Flight performance of the malaria vectors *Anopheles gambiae* and *Anopheles atroparvus*

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ABSTRACT: The flight potential and metabolism of two malaria vectors, *Anopheles gambiae s.str*. and *An. atroparvus*, were analyzed on flightmills. The flight distance, the flight time, and individual flight activities of females were recorded during 22 h flight trials. The glycogen and lipid before flight, after flight, and of unflown controls were measured for starved, sugar-, or blood-fed females. Maximal flight distances of *An. gambiae* were 9 km when sugar-fed and 10 km when blood-fed, while in starved females it was below 3 km and the average speed was around 1 km/h. In *Anopheles atroparvus,* the maximal flight distances were 10-12 km when sugar-fed , 4.5 km when blood-fed, and below 3.5 km when starved, with an average speed of 1.3 km/h. Flight performances consisted of 1-4 h intervals of continuous flights, but mainly of bouts shorter than one h, randomly distributed during the long flight trials in both species. *An. gambiae* utilized an average of 47% of its pre-flight carbohydrate reserves for survival and 38% for flight at a rate of 0.07 cal/h/female. After a blood meal they utilized 11% for survival and 61% for flight at a rate of 0.04 cal/h. At the same time, 25% of the pre-flight lipid was mobilized for flight at a rate of 0.09 cal/h when sugar-fed and 22% when blood-fed at a rate of 0.06 cal/h; lipid was barely mobilized for survival. *An. atroparvus* differed: carbohydrate mobilization was 28% for survival and 41% for flight at a rate of 0.15 cal/h when sugar-fed; lipid mobilization for flight was only 13% at a rate of 0.06 cal/h. After a blood meal only 2% of the pre-flight lipid was used (0.02 cal/h). The contribution of carbohydrate reserves for flight metabolism at the high rate of 0.21 cal/h could not be fully elucidated because its decrease coincided with a pronounced resynthesis from the blood meal. *An. atroparvus* always depended on sugar meals for its flight activities and barely utilized lipid reserves. *An. gambiae* was independent of sugar sources for strong flights due to its early blood feeding and because of its equicaloric lipid mobilization during flights. Strong evidence for lipid oxidation during its flight is discussed. ***Journal of Vector Ecology* 29 (1): 140-153. 2004.**

Keyword Index: *Anopheles*, flight, distance, metabolism.

INTRODUCTION

Reproductive success in insects is often dependent on their flight potential, and in mosquitoes this is an extremely important parameter because seeking a host for blood meals often takes place far away from their breeding places. Furthermore, from an epidemiological perspective, possible flight distances are important parameters. Therefore, we have investigated the flight potential of two *Aedes* species in the laboratory under controlled, constant conditions (Briegel et al. 2001a, b) to provide a quantitative basis for comparisons with data reported from field studies based on release-recapture experiments (Jensen and Washino 1994, Schäfer et al. 1994, Gillies 1961). Our data primarily reflect the maximal flight potential rather than actual flight patterns in the field. Nevertheless, such data provide a solid basis for evaluations of earlier or future investigations.

In this study we report our results on the flight distances and metabolism of two malaria vector species: the most important tropical vector, *An. gambiae*, in comparison to a former vector species from the temperate regions, *An. atroparvus* from the *An. maculipennis* complex. For *An. gambiae,* an average dispersal of only a few hundred meters was reported (Sabatinelli et al. 1986, Costantini et al. 1996). Despite their different sizes, environmental conditions, and general biology, females of the two species achieved similar flight potentials, although following different metabolic strategies. Nayar and Van Handel (1971) studied the energy substrate during flight of *Ae. sollicitans* and *Ae. taeniorhynchus*, revealing sugar and glycogen as the flight substrates, but

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not lipids (Nayar and Sauerman 1973). However, for *Ae. vexans* we found evidence for some lipid to be used during flight (Briegel et al. 2001b). The discrepancies concerning lipid utilization might be caused by short flight trials (Nayar and Van Handel 1971) *versus* long flights (Briegel et al. 2001a, b). The recent findings on proline oxidation during flight of *Ae. aegypti* by Scaraffia and Wells (2003) appear to explain the disappearance of lipids during lasting flight activities, along similar lines as shown for *Glossina* by Bursell et al. (1974). In this study, we demonstrate the possible role of lipids as a flight substrate for *An. gambiae*, but not for *An. atroparvus*, further stressing the physiological diversities among various mosquito species.

MATERIALS AND METHODS

Mosquito colonies

All studies were carried out with *Anopheles (Cellia) gambiae s.s.* and with *Anopheles* (*Anopheles*) *atroparvus*. For routine maintenance, *An. gambiae* was kept in 30 x 50 x 60 cm cages at 27 ± 0.5°C, 85 ± 5% relative humidity, long-day conditions (14L, 10D) and with permanent access to 10% sucrose solution. *An. atroparvus* were kept in cages of the same size with the same feeding conditions, but at 22 ± 2°C, 40 ± 20% relative humidity, under natural day-light, and long-days (15L, 9D). Blood meals were given from a restrained guinea pig or from a human arm. All hatched larvae were counted and raised as described by Timmermann and Briegel (1993).

The body size of all mosquitoes was recorded by their wing lengths, measured from the alula to the tip, including the fringes. When required, the population of *An. gambiae* was split into size groups of small (2.9-3.1 mm) and large females (3.2-3.5 mm). The wing lengths of *An. atroparvus* varied between 4.2 and 5.0 mm; small sizes were 4.2-4.6 mm and large sizes 4.7-5.0 mm.

The flightmill system

Our flightmills were built according to Rowley et al. (1968), with circumferences of the flight path of 32.7 cm; the number of revolutions was registered by the computer at 30 s intervals. Further details were described by Briegel et al. (2001a, b). Flight experiments usually started around 3:00 pm at 24 ± 2°C under controlled light regimes of 12 h, but mainly during the scotophase. Each flight trial lasted 22 h and the computer printout provided information on the total flight distance covered during the period, the temporal pattern of flight activities, i.e. bursts of continuous flights or erratic flight pulses, and pauses for each female tested. Additional experiments were performed with *An. gambiae* that were flown for only 4 h (starting at 6:00 pm), also during the scotophase. These experiments were designed to simulate the shorter flight trials that were applied by Nayar and Van Handel (1971).

For metabolic analyses, females were fixed after termination of the flight trials. Two different controls were used. Sisters of same body sizes were fixed as pre-flight controls at the time when the flights started, and as a second control, sisters were kept individually in test tubes, restrained by cotton plugs to very narrow spaces to prevent flight movements (unflown controls). After the flight trials ended, all females were fixed for analysis in test tubes (13x100 mm) by heating in 100 µl of ethyl alcohol for 10 min at 90°C.

