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Flight Capacity of *Bactrocera dorsalis* (Diptera: Tephritidae) Adult Females Based on Flight Mill Studies and Flight Muscle Ultrastructure

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Subject Editor: Juan Rull

J. Insect Sci. *(2015)* 15(1): 141; DOI: 10.1093/jisesa/iev124

ABSTRACT. The oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), is considered a major economic threat in many regions worldwide. To better comprehend flight capacity of *B. dorsalis* and its physiological basis, a computer-monitored flight mill was used to study flight capacity of *B. dorsalis* adult females of various ages, and the changes of its flight muscle ultrastructures were studied by transmission electron microscopy. The flight capacity (both speed and distance) changed significantly with age of *B. dorsalis* female adults, peaking at about 15 d; the myofibril diameter of the flight muscle of test insects at 15-d old was the longest, up to 1.56 µm, the sarcomere length at 15-d old was the shortest, averaging at 1.37 µm, volume content of mitochondria of flight muscle at 15-d old reached the peak, it was 32.64%. This study provides the important scientific data for better revealing long-distance movement mechanism of *B. dorsalis.*

Key Words: *Bactrocera dorsalis*, flight capacity, flight muscle, ultrastructure

The oriental fruit fly, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae: Dacinae), is native to Southeast Asia (Koyama et al. 1984, Aketarawong et al. 2007) and is one of the most destructive insect pests of tropical and subtropical fruits and vegetables in Asia. *B. dorsalis* ranges from the Indian subcontinent (and Andaman Island), across into southern China and mainland South-east Asia but has also been introduced to Hawaii, the Mariana Islands and Tahiti, and to Africa (formerly *Bactrocera invadens*) (Aketarawong et al. 2007, Drew and Romig 2013, Wang et al. 2014). As a result of its potential to cause severe damage to agricultural products, high fecundity, and wide host range, *B. dorsalis* has been listed as an important quarantine pest in most countries (Koyama et al. 1984, Li and Ye 2000, Clarke et al. 2005, Xie and Zhang 2005, Chen et al. 2007, Zhang et al. 2008, Froerer et al. 2010, Drew and Romig 2013).

Research has shown that *B. dorsalis* has strong flight and dispersal capacity (Fletcher 1989). Steiner (1957) found that *B. dorsalis* in Hawaii could spread out extensively after fruit harvests, with a dispersal radius up to 37 km. In the Ogasawara Islands, *B. dorsalis* could fly over water up to 50 km (Yan 1984). Tan and Serit (1994) reported that *B. dorsalis* was capable of long-distance dispersal based on mark-recapture studies that were conducted in Penang, Malaysia. Zhu and Qiu (1989) reported that *B. dorsalis* could fly from Taiwan to Ryukyu a distance of 27 km. It is believed that the ability to perform long-distance flights has enabled this insect to disperse widely in Asia (Yan 1984, Tan and Serit 1994, Liang et al. 2001; Chen and Ye 2007, Chen et al. 2007, Froerer et al. 2010, Wan et al. 2011).

Although the flight capacity of *B. dorsalis* has been well studied, few researchers have attempted to study internal changes within the fly that are related to long-distance flight. Normally, the flight capacity of insects is controlled by many factors, including physiological and environmental factors such as food and intraspecific competition. Among these factors, the flight muscle of insects play a crucial role in regulating flight capacity (Heinrich 1971, Liu and Ye 2006). To better understand the flight capacity of *B. dorsalis*, we tested average flight speed and flight distance of *B. dorsalis* adult females of various ages on a computer-monitored flight mill, which can provide useful information on the flight capacity of insects (Cui et al. 2013, Hao et al. 2013). Flight mills can provide the exact measurement of flight distance, speed, and duration, which is the most reliable parameters to evaluate the flight capacity of insects (Thomas and William 1992). Therefore, this method is considered the model system for investigation of flight behavior (Schumacher et al. 1997, Ishiguri and Shirai 2004, Tu et al. 2010).

We also compared the flight data with the flight muscle ultrastructure of *B. dorsalis* adult females of similar age, including myofibril diameter, sarcomere length, and volume content of mitochondria, which are regarded as the main indicators of flight capacity of insects (Pan et al. 2013). In general, flight capacity in insects has been shown to increase with longer myofibril diameter (Luo and Li 1996, Liu et al. 2008), shorter sarcomere length (Luo and Li 1996, Liu et al. 2008), and higher volume amounts of mitochondria (Liu et al. 2008).

Understanding the flight capacity of *B. dorsalis*, and the corresponding flight muscle ultrastructure, will contribute to our comprehension of the physiological basis of flight capacity in this insect. In addition, such information will allow better prediction of potential *B. dorsalis* spread and aid in development of prevention and control strategies.

