

# Flight of the Chinese white pine beetle (Coleoptera: Scolytidae) in relation to sex, body weight and energy reserve

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## Abstract

The flight distance, flight time and individual flight activities of males and females of *Dendroctonus armandi* were recorded during 96-h flight trials using a flight mill system. The body weight, glucose, glycogen and lipid content of four treatments (naturally emerged, starved, phloem-fed and water-fed) were compared among pre-flight, post-flight and unflown controls. There was no significant difference between males and females in total flight distance and flight time in a given 24-h period. The flight distance and flight time of females showed a significant linear decline as the tethered flying continued, but the sustained flight ability of females was better than that of males. The females had higher glycogen and lipid content than the males; however, there was no significant difference between both sexes in glucose content. Water-feeding and phloem-feeding had significant effects on longevity, survival days and flight potential of *D. armandi*, which resulted in longer feeding days, poorer flight potential and lower energy substrate content. Our results demonstrate that flight distances in general do not differ between water-fed and starved individuals, whereas phloem-fed females and males fly better than water-fed and starved individuals.

**Keywords:** *Dendroctonus armandi*, flight performance, body size, energy reserve

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## Introduction

The flight of bark beetles plays an important role in migration because each generation needs to find new habitats to complete the life cycle (Forsse & Solbreck, 1985). Thus, the beetles must have a certain level of flying ability and a certain degree of flight energy reserve to achieve migration (Atkins, 1967; Nijholt, 1967; Salom & McLean, 1991; Elkin & Reid, 2005; Safranyik & Carroll, 2006). In addition, the dispersal distance of bark beetles is related to beetle size and lipid content

(Thompson & Bennett, 1971; Hedden & Billings, 1977). For example, *Dendroctonus pseudotsugae* individuals with increased flight activity tend to be larger or contain a higher percentage of lipids (Atkins, 1969, 1975). Kinn *et al.* (1994) found a significant correlation between weight and distance flown for both male and female southern pine beetles. Generally, southern pine beetles are smaller in summer and tend to be larger and heavier in spring (Thatcher & Pickard, 1967; Hedden & Billings, 1977). Barras & Hodges (1974) concluded that the greater flight duration of males than females is associated with the males' larger size and greater lipid content. Further evidence that lipids are metabolised during southern pine beetle dispersal shows that lipids decline with the increase of flight time for both males and females (Thatcher & Pickard, 1967; Barras & Hodges, 1974;

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Hedden & Billings, 1977); however, the flight activity of other smaller individuals tend to increase, like *Ips typographus*, with a flight behaviour that is not affected by beetle size, fat content or sex (Botterweg, 1982). There is much variation in flight duration among individuals, which apparently is not an artefact of the method and is unrelated to sex, size or environmental condition earlier in the life of the beetle (Forsse & Solbreck, 1985). Slansky & Haack (1986) found weak, positive correlations between body weight and lifetime flight duration, and poor correlation between lifetime flight duration and longevity of *Ips calligraphus* (Gries *et al.*, 1990). Ilse & Hellgren (2007) indicated that trees colonised by beetles have phloem with higher concentrations of fructose and glucose and lower percent composition of limonene, sabinene and terpinolene than uncolonised trees.

Chinese white pine beetle, *Dendroctonus armandi* Tsai *et al.* (Coleoptera: Scolytidae), is the most destructive scolytid in the coniferous forest of the Qinling Mountains, and its outbreaks result in the destruction of millions of Chinese white pine (*Pinus armandii* Fr.) (Ren & Dang, 1959; Cai, 1980; Chen *et al.*, 1999; Chen & Tang, 2007). Most *D. armandi* overwinter under the bark of the Chinese white pine as larvae and then pupate in the last ten days of April of the following year (Yin *et al.*, 1984; Chen & Yuan, 2000). After emerging from May to August, adults of *D. armandi* continue to feed (maturation feeding) until they migrate toward new host trees from early July to September. Their flight period focuses on four months from June to September (Ren & Dang, 1959; Cai, 1980; Chen & Tang, 2007).

Despite a fairly large amount of information available about the effects of temperature, humidity, age, sex, population density and energy reserve on the flight activity of bark beetles (Atkins, 1969; Hedden & Billings, 1977; Botterweg, 1982; Slansky & Haack, 1986; Jactel, 1993; Kinn *et al.*, 1994; Elkin & Reid, 2005), little is known about the flight capability of *D. armandi*, which is closely related to dispersal or migration in the Qinling forest ecosystem and plays a critical role in the management of the bark beetle. The aim of our research was to determine the sustained flight capability and the flight behaviour of *D. armandi* in relation to sex, body weight and energy reserve. We speculated that the concentration of the principal energy substrates affects flight duration, frequency and speed of the Chinese white pine beetle and that males and females would be reluctant to engage in long-distance flight prior to host selection and copulation. In this study, we examined the flight performance of *D. armandi* in relation to sex, body weight and energy reserve using a laboratory flight mill system.

## Methods

### *Insect collection*

Four Chinese white pines (*Pinus armandi* Fr.) infested by *D. armandi* on the southern slope of the middle Qinling Mountains (33°18'–33°28'N, 108°21'–108°39'E) were selected in July and September 2008, respectively. The felled trees were cut into 80-cm logs and placed in emergence cages measuring 1×3 m with screen and kept at 23–25°C under 16:8 light: dark in the laboratory until adult eclosion. Emerged parental adult *D. armandi* from logs were collected daily, separated by sex and used immediately in the experiments described below.

