



## Flight response, body weight, and lipid content of *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae) as influenced by strain, season and phenotype

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### Abstract

Effects of geographical origin of strain, season of field collection, genetic background, and number of generations of laboratory rearing on flight initiation, body weight, and lipid content of lesser grain borer, *Rhyzopertha dominica*, were studied. Significant differences in flight initiation, body weight, and total lipid content occurred among the four field strains collected from Kansas, Oklahoma, Texas, and Mexico. Flight activity tended to be higher for strains with higher average body weight. Oleic, palmitic, and linoleic acids accounted for about 95% of all fatty acids present in the strains tested. However, the percentage of lipids per fresh body weight was not significantly different among these four field strains. Beetles collected in summer tended to fly more and have a higher percentage of lipid content than beetles collected in spring and autumn. Results from crosses between strains with high and low flight responses suggested that the female contributes a higher proportion of additive genetic variance for flight initiation than the male. Rearing for 17 generations in laboratory conditions had no discernible effect on flight initiation of a strain of *R. dominica* collected from the field. Thus, flight behavior can persist for many generations of laboratory rearing. © 1999 Published by Elsevier Science Ltd. All rights reserved.

*Keywords:* *Rhyzopertha dominica*; Flight initiation; Strain; Body weight; Lipid content

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### 1. Introduction

The lesser grain borer, *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae), is a destructive pest of stored grains throughout the world (Khorramshahi and Burkholder, 1981; Cogburn

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et al., 1984; Hagstrum et al., 1994). Both larvae and adults are able to attack whole, sound grain (Mayhew and Phillips, 1994). Adults of *R. dominica* are long-lived and lay an average of one to seven eggs per day over several months (Hagstrum and Flinn, 1994). Eggs are laid externally on the wheat kernels. After hatching, larvae bore into and feed inside the kernels. Larvae pupate inside the kernels, and adults remain inside for several days after eclosion (Hagstrum and Flinn, 1994).

*Rhyzopertha dominica* is a strong flyer and is commonly found flying outside and inside grain-handling facilities during warm months (Sinclair and Haddrell, 1985; Fields et al., 1993; Throne and Cline, 1994; Dowdy and McGaughey, 1994). This pest is a crepuscular species that has a small peak of flight activity around sunrise, a large flight response at sunset, and minimal flight activity during the night (Leos-Martinez et al., 1986; Wright and Morton, 1995). Its greatest flight activity occurs in late afternoon and evening (Leos-Martinez et al., 1986; Sinclair and Haddrell, 1985), mainly 2 hours before sunset when the temperature is 37°C (Wright and Morton, 1995). Aslam et al. (1994) showed that *R. dominica* tends to fly throughout the photophase but flight activity is significantly reduced in the scotophase. Young adults (3–6 days old) tend to fly more than older adults (Aslam et al., 1994). Adults exposed to high population densities fly more than adults exposed to low population densities (Barrer et al., 1993; Perez-Mendoza, 1997). Also, temperature must be between minimum and maximum thresholds for flight to occur. In a laboratory study, Dowdy (1994) found that 19.9 and 41.6°C were the lower and upper temperature thresholds for flight, respectively, and the optimal temperature to initiate flight was 30.7°C in U.S.A. populations. Wright and Morton (1995) found that 16 and 37°C were the minimum and maximum temperature thresholds for flight in Australian populations.

The frequency of insect flight depends on internal and external factors such as feeding, adult age, food reserves, light intensity, temperature, humidity, and photoperiod (Chapman, 1982). Light intensity is usually the factor that affects the time of flight, whereas temperature influences amplitude of flight (Lewis and Taylor, 1964). The energy used during insect flight is derived ultimately from biochemical reactions taking place within the flight muscles (Beenackers et al., 1985). Lipids and carbohydrates are the major sources of energy for flight in most insects but various amino acids can also act as sources of energy in some species (Bailey, 1975). Most insect lipids are usually found in the fat body and predominantly include triglycerides (Bailey, 1975), which serve as a reserve of metabolic energy that can be mobilized and utilized in response to bioenergetic demands (Downer, 1985). Many migratory insects, including several Scolytidae (Hedden and Billings, 1977; Slansky and Haack, 1986; Jactel, 1993) and some Bruchidae (Gilbert, 1967; Nwanze et al., 1976) tend to utilize lipids rather than carbohydrates as the main source of energy during prolonged flight.

Several aspects of flight activity of *R. dominica* have been studied. These include the effects of photoperiod, temperature, humidity, age, sex, population density, starvation, and food source (Barrer et al. 1993, Aslam et al., 1994, Dowdy, 1994, Perez-Mendoza, 1997). In this study, we examined the relationships of body weight, lipid content, and flight initiation of *R. dominica* to strains, season of collection, genetic background, and number of generations of laboratory rearing.