Biochemical analyses

Sugar, glycogen, and total lipid were measured in the same individual females according to Van Handel and Day (1988). Sugar in the aqueous fraction and glycogen in the precipitate were both measured with the hot anthrone reaction (Van Handel, 1985b), with glucose (Merck 8337) 0.1% in ethyl alcohol (25%) as standard. The lipid content was quantified by a vanillin-phosphoric acid reaction (Van Handel 1985a). The vanillin-reagent (Merck 818718) was used to initiate the color reaction. Soybean oil (Sigma S-7381) 0.1% in chloroform was used as a standard. The photometric readings were converted to µg and finally to calories per female.

Utilization of a given substrate for flight was obtained by subtraction of post-flight caloric values from pre-flight values. Alternatively, the rate of substrate utilization was calculated by expressing these absolute differences per hour of actual flight activities. The same was achieved for survival data when pre-flight values were compared to the values of non-flown, resting controls.

RESULTS

Flight performance of *An. gambiae*

Female *An. gambiae* were tested for their daily flight performance on flightmills after various treatments: starvation (i.e. access to water only), sugar-fed, and blood-fed. Four typical examples of 2-d-old females have been selected for Figure 1: a starved female, a sugar-fed female, and 2 blood-fed females. Of the latter, one was an average, the other a vigorous flier, as reflected by their total flight distances. We arbitrarily decided to discard as "noise" those flights of less than 0.5 km or pulses lower than 2 m/min, assuming that such animals were not in good condition or poorly mounted on the mill.

The total flight distances for all experiments are

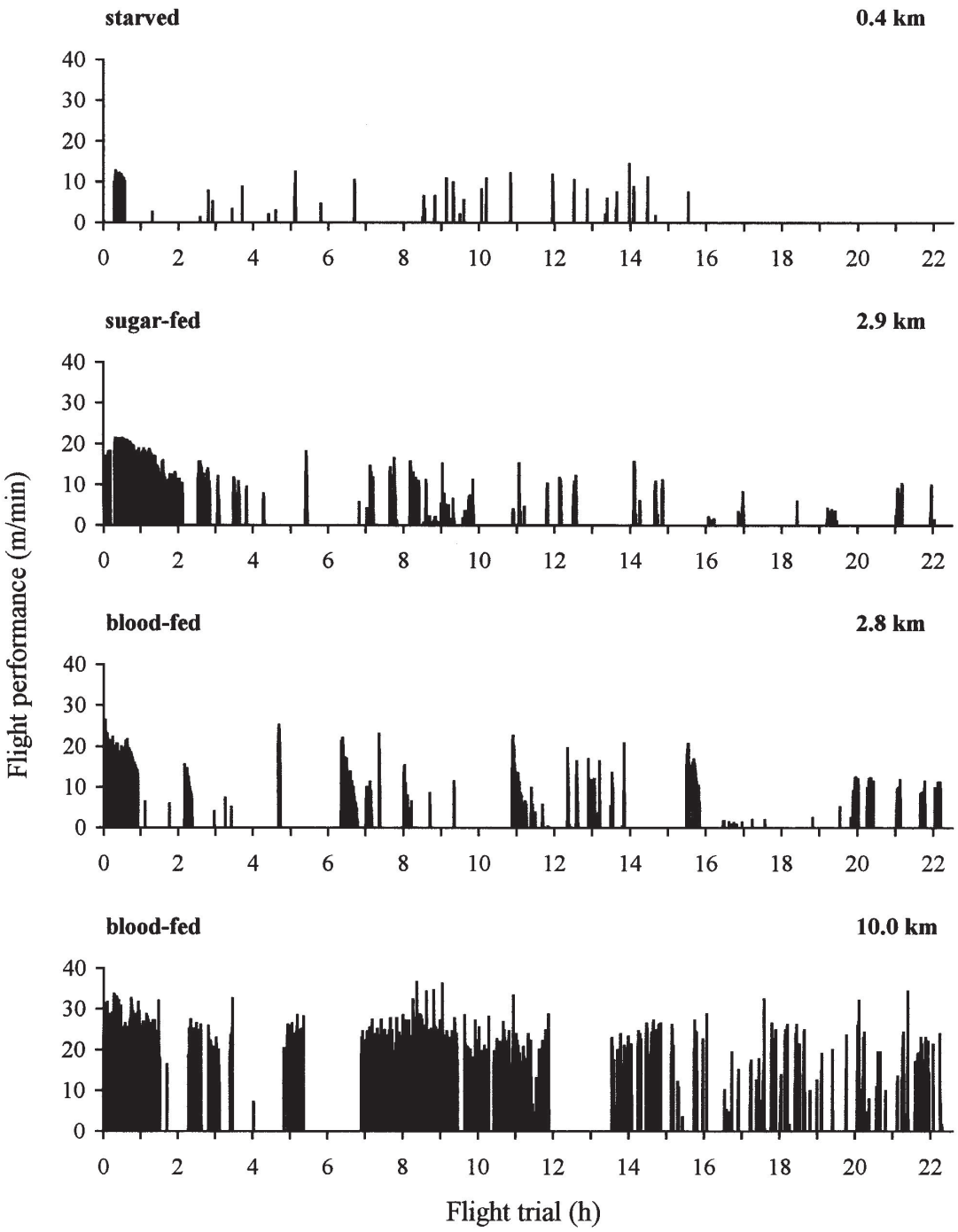

Figure 1. Selection of four individual flight patterns and the total flight distances of female of *An. gambiae* that were 2-d-old and starved, sugar-fed or blood-fed; blood meals were given at days 1 and 2 post-eclosion. Each peak shows a flight pulse during a half-minute interval. Note the difference in flight performance between weak, normal fliers and a vigorous flier.