## *Overview of experimental design*

### *Measuring flight activity*

The flight activity was monitored with a flight mill system similar to that described by Rowley *et al.* (1968), Briegel *et al.* (2001) and Chen *et al.* (2006). Each experimental run consisted of ten individual flight mills operated concurrently. Ten *D. armandi* adults (five males and five females) were anaesthetised on ice for 30 s and then mounted, via their thoraces, on 2-cm segments of fine steel wire (0.14 mm in diameter) using molten candle wax. The wire segments were then immediately attached to the flight mill rotors, with a dead beetle attached similarly to the opposite end of each rotor to serve as a counter weight. Flight mill signals (number of rotor revolutions per 5-s interval) were recorded with a data logger (Model CR1000 with SDM-SW8A switch closure module; Campbell Scientific, Logan, UT) and converted into total flight distance, total flight time and maximum uninterrupted time (i.e. the maximum number of consecutive 5-s intervals with flight activity) for each insect. All experiments started around 10:00 h and continued for 24 h, except those on sustained flight activity (described below), in which three consecutive 24-h periods were monitored. Unless stated otherwise, the experiments were carried out under natural light conditions with no extra lighting in the laboratory (day length 13.5 h, maximum photon flux density  $\approx 4.37 \text{ W m}^{-2} \text{ s}^{-1}$ ).

### *Overall experimental design*

Emerged males and females were placed individually according to size and randomly assigned to naturally emerged, starvation, deionised water feeding and phloem feeding treatments. In the starvation treatment, emerged males and females were housed individually in 1.5-ml microcentrifuge tubes with holes for air exchange. In the deionised water feeding and phloem feeding treatments, the 1.5-ml microcentrifuge tubes were lined with either a paper towel moistened with deionised water or fresh Chinese white pine phloem tissues. All treatments were kept at room temperature (22–26°C) on a 16L:8D cycle for two, four and six days. Three independent runs of the experiment were carried out for each experimental group and each independent run was performed using five male and five female beetles.

### *Sustained flight treatments*

Individuals flew uninterruptedly for one, two, three or four days for processing under naturally emerged, starvation, deionised water feeding and phloem feeding treatments. Three independent runs of each experiment were carried out, each run with ten adults (five females and five males).

### *Control groups and post-flight measurements*

For metabolic analyses, insects were killed after termination of the flight trials. Two controls were used. Before the flight trials, ten *D. armandi* adults (five males and five females) with equivalent body weight were fixed as a pre-flight control. Another ten *D. armandi* adults (five males and five females) were kept individually in 1.5-ml microcentrifuge tubes with holes to allow air exchange and restrained by cotton plugs to very narrow spaces to prevent flight movements (unflown controls) at room temperature (22–26°C) on a 16L:8D cycle

until they were used. After the flight tests ended, all insects were fixed for analysis in the test tubes (13 × 100 mm) by heating in 100 µl of ethyl alcohol for ten minutes at 90°C.

### Biochemical analysis

Sugar, glycogen and lipid content were measured from the same individual males and females according to Van Handel & Day (1988) and Kaufmann & Briegel (2004). Glucose and glycogen were measured by the hot anthrone method (Van Handel, 1985b), and the vanillin-phosphoric acid reaction method (Van Handel, 1985a) was used to test the lipid content. The photometric readings were converted into micrograms and finally to calories per female: 1 mg consumption of glycogen and fat to release 17 J and 39 J energy, respectively (Chapman, 1982).

The caloric values subtraction of post-flight from pre-flight gives the use of a specific substrate for flight. The rate of substrate use was calculated by expressing these absolute differences per hour of actual flight activities alternatively. The same was done for survival data when pre-flight values were compared to the values of non-flown, resting controls.

### Statistical analysis

Because of a lack of normality in the data set (PROC UNIVARIATE in SAS version 8.1, SAS Institute), flight performance data were  $\log_{10}$ -transformed and subjected to analysis of variance (ANOVA) (PROC GLM in SAS version 8.1, SAS Institute) and linear regression analysis (PROC REG in SAS version 8.1, SAS Institute) (Gomez & Gomez, 1984) to compare the total flight distance, total flight time and maximum uninterrupted flight time between males and females during different nutrition treatments, and means were compared using least significant differences (LSD) in SAS. Wilcoxon-Mann-Whitney (SAS Institute, 1991) tests were used to analyse the differences in body weight, body weight loss, body weight loss rate and glucose, glycogen and lipid content between males and females in four treatments (Kinn *et al.*, 1994). In all cases, significant was indicated at the 5% level.

## Results

### The performance of sustained flight

The flight distance and flight time showed a continuous downward trend within 96 h of tethered flying time (fig. 1). The total flight distance and time of females showed a significant linear decline as the tethered flying time continued (distance  $r^2=0.9445$ ,  $P=0.0281$ ; time  $r^2=0.9955$ ,  $P=0.0022$ ); the total flight distance for males presented a highly significant linear decline ( $r^2=0.9849$ ,  $P=0.0076$ ), but there was no significant linear decline in their total flight time as the tethered flying time continued ( $r^2=0.8631$ ,  $P=0.0710$ ). Moreover, the total flight time was 3252 s and 2338 s on day 1 and day 2 for females, and 3972 s and 1812 s for males on day 1 and day 2, respectively. According to one-way ANOVA results, there was no significant difference between males and females in total flight distance and time in a single 24-h period ( $P=0.1506$ – $0.5040$ ), but females had better sustained flight ability than males.