Materials and Methods

Test Insects. The *B. dorsalis* test insects used in this study, which was conducted during 2012–2014, originated from a mango orchard, about 120 ha in size (23° 18′ N, 101° 39′ E, 395 m a.s.l,) in Yuanjiang County, Yunnan Province, China. First, *B. dorsalis* were collected as larvae from infested mango, *Mangifera indica* L., and then the larvae were reared with an artificial diet containing wheat bran, sugar, dry yeast, sodium benzoate, and HCl under room conditions of 25°C, 60% RH, and 12 h photophase (6 a.m. to 6 p.m.); adults were released in a cage (35 by 30 by 30 cm) with water and a mixture of protein hydrolyzate and sugar under a constant temperature of 25°C and 12 h

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photophase (Chiu 1978, Vargas and Chang 1991). To keep consistency, tested insects were collected from mass-reared strains of *B. dorsalis*, which was given an artificial diet for about 10 generations after colonization. The *B. dorsalis* adults usually lived 25–30 d under above conditions. The adult females were reared separately from the males on day 0 after eclosion. Adult females of the same day age were put into a single cage (35 by 30 by 30 cm) and allowed to feed on cotton balls that were immersed in a diet of sugar: water (1 part sugar to 3 parts water) and liquid yeast (1 part yeast powder to 3 parts water), and changed every 12 h.

Measurement of Flight Capacity. A computer-monitored flight mill was custom-made for the monitoring of insect flight ability from Jiaduo Industry & Trade co., LTD, Hebi, China, which was similar to the equipment described by Chambers et al. (1976), Cheng et al. (1997), and Hao et al. (2013). In total, 12 individual flight mills were linked to a recorder, which was connected to a computer and placed on glass shelves in a room where temperature, RH, and light intensity could be adjusted. Same size female adult *B. dorsalis* were captured in 15 mm by 150 mm test tube directly from the rearing cage. A cotton sliver with 200 µl diethyl ether was put into the test tube lightly to anesthetize above adults for 30 s. The adults were then put on glass slides and mounted, via the pronotum, on 12-cm-long segments of steel wire (0.4 mm in diameter) with a droplet of 502 Glue (Quanzhou Changde Chemical Engineering Co., Ltd., Quanzhou, China) (Cui et al. 2013). The steel cantilever was placed between two miniature magnets on the flight mill immediately thereafter, ensuring the fruit fly was placed horizontally for the sake of smooth flight. Data recorded by the software included the time of flight initiation and each revolution and the number of mill revolutions that occurred in consecutive 5-s intervals. Flights interrupted by a 5-min interval were considered separate flights.

Twelve female adults of the same age and similar size were tested at one time. Each test was conducted for 13 h. Each adult female was tested only once in her lifetime. The total number of flight mill revolutions was recorded and flight distance, speed, duration, and the maximum speed of each flight for each one were computed using a custom-made software package (Cheng et al. 1997). During the process, the temperature was maintained at 25°C, 60% RH, and a light intensity of 1.2205klx.

Flight Muscle Sampling and Ultrastructure Observations. *B. dorsalis* female adults were selected randomly from rearing cages at ages of 5, 10, 15, 20, and 25 d, killed with ethyl acetate vapor. Thoracic dorsal-longitudinal muscles of these flies were carefully observed under transmission electron microscope (JEM-1011, JEOL Ltd., Japan) on each sampling date, five were used for cross-sectional observations and the other five insects were used for vertical section observations. Flight muscle (thoracic dorsal-longitudinal muscle) samples were made using primary fixation in 3.5% glutaraldehyde solution and secondary fixation in 1% osmic acid. Samples were then treated by gradient dehydration by ethyl alcohol and acetone, and penetration and embedding by 618 epoxy resins. Afterward, semithin sections of the samples were made, using a light microscope for positioning, trimmed with an ultramicrotome section by LEICA-R, double staining by citrate-uranium acetate, and finally observed with transmission electron microscope (JEM-1011, JEOL Ltd.).

Analysis of Transmission Electron Microscopy Photographs. The cross-sectional diameter of myofibrils and the length of the sarcomere (longitudinal section) from the Electron micrograph of the samples were directly measured using Photoshop software (Adobe Photoshop CS6). Six myofibrils and sarcomeres in each image were randomly sampled to measure their diameter and length. The cross-sectional diameter measurement was made using the longest axis of the cross-section. The length of the sarcomere was the distance between two adjacent Z-lines. The mitochondrial volume was measured by the three-dimensional principle of Steer (1981), and the percentage of mitochondrial volume in each myofibril was calculated using transmission electron microscopy photos that were covered by graph paper with a known number of points. The ratio of mitochondrion points to total points was calculated. A counter was used to check the number of thick filaments from the cross-section photos.