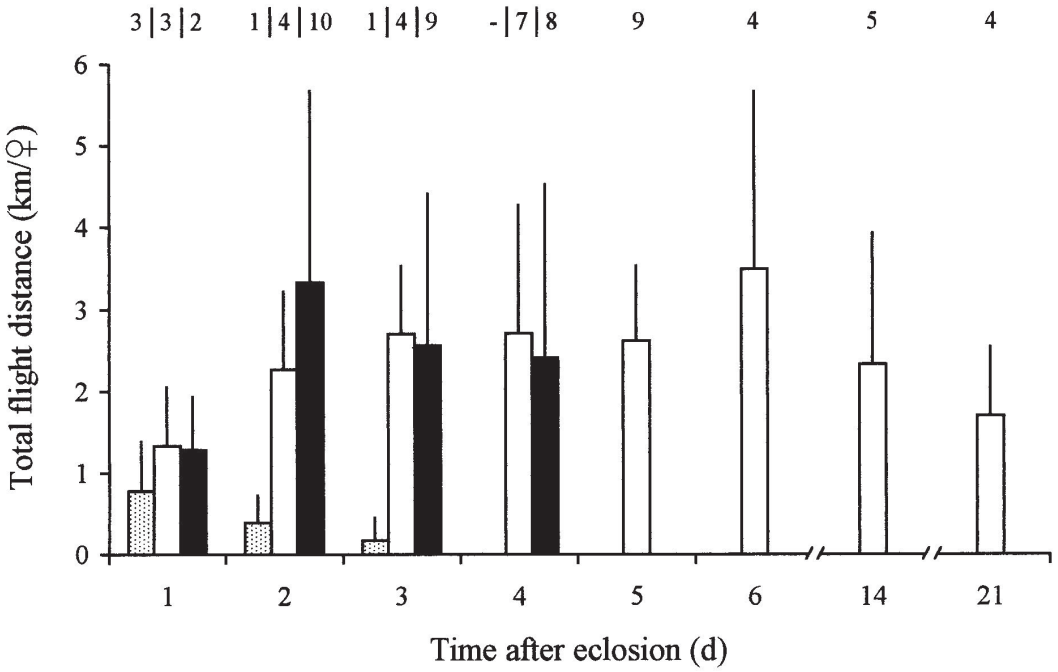

Figure 2. Total flight distances of female *An. gambiae* with access to sucrose for 3 wk (white). For comparison, the flight distances of starved (dotted) and blood-fed females (black) are included; blood meals were given at day 1 and 2 after eclosion (Mean ± S.E., N = 9 – 30 for each bar). Numbers on top of each bar indicate the maxima observed in each group.

Table 1. Mean distances and total flight time of female *An. gambiae* and *An. atroparvus* under different feeding conditions. The duration of continuous flight periods have been categorized arbitrarily in 3 segments, and their frequencies are given (% of total flight time).

			Continuous flights (h)		
			0.5 -1	1-4	>4
	Distance (km)	Total flight time (h)		(%)	
An. gambiae					
Starved*	0.4±0.3	0.7±0.5	16	4	0
Sugar-fed**	2.4±0.6	2.5±0.5	45	49	2
Blood-fed at***					
d 1	1.3 ± 0.7	1.8 ± 0.9	30	9	1
d 2	1.3 ± 0.5	1.8 ± 0.8	44	12	1
d 3	1.4 ± 0.7	1.6 ± 0.6	40	12	0
d l+2	2.8 ± 0.5	3.3 ± 0.6	59	34	1
d 2+3	2.5 ± 0.5	2.8 ± 0.5	60	35	1
An. atroparvus					
Starved*	0.9 ± 0.1	1.2 ± 0.6	66	12	0
Sugar- fed**	3.9 ± 1.1	3.7 ± 1.1	44	52	4
Blood-fed at***					
d l + 2	2.5 ± 0.3	2.0 ± 0.1	76	24	0

* N= 11-15; ** N = 8 - 24;*** N = 11 - 30 for each day

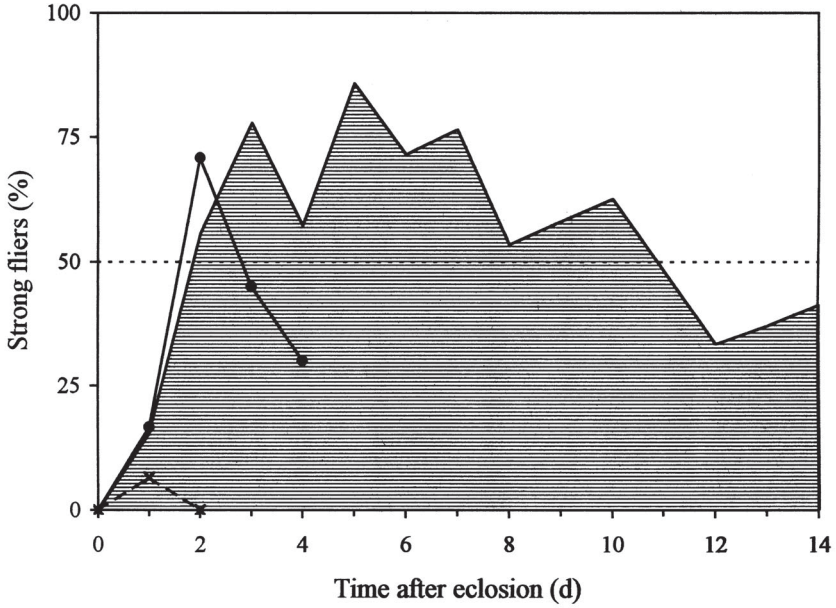

Figure 3. Distribution of strong fliers (> 2 km/female) and weak fliers (< 2 km/female) of *An. gambiae* with access to sucrose (hatched area) or two blood meals at day 1 and 2 (closed circles). For comparison, flights of starved females are included (x). During the first 2 days the frequencies of strong fliers largely coincided with sugar-fed and protein-fed females. For absolute flight distances compare Figure 2.

summarized in Figure 2. Sugar-fed females reached their maximal performance within 3-6 d after eclosion with a mean of 3 km per female per night. The range was very broad, with maxima of 8.5 km within the 22 hr trial. After 2 and 3 wk their performance slightly declined but remained always higher than shortly after eclosion. Females that had obtained human blood meals at day 1 or days 1+2 post eclosion, revealed the same performances as sugar-fed sisters, with maximal values of 10 km/female/night already by day 2 (Figures 1and 2). When we correlated the total flight distances per female with their actual flight times, a highly significant linear regression was obtained (not shown), from which an average flight speed was deduced: about 1.0 km/h in sugar-fed, and about 0.9 km/h in blood-fed females; these differences were considered irrelevant in biological terms, because speeds ranged between 0.4 km/h and in rare cases 2.1 km/h. A more conclusive analysis of the flight performance was obtained when we categorized the flight distances in 3 arbitrarily chosen segments of continuous flight periods (Table 1). Weak and strong fliers were recognized and their percentages within the cohort were plotted over time after eclosion (Figure 3, Table 1). Within 2 d strong fliers with means between 2-5 km/female prevailed (>50%) and dominated for more than a week (Figure 3). Flight performances improved in a similar pattern whether the females had sugar or blood, with maxima observed already by day 2-3 after eclosion.

When flown at day 1, 3, and 5, during a period of only 4 h, the total flight distances were very similar to the ones observed during 22 h flights. Obviously, the most intense flight activities of sugar-fed females usually occurred during the first few hours, as shown in Figure 1.

