal TG of non-flown males (Table 2), the levels of the four unsaturated fatty acids significantly decreased with age (ANOVA, linolenic acid (C 18:3): $P=0.0030$; linoleic acid (C 18:2): $P=0.0016$; oleic acid (C18:1): $P=0.0034$; palmitoleic acid (C16:1): $P=0.0003$). The level of stearic acid (C18:0) decreased in 3 days after emergence, but did not change thereafter. On the other hand, the

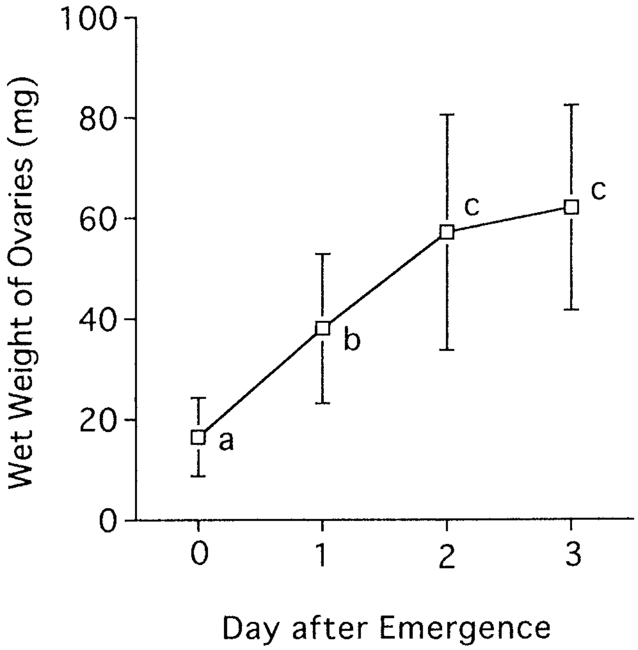

Fig. 2. Changes in the wet weight of the ovaries in non-flown *S. litura* females (n=5). Adults were separately maintained without food after emergence. Values (mean±SD) with different letters are significantly different ($P < 0.05$, U-test).

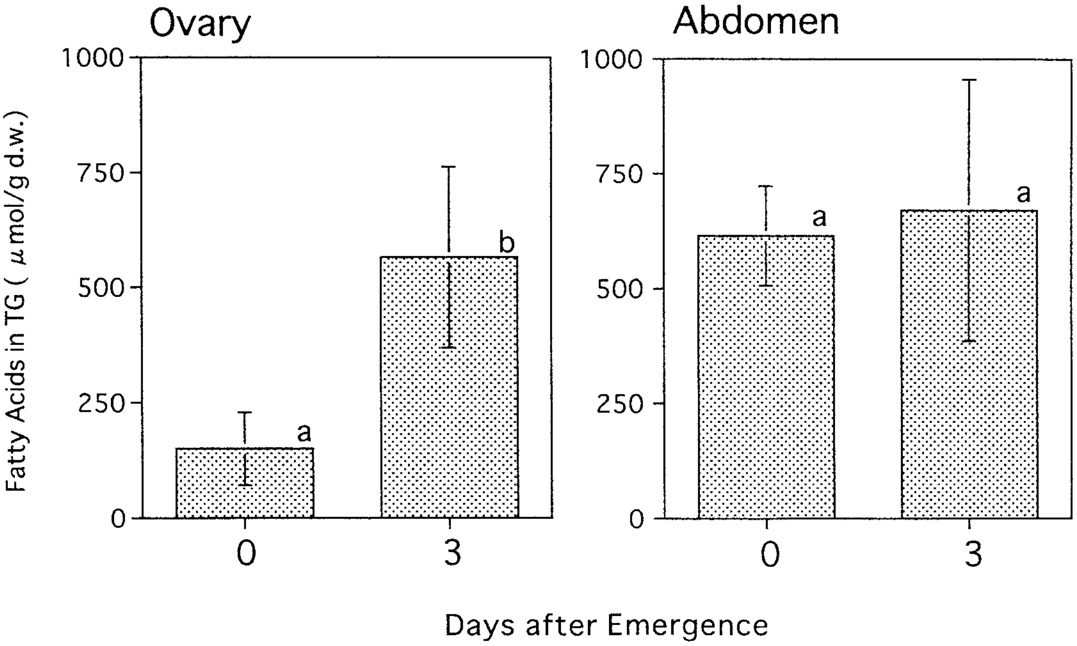

Fig. 3. Changes in the TG level in the ovaries and abdomens of *S. litura* females (n=5). Females were separately maintained without food and flight experience. Values (mean±SD) with different letters are significantly different ($P<0.05$, U-test).

other three saturated fatty acids did not change (ANOVA, palmitic acid (C 16:0): *P*=0.1128; miristic acid (C 14:0): *P*=0.9138; lauric acid (C 12:0): *P*=0.3124) (Table 2).