Statistical Analyses. Flight distance, duration, and speed of the fruit fly at different day old; myofibril diameter, sarcomere length, and volume content of mitochondria of its flight muscle were compared using one-way analysis of variance followed by the least significant difference test. Before analysis, we ensured the data met the necessary assumptions of normality and homoscedasticity. Statistical analyses were executed using SPSS 13.0 (SPSS, Chicago, IL).

Results

Flight Capacity of Female Adults. The flight parameters of the *B. dorsalis* test females over the 13-h test period varied significantly by age ($P < 0.01$; $F = 32.85$; df = 4). The 15-d-old females had the longest flight duration, averaging 1.30 ± 0.16 h (mean ± SE, $n = 12$); had the longest accumulative flight distance, averaging 3.57 ± 0.16 km (mean ± SE, $n = 12$); had the fastest average flight speed, averaging 0.98 ± 0.18 m/s (mean ± SE, $n = 12$); and had the average fastest flight speed as well, reaching to 1.58 ± 0.10 m/s (mean ± SE). These results clearly show that the flight capacity (both speed and distance) change with age of *B. dorsalis* female adults, peaking at about 15 d (Table 1).

Structure and Development Dynamic of flight Muscle.

Myofibril. Flight muscle myofibrils of *B. dorsalis* composed of actin filaments and myosin filaments (Fig. 1). Each actin filament was enclosed by six myosin filaments arranged equidistantly in a hexagon pattern (Fig. 1).

In cross-section, the myofibrils were elliptic in shape (Fig. 2) and the average diameter (measured along the longest axis) differed significantly with age ($P < 0.01$; $F = 14.97$; df = 4). The average diameter of the myofibrils at 15 d was 1.56 ± 0.04 µm (mean ± SE, $n = 30$), which was significantly larger than at 5 d, 1.30 ± 0.01 µm (mean ± SE, $n = 30$); 10 d, 1.24 ± 0.02 µm (mean ± SE, $n = 30$); 20 d 1.36 ± 0.02 µm (mean ± SE, $n = 30$); and 25 d, 1.35 ± 0.05 µm (mean ± SE, $n = 30$) (Fig. 3).

Sarcomere Length. In longitudinal view, the sarcomeres were cylindrical in shape (Fig. 4). Z lines were obvious and regularly shaped, which accounted for around 3% of the sarcomere length. Bands were

Table 1. Flight parameters of *B. dorsalis* adult females at various days after adult emergence, tested at 25°X, no wind, photoperiod of 12:12 (L:D) h, and 60% RH for tethered-flight 13 h

Days	No. of test insects	Mean accumulative flight duration (h) (mean ± SE)*	Mean accumulative flight distance (km) (mean ± SE)*	Mean flight speed (m/s) (mean ± SE)*	Mean fastest flight speed (m/s) (mean ± SE)*
5	12	1.15 ± 0.16 b	0.95 ± 0.19 c	0.30 ± 0.13 bc	0.88 ± 0.14 c
10	12	0.78 ± 0.17 c	1.44 ± 0.11 b	0.51 ± 0.16 b	1.26 ± 0.16 b
15	12	1.30 ± 0.16 a	3.57 ± 0.16 a	0.98 ± 0.18 a	1.58 ± 0.10 a
20	12	0.64 ± 0.12 c	1.20 ± 0.14 b	0.45 ± 0.19 b	1.08 ± 0.14 b
25	12	0.95 ± 0.11 b	1.12 ± 0.12 b	0.33 ± 0.14 bc	0.73 ± 0.14 c

*Means within a column followed by the same letter are not significantly different ($P > 0.05$, Duncan test).