## 2. Materials and methods

### 2.1. Culture methods

Adults of *R. dominica* used in these experiments were obtained from immatures reared at two different densities on hard red winter wheat at  $27 \pm 2^\circ\text{C}$ ,  $65 \pm 5\%$  r.h., and 14:10 Light:Dark (L:D) photoperiod. The uncrowded condition was obtained by placing individual newly hatched larvae on single kernels of wheat in multiple-well tissue culture plates (Corning Laboratory Sciences Co., Corning, NY). Emerging adults were collected for bioassays. The crowded condition was obtained by introducing 350 adults on 400 g of wheat in 1 l jars. All founding adults were removed 7 days after introduction. Adult progeny from both culturing methods were used in flight bioassays.

All rearing and flight experiments were conducted in light-tight plywood boxes (Aslam et al., 1994) containing light sources (Phillips F8T5/CW fluorescent lights 425–470 lux) to maintain a 14:10 L:D photoperiod. Each box contained baffles to keep them light tight and to allow electric fans to circulate air through the boxes. The temperature and relative humidity in the boxes were  $27 \pm 2^\circ\text{C}$  and  $65 \pm 5\%$ , respectively.

### 2.2. Flight bioassay

Flight activity of *R. dominica* was measured using a flight bioassay developed by Aslam et al., (1994). The bioassay chamber was a 95-mm-diameter glass funnel with the inner surface coated with sticky material (Sticky Stuff, Olson Products, Medina, OH). The funnel was inverted over a Petri dish (10×85 mm) containing adult insects. The sides of the Petri dish were coated with Teflon PTFE 30 fluorocarbon resin (DuPont, Wilmington, DE) to prevent adults from walking onto the funnel edge. Flying insects were trapped on the sticky inner surface of the funnel. Adults used in flight tests generally were not fed for 18 h prior to the experiment. On the day prior to the test, 10 batches of 50, 4–6-day-old, adults were weighed and placed into Petri dishes without food. The covered dishes were transferred to the light-tight plywood boxes. After 18 h, (7:30 a.m. the next day), the Petri dish covers were replaced with funnels, and the plates with the funnels remained in the boxes. The number of adults adhering to the funnels was recorded after 24 h. This flight bioassay was replicated 10 times using 50 randomly selected adults per replicate. Additionally, the number of adults that initiated flight after 24, 48, 72, and 96 h was recorded in another experiment.

The effect of number of adults released in the flight chamber on the rate of flight initiation was tested in a preliminary experiment. The insects were randomly placed in groups of 10, 25, 50, 75, and 100 adults. The number of adults adhering to the funnels was recorded after 24, 48, 72, and 96 h. This flight bioassay was replicated 10 times with insects of the field strain reared in crowded conditions.

### 2.3. Strain variations in body weight, lipid content, and flight initiation

Variations in body weight, lipid content, and flight initiation of different strains of *R. dominica* were tested in this experiment. Flight bioassays were carried out with two laboratory

strains and four field strains of *R. dominica*. One laboratory strain was provided by the Grain Marketing and Production Research Center ARS-USDA, Manhattan, KS, U.S.A. and the other was provided by the stored-product insects laboratory in the Department of Entomology at Kansas State University. Both strains have been reared under laboratory conditions for at least 20 y. The field strains were collected on September 12 and 15, 1994 in Manhattan, Kansas and Payne County, Oklahoma, respectively, using Lindgren funnel traps (Lindgren, 1983) baited with wheat and aggregation pheromone (Trece, Inc. Salina, CA), and on August 30 and September 8, 1995 in Celaya, Mexico, and Amarillo, Texas, respectively, from stored wheat in commercial bins. At least 50 trapped adults were used to start cultures of the field strains. The adults were reared under crowded or uncrowded conditions. Flight initiation rate, body weight, and lipid content were bioassayed with the 4th generation of adults of each field strain. The flight bioassay was replicated 10 times with each strain and both crowded and uncrowded rearing conditions for a total of 6,000 beetles with 500 tested for each strain-by-rearing condition combination. The experimental design was split-plot with strains arranged in a 5-by-2 factorial configuration as the main plot and with rearing method at the subplot level.

Three batches of 200 4th generation adults, 8- to 12-days-old, for each strain reared in crowded conditions were collected, weighed to the nearest 0.1 mg, and held at  $-70^{\circ}\text{C}$  until lipid analysis.