Flight capability, TG content and fecundity in flown females

The wet weight of the ovaries in non-flown female adult increased in 3 days after emergence (ANOVA, *P*<0.001) (Fig. 2). In this period, TG in the abdomen including ovaries did not change (U-test, *P*>0.05), but the TG level in the ovaries per g dry weight increased from 148 μmol, i.e., 24% of the total TG in the abdomen at emergence, to 566 μmol, *i.e.*, 88% of the total abdominal TG (U-test, *P*<0.05) (Fig. 3). The proportion of unsaturated fatty acids in the abdominal TG fatty acids slightly changed during the first three days of adult development (from 37 to 44%), but the proportion in ovarian TG' greatly changed (from 4% at day 0 to 48% at day 3) (Fig. 4).

The TG content per g dry weight of the abdomen in females decreased with prolongation of flight, from 672 μmol in non-flown to 198 μmol after 12 hr of flight (r=–0.649, *P*=0.0026); the average loss of TG per g dry weight per hr being 37 μmol (Fig. 5A). When females mated after tethered flight, the number of eggs they deposited significantly

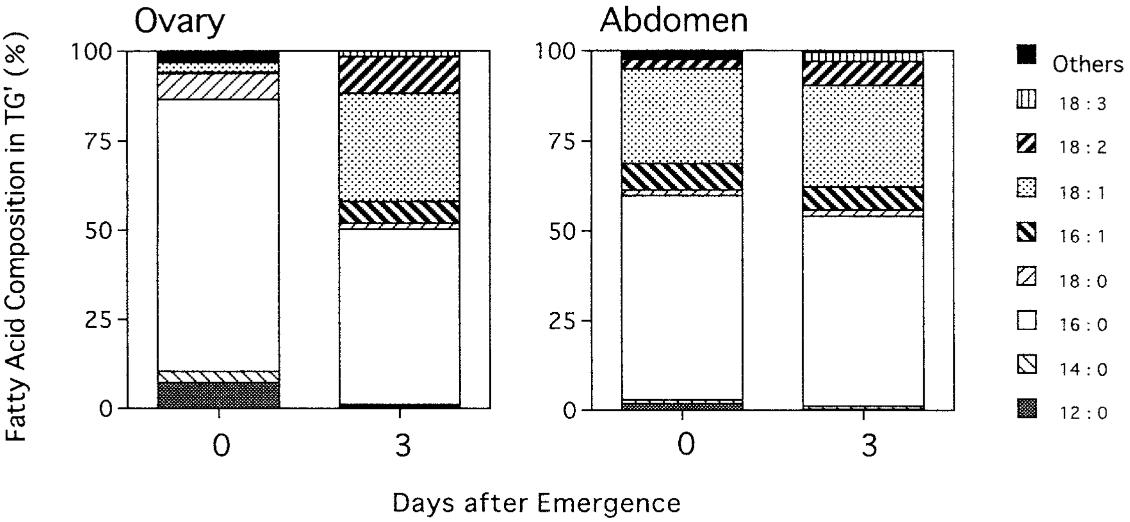

Fig. 4. Comparison of the fatty acid composition in TG in the ovaries and abdomens of *S. litura* females (n=5) in the experiment conducted in Fig. 3.