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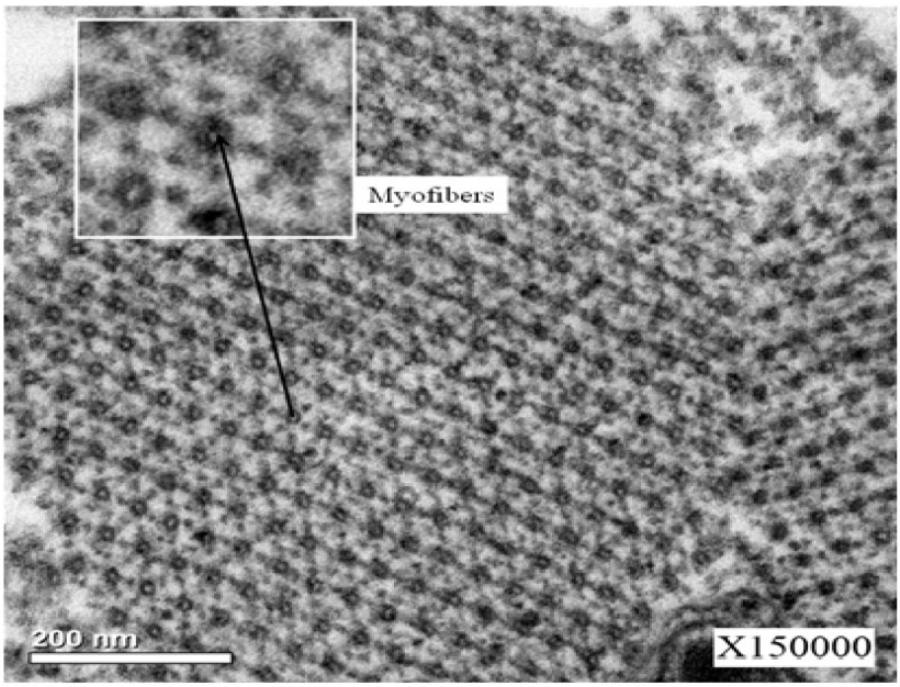

Fig. 1. Cross-section of the myofibrils of the flight muscle of a *B. dorsalis* adult female at 15 d after adult emergence.

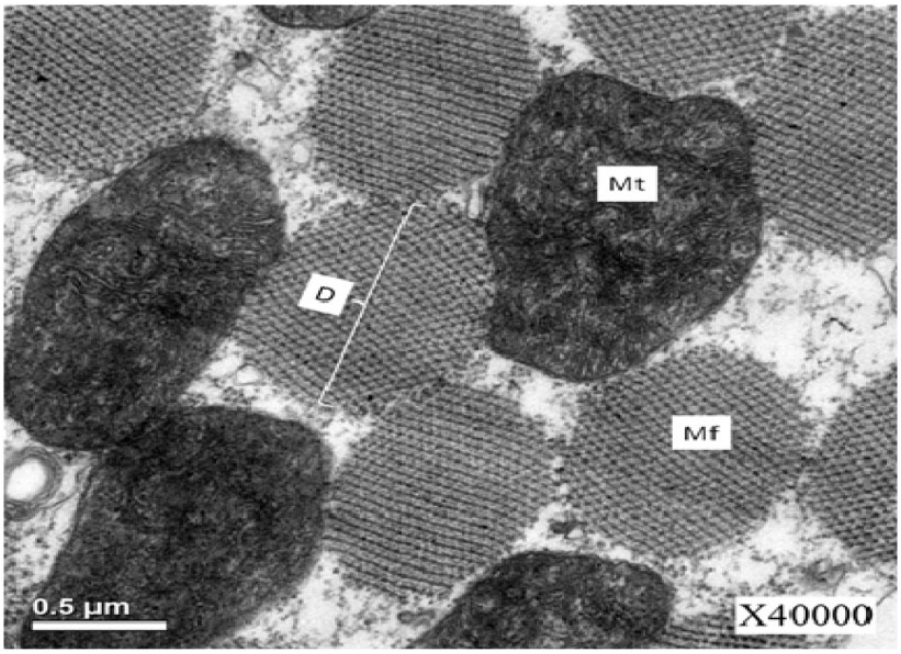

Fig. 2. Cross-section of the myofibril of the flight muscle of a *B. dorsalis* adult female at 15 d after adult emergence (Mf, myofibril; Mt, mitochondria; D, myofibril diameter).

wide, accounting for more than 95%. However, the sarcomere's I band was not clear (Fig. 4).

The sarcomere average length in the flight muscles of *B. dorsalis* female adults varied with age (Fig. 5). The average sarcomere length was shortest at 15 d, averaging 1.37 ± 0.01 µm (mean ± SE, $n = 30$) and being significantly less than the other four age groups ($P < 0.01$; $F = 1{,}643$; df = 4). Average length was 2.52 ± 0.01 µm (mean ± SE, $n = 30$) at 5 d, 2.68 ± 0.02 µm (mean ± SE, $n = 30$) at 10 d, 2.83 ± 0.02 µm (mean ± SE, $n = 30$) at 20 d, and 2.84 ± 0.02 µm (mean ± SE, $n = 30$) at 25 d.