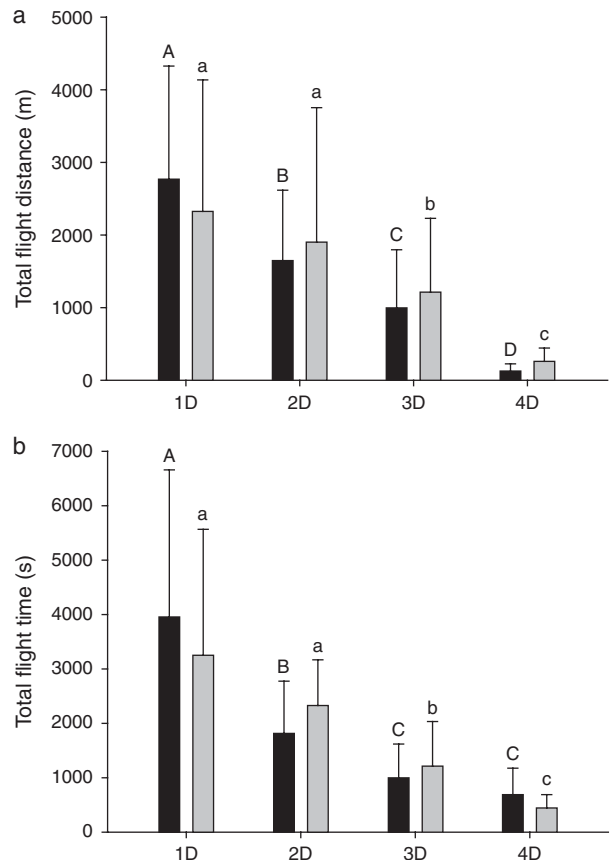


Fig. 1. Sustained flight performance of *D. armandi* in the laboratory. The sustained flight (a) distance and (b) time (mean  $\pm$  SE,  $n=11$ – $14$  for each bar) for males and females. Flight performances were significantly different, and histogram bars during four days are marked with different letters (ANOVA,  $P < 0.05$ ) (■, male; □, female).

### Effect of body weight

Although there was a significant difference in body weight between the sexes, we detected no sex differences in body weight loss after 24-h flight (1.56 mg for females, 1.78 mg for males) or body weight loss rate (18.44% for females, 22.32% for males) (fig. 2). The total flight time of *D. armandi* was significantly correlated with initial pre-flight body weight and weight loss with flight ( $r^2=0.1604$ ,  $r^2=0.1519$ , respectively,  $n=327$ ), but the total flight distance was not significantly correlated with body weight or weight loss ( $r^2=0.01321$ ,  $r^2=0.01012$ , respectively,  $n=327$ ).

### Metabolism of the Chinese white pine beetle during flight

Wilcoxon-Mann-Whitney tests identified no significant difference in the glucose content between males and females (18.24 µg per female and 16.36 µg per male). The females had significantly higher glycogen (81.91 µg) and lipid content (211.15 µg), compared to the males (74.71 µg and 175.14 µg) (fig. 3).

Correlation analysis showed that body weight was correlated with glycogen and lipid content ( $r^2=0.4617$ ,  $r^2=0.2383$ ,

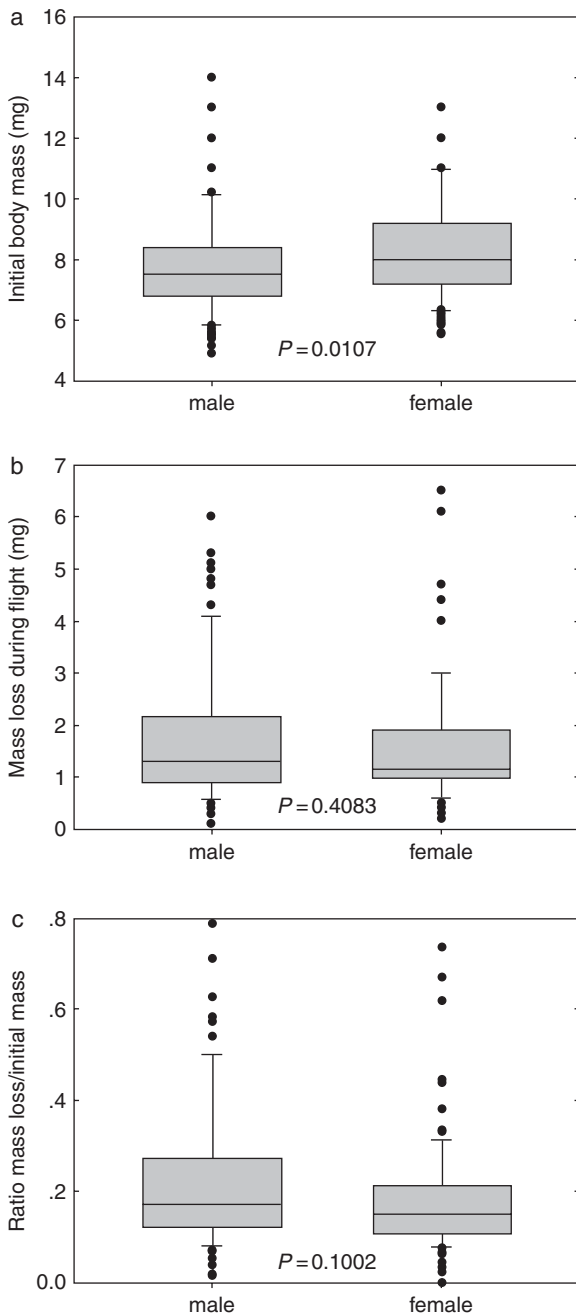


Fig. 2. Box-whisker plots summarizing body mass variables of male ( $n=107$ ) and female ( $n=107$ ) *D. armandi* in flight mill experiments in the laboratory. The boxes represent the interquartile range, with the line within each box indicating the median value.  $P$ -values are based on Wilcoxon-Mann-Whitney tests for the null hypothesis of no significant difference between both sexes.

respectively,  $n=214$ ). The lipid content was significantly correlated with total flight distance and time ( $r^2=0.1983$ ,  $r^2=0.2112$ , respectively,  $n=214$ ), but there was no significant correlation between total flight distance and time in glucose or glycogen content (glucose:  $r^2=0.0698$ ,  $r^2=0.0363$ , respectively; glycogen:  $r^2=0.1080$ ,  $r^2=0.0910$ , respectively;  $n=214$ ).