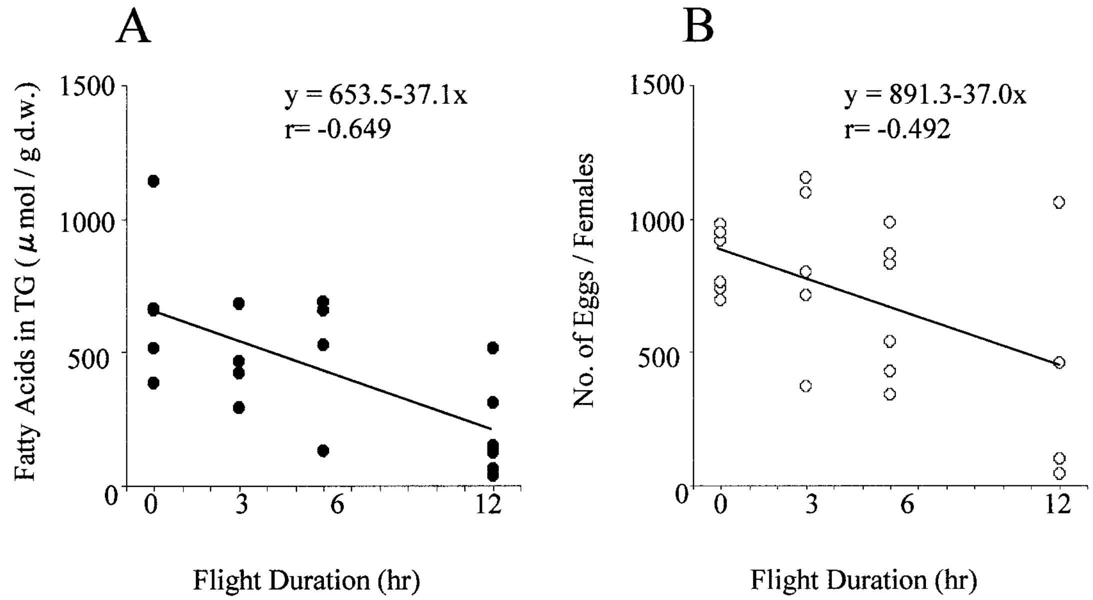

Fig. 5. Changes in the TG fatty acid level in the abdomens of *S. litura* females flown for different periods (A), and the number of eggs laid per female after flight. Females were separately maintained for three days after emergence without food, and then flown by tethered flight for the periods shown in the abscissa. After the flight, half the females (n=4–6) were kept with two respective males for copulation with 10% honeydew solution and the number of eggs laid were counted three days later. The other half of the flown females (n=4–6) were used for lipid analysis. The corresponding regressions are given in the figures (*P*<0.0001, n=19 for flown males and *P*=0.0012, n=23 for non-flown males).

declined with the increase of flight periods (r=–0.493, *P*=0.0168), but half of the females could lay eggs even after 12 hr of flight in quantities similar to some of the non-flown controls (Fig. 5B).

DISCUSSION

Utilization of fatty acids in TG in long flights

In long-distance migratory insects, a rapid decline in carbohydrate followed by an increase in lipid (diacylglycerol) in the hemolymph during flight have been generally accepted to indicate the utilization of carbohydrate for initial flight, and then lipid for sustained flight (Van der Horst *et al.*, 1980; Teo *et al.*, 1987). However, virtually no studies have been published on the fluctuations of even lipid levels in the whole body or fat body, the main reserve organ of lipids, during long flights near exhaustion except for the following data: 40–58% decrease in lipid during 16–32 hr of tethered flight in *Spodoptera frugiperda*, and 34–85% decrease in lipid during 23–40 hr of tethered flight in *Heliothis zea* (Van Handel, 1974).

Here, we demonstrated that the TG fatty acid level in the abdomen of 3-day-old male *S. litura* moths declined with prolongation of tethered flight, at a rate of 39 μmol per g dry weight per hr, being 28 times higher compared to non-flown starved males (Fig. 1). In females, the average loss of TG per g dry weight per hr was 37 μmol (Fig. 5A). But, restricting to the changes during 3 hr of flight, the TG fatty acid level did not significantly decrease as being supported by non-significant declines of any TG fatty acids (Table 1). This seems to indicate that TG fatty acids were not consumed during early flight, and may suggest initial utilization of carbohydrates as flight fuel, as being demonstrated in other long-distance migratory insects (Van der Horst *et al.*, 1980; Teo *et al.*, 1987).

During flight from 3 hr up to 15 hr, the levels of all unsaturated fatty acids in the TG significantly decreased, while those of all saturated fatty acids did not change and rather seem to increase except palmitic acid (Table 1). In non-flown males, the four unsaturated fatty acids in TG declined from 3 to 7 days of starvation, while a decrease in quantity was not observed in any of saturated fatty acids (Table 2). So, the utilization of respective TG fatty acids seems to proceed similarly during starvation and flight, but to be highly enhanced by flight. As the level of respective fatty acid reflects the difference between the synthesis and consumption, the present result may indicate that synthesis and consumption equally proceeded in saturated fatty acids, while consumption overwhelmed synthesis in unsaturated fatty acid.