Mitochondria. The flight muscle mitochondria of *B. dorsalis* were mostly oval to round in shape, but some were irregular (Fig. 6). Volume content of mitochondria occupying the total myofiber volume in each image varied significantly with age of the adult females ($P < 0.01$; $F = 8.46$; df = 4), peaking at about 32.6 ± 1.05% (mean ± SE, $n = 5$) of myofiber volume at 15 d (Fig. 6). In contrast, the mitochondria occupied 25.32 ± 0.99% (mean ± SE, $n = 5$) of myofiber volume at 5 d, 26.3 ± 0.97% (mean ± SE, $n = 5$) of myofiber volume at 10 d, at 29.0 ± 1.26% (mean ± SE, $n = 5$) of myofiber volume at 20 d, and 26.2 ± 0.83% (mean ± SE, $n = 5$) of myofiber volume at 25 d.

Discussion

Computer-monitored flight mills have been used to characterize flight aptitude of a number of insect species, such as *Cnaphalocrocis*

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medinali (Guenée) (Lepidoptera: Crambidae), *Sogatella furc*ifera Horvath (Homoptera: Delphacidae), and *Sitodiplosis mosellana* Gehin (Diptera: Cecidomyiidae) (Cheng et al. 1997, Wang and Zhai 2004, Huang et al. 2010, Hao et al. 2013).

Most studies related to *B. dorsalis* long-distance flight have been carried out under field conditions, which are often complicated by local weather events (Sharp et al. 1975, Sharp and Chambers 1976, Yan 1984, Tan and Serit 1994, Froerer et al. 2010). For example, Chen et al. (2007) found that wind within a valley greatly affected long-distance flight of *B. dorsalis*, given that *B. dorsalis* flew 20 km upwind compared with 97 km downwind along the Nujiang River (Chen et al. 2007). Marked sterile males of *B. dorsalis* have been recovered up to 24 miles away from their release point (Steiner 1957). Based on flight mill experiment, Sharp et al. (1975) found that *Dacus* (*Bactrocera*) *dorsalis* females were better fliers, and their flight abilities were varying with adult day ages. Normally, flight ability of adult *B. dorsalis* females could largely determine the survival and fecundity of its population (Chen et al. 2014). Our research provided insights into understanding flight ability and flight muscle ultrastructure of various age adult *B. dorsalis* females.

Under indoor conditions, at 25°C and no wind, the average accumulative total flight distance of adult *B. dorsalis* females at 15 d of age in this study reached 3.5 km within 13 h, and its maximum distances flown by one individual were 7.68 km, and average velocity reached at 0.98 m/s, which was similar with results of Sharp et al. (1975), who found that maximum distances flown by individual *B. dorsalis* females

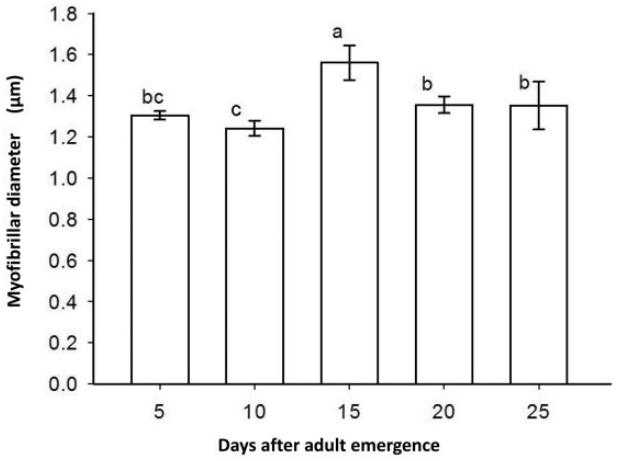

Fig. 3. Variations in the myofibrillar diameter of *B. dorsalis* female adults at different days after adult emergence. Mean ± SE. Bars with different letters represent significant differences at the 5% level. Bars with the same letter are not significantly different at the 5% level (test).

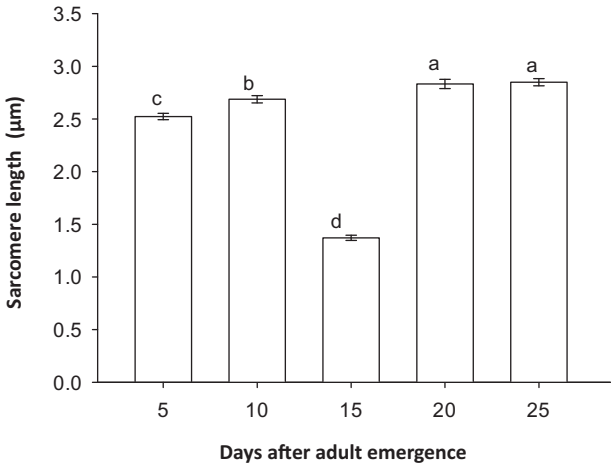

Fig. 5. Variations in the sarcomere length of *B. dorsalis* female adults at different days after adult emergence. Mean ± SE. Bars with different letters represent significant differences at the 5% level. Bars with the same letter are not significantly different at the 5% level (test).