#### 2.4. Seasonal variations in flight initiation

Effects of the season in which the insects were collected on body weight, lipid content, and flight initiation was tested. Field strains of *R. dominica* were collected in Manhattan, Kansas, in early May (spring), late July (summer), and late September (autumn) of 1996 using Lindgren funnel traps baited as previously described. At least 50 trapped adults were used to start cultures of the field strain. Flight bioassays were carried out with the second generation of beetles from each population, which was reared under crowded conditions. Each treatment was replicated 10 times for a total of 500 adults tested for each population. The experiment was conducted in a 3-by-2 factorial arrangement, and data were analyzed using a split-plot design, with season of collection as main plot and rearing method as subplot.

Three batches of 200, 5-day-old adults for each population from the 2nd generation were collected, weighed, and held at  $-70^{\circ}\text{C}$  for lipid analysis.

#### 2.5. Genetic crosses

Virgin males and females from Mexican ( $F_{10}$ ) and Manhattan, KS 1994 ( $F_{16}$ ) strains were reared as isolated individuals. Reciprocal single-pair crosses between high and low flight propensity field strains were made to determine mating success and flight response of the hybrids. The following crosses were made: Mexico ♀ $\times$ Mexico ♂, Mexico ♀ $\times$ KS ♂, KS ♀ $\times$ Mexico ♂, and KS ♀ $\times$ KS ♂. Virgin adults were paired in plastic Petri dishes (35 $\times$ 10 mm) containing five to seven wheat kernels. After 72 h, each pair was placed in a 250 ml jar containing 25 g of wheat in a light-tight box at  $27 \pm 2^{\circ}\text{C}$ ,  $65 \pm 5\%$  r.h., and 14:10 L:D photoperiod. The number of days from egg hatch to adult emergence was

determined. Adult weights were obtained by weighing 100 individual  $F_1$  progeny from the four crosses on a Mettler UMT2 microbalance (USA Mettler Instrument Corporation, Hightstown, NJ).

Progeny ( $F_1$ ) from the single-pair crosses were self-crossed to obtain a second generation and to increase the number of beetles. The 2nd generation was reared in crowded and uncrowded conditions, and 4- to 6-day-old adult progeny were tested for flight initiation rate. Beetles were separated by cross, and each cross-by-rearing method combination was replicated 10 times with 50 beetles per replicate for a total of 500 beetles tested for each combination. The experimental design was a split-plot with cross arranged in a 4-by-2 factorial configuration as the main plot and rearing method as subplot.

Three batches of 200, 5-day-old adults for each test population were collected from the 2nd generation, weighed, and held at  $-70^\circ\text{C}$  for lipid analysis.

### 2.6. Effect of number of generations of laboratory rearing on flight propensity

The effect of laboratory rearing on flight initiation in a field strain of *R. dominica* was determined. The Manhattan, KS 1994 strain was maintained in crowded and uncrowded conditions in a culture chamber at  $27 \pm 2^\circ\text{C}$ ,  $65 \pm 5\%$  r.h., and 14:10 L:D photoperiod for 17 generations. Flight bioassays were conducted with adults from the 4th, 6th, 8th, 14th, and 17th generations. The experiment was conducted in a 5-by-2 factorial arrangement, and data were analyzed using a split-plot design, with generation as main plot and rearing method as subplot, and replicated 10 times, with 500 beetles tested for each generation-by-rearing method combination for a total of 2,500 beetles.

### 2.7. Lipid extraction and fatty acid composition analysis

Batches of 200 adults were placed in glass vials containing liquid nitrogen and ground to a fine powder with a glass rod. The liquid nitrogen was allowed to evaporate and chloroform (10 ml) was added to each sample to extract the lipids; left to stand for 1 h. The chloroform extract was filtered through two thicknesses of Whatman No. 1 filter paper and evaporated to dryness under a stream of nitrogen in a preweighed vial. After the lipid weight was determined, the sample was dissolved in chloroform. Aliquots containing at least 2 mg lipid were used for fatty acid analysis.

The fatty acid composition of lipid samples was determined as follows. The chloroform added to the 2 mg lipid samples was evaporated under nitrogen, and the samples were placed in reaction vials that contained 200  $\mu\text{l}$  of 0.5 M NaOH in methanol, the vials were capped, heated at  $100^\circ\text{C}$  for 1 h, and cooled. Then 200  $\mu\text{l}$  of  $\text{BF}_3$  in methanol was added to each vial. The vials were capped again and heated at  $100^\circ\text{C}$  for 2 min. After cooling, the contents of these vials were partitioned against 500  $\mu\text{l}$  of hexane. The hexane layer containing the fatty acid methyl esters was collected, and 2  $\mu\text{l}$  was injected into a Tracor 540 Gas chromatograph equipped with a capillary column (SGE 0.33 mm ID  $\times$  25 m) and a flame ionization detector. Nitrogen carrier gas had a head pressure of 40 kPa (6 psi), and the column oven was temperature programmed from  $150^\circ\text{C}$  (1 min hold) to  $300^\circ\text{C}$  (5 min hold) at  $3.5^\circ\text{C}/\text{min}$ . The

temperatures of the injector and detector were 325°C. Fatty acid methyl ester standards of myristic, palmitic, palmitoleic, stearic, oleic, and linoleic acids were prepared as above. Retention times and peak areas of each fatty acid were recorded with a Shimadzu integrator (Kyoto, Japan). These were compared with those of the standards, and the percentage compositions of fatty acids in the lipid extract of each strain were calculated. Data were analyzed using a completely randomized design with three replications, and 200 beetles per replicate.