As the moths used for tethered flight were maintained only on water, so all materials with carbon skeleton should be supplied by themselves. One of resources for fatty acid synthesis will be carbohydrate, but carbohydrates would be exhausted if these were the major fuels during early flight as mentioned above. Other possible sources for the synthesis will be from inter-conversion of saturated and unsaturated fatty acids, but metabolic conversion between them during degradation by β-oxidation have not known (Conn *et al.*, 1987). So, it may be also possible to explain that the decline of respective fatty acids in TG was mostly due to consumption of them and so, the present data may indicate utilization of unsaturated fatty acids preceding to that of saturated fatty acids in flight longer than 3 hr. More detailed studies are required to conclude either both saturated and unsaturated were utilized equally or selectively during tethered flight.

In other long-distance migratory insects, a change of unsaturated fatty acid level during flight has been reported, *e.g.*, in *Mythimna separata*, oleic acid decreased in the fat body and increased in the flight muscle during tethered flight (Zongshun and Ouyang, 1995). In *Cnaphalocrosis medinalis,* linolenic acid in TG seemed to be utilized first because migrants contained TG with essentially no linolenic acid, while non-immigrants had a high level of linolenic acid in TG (Murata and Tojo, 2001). In the migratory locust *Schistocerca gregaria,* the ratio of unsaturated fatty acids in TG' is kept over 60% during one month of feeding in adulthood, supporting the hypothesis that unsaturated fatty acids are the major flight fuel, although analyses of adults after long flights were not conducted (Schneider and Dorn, 1994).

Flight capability of reproductively mature moths

In *S. litura*, the females release sex pheromones within one or two days after emergence, and the males become able to respond to the pheromones a little later (Yushima *et al.*, 1973). Since the females used in the present experiment matured ovaries within 3 days of emergence (Fig. 2), both the 3-day-old males and females used in the tethered flight could be said to be sexually mature. Here, we demonstrated that even these sexually mature males and females could fly for over 18 and 12 hr, respectively, in tethered flights, although they had been maintained without food for 3 days (Figs. 1 and 5), supporting their potential to undertake long-distance migration. It seems likely that they are able to fly longer if they were given food during these three days. Since females lost nearly two-thirds of their TG during 12 hr of flight, but still maintained a high level of TG (Fig. 5) similar to the 12 hr-flown males (Fig. 1), they would be able to fly for several more hours. In males which were flown for more than 18 hr, the abdominal TG per g dry weight was 144 μmol (Fig. 1), while the level was approximately 50 μmol in those moths caught at the time of a typhoon approach, which were expected to have immigrated overseas on the typhoon winds (Murata, 2001). Judging from the decrease of abdominal TG in males during tethered flight (Fig. 1), the males caught at the time of the typhoon approach were estimated to have flown for nearly 24 hr (Murata, 2001). In such cases, saturated fatty acids would be utilized for the flight activity. The reason why the unsaturated fatty acids in TG are utilized initially as the flight energy source before the saturated acids remains unclear, although it might be due to the presence of specific enzymes necessary for the isomerization and oxidation of the unsaturated fatty acids in muscles (Conn *et al.*, 1987)

We showed a prominent accumulation of TG in the ovaries during three days of ovarian development with yolk deposition. During this period, the proportion of unsaturated fatty acid in abdominal TG's remained 40% (Fig. 4). This suggests the increase of TG fatty acids in the ovaries being mostly due to the uptake of these fatty acids, possibly bound with vitellogenin, by the ovaries, as have been shown in many insect species (Kunkel and Nordin, 1985; Raikhel and Dhadialla, 1992). In fact, vitellogenin with 9% of lipid content in *S. litura* first appears in the hemolymph one day before adult emergence, and prominently increases the concentration shortly after emergence (Maruta *et al.*, 2002), preceding the yolk deposition, *i.e.*, vitellogenin uptake by oocytes (Fig. 2). When 3-day-old females were flown, 37 μmol of abdominal TG fatty acids per g dry weight was consumed per hr as in the flown males (39 μmol). It is reasonable to assume that the TG deposited in the yolk of the ovaries in 3-day-old females would become the major source of flight energy, since 88% of the TG was distributed in the ovaries at the time of flight initiation (Fig. 4). Absorption of oocytes is known in many insects, when they are starved or not inseminated (Chapmann, 1998), but virtually no studies have been published on the possible utilization of the fatty acids deposited in the oocytes as an energy resource for the flight muscles.