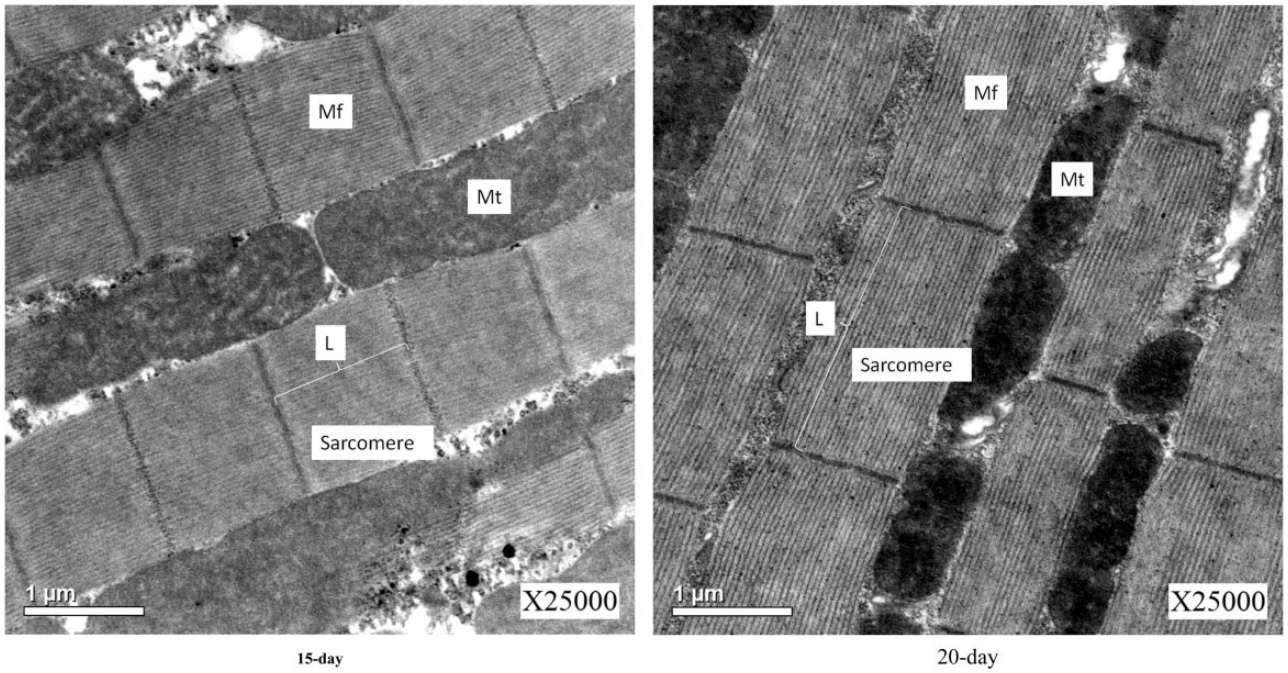

Fig. 4. Longitudinal section of the myofibril of the flight muscle of *B. dorsalis* female adult at 15 d and 20 d after adult emergence. Mf, myofibril; Mt, mitochondria; L, sarcomere length.

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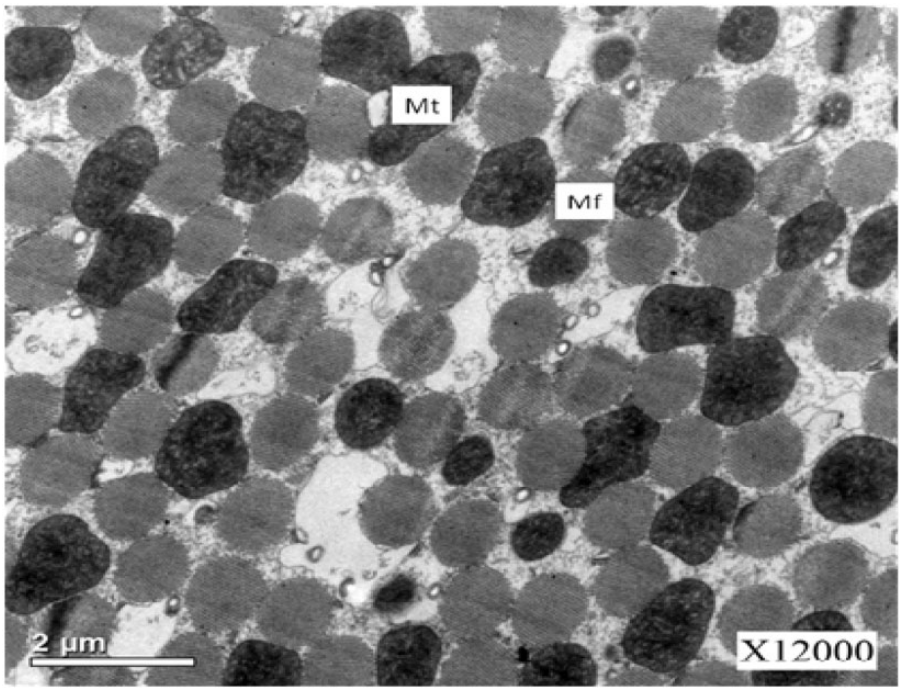