## 2.8. Statistical analysis

Data from the experiments were analyzed with analysis of variance (ANOVA) (SAS Institute, 1985), and means were compared using least significant differences (LSD) (Steel and Torrie, 1980). Data from the experiment, in which flight initiation was recorded after 24, 48, 72 and 96 h were analyzed with repeated-measures analysis of variance (SAS Institute, 1991).

## 3. Results

### 3.1. Flight response of strains

Flight initiation among field strains of *R. dominica* collected from different locations was significantly affected by strain ( $df = 5,108$ ;  $F = 82.8$ ;  $P < 0.01$ ) and rearing method ( $df = 1,108$ ;  $F = 446.0$ ;  $P < 0.01$ ). The interaction for strain-by-rearing method was also highly significant ( $df = 5,108$ ;  $F = 31.1$ ;  $P < 0.01$ ). Therefore, we analyzed the data by rearing method. The rate of flight initiation of beetles from the Mexican strain reared in crowded conditions was significantly higher than the rates of beetles from laboratory or field strains collected in Kansas, Oklahoma, and Texas ( $df = 3,36$ ;  $F = 38.4$ ;  $P < 0.01$ ) (Fig. 1). Also, beetles reared in uncrowded conditions from strains collected in Mexico and Texas had significantly higher rates of flight initiation than those collected in Kansas and Oklahoma ( $df = 3,36$ ;  $F = 24.9$ ;  $P < 0.01$ ) (Fig. 1).

In general, the rates of flight initiation of beetles from field strains was significantly higher than the rates of beetles from laboratory strains from both crowded ( $df = 5,54$ ;  $F = 63.8$ ;  $P < 0.01$ ) and uncrowded rearing conditions ( $df = 5,54$ ;  $F = 25.2$ ;  $P < 0.01$ ) (Fig. 1). However, the rate of flight initiation of uncrowded beetles from the USDA laboratory strain was not significantly different than that of the Kansas, Oklahoma and Texas field strains.

Flight initiation of all strains of *R. dominica* was affected strongly by rearing condition ( $df = 5,108$ ;  $F = 31.1$ ;  $P < 0.01$ ). The rates of flight initiation of beetles of all the strains reared in crowded conditions were significantly higher than the rates of beetles reared in uncrowded conditions ( $df = 1,108$ ;  $F = 446.0$ ;  $P < 0.01$ ) (Fig. 1). However, the number of insects released in the flight chamber did not affect the proportion of beetles initiating flight ( $df = 4,45$ ;  $F = 1.8$ ;  $P < 0.46$ , data not shown).

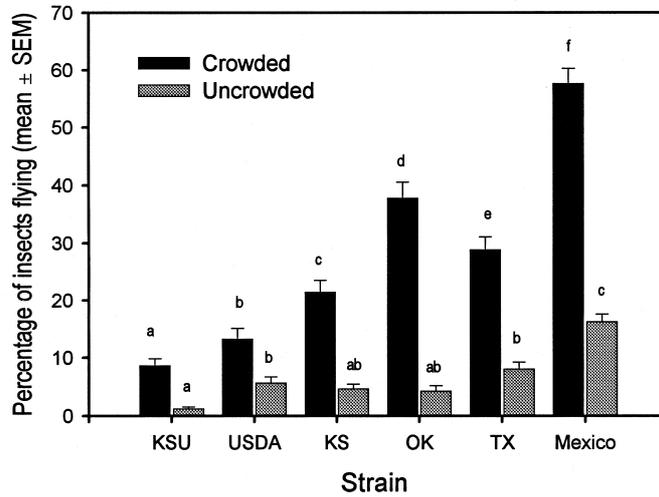


Fig. 1. Flight initiation of six strains of lesser grain borer, *Rhizopertha dominica*, collected in different locations. Percentage of insects flying within 24 h in the flight bioassay. Mean  $\pm$  SEM of 10 replicates per strain, 50 insects per replicate. Bars within the same rearing method marked with the same letter were not significantly different at  $P < 0.01$  (LSD test).