Metabolism of *An. gambiae* during flight

All the females were analyzed for their carbohydrate and lipid contents before and after flight and the values were corrected for the amounts utilized for survival during the same time interval by non-flown sisters. These studies aimed at the recognition of the flight substrates. Means are compiled in Table 2, together with the respective teneral values of females of the same body size. The daily results are presented in Figure 4. During day 1, shortly before flight, glucose had increased considerably over teneral values because of sugar feeding, whereas glycogen increased only after 2 d, and remained above teneral values for the rest of their lives. Lipid synthesis was much slower, reaching its peak by the end of the first week of sugar feeding. The blood meals, however, led to a dramatic lipid synthesis within 2-4 d (Figure 4).

After flight the carbohydrates were markedly reduced, 38% of the pre-flight conditions being utilized for flight in sugar-fed females and 61% in blood-fed

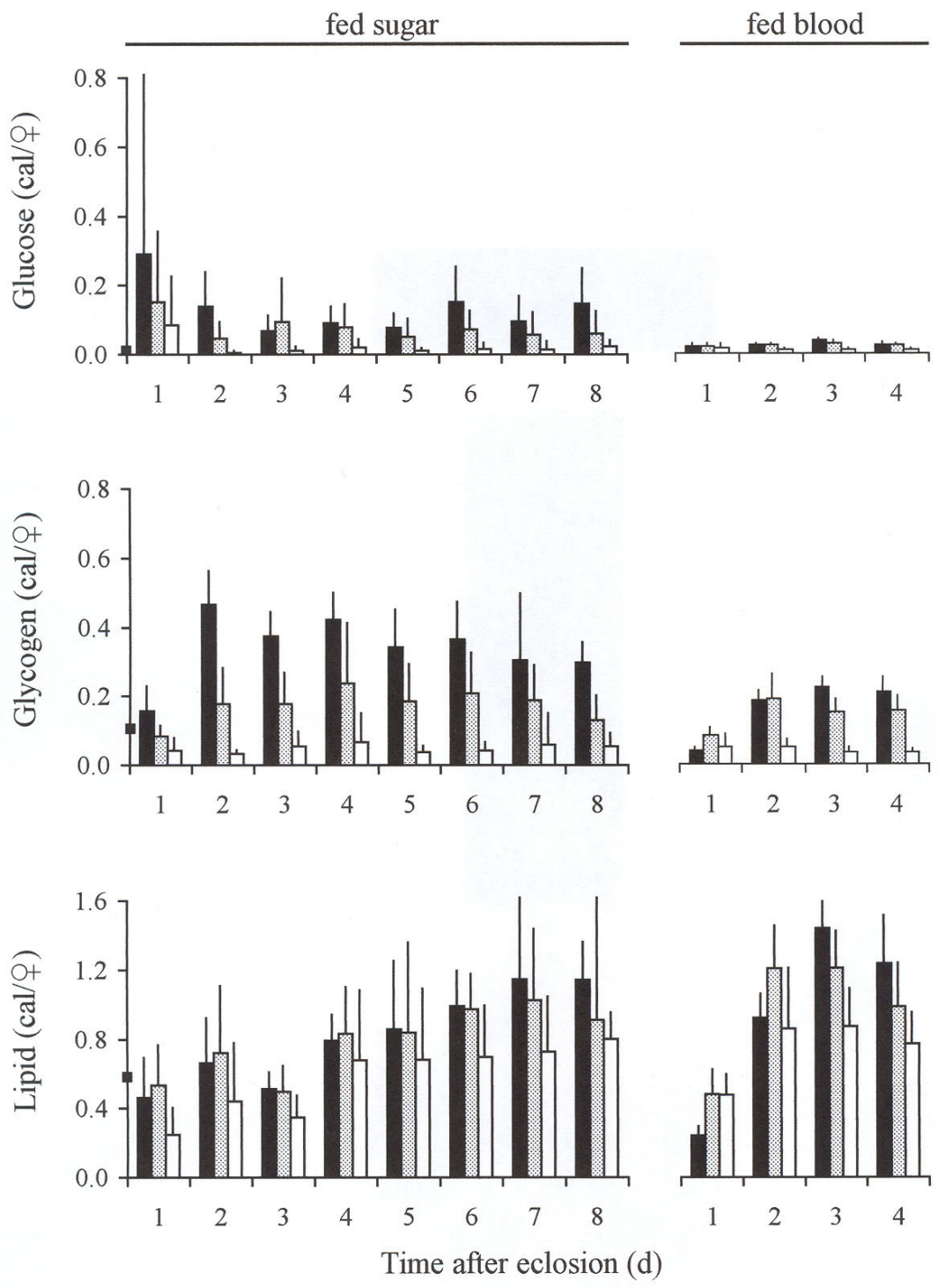

Figure 4. Profile of caloric content of carbohydrates and lipids of *An. gambiae* with access to sucrose (left side) and with two blood meals at days 1 and 2 (right side). Black bars are the pre-flight controls, dotted bars the non-flown controls, and white bars the females after the flights presented in Figure 2. The filled squares illustrate the level of teneral reserves (Mean ± S.E., N = 9-30 for each bar).

Table 2. Caloric data for pre-flight *An. gambiae* and *An. atroparvus:* teneral and pre-flight content of carbohydrates and lipid and the absolute amounts utilized for survival and during flight. For the latter, the percentage of pre-flight contents are in parentheses (Mean ± S.E./female).

	An. gambiae	
	Sugar-fed for 7 days (N = 105)	Blood-fed at day 1 +2* (N = 76)
Carbohydrates (cal/female)		
teneral	0.13±0.03	
pre-flight	0.47±0.07 (100%)	0.18±0.08 (100%)
used for survival	0.22±0.07 (47%)	0.02±0.05 (11 %)
used for flight	0.18±0.05 (38%)	0.11± 0.05 (61%)
Lipid (cal/female)		
teneral	0.59±0.06	
pre-flight	0.82±0.26 (100%)	0.89±0.48 (100%)
used for survival	0.03±0.10 (4%)	0**
used for flight	0.21±0.08 (25%)	0.21±0.15 (22%)
Distance (km)	2.6±0.6	2.4±0.8

	An. atroparvus	
	Sugar-fed for 7 days (N = 71)	Blood-fed at day 1 +2* (N = 26)
Carbohydrates (cal/female)		
teneral	0.61±0.17	
pre-flight	1.33±0.61 (100%)	0.40± 0.19 (100%)
used for survival	0.37±0.22 (28%)	0**
used for flight	0.54±0.21 (41%)	0.41± 0.13 (103%)
Lipid (cal/female)		
teneral	1.08± 0.19	
pre-flight	1.74±0.70 (100%)	1.28± 0.33 (100%)
used for survival	0**	0**
used for flight	0.22± 0.14 (13%)	0.03±0.05 (2%)
Distance (km)	3.8±1.1	2.5±0.1

*After blood meal the females had access to water until day 4 or 5.