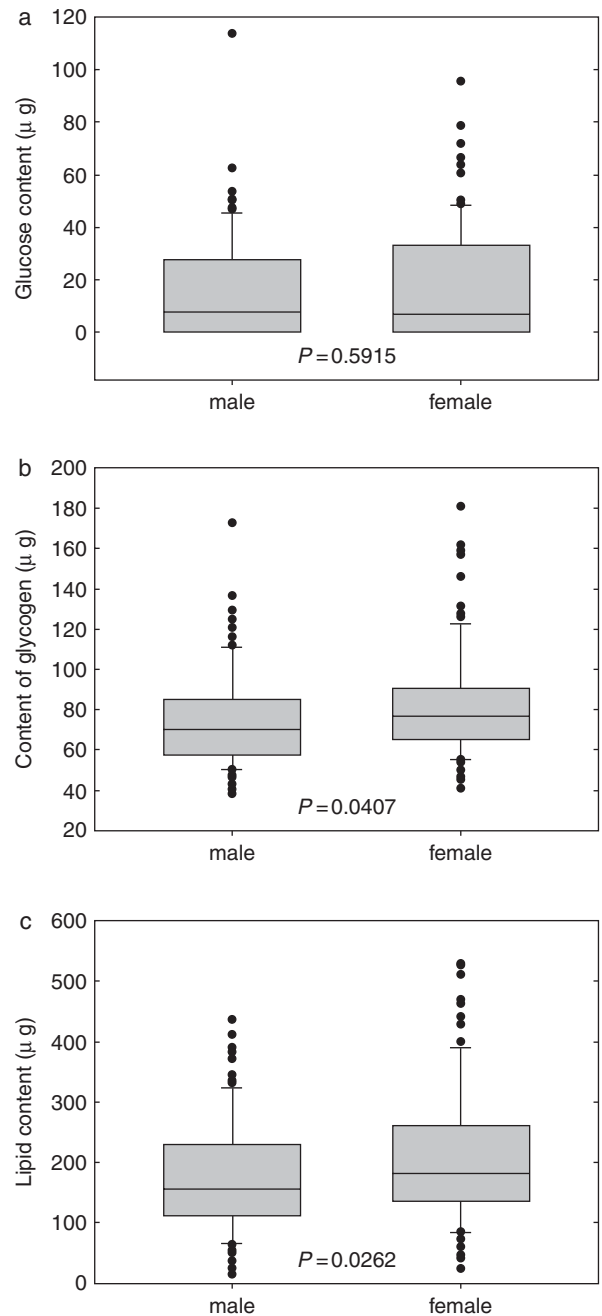


Fig. 3. Box-whisker plots summarizing (a) glucose, (b) glycogen and (c) lipid contents of male ( $n=107$ ) and female ( $n=107$ ) *D. armandi* in flight mill experiments.  $P$ -values are based on  $t$ -tests for the null hypothesis of no significant difference between both sexes.

Moreover, the lipid level was much higher than that of glucose and glycogen. After three days and four days of flight, the glucose levels reached the minimum value (an average value of  $0.04\mu\text{g}$ ), but there was still a considerable amount of storage of glycogen and lipids during the fourth day (fig. 4).

We also introduced the concept of rates of substrate use (Kaufmann & Briegel, 2004), i.e. joules per hour of active flight