### 3.2. Strain variations in body weight, lipid content, and fatty acid composition

Body weight of adults reared in crowded conditions was slightly but significantly different ( $df = 4,45$ ;  $F = 130.9$ ;  $P < 0.01$ ) among some strains (Table 1). Although beetles from the laboratory strain of *R. dominica* (USDA) had the highest body weight and lipid content, their flight initiation rate was significantly lower than the rates of beetles from the field strains ( $df = 4,45$ ;  $F = 20.6$ ;  $P < 0.01$ ) (Table 1). Among the four field strains, beetles from the Mexican and Oklahoma strains had significantly higher fresh body weight ( $df = 4,10$ ;  $F = 38.5$ ;

Table 1

Body weight, lipid content, % of lipid, and flight initiation in five strains of the lesser grain borer, *Rhizopertha dominica*, reared in crowded conditions

Strains	Fresh body weight (mg/insect)*	Lipid content ( $\mu\text{g}/\text{insect}$ )*	% of lipids/fresh body weight*	% of insects flying**
USDA-Lab	1.22 $\pm$ 0.08 a	67.2 $\pm$ 2.5 a	5.5 $\pm$ 0.1 a	55 $\pm$ 8 a
Manhattan, KS	1.07 $\pm$ 0.07 b	49.2 $\pm$ 4.3 b	4.6 $\pm$ 0.4 a	75 $\pm$ 11 b
Payne, OK	1.16 $\pm$ 0.01 c	57.8 $\pm$ 2.4 ab	5.0 $\pm$ 0.2 a	91 $\pm$ 8 c
Amarillo, TX	1.09 $\pm$ 0.02 b	51.3 $\pm$ 2.8 b	4.7 $\pm$ 0.2 a	77 $\pm$ 9 b
Celaya, Mex.	1.16 $\pm$ 0.01 c	64.3 $\pm$ 1.5 a	5.5 $\pm$ 0.2 a	93 $\pm$ 5 c

\* Table shows mean  $\pm$  SEM of three replicates per strain, 200 insects were used per replicate.

\*\* Percentage of insects flying within the first 24 h of the flight bioassay. Mean  $\pm$  SEM of 10 replicates per strain, 50 insects were tested per replicate.

Means within a column followed by different letters are significantly different ( $P < 0.05$ ).

$P < 0.01$ ) and total lipid content ( $df = 4,10$ ;  $F = 7.5$ ;  $P < 0.047$ ) than the Kansas and Texas strains (Table 1). However, the percentage of lipids per fresh body weight was not significantly different ( $df = 4,10$ ;  $F = 2.8$ ;  $P < 0.09$ ) among the four field strains (Table 1).

Fatty acid compositions from the lipid extract of whole insects reared in crowded conditions were not significantly different among strains ( $df = 4,10$ ;  $F = 1.9$ ;  $P < 0.32$ ). The predominant fatty acid in the five strains was oleic acid, which averaged around  $45 \pm 2\%$  of the total fatty acids. Palmitic, linoleic, and stearic acids averaged about  $33 \pm 0.5$ ,  $18 \pm 0.2$ , and  $3.5 \pm 0.1\%$ , respectively. The concentrations of myristic and palmitoleic acids were much lower and averaged  $0.4 \pm 0.02$  and  $0.7 \pm 0.03\%$ , respectively.

### 3.3. Strain variations in time of flight initiation

Time had a significant effect on flight initiation ( $df = 3,18$ ;  $F = 93.6$ ;  $P < 0.01$ ), and because the interaction between time and rearing method was highly significant ( $df = 3,18$ ;  $F = 54.4$ ;  $P < 0.01$ ), we analyzed the rate of flight initiation separated by rearing method. Beetles from the Mexican strain reared under both crowded ( $df = 3,36$ ;  $F = 8.2$ ;  $P < 0.03$ ) and uncrowded ( $df = 3,36$ ;  $F = 8.2$ ;  $P < 0.03$ ) conditions initiated flight significantly more often within the first 24 h (Fig. 2). Beetles from all strains from both rearing conditions flew throughout the 96 h period in the flight chamber. However, adults from the four field strains reared in crowded conditions tended to initiate flight significantly more within the first 24 h of exposure in the flight chamber than the USDA-Lab strain ( $df = 3,36$ ;  $F = 323.2$ ;  $P < 0.01$ ) (Table 1).