**Renewed syntheses from the blood or sugar-meal obscured the decrease in non-flown controls.

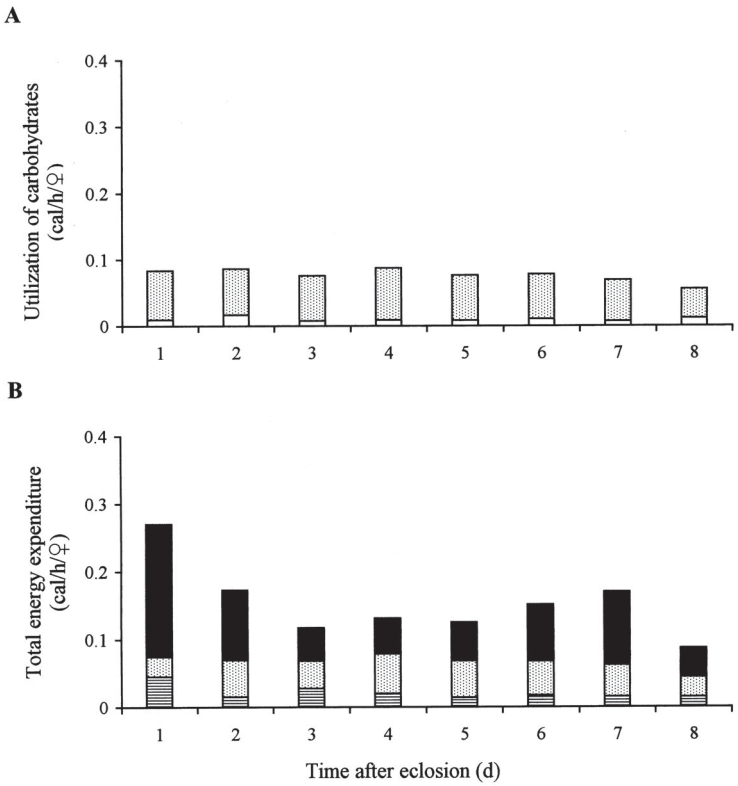

Figure 5. Rates of energy expenditure by female *An. gambiae* with access to sucrose during the first eight d after eclosion (N = 9-24 per day). **A** Carbohydrate utilized per hour for survival (white) and for flight (dotted). **B** Total energy expenditure during flight: glucose (hatched), glycogen (dotted), and lipid (black).

females (Table 2). The decrease in reserves of non-flown females revealed the requirements for survival which was 47% in sugar-fed females and 11% in blood-fed females. Surprisingly, lipid was also reduced after flight, indicating a lipid utilization of 25%, whereas for survival lipid contributed only 4% (Table 2). Obviously, sugar and glycogen were assigned similarly for both survival and flight. The lipids differed. In sugar-fed females only 4% were used for survival, but 25% of the pre-flight lipid was utilized for flight, and 22% by blood-fed females (Table 2). No reduction of lipid was observed in the blood-fed, non-flown controls because of concurring syntheses of lipid from the blood meal.

Because the pre-flight contents of reserves as a consequence of their feeding history differed considerably among the female cohorts tested, more conclusive data were presented when expenditures were expressed as rates of substrate utilization, i.e. cal per hour of active flight per female (cal/h). The contributions of the three reserve components for survival and flight of sugar-fed females are presented in Figure 5. For carbohydrates a mean rate of 0.01±0.003 cal/h for survival and 0.07±0.01 cal/h for flight were found to be constant for a whole week after eclosion (Figure 5A). Lipid utilization for flight clearly differed (Figure 5B). The first day after eclosion 0.20 cal/h disappeared during flight, the second day this decreased to 0.10 cal/h, and subsequently it remained at an average of 0.09±0.05 cal/h, equal to carbohydrate utilization for flight (Figure 5B). Despite an enormous lipid synthesis of blood-fed females (Figure 4), its utilization for flight was equal to females fed sugar (Table 2).

The prevalence of lipid as a major energy substrate for flight during the first and second day of imaginal life is explained by the large amounts present at eclosion (Figure 4), and equally so in blood-fed females by the strong lipogenesis from the blood meal. The lower carbohydrate content in teneral females, on the other hand, is quickly enhanced by feeding on sugar and is accompanied by substantial glycogenesis from day 2 onwards, saving the lipids from being used for flight during the later periods.

Flight performance of *An. atroparvus*

Four individual flight protocols were selected for Figure 6, and the total distances flown by starving, sugar-