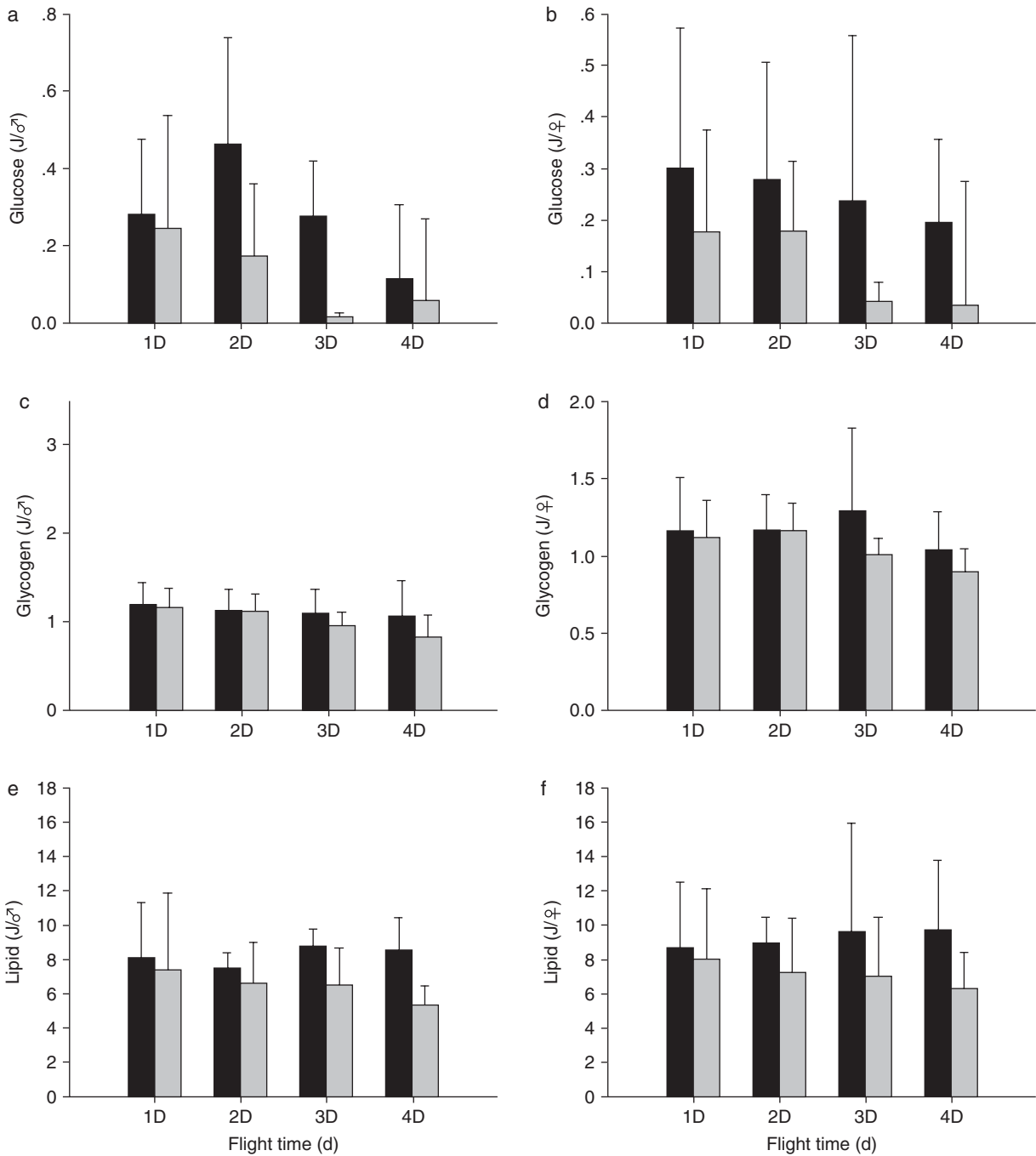


Fig. 4. Profile of caloric content of carbohydrates and lipids of *D. armandi* under different flight days, with male on the left, female on the right (mean  $\pm$  SE,  $n = 11-14$  for each bar) (■, non-flown; □, flight).

per adult ( $J h^{-1}$ ), to analyse energy consumption. Figure 5 and table 1 present the contributions of the three reserve components for survival and flight of both sexes.

After conversion, the consumption of carbohydrates for flight was far more than what was used for survival: the mean flight rate for males was  $0.167 \pm 0.041 J h^{-1}$ , while for survival it was only  $0.008 \pm 0.003 J h^{-1}$ ; the mean flight rate for females was  $0.177 \pm 0.026 J h^{-1}$  and for survival was  $0.013 \pm 0.004 J h^{-1}$

(fig. 5a,b, table 1). During the sustained flight days, the average lipids consumed was  $0.859 \pm 0.177 J h^{-1}$  for males and  $0.863 \pm 0.136 J h^{-1}$  for females (fig. 5c,d, table 1).

*Effect of nutrition on the flight performance*

The total flight distance of *D. armandi* over 24h under different nutritional status was compared. There was no

