MOLECULAR ECOLOGY AND EVOLUTION

Genetic Variation in Flight Activity of *Ophraella communa* (Coleoptera: Chrysomelidae): Heritability Estimated by Artificial Selection

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ABSTRACT

The exotic beetle *Ophraella communa* LeSage (Coleoptera: Chrysomelidae) was first found in 1996 in Japan and has rapidly expanded its distribution. This study investigated variation in flight activity and its genetic basis in this beetle by measuring its flight time on a flight mill system. The *O. communa* population exhibited substantial variation in flight activity among individuals. More than 30% of the beetles did not fly at all during a 23-h experimental period, whereas 20–26% of the beetles flew for over 60 min. Bidirectional artificial selection based on total flight time (0 or >60 min) significantly shifted the distributions of flight time and percentage of beetles flying after several generations. Repeatability of the following five flight components was analyzed: the total flight time, longest duration of single flight, mean duration of single flights, number of single flights, and a fly-or-not criterion (flying at least once [1] or nothing at all [0]) because it defines a theoretical upper limit of heritability. Among them, the fly-or-not criterion had the highest repeatability (0.797), followed by the total flight time (0.648). The fly-or-not criterion assumes a threshold trait, whereas the total flight time is regarded as a continuous trait. The realized heritabilities of these traits were estimated at 0.206–0.864 based on the threshold trait and 0.125–0.531 based on the continuous trait.

KEY WORDS  beetle, exotic insect, bidirectional selection, repeatability, realized heritability
lecion and estimate the heritability in this trait using the selected beetle lines.

Materials and Methods

Insects. For a preliminary experiment of repeated measurements (see below), the overwintering adults of *O. communa* were caught in the field at the National Institute for Agro-Environmental Sciences (NIAES) in May 2001, and their progeny were used. Then, I established two laboratory lines of *O. communa* that were derived from first-generation adults collected in the field at NIAES in June 2001 (2001 line) and June 2003 (2003 line). These lines were successively reared by a modified version of the method described by Moriya (1999) at 25°C, 60% RH, and a photoperiod of 16:8 (L:D) h (light phase 0400–2000 hours). The insects were supplied with ragweed, *Ambrosia artemisiifolia* L., which was grown in polyethylene pots (9 cm in diameter by 8 cm in height) in a greenhouse from seeds obtained from Herbiseed (Twyford, England). A ragweed leaf was put into a plastic petri dish (9 cm in diameter by 2 cm in height) lined with moist filter paper. Four adult females =10 d posteclosion were introduced into the petri dish for oviposition. After 1 d, a small piece of leaf bearing an egg mass of *O. communa* was cut out and placed on moist filter paper in a plastic petri dish. Hatching larvae were released onto a potted ragweed plant placed on a plastic tray filled with water. At =10 d after hatching, the larvae made cocoons, usually on leaves, and pupated inside the cocoons. The cocoons were cut off with a piece of leaf and placed into a plastic petri dish. Ecloring adults were released onto a potted ragweed plant placed inside an insect-rearing cage (30 by 27 by 30 cm; Fujiwara Scientific Co., Tokyo, Japan).

Plastic and Metal Petri Dishes. Hatching larvae were released onto a petri dish for oviposition. After 1 d, a small piece of leaf bearing an egg mass of *O. communa* was cut out and placed on moist filter paper in a plastic petri dish. Hatching larvae were released onto a potted ragweed plant placed on a plastic tray filled with water. At =10 d after hatching, the larvae made cocoons, usually on leaves, and pupated inside the cocoons. The cocoons were cut off with a piece of leaf and placed into a plastic petri dish. Ecloring adults were released onto a potted ragweed plant placed inside an insect-rearing cage (30 by 27 by 30 cm; Fujiwara Scientific Co., Tokyo, Japan).

Adult Morphology of Selected Lines. To examine the effect of the artificial selection on flight activity on adult morphology, particularly wing size, I compared morphology between the selected lines. Using a binocular dissecting scope with an ocular micrometer, I measured the following morphological traits in adults after two generations without selection (2003-F2), and selected after eight and 17 generations of selection (2001-NF8) were tested at the ages of seven and 14 d, and after 1 and 2 d of starvation, i.e., with water but no food.

Estimation of Heritability of Flight Activity. To determine the traits to be used in heritability estimation, I estimated the repeatability of flight activity because the repeatability defines a theoretical upper limit to the heritability (Falconer 1989). I analyzed five flight components, i.e., the total flight time, longest duration of single flight, mean duration of single flights, number of single flights, and a fly-or-not criterion (flying at least once [1] or nothing at all [0]) during the 23-h period, by using the data of preliminary experiment where the same individuals were measured twice. The repeatability was estimated according to Falconer (1989) and its standard error was calculated following Becker (1992). Thus, the traits to be used were determined and the realized heritability measurement, the beetles were individually housed in a petri dish with food and water for 3 d and tested again.