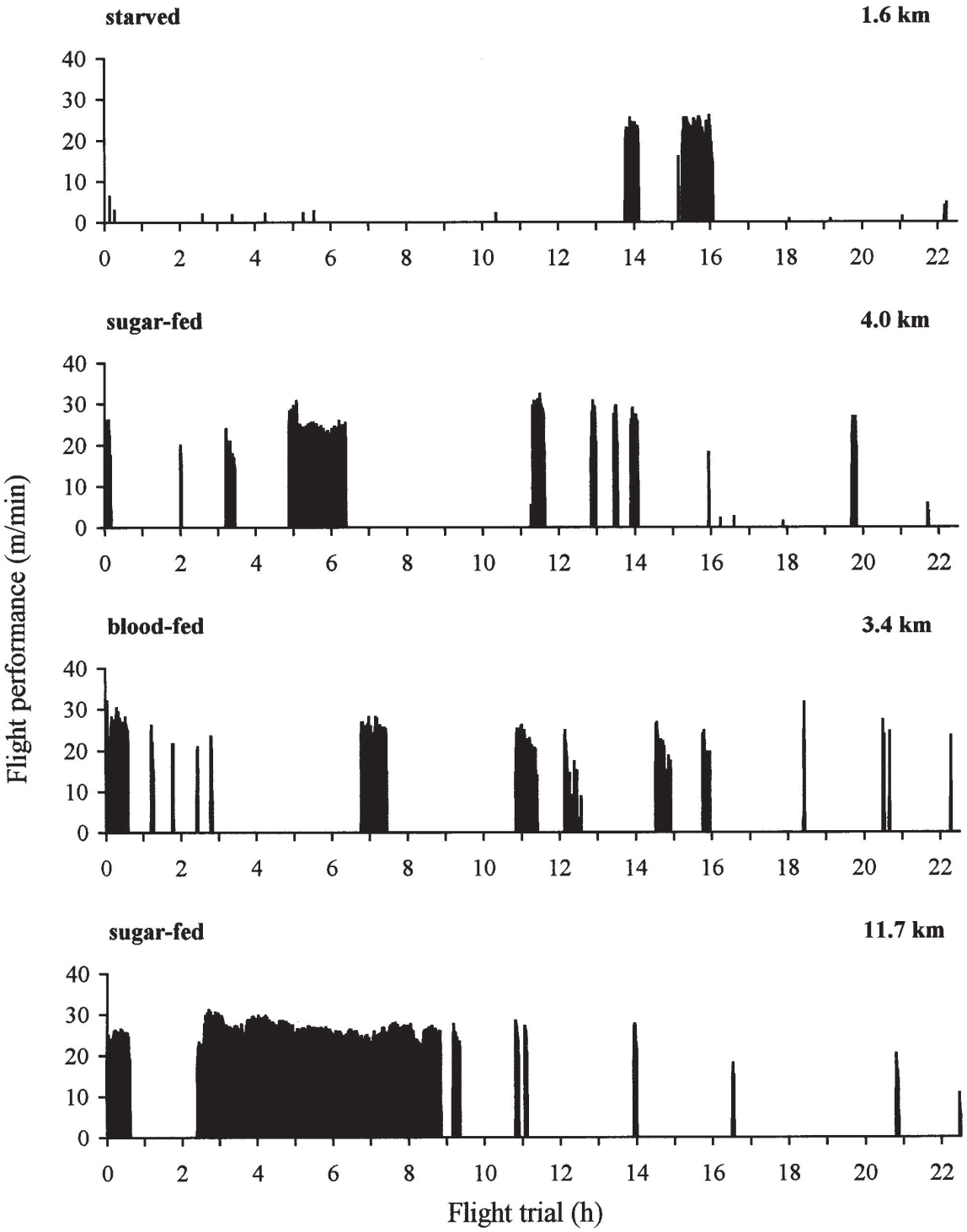

Figure 6. Selection of four individual flight patterns of *An. atroparvus*; females were starved or sugar-fed for two days or blood-fed with blood meals given at day 1 + 2. A vigorous, strong flier (bottom) with access to sugar for 7 d is also depicted; note the 6 h interval of non-stop flight.

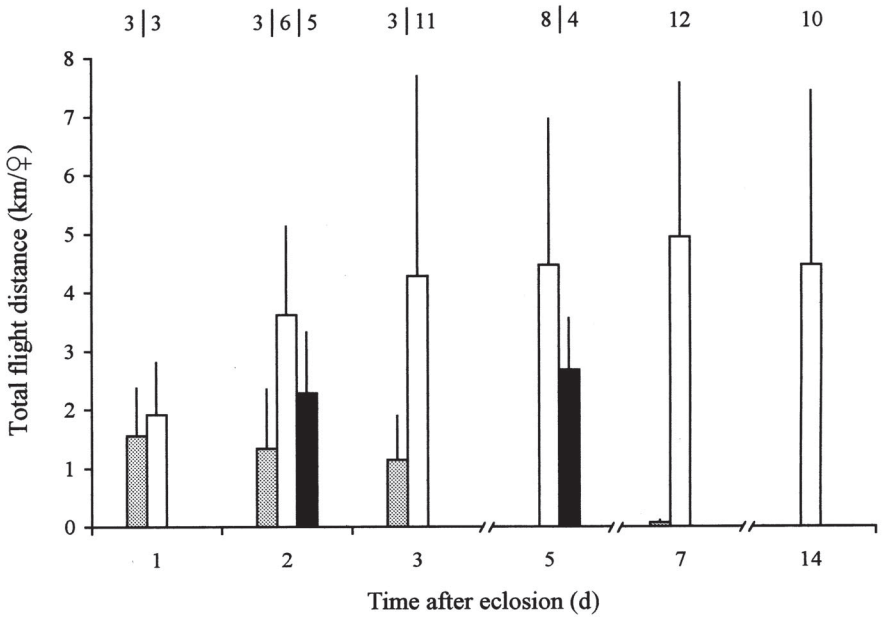

Figure 7. Total flight distances of female *An. atroparvus* with access to sucrose (white) and of starved (dotted) females; for comparison, the flight distances of blood-fed females (black) are included. Blood meals were given at days 1 and 2 after eclosion (Mean ± S.E., N = 8 – 18 for each bar). Numbers on top of each bar indicate the maxima observed for each group.

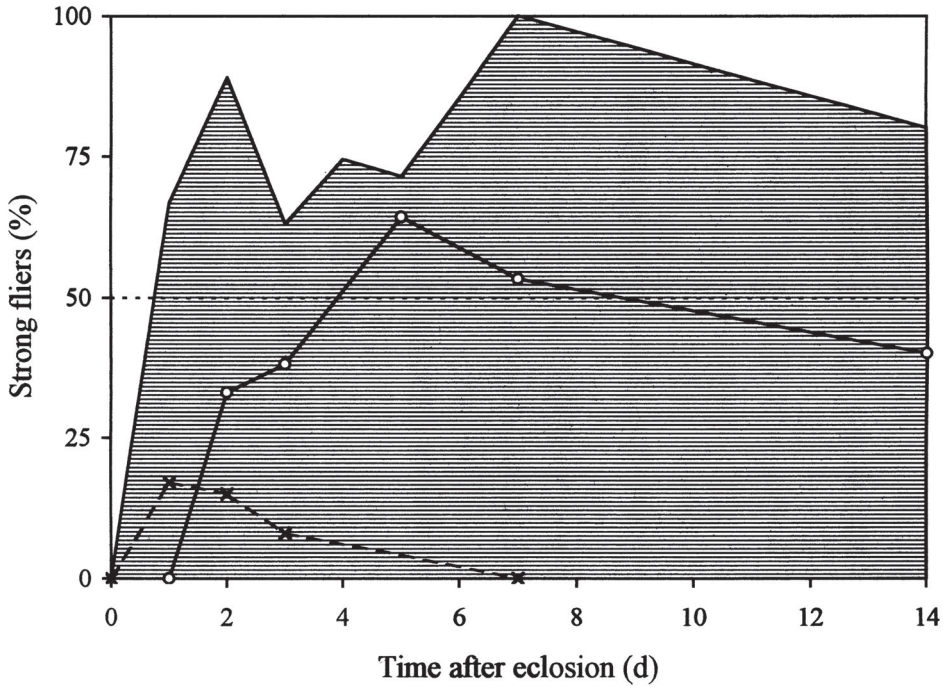

Figure 8. Distribution of strong fliers (> 2 km/female; hatched area) and weak fliers (< 2 km/female; white area) of *An. atroparvus* with access to sucrose. For comparison, starved females are included (**x**) together with females that flew more than 4 km (open circles).