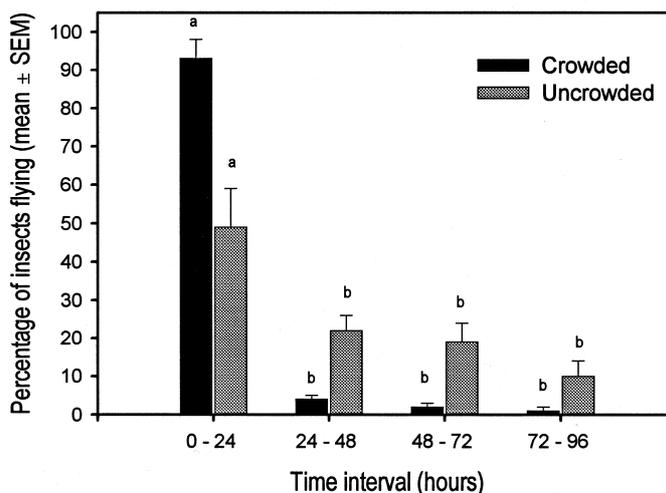


Fig. 2. Percentage of insects flying at 24-h intervals during bioassay of a Mexican strain of the lesser grain borer, *Rhyzopertha dominica*, reared in crowded or uncrowded conditions. Mean  $\pm$  SEM of 10 replicates per strain, 50 insects per replicate. Bars within the same rearing method marked with the same letter were not significantly different at  $P < 0.01$  (LSD test).

Table 2

Body weight, total lipid, % of lipid, and flight initiation in a field strain of the lesser grain borer, *Rhyzopertha dominica*, collected in different seasons from the same facility in Manhattan, KS, and reared in crowded conditions

Season	Fresh body weight (mg/insect)*	Lipid content ( $\mu\text{g}/\text{insect}$ )*	% of lipids/fresh body weight*	% of insects flying**
Spring	0.99 $\pm$ 0.01 b	59.2 $\pm$ 4.4 b	5.9 $\pm$ 0.4 b	44.0 $\pm$ 3.0 a
Summer	1.02 $\pm$ 0.02 b	87.5 $\pm$ 5.8 a	8.5 $\pm$ 0.4 a	67.4 $\pm$ 2.6 c
Autumn	1.06 $\pm$ 0.01 a	68.2 $\pm$ 8.9 ab	6.4 $\pm$ 0.8 b	54.8 $\pm$ 3.2 b

\* Table shows mean  $\pm$  SEM of three replicates per season, 200 insects were used per replicate.

\*\* Percentage of insects flying within 96 h of the flight bioassay. Mean  $\pm$  SEM of 10 replicates per season, 50 insects were tested per replicate.

Means within a column followed by different letters are significantly different ( $P < 0.05$ ).

### 3.4. Seasonal variation in flight initiation and lipid content

The season during which *R. dominica* was collected in the field had a small but statistically significant effect on flight initiation ( $df = 2,27$ ;  $F = 15.6$ ;  $P < 0.01$ ). Flight initiation was significantly higher in insects collected in the summer than those collected in spring and autumn (Table 2).

Total lipids tended to be higher in the insects collected in summer ( $df = 2,6$ ;  $F = 4.0$ ;  $P < 0.05$ ) but fresh body weight was significantly higher in progeny of the insects collected in autumn ( $df = 2,6$ ;  $F = 9.8$ ;  $P < 0.01$ ) (Table 2). Percent lipid/fresh body weight ( $df = 2,6$ ;  $F = 5.4$ ;  $P < 0.04$ ) was significantly higher in  $F_2$  progeny of insects collected in summer than in those collected in spring and autumn (Table 2). Fatty acid compositions were very similar in the three populations collected in spring, summer, and autumn and similar to the fatty acid composition from the field strains tested in a previous experiment.

### 3.5. Genetic crosses

Sixteen of 20 reciprocal crosses between the Mexican and Kansas strains produced progeny. Egg hatch (8.5–9.0 day), adult emergence (43.1–44.8 day), and body weight (1.1–1.2 mg) of progeny from all crosses tended to be similar. Flight initiation of progeny from crosses between Mexico  $\text{♀} \times \text{KS } \text{♂}$  tended to be similar to that of progeny from the Mexican strain, whereas that of progeny from the cross of KS  $\text{♀} \times \text{Mexico } \text{♂}$  tended to be similar to that of progeny from the Kansas strain (Fig. 3). However, the rates of flight initiation between the two parent strains were significantly different in both crowded ( $df = 3,36$ ;  $F = 16.9$ ;  $P < 0.01$ ) and uncrowded rearing conditions ( $df = 3,36$ ;  $F = 6.3$ ;  $P < 0.01$ ).

Fresh body weight ( $df = 3,8$ ;  $F = 10.2$ ;  $P < 0.01$ ); total lipid ( $df = 3,8$ ;  $F = 12.8$ ;  $P < 0.01$ ); and percentage of lipid/fresh body weight ( $df = 3,8$ ;  $F = 9.0$ ;  $P < 0.01$ ) of progeny from the Mexican strain were significantly different from those of progeny from the Kansas strain (Table 3), whereas these parameters were not significantly different between hybrid progeny in both crosses.