Fig. 6. Mitochondria distribution in *B. dorsalis* female adult flight muscles at 15 d after adult emergence. Mf, myofibril; Mt, mitochondria.

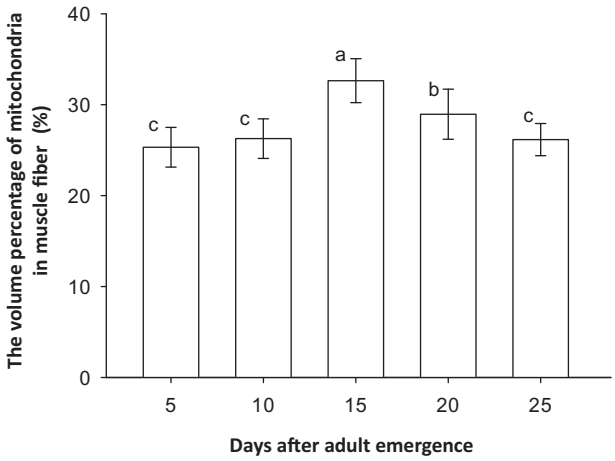

Fig. 7. Percentage of mitochondria volume in the muscle fiber of *B. dorsalis* female adults at different days after adult emergence. Mean ± SE. Bars with the same letters are not significantly different at the 5% level (test).

(8-d old) were 8.025 km and 8.301 km by 2 which flew 91.2 and 100% of the time, respectively, at velocities of 0.9 m/s. In comparison, at 18–24°C, 7-d-old adult female *Culex pipiens pallens* Coquillett (Diptera: Culicidae) flew an average of 2.6 km within 22 h with an average speed of 0.33 m/s (Cui et al. 2013). At 16°C, 1-d-old adult female *S. moselana* Gehin (Diptera: Cecidomyiidae) flew an average of 0.74 km within 24 h with an average speed of 0.16 m/s; while at 24°C they flew on average only 0.28 km within 24 h with an average speed of 0.13 m/s (Hao et al. 2013). Results from this study indicate that *B. dorsalis* has stronger flight capabilities than above insects.

Liu (2005) suggested that during long-distance flight, *B. dorsalis* likely experiences many flight episodes. According to marked flies with fluorescence powder in the Nujiang River Basin of Yunnan Province, Chen et al. (2007) found that longest flight distance of *B. dorsalis* in 7 d could reach 97 km and assumed that *B. dorsalis* adults would replenish nutrients and moisture and rest during its long distance flight (Chen et al. 2007). Steiner (1957) indicated that dispersal of *B. dorsalis* adults was not likely completed all at one time. In this study, the tests to flight capability of *B. dorsalis* were lasted 13 h, during which time the flies were not provided food or water. In addition, these tested fruit flies belonged to laboratory-reared colonies, normally, fruit flies of the wild colonies could travel a greater distance than those from the artificial rearing (Hiroaki and Hiroshi 1981). Therefore, it might be underestimated for flight distance compared *B. dorsalis* in the field.

Myofibrils, sarcomeres, and mitochondria are key components of flight muscle that are closely related to flight capability of insects (Martyn et al. 2002, Liu et al. 2008, Bullard and Pastore 2011, Holmes 2011). Structure and development dynamics of flight muscle are the material guarantee of insects with strong flight ability, and the structural characteristics of the flight muscle directly affect its flight potential, making chemical energy transfer mechanical energy (Luo and Li 1996).