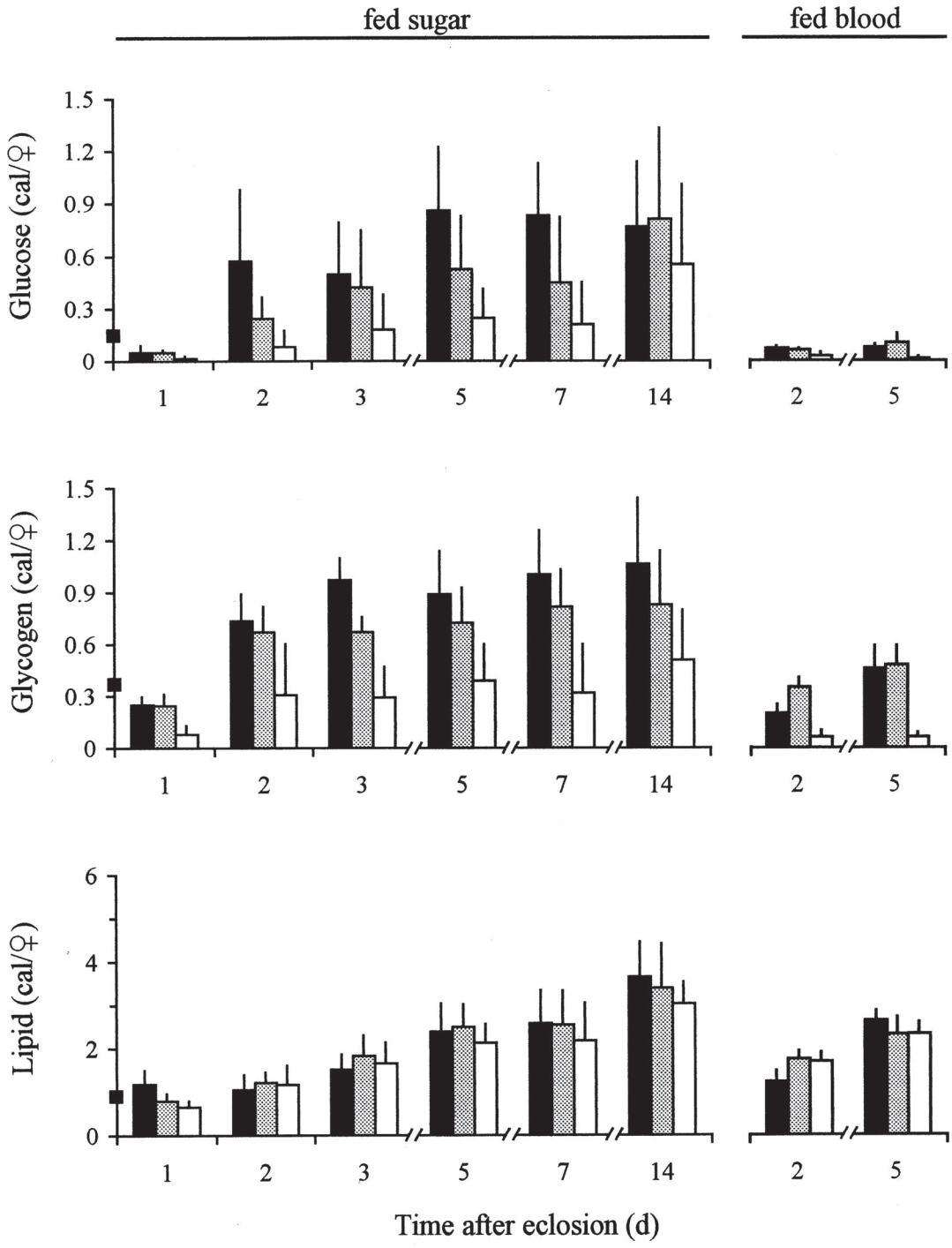

Figure 9. Profile of caloric content of carbohydrates and lipid of *An. atroparvus* with access to sucrose (left side) and with two blood meals at days 1 and 2 (right side). Black bars are the pre-flight controls, dotted bars the non-flown controls, and white bars the females after flight. The filled squares illustrates the teneral reserves (Mean ± S.E., N = 8-18 for each d).

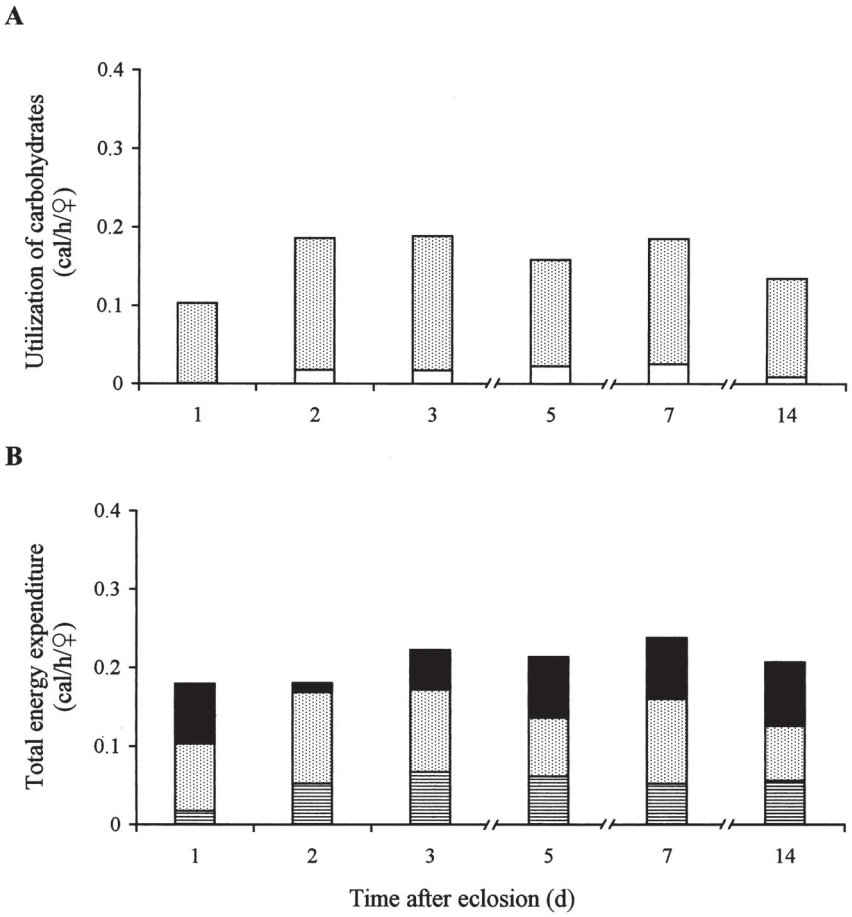

Figure 10. Energy expenditure by female *An. atroparvus* with access to sucrose during the first eight d after eclosion (N = 8-18 per d). **A** Rate of carbohydrate utilization for survival (white) and for flight (dotted). **B** Total energy expenditure during flight: glucose (hatched), glycogen (dotted), and lipid (black).

fed, and blood-fed female *An. atroparvus* are summarized in Figure 7. Starving females died within 5-7 d after eclosion, and their flight potential gradually decreased, although much more slowly than in *An. gambiae*. Sugar-fed females, tested during two wk, developed their full flight potential within 3 d whereupon it remained stable with an average of 4-5 km/night/female; the range was 0.6-14.1 km (Figure 7). We also chose the arbitrary segments of continuous flights as before, and compared their percentages in Table 1. In Figure 8, we split the experimental cohort of sugar-fed females into weak (<2 km/female) and strong fliers (>2 km/female); an appreciable flight potential developed already within the first day after eclosion, and it always remained over 50%. Even when we decided on a 4 km/female threshold for strong flights, the curve followed a similar steep pattern after day 1. Obviously, this species was already capable of powerful and enduring flights within one d of eclosion and for at least two wk. Females given blood at day 1 and 2 were tested 2 and 5 d after eclosion. Unlike *An. gambiae*, they did not reach the same flight performances as their sugar-fed sisters; 65% were strong flyers (>2 km), but only 4% when we applied a >4 km performance.