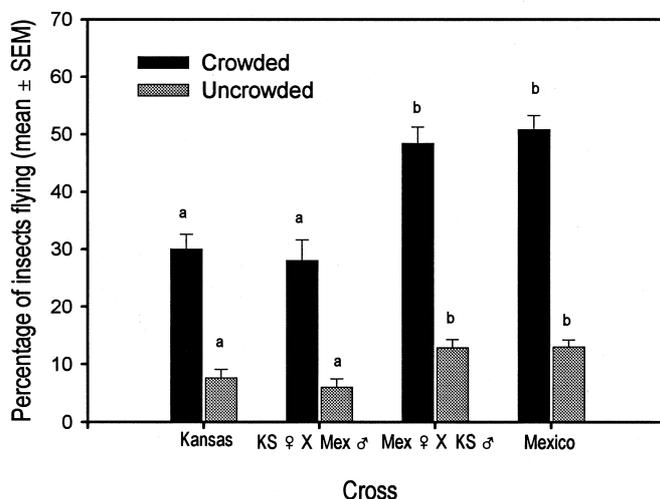


Fig. 3. Flight initiation of second generation progeny of reciprocal crosses between Kansas and Mexican field strains of the lesser grain borer, *Rhyzopertha dominica*. Percentage of insects flying within 24 h of the flight bioassay. Mean  $\pm$  SEM of 10 replicates per cross, 50 insects per replicate. Bars within the same rearing method marked with the same letter were not significantly different at  $P < 0.01$  (LSD test).

### 3.6. Effect of number of generations of laboratory rearing

Rearing *R. dominica* in the laboratory for several generations resulted in a small but statistically significant increase in flight initiation rate ( $df = 4,90$ ;  $F = 68.9$ ;  $P < 0.01$ ). There was also a difference between rearing methods ( $df = 1,90$ ;  $F = 1730.6$ ;  $P < 0.01$ ). The interaction between generation and rearing method was highly significant ( $df = 4,90$ ;  $F = 33.1$ ;  $P < 0.01$ ). Therefore, data on flight initiation were analyzed separately by rearing method. The rate of flight initiation increased significantly in both crowded ( $df = 4,45$ ;  $F = 3.3$ ;  $P < 0.02$ ) and uncrowded rearing conditions ( $df = 4,45$ ;  $F = 8.8$ ;  $P < 0.01$ ) through the different generations (Fig. 4). The rate of flight initiation reached a maximum at the 14th generation and decreased by the 17th generation in insects reared in crowded conditions. With uncrowded

Table 3

Body weight, total lipids, and % lipid in hybrid progeny and parental strains of the lesser grain borer, *Rhyzopertha dominica*, reared in crowded conditions

Cross	Fresh body weight (mg/insect)*	Total lipids (mg/insect)*	% lipids/fresh body weight*
Mex ♀ × Mex ♂	1.19 $\pm$ 0.01 a	113.3 $\pm$ 10.0 a	9.6 $\pm$ 0.8 a
Mex ♀ × KS ♂	1.10 $\pm$ 0.01 ab	89.3 $\pm$ 4.8 b	8.1 $\pm$ 0.5 ab
KS ♀ × Mex ♂	1.09 $\pm$ 0.01 ab	70.3 $\pm$ 5.5 bc	6.4 $\pm$ 0.5 b
KS ♀ × KS ♂	1.05 $\pm$ 0.01 b	62.0 $\pm$ 3.3 c	5.9 $\pm$ 0.3 b

\* Table shows mean  $\pm$  SEM of three replicates per population, 200 insects were used per replicate. Means within a column with different letters are significantly different ( $P < 0.05$ ).

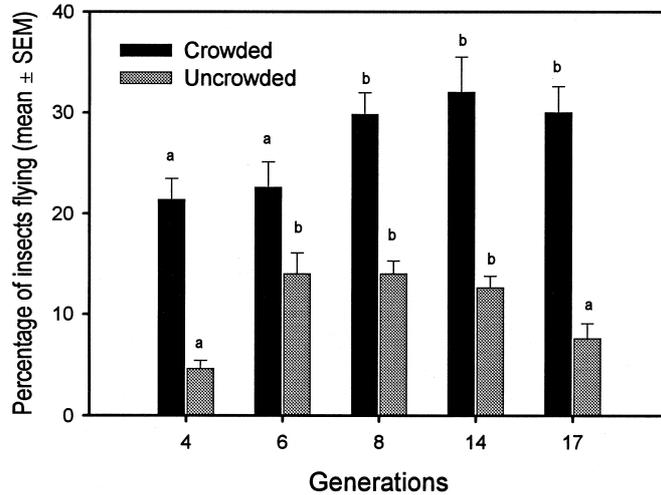


Fig. 4. Effect of number of generations of laboratory rearing on flight initiation of the Kansas field strain of *Rhyzopertha dominica* collected in Manhattan in 1994. Percentage of insects flying within 24 h in the flight bioassay. Mean  $\pm$  SEM of 10 replicates per generation, 50 insects per replicate. Bars within the same rearing method marked with the same letter were not significantly different at  $P < 0.01$  (LSD test).

reared insects, flight initiation was higher in the 6th, 8th and 14th generation but decreased by the 17th generation (Fig. 4).