Generally, insects with longer diameter of the myofibrils, shorter sarcomere length, and higher volume content of mitochondria in each myofibril possess greater flight capacity (Martyn et al. 2002, Liu et al. 2008, Bullard and Pastore 2011, Holmes 2011). When the diameter of the myofibrils of insects is increasing, the strength and toughness of the flight muscles will be energized, and its flight ability will be improving as well. Length of sarcomere determines overlapping degree of thin filaments and thick filaments. The longer sarcomere, the less overlap of thin filaments and thick filaments, and shorter shrinkage of muscle tension (Yang et al. 2005). Mitochondria are the main site of releasing ATP. Flight ability of insects is closely related to mitochondrial content volume in myofibrils and to activities of flight muscle. Therefore, the higher the mitochondrial content, the higher flight ability (Patricia et al. 1997).

The study found that the structure of the flight muscle has varied greatly with age changes of adult *B. dorsalis* female after eclosion. Fifteen-d-old female adults had the longest diameter of the myofibrils, the shortest sarcomere length, and highest volume content of mitochondria. These flight muscle structure characteristics may be one of the important reasons for the 15-d-old female *B. dorsalis* adults, whose flight abilities are significantly stronger than the flies on the other d.

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In flight muscle of *B. dorsalis*, the ratio of actin filaments to myosin filaments was 1:6, with each muscle filament being surrounded by six fine ones in a hexagonal shape, which is typical structure expressing the strongest contractile function of the flight muscle (Fig. 1). This kind of highly contractile structure only appears in insects with stronger flight capability (Carnevali and Reger 1982, Liu et al. 2008) that might suggest why *B. dorsalis* would have stronger long-distance flight ability.

Sarcomere length is closely related to the flight capacity of insects (Luo and Li 1996, Liu et al. 2008). Sarcomere length in the oriental armyworm adult, *Mythimna separata* Walker (Lepidotera : Noctuidae) is between 2.2 µm and 2.6 µm (Luo and Li 1996). Sarcomere length of *Manduca sexta* L. (Lepidoptera : Sphingidae) are 3–4 µm (Jiang and Luo 2008). As for some Saturniidae, the length is about 4 µm (Carnevali and Reger 1982). Our study found that average sarcomere length of *B. dorsalis* varied from 1.37 to 2.84 µm, being shortest at 1.37 µm when adults were about 15-d old, suggesting that flight capacity of *B. dorsalis* may be greater than many insects, such as saturniid moths.

Mitochondria provide continuously energy for flight muscles, and their numbers in each myofibril are positively correlated with flight capability (Luo and Li 1996). For example, in 10-d-old gregarious-phase *L. migratoria manilensis*, flight capability peaked and its volume content of mitochondria occupied about 41.3% of myofiber volume (Liu et al. 2007). In *Calliptamus italicus* L. (Orthoptera: Locustidae), it occupied as much as 45% of myofiber volume, guaranteeing sufficient energy for long-distance flight of *C. italicus* (Zhang 2011). In this study, 15-d-old female *B. dorsalis* had the highest volume content of mitochondria and matching longest flight distance and fastest flight velocity (Table 1, Fig. 6 and Fig. 7), indicating that special flight muscle ultrastructure of *B. dorsalis* supports its stronger flight capacity.

In this study, *B. dorsalis* adults usually lived 25–30 d under our artificial rearing condition, the flight capability of these fruit flies peaked around day 15 (Figs. 1 and 2), which was its peak period of oviposition as well (Chen et al. 2014). The ovaries of these laboratory-reared fruit flies usually become mature after 10 d eclosion (Chen et al. 2014). Obviously, it is different from wild colonies of *B. dorsalis*, its peak oviposition of wild or F1 has been found to take place at 4 wk or at a greater age (Tan and Serit 1994). Therefore, *B. dorsalis* might focus on reproductive development before maturation of its ovaries (10 d eclosion for artificial reared group). When its reproductive organ becomes mature, it possesses strong enough flight ability that they can fly long distance or even fly to a high altitude and then disperse via moving air currents (Steiner 1957, Chen et al. 2007).

Flight muscle ultrastructure of *B. dorsalis* shows that the oriental fruit fly possesses long-distance flight ability. However, compared with many migratory insects, such as locust, *B. dorsalis* may not belong to a typical migratory insect. Normally, migratory flight behavior of migratory insect often occurs at the initial stage of ovarian development in the adults (Xiao et al. 2013). In contrast, flight ability peak of *B. dorsalis* appears within its peak period of oviposition (Chen et al. 2014). Therefore, clearly much more research is needed to fully elucidate dispersal mechanism of *B. dorsalis* in future.

Acknowledgments

This study was supported by the Natural Science Foundation of China (31160162), National Sci-technology Promotion Project of China ([2014]TZYN03), and Yunnan Provincial Natural Science Foundation (2013FA055). We thank Robert A. Haack for English assistance.

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Received 11 April 2015; accepted 12 September 2015.

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