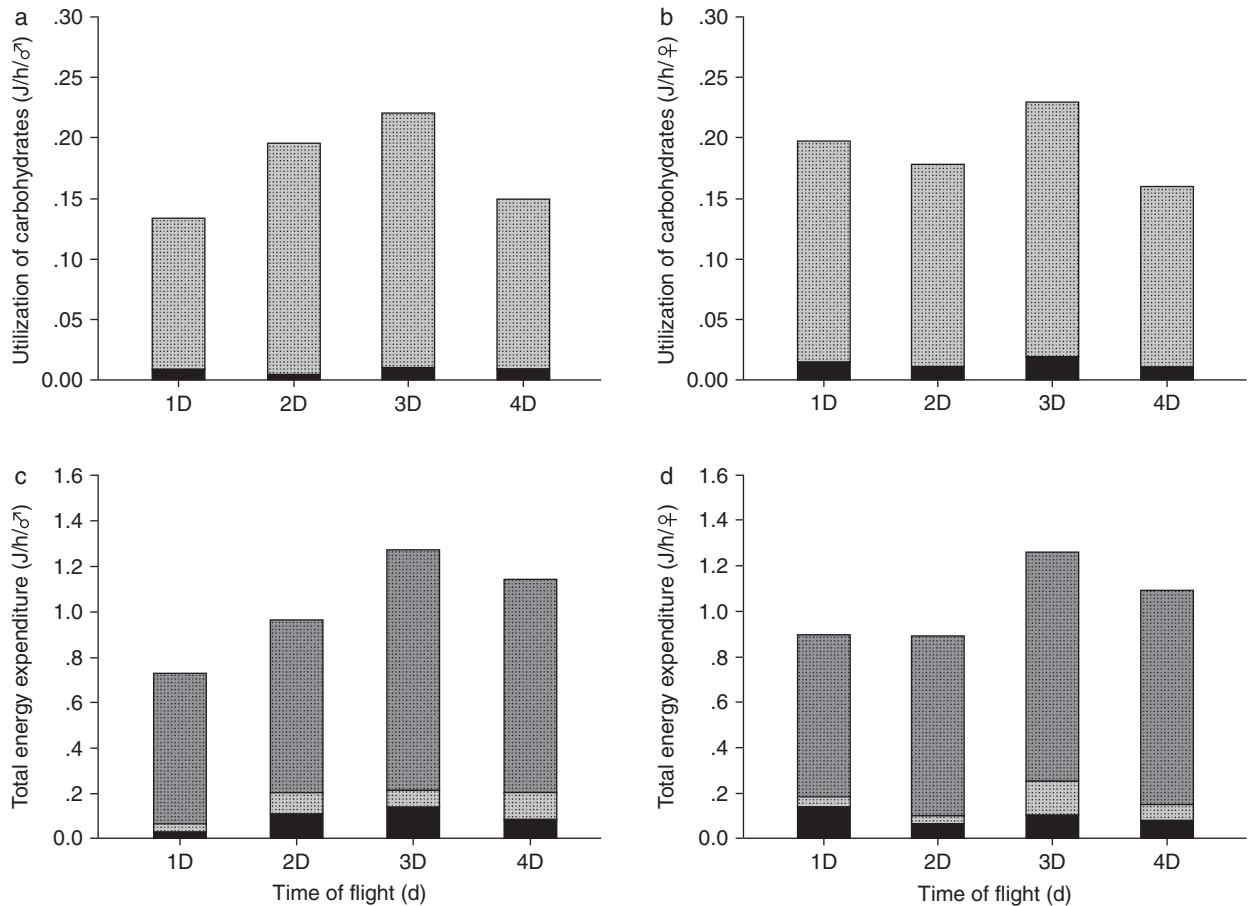


Fig. 5. Rates of energy expenditure by *D. armandi* under different flight hours ( $n=14$  for each bar). Carbohydrate used per hour for survival (black) and for flight (light grey) for (a) males and (b) females (■, survival; □, flight); total energy expenditure during flight: glucose (black), glycogen (light grey), lipid (dark grey) for (c) males and (d) females (■, glucose; □, glycogen; ▒, lipid).

Table 1. Caloric data for pre-flight *D. armandi*: teneral and pre-flight content of carbohydrates and lipid and the absolute use for survival and during flight.

	Male ( $n=107$ )	Female ( $n=107$ )
<b>Carbohydrate (<math>\text{J adult}^{-1}</math>)</b>		
Teneral	$1.14 \pm 0.37$	$1.16 \pm 0.31$
Pre-flight	$1.92 \pm 0.49$ (100%)	$2.21 \pm 0.65$ (100%)
Used for survival	$0.51 \pm 0.06$ (26.6%)	$0.80 \pm 0.07$ (36.0%)
Used for flight	$0.27 \pm 0.11$ (13.9%)	$0.26 \pm 0.13$ (11.8%)
<b>Lipid (<math>\text{J adult}^{-1}</math>)</b>		
Teneral	$6.45 \pm 2.15$	$7.16 \pm 1.59$
Pre-flight	$8.63 \pm 1.60$	$9.37 \pm 1.92$ (100%)
Used for survival	0	0
Used for flight	$1.78 \pm 0.79$ (20.7%)	$2.09 \pm 0.72$ (22.3%)
Distance* (m)	$1389.2 \pm 458.7$	$1429.1 \pm 612.3$

\*, mean  $\pm$  SE.

significant difference between the naturally emerged and the phloem-fed animals during 24-h flight ( $P=0.1128$ – $0.5662$ ). The total flight distances for males and females under phloem feeding for six days were still 1509 m and 2313 m, with a total

flight time of 2604 s and 4798 s, respectively. There was also no significant difference for flight performance between the starved and deionised water feeding conditions ( $P=0.1332$ – $0.2538$ ). With feeding time prolongation in the starving and deionised water, the flight distance and total flight time declined. ANOVA identified a significant difference ( $P<0.05$ ) in total flight distance and flight time among the phloem-fed, starved and water-fed conditions (fig. 6).

Carbohydrate and lipid content of *D. armandi* under different feeding status showed that the glucose and glycogen contents of *D. armandi* adults were increased with prolonged phloem feeding time so that individual beetles reserved more energy for flight (phloem-fed from  $0.39$  to  $0.55 \text{ J adult}^{-1}$  for the flight; normal emerged was  $0.26 \text{ J adult}^{-1}$ ). For lipids, however, there was no significant difference during the phloem feeding period (phloem-fed from  $1.68$  to  $1.85 \text{ J adult}^{-1}$  for the flight; naturally emerged ranged from  $1.78$  to  $2.06 \text{ J adult}^{-1}$ ). Under starved and deionised-water feeding conditions, carbohydrate and lipid content were both reduced as the feeding time prolonged. For 24-h uninterrupted flights, *D. armandi* used lipids, which ranged from  $1.5\%$  to  $4.3\%$  and carbohydrates from  $0.26$ – $0.55 \text{ J adult}^{-1}$  to  $0.03$ – $0.17 \text{ J adult}^{-1}$  (table 2).