#### 4. Discussion

Flight initiation, body weight, lipid content, and percentage lipid of *R. dominica* varied significantly among field strains collected in different geographical locations. These parameters generally increased from north to south. Rearing density influenced flight initiation nearly as much as strain differences. Flight activity tended to be higher for strains of insects with higher body weight and thus higher lipid content. Similarly, increased body weight and lipid content were also correlated with increased flight activity in *Ips paraconfusus* (Lanier) (Hagen and Atkins, 1975) and *I. calligraphus* (Germar) (Slansky and Haack, 1986). Kinn et al. (1994) also found that females of *Dendroctonus frontalis* were heavier, had more lipid, and flew more than males. Percentage composition of the fatty acids of the five strains of *R. dominica* varied only slightly, indicating that the increase in total lipids in strains most likely to fly was not accompanied by changes in ratios of fatty acids.

Variability in flight initiation rate and body weight may occur between populations of insects collected at different latitudes because those at southern latitudes may have suitable weather conditions for growth and reproduction throughout more of the year than those found at northern latitudes. Celaya, Mexico, has temperatures above 16°C during at least 10 mo of the year (personal observation by Perez-Mendoza). This temperature is the lower threshold for flight reported by Wright and Morton (1995). Therefore, in Mexico, adults of *R. dominica* are able to reproduce and disperse by flight almost all year. In the three locations in the U.S.,

temperatures are warm enough for flight for only about 6 mo (April to September) of the year (Hagstrum and Flinn, 1994). Thus, at northern latitudes, insects have only a short period of time in which they are able to accumulate fat resources to reproduce and disperse by flight, and they may spend the rest of the time overwintering inside the grain mass in commercial and farmers' bins (Fields et al., 1993).

Variations in flight initiation, body weight, and lipid content found in field strains suggest that each population may represent a different genotype. Parker and Gatehouse (1985) also found that variation in flight capacity of *Spodoptera exempta* (Walker) was discontinuous, with some populations containing both long-flyers and short-flyers in varying proportions. Evidence for the role of genetic factors in flight behavior also was reported in *Tribolium castaneum* (Herbst) by Diez and Lopez-Fanjul (1979), who found that the ability of this species to fly was heritable and responded rapidly to selection. Parker and Gatehouse (1985) also pointed out that genetic factors play a major role in the control of flight migration in *Spodoptera exempta*. The presence of a possible genetic component in the determination of flight initiation, body weight, and lipid content in *R. dominica* is supported by results from the experiment in which crosses were made between field strains with higher and lower flight initiation responses. Flight initiation in hybrid progeny paralleled that of the mother, regardless of strain. These preliminary results suggest that the female contributes a higher proportion of additive genetic variance for flight behavior than the male. However, more detailed studies are necessary to elucidate the complete genetic basis for flight behavior in this species.

The possible influences of suitable temperatures on flight initiation, body weight, and lipid content in *R. dominica* may be supported further by results obtained for progeny of adults trapped during the spring, summer, and autumn at the same site in Manhattan, KS. In these tests, higher lipid content and flight initiation occurred in progeny of adults trapped during the summer. However, there may be another explanation for these results. Continual immigration and emigration of insects from bins probably occurred throughout the trapping season. As a result, the insects trapped with pheromones during the spring, summer, and autumn may have been from populations with significantly different genetic compositions, and these differences could have been responsible for both the biochemical variations and differences in flight behavior that we documented.

Adults of *R. dominica* were more likely to fly within the first 24 hours of exposure inside the flight chamber. More flight initiation within the first 24 h also was noted by Aslam et al. (1994), who found that one third of the flights by field strain adults occurred during the initial 2–4 h of the flight test.

In the current study, progeny from field strains of *R. dominica* flew significantly more than the laboratory strain tested, even though the laboratory strain had the highest body weight and total lipids. This tendency also was noted by Aslam et al. (1994) and Perez-Mendoza (1997). This suggests that when populations become adapted to laboratory conditions, they may fly less, because in this environment, flight does not increase their chance of finding mates or food sources. However, no real effect on flight frequency was discernible for the field strain of *R. dominica* reared for 17 generations in laboratory conditions. This suggests that flight behavior of field strains is relatively stable in laboratory conditions, and that no rapid selection for reduced flight occurs with 17 generations of laboratory rearing.

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