Metabolism of *An. atroparvus* during flight

In contrast to *An. gambiae*, this species bears considerably higher values of carbohydrates at eclosion (Figure 9). The caloric differences between pre-flight conditions and non-flown controls (Figure 9) indicated that during the first week of imaginal life substantial parts of sugar were metabolized for survival, more than glycogen; together 28% of pre-flight carbohydrates for survival and 41% for flight (Table 2). Glycogen appeared

to be utilized mainly for flight, but glycogen synthesis exceeded the teneral level already at day 2 (Figure 9). With the lipids there was a different situation: nothing was used for survival during 7 d and only 13% for flight (Table 2). During their first day of imaginal life, females appeared to utilize little lipid for survival, while from 2 d onwards a slow, steady lipogenesis was observed during two wk. The extent of substrate utilization for flight versus survival was obtained again by the rate of its disappearance during flight (Figure 10). The mean rate of carbohydrate utilization for survival was 0.02±0.01 cal/h during 2 wk, whereas for flight it was 0.14±0.03 cal/h, 7-10-times higher than for survival (Figure 10A). Mean lipid utilization for survival was extremely low with 0.001±0.012 cal/h during 2 weeks, whereas for flight it was 0.06±0.03 cal/hr (black segment in Figure 10B).

DISCUSSION

Flight performance and metabolism

The maximal flight distances were reached in both species 2-3 d post-eclosion. In *An. atroparvus,* the means were somewhat higher than in *An. gambiae*, with maxima of 10 and 14 km per female per night, respectively. In *An. gambiae* the flight distances in general did not differ whether they were fed sugar or blood before, whereas sugar-fed females of *An. atroparvus* flew better than blood-fed sisters. For survival, females of both species utilized approximately equal amounts of carbohydrates as for flight, but they clearly differed in their lipid utilization. In *An. gambiae*, half of the flight substrates utilized consisted of lipids and minimal amounts during rest. In *An. atroparvus*, lipid contributed only one-third to the total flight energy, thus sparing the rest for oogenesis instead. The extent of pre-flight lipid that was lost during flight of *An. gambiae* (22-25%) and of *An. atroparvus* (2-13%) under all circumstances was new and supports our earlier evidence for lipid disappearance during flight of *Ae. vexans* (10-20%; Briegel et al. 2001b). These results were surprising in view of the evidence by Nayar and Van Handel (1971) that carbohydrates form the energy substrate during flight of *Ae. sollicitans* and *Ae. taeniorhynchus*. This discrepancy might be explained by the duration of the flight experiments which lasted 3-4 times longer in our laboratory.

The recent findings by Scaraffia and Wells (2003) for proline oxidation as a source of flight energy emphasize the possible role of lipids as an energy reserve for flying mosquitoes, similar to the tsetse-fly *Glossina* (Bursell et al. 1974). However, two different metabolic strategies need to be recognized among mosquitoes. Species such as *An. atroparvus*, *Ae. aegypti*, *Ae. albopictus*, *Ae. sollicitans,* and *Ae. taeniorhynchus* mainly depend on carbohydrate sources to gain their flight energy, while species like *An. gambiae* and *Ae. vexans* appear to mobilize lipids during their extended flight periods. Interestingly, flight activities were always composed of longer and shorter bouts of intense flights (Briegel et al. 2001a,b, this report) and the intermittent pauses possibly represent periods of hormonal reserve mobilizations by either adipokinetic or hyper-trehalosemic hormones.

Reserves and starvation

The different body sizes of these two species strongly relate to their teneral reserves, as shown by Fernandes and Briegel (unpublished data) and earlier by Briegel (1990). In absolute terms, *An. atroparvus* carried over twice the amounts of lipids from the larval/pupal stages than did *An. gambiae*, and almost 5 times as much glycogen (Table 2). These values roughly doubled in *An. atroparvus* through sugar feeding, whereas in *An. gambiae* the synthesis of additional reserves was less pronounced. When normalized for body size however, *An. atroparvus* had 1.5-fold higher glycogen reserves than *An. gambiae*, whereas the latter had about 1.5-fold higher lipid reserves than the former. These conditions also determined the flight performance of starving females which was 1.2 h in *An. atroparvus* and 0.7 h in *An. gambiae*, or 1.6 km during the first day of *An. atroparvus*, while starving *An. gambiae* reached 1.4 km only during 3 d. The survival of starving females was only 3 d in *An. gambiae* and 7 d in *An. atroparvus*, again reflecting the availability of teneral reserves. Therefore, there is an obvious need to acquire additional energy reserves, be it from sugar or from blood.

In sugar-fed *An. gambiae,* lipogenesis reached its maximal level within 7 d and the maximal glycogen within 2 d. When fed blood however, lipid maxima were attained already within 1 d of the blood meal, but glycogenesis now was slower. Taken together, *An. gambiae* is characterized by the synthesis of lipids as well as for its mobilization for flight. *An. atroparvus* on the other hand, saves the lipid reserves mainly for oogenesis and possibly for hibernation, leaving the carbohydrates for fueling its flight. However, both species could be maintained on blood meals alone: maximal survival times were 90 d for *An. atroparvus* when fed blood every other day and 55 d for *An. gambiae* with permanent access to oviposition sites[2] which confirms earlier observations from the field for *An. gambiae* (Straif

[2]Fernandes, L. 2003. Ph.D. dissertation, University of Zürich, Zürich, Switzerland.

and Beier 1996, Gary and Foster 2001).

As long as blood donors are available, *An. atroparvus* does not require sugar sources for survival and reproduction, although additional sugar meals strongly improve flight performance, besides reproduction. The caloric blood meal input is diverted primarily to oogenesis, thus limiting flight performance. In contrast, in *An. gambiae* flight metabolism does not differ whether it feeds on sugar or blood because of a more efficient lipogenesis from the blood protein. This strategy relates to the multiple blood meals that are ingested by *An. gambiae* and their relative independence of sugar meals, as observed by Fernandes[2].

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