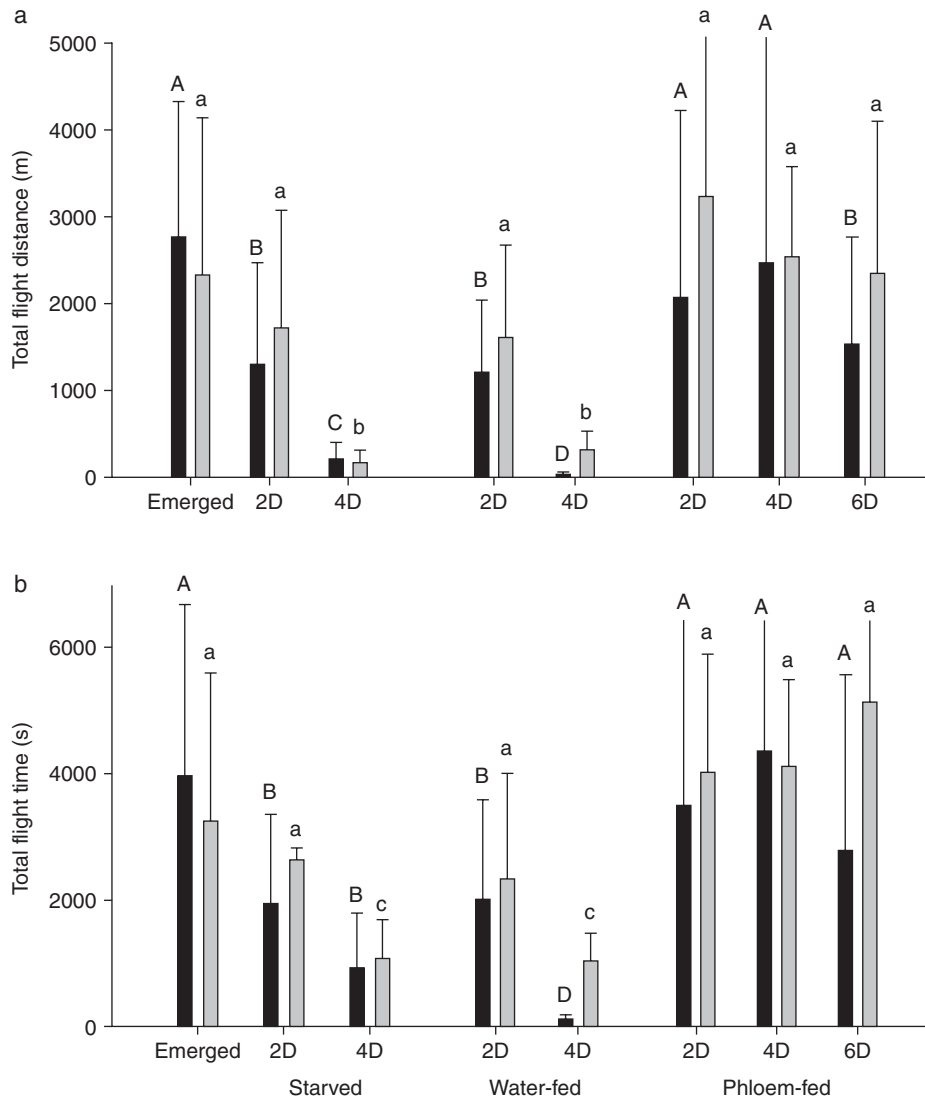


Fig. 6. (a) Total flight distances and (b) flight times of *D. armandi* under different feeding conditions in the laboratory. The filled squares illustrate the sustained flight distance and time (mean  $\pm$  SE). Flight performances are significantly different during six days and histogram bars are marked with different letters (ANOVA,  $P < 0.05$ ) (■, male; □, female).

**Discussion**

Our results revealed that female *D. armandi* tended to have higher flight activity during 96h in the flight mill, indicating perhaps that the two sexes are similarly capable of escape-type flight but that females are better sustained fliers. Moreover, the flight distance reached maximum during 2–3d post-eclosion for the Chinese white pine beetle, and the flight activity decreased as tethered flight tests time increased.

Although tethered flight assays have provided some of the best corroborating evidence of field observations, field observations cannot be compared directly with laboratory-derived results. For example, the proximate cues of temperature, light and photoperiod necessary for migration of bark beetle populations were provided in all flight tests, but field conditions are likely to be much more variable. Mark-release-recapture studies recovered adult spruce beetles in locations

90–600m from the point of release in the direction of the prevailing winds (Werner & Holsten, 1997). On the other hand, in the forest ecosystem, bark beetles have the opportunity to fly at any appropriate time, rather than only once every three or four days as in these experiments.

Nevertheless, the present laboratory evaluation revealed little difference in flight distance, in general, whether beetles were fed with water or starved before flight, but phloem-fed females and males flew better than water-fed and starved ones. Specifically, beetles that had been provided with phloem of the host tree as a food source for two days after emergence showed considerably improved flight performance compared with those given no food or only water during the same period. This result is not surprising given that flight is a very energy-intensive activity (Thompson & Bennett, 1971).

We found that beetles flight capacity depended on energy reserves and the length of the dispersal period; hence, the

Table 2. Caloric data for pre-flight *D. armandi* under different feeding conditions: general and pre-flight content of carbohydrates and lipid and the absolute amounts used for survival and during flight. For the latter, the percentage of pre-flight contents is in parentheses (mean  $\pm$  SE).