We further showed that some sexually mature females laid a similar number of eggs to the non-flown ones, even after 12 hr of flight (Fig. 4). The *S. litura* females in sexually immature stages show similar high flight activity to those in mature stages (data not shown). These results seem to coincide with those obtained by actographs in which the moths were allowed to fly freely: females of *S. litura* actively flew at night for several days, and males were more active for longer periods (Saito, 2000a). This would be an advantageous characteristic for the survival of a migratory insect: females first migrate and then reproduce. In a long-distance migratory cotton bollworm *Helicoverpa armigera,* the females have mature eggs within three days after emergence as in *S. litura*, and showed nearly ten days of active flight activity by actographs, although copulation significantly reduced their flight activity (Saito, 2000b). Studies are now in progress to see whether or not preceding copulation has any effect on the long-distance migratory capability of *S. litura* females.

Noda and Kamano (1988) demonstrated that, during 10 hr experiments with a flight mill, 3-day-old females and males of *S. litura* flew for only 3 or 4 hr, and estimated that they would be able to fly less than 100 km in a night, thus denying a long flight capability of this species. In another tethered flight experiment, *S. litura* could fly only for 10 min at the maximum (Oyama, 1976). Although such contradictory results might be due to the different methods applied to check the flight ability, the results seem to suggest genetic differences in the migratory potentials of *S. litura* populations, as has been observed in several species of insects (for a review: Gatehouse, 1997). We are finding such variations among field-collected *S. litura* and these data will be published elsewhere.

Recent trajectory analyses of 850 hPa air masses with strong winds of over 10 m/s and records of moths trapped in pheromone traps strongly suggest the overseas immigration of *S. litura* to Japan in spring and autumn rainy seasons within 24 hr from mainland China and the Korean Peninsula (Murata, Inoue, Cheng and Tojo, unpublished). Our present data support the hypothesis that their lipid reserve is sufficient for long flights, and show that they have a high flight capability in no-wind conditions for the period nearly corresponding to the duration estimated to be necessary for immigration to Japan with the aid of air masses at 850 hPa. In the case of wind-born migration, the moths can be expected to migrate or disperse for longer distances than those estimated in laboratory experiments.

ACKNOWLEDGEMENTS

We would like to thank Makoto Hatakoshi of Sumitomo Chemical Co. Ltd. for supplying the *Spodoptera litura* eggs. This work was partly supported by a Grant-in-Aid from the Japan Society for Promotion of Science (No. 13460023).

REFERENCES

Asahina S, Turuoka Y (1968) Records of the insects visited a weather ship located at the Ocean Weather Station 'Tango' on at the Pacific II. Kontyu 36: 190–202

Beenakkers AMTh, Van der Horst DJ, Van Marrewijk WJA (1985) Insect lipids and lipoproteins, and their role in physiological processes. Prog Lipid Res 24: 19–67

Blacklock BJ, Ryan RO (1994) Hemolymph lipid transport. Insect Biochem Mol Biol 24: 855–873

Chino H (1985) Lipid transport: biochemistry of hemolymph lipophorin. In "Comprehensive Insect Physiology, Biochemistry and Pharmacology Vol 10" Ed by Kerkut G A, Gilbert L I , Pergamon Press, Oxford, pp 115–134

Chapman RF (1998) the insects, structure and function, 4th ed. The English Universities Press, St Paul's House

Conn EE, Stumpf PK, Bruening G, Doi RH (1987) Outlines of Biochemistry 5 th Ed., John Wiley & Sons Inc., New York

Folch J, Lees M, Stanley GHS (1957) A simple method for the isolation and purification of total lipids from animal tissues. J Biol Chem 226: 497–509

Gatehouse AG (1997) Behavior and ecological genetics of windborne migration by insects. Annu Rev Entomol 42: 475–502

Ishida S, Miyashita K (1976) Effects of photoperiod and temperature on development and overwintering of *Spodopera litura* F. (Lepidoptera: Noctuidae). Appl Entomol Zool 11: 248–257