Variable	Starved		Deionized water		Phloem feeding	
	Male (n = 24)	Female (n = 24)	Male (n = 24)	Female (n = 24)	Male (n = 41)	Female (n = 41)
<b>Carbohydrate (J adult<sup>-1</sup>)</b>						
General	0.75 $\pm$ 0.17	0.89 $\pm$ 0.22	1.08 $\pm$ 0.28	1.05 $\pm$ 0.25	1.41 $\pm$ 0.40	1.56 $\pm$ 0.42
Pre-flight	1.26 $\pm$ 0.54 (100%)	1.39 $\pm$ 0.39 (100%)	1.53 $\pm$ 0.25 (100%)	1.46 $\pm$ 0.35 (100%)	2.48 $\pm$ 0.81 (100%)	2.64 $\pm$ 0.74 (100%)
Used for survival	0.35 $\pm$ 0.10 (27.3%)	0.39 $\pm$ 0.14 (27.9%)	0.43 $\pm$ 0.25 (27.9%)	0.33 $\pm$ 0.13 (22.5%)	0.73 $\pm$ 0.19 (29.5%)	0.52 $\pm$ 0.08 (19.9%)
Used for flight	0.17 $\pm$ 0.12 (13.3%)	0.12 $\pm$ 0.08 (8.5%)	0.03 $\pm$ 0.02 (2.0%)	0.08 $\pm$ 0.12 (5.7%)	0.39 $\pm$ 0.13 (14.9%)	0.55 $\pm$ 0.27 (21.0%)
<b>Lipid (J adult<sup>-1</sup>)</b>						
General	6.48 $\pm$ 2.29	6.68 $\pm$ 2.03	5.85 $\pm$ 1.27	5.93 $\pm$ 2.52	6.26 $\pm$ 1.82	6.12 $\pm$ 1.03
Pre-flight	6.92 $\pm$ 1.31 (100%)	7.57 $\pm$ 0.78 (100%)	6.48 $\pm$ 1.13 (100%)	6.98 $\pm$ 0.94 (100%)	7.92 $\pm$ 2.59 (100%)	7.99 $\pm$ 2.36 (100%)
Used for survival	0.21 $\pm$ 0.13 (3.0%)	0.11 $\pm$ 0.06 (1.5%)	0.28 $\pm$ 0.20 (4.3%)	0.19 $\pm$ 0.17 (3.3%)	0	0.09 $\pm$ 0.02 (1.3%)
Used for flight	0.65 $\pm$ 0.37 (9.3%)	0.77 $\pm$ 0.41 (10.2%)	0.34 $\pm$ 0.24 (5.3%)	1.06 $\pm$ 1.08 (14.3%)	1.85 $\pm$ 0.77 (23.5%)	1.68 $\pm$ 0.55 (21.1%)
Distance* (m)	758.6 $\pm$ 479.2	944.8 $\pm$ 550.2	605.3 $\pm$ 402.8	947.3 $\pm$ 624.7	1991.3 $\pm$ 856.7	2665.2 $\pm$ 1045.4

\* , mean  $\pm$  SE.

distance covered during flight is extremely variable among *D. armandi* individuals of both sexes under different feeding status, ranging from a few meters to several kilometers. Therefore, the individual variation in energy appears to explain the variable flight capacity of *D. armandi*. For survival, male and female *D. armandi* used approximately equal amounts of carbohydrates for flight, but they clearly differed in their lipid, glucose and glycogen use during flight. However, the Chinese white pine beetle, like most ambrosia bark beetles, uses a combination of lipids/carbohydrates for flight; and the current results indicate that the metabolic pattern of lipids and carbohydrates during starvation may be similar to *I. typographus* (Byers & Löfqvist, 1989). The lack of carbohydrates during starvation is most likely the reason for reduced flight performance of the Chinese white pine beetle, as there is no shortage of lipids. In fruit beetles, two substrates for flight are carbohydrates and praline; but, without them, flight activity can still be carried out. Carbohydrate is the major energy material at the start-up stage of insect flight (Friedman, 1985), but lipids may become the major energy material at sustained flight stage. Atkins (1969) observed a reduction from 46% lipids in control beetles to 37% in female Douglas-fir beetles flown an average of 3.5 h, and Thompson & Bennett (1971) found a reduction in lipids from 15% to 5% in male Douglas-fir beetles flown over a 5-h period. Hodges & Barras (1974) speculated that lipids are metabolised for southern pine beetle flight and that a degradation of triglycerides to short-chain fatty acids may occur between emergence and tree colonisation. Kinn *et al.* (1994) indicated that triglycerides account for 83% of the total lipid content in southern pine females and 74% in males. Our results indicated that lipid content had significant correlation with flight capability of Chinese white pine beetle. Moreover, carbohydrates were the main energy for the survival of *D. armandi*; 26.6% of males and 36.0% of females used carbohydrates for survival, but lipid was the major energy source of flight material within 24 h. The average consumption was 1.78 J adult<sup>-1</sup> for males and 2.09 J adult<sup>-1</sup> for females; carbohydrates were consumed less than lipids during the flight; and energy level of lipids was much higher than that of glucose and glycogen. When the adults sustained flight for three days and four days, their glucose levels declined to a minimum value (an average of 0.04  $\mu$ g), but there was still considerable storage of glycogen and lipid content during the fourth day.

Studies suggest a link between lipid content and dispersal, the dispersal distance of *D. armandi* strongly relates to body size and energy reserve, as shown by Hedden & Billings (1977) and Barras & Hodges (1974). It is believed that during spring, southern pine beetles are more likely to disperse than during other seasons; and the lipid content of beetles emerging in the spring tends to be high (Hedden & Billings, 1977). Similarly, increased body weight and lipid content are also correlated with increased flight activity in *I. paraconfusus* (Hagen & Atkins, 1975) and *I. calligraphus* (Slansky & Haack, 1986). In general, however, it seems that only vigorous beetles with an abundant lipid reserve can afford the luxury of extended dispersal and are by their nature committed to it for a requisite period. On the other hand, lipid-poor beetles cannot disperse readily. However, if they encounter suitable hosts or pheromone sources, they can respond immediately, thus ensuring that peripheral as well as distant hosts are exploited.

In summary, our results suggest that flight potential and energy reserve are important factors for the spatial dispersal



and migration of *D. armandi*. Although there was no significant difference in body weight or energy reserve between the sexes, dispersal potential (such as that required to meet the need to locate suitable oviposition sites) and energy reserve might lead to changes in flight capability of females and males, but females are better sustained fliers and spend more energy reserves to maintain dispersal, especially if no food or water is provided. Starvation had significant effects on survival days and flight potential of *D. armandi*. This result provides a framework for the development of a spatial model to examine the implications of these results for the attack dynamics of beetle populations. Further studies of the flight behavior of this species should provide a better understanding of *D. armandi* population dispersal and migration, which could guide proper management of this destructive pest.

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