Itoyama K, Kawahira Y, Murata M, Tojo S (1999) Fluctuation of some characteristics in the common cutworm, *Spodoptera litura* (Lepidoptera: Noctuidae) reared under different diets. Appl Entomol Zool 34: 315–321

Kawasaki K (1986) Activity rhythms and behavior of adult *Spodopera litura* F. (Lepidoptera: Noctuidae) at night: factors determining male attraction time by females. Appl Entomol Zool 21: 493–499

Kunkel JG, Nordin JH (1985) Yolk proteins. In "Comprehensive Insect Physiology, Biochemistry and Pharmacology Vol 1" Ed by Kerkut GA, Gilbert LI , Pergamon Press, Oxford, pp 83–109

Maruta K, Yoshiga T, Katagiri C, Ochiai M, Tojo S (2002) Purification and characterization of biliverdin-binding vitellogenin from the common cutworm, *Spodoptera litura*. Arch Insect Biochem Physiol 50: 97–106

Murata M (2001) Researches on long-distance migration in the common cutworm, *Spodoptera litura*. Ph.D. Dissertation, United Graduate School of Agriculture, Kagoshima University

Murata M, Tojo S (2001) Seasonal fluctuation of residual flight energy source in the rice leaf roller, *Cnaphalocroris medinalis* (Lepidoptera: Pyralidae) adults. Jpn J Entomol (N.S.) 4: 1–9 (in Japanese)

Murata M, EthoT, Itoyama K, Tojo S (1998) Sudden occurrence of the common cutworm, *Spodopera litura* (Lepidoptera: Noctuidae) in southern Japan during the typhoon season. Appl Entomol Zool 33: 419–427

Noda T, Kamano S (1988) Flight capacity of *Spodoptera litura* (F.) (Lepidoptera: Noctuidae) determined with a computer-assisted flight mill: effect of age and sex of the moth. Jpn J Appl Entomol Zool 32: 227–229 (in Japanese)

Okamoto D, OkadaT (1968) Studies on the tobacco cutworm, *Prodenia litura* Fabricius, as insect pest of the forage crops. Bull Chugoku Nat Agr Exp Stat E2: 111–141(in Japanese)

Oyama M (1976) Mating and flying abilities of the wild- and laboratory-reared males of *Spodoptera litura* F. (Lepidoptera: Noctuidae). Jpn J Appl Entomol Zool 20: 203-207 (in Japanese)

Raikhel AS, Dhadialla TS (1992) Accumulation of yolk proteins in insect oocytes. Annu Rev Entomol 37: 217–251

Ryan RO, Van der Horst DJ (2000) Lipid transport biochemistry and its role in energy production. Annu Rev Entomol 45: 233–260

Saito O (2000a) Flight activity of three *Spodoptera* spp., *Spodoptera litrua, S. exigua* and *S. depravata*, measured by flight actograph. Physiol Entomol 25: 112–119

Saito O (2000b) Flight activity changes of the cotton bollworm, *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae), by aging and copulation as measured by flight actograph. Appl Entomol Zool 35: 53–61

Schneider M, Dorn A (1994) Lipid storage and mobilization by flight in relation to phase and age of *Schistocerca gregaria* females. Insect Biochem Mol Biol 24: 883–889

Soulages JL, Wells MA (1994) Lipophorin: the structure of an insect lipoprotein and its role in lipid transport in insects. Adv Prot Chem 45: 371–415

Teo L-H, Fescemyer HW, Woodring JP, Hammond AM (1987) Carbohydrate and fatty acid titres during flight of the migrant Noctuid moth, *Anticarsia gemmatalis* Hubner. Insect Biochem 17: 777–781

Van der Horst DJ, Houben NMD, Beenakkers AMTh (1980) Dynamics of energy substrates in the haemolymph of *Locusta migratoria* during flight. J Insect Physiol 26: 441–448

Van Handel E (1974) Lipid utilization during sustained flight of moths. J Insect Physiol 20: 2329–2332

Zongshun W Ouyang,Y (1995) Flight activity and fatty acid utilization in *Mythimna separata* (Walker) moths. Entomol Sinica 2: 370–376

Yushima T, Noguchi H, Tamaki Y (1973) Mating and sex pheromone of *Spodoptera litura* F. (Lepidoptera: Noctuidae): an introductory report. Appl Entomol Zool 8: 18–26

(Received May 27, 2003 / Accepted October 21, 2003)