Artificial Selection Based on Flight Time. Each F1 progeny of the 2001 and 2003 lines was used for the artificial selection. The sex of *O. communa* adults was identified within 24 h of eclosion, and the females and males were reared separately. Six beetles were housed per petri dish, each containing moist filter paper and ragweed leaves. Because *O. communa* adults attain high flight activity after the age of 6 or 7 d (Tanaka and Yamanaka, 2009), beetles aged 7–9 d were used for the flight measurements. Beetles were selected in opposite directions, i.e., well-flying (flyers) and no flying (nonflyers). Beetles which flew >60 min during 23 h were chosen as flyers, and those which did not fly at all as nonflyers. To allow mating, two or three pairs of classified beetles were housed in a petri dish with moist filter paper and ragweed leaves. After three or more days, egg masses were obtained and offspring were reared using the procedures outlined above. Each line was reared separately in an incubator, and selections were carried out successively.

In addition, to determine whether the nonflyers would fly under different experimental conditions, I tested the effects of starvation and adult age on the flights of the beetles. The flight activities of the 2001 nonflyer line after eight generations of selection (2001-NF8) were tested at the ages of seven and 14 d, and after 1 and 2 d of starvation, i.e., with water but no food.
of these traits was estimated using artificial selection data according to the following equation (Falconer 1989):

\[ R = h^2 S \]

where \( R \) is the response to selection (deviation of offspring mean from the population mean in the parental generation), \( h^2 \) is heritability, and \( S \) is the selection differential (deviation of mean of selected parents from the population mean). The heritability was estimated as a regression coefficient, i.e., slope, in the linear regression of \( R \) on cumulated \( S \). The fly-or-not criterion assumes a threshold trait (Falconer 1989; Roff 1996, 1997). For the threshold trait, an underlying continuous variable with a threshold (termed liability), e.g., a physiological basis determining the expression of a few distinct phenotypes, is assumed (Falconer 1989). When the underlying variable is above the threshold the individual exhibits one phenotype, flyer in the present case; when it is below the threshold the individual has another phenotype, nonflyer. To estimate heritability of the threshold trait, the proportion of one phenotype is required to be transformed to liability, i.e., deviations of means of selected parents and offspring from the population mean, assuming a normal distribution of liability. Then the regression coefficient (slope) in liability was calculated like the continuous trait described above.

Data Analysis. For statistical analyses, flight time including total flight time and single flight duration was transformed by \( \log_{10}(x + 0.5) \) (Yamamura 1999). To test the effect of artificial selection on flight time, I performed factorial analysis of variance (ANOVA) with three main effects, i.e., origin (original beetle line), selection (artificially selected line), and sex by using the data for the beetles before and after eight generations of selection. To determine whether the increased total flight time of the flyer line was due to an increase in the number of single flights during the 23-h period or to an increase in the mean duration of single flights, I also conducted factorial ANOVA with the same effects. To test the effects of starvation and adult age on the flight of the nonflyer line, I used ANOVA for flight time and a logistic fit model for percentage of beetles flying. Wing length and relative wing length (arcsine-transformed) were compared between the selected beetle lines by ANOVA and the Tukey–Kramer method.

Results

Repeatability. Among the five flight components analyzed, the fly-or-not criterion showed the highest repeatability (Table 1). Other criteria, e.g., 1, 10, 30, 60 min (flying > each minute [1] or flying ≤ each minute [0]), had lower repeatabilities, 0.637, 0.471, 0.394, and 0.322, respectively. The total flight time had the second highest value (Table 1). Accordingly, I used the percentage of beetles flying at least once and the total flight time during the 23-h period in this study. The percentage of beetles flying assumes a threshold trait, whereas the total flight time is regarded as a continuous trait.

In the two successive measurements of same individuals, the linear regression of total flight time between the first (\( X \)) and second (\( Y \)) measurements was as follows:

\[ Y = -1.123 + 0.347X \quad (N = 82, \quad r^2 = 0.432, \quad t = 7.80, \quad P < 0.0001) \]

The regression coefficient was significantly smaller than 1.0 (\( t = 14.7, \quad P < 0.0001 \)), indicating that the beetles reduced the flight activity at the second test. Accordingly, individual beetles were measured only once in the other experiments.

Effect of Artificial Selection on Flight Time. There was variation in flight times of the field population of \( O. \) communa, represented by the \( F_1 \) progeny of the 2001 and 2003 lines (Fig. 1). More than 30% of the beetles did not fly at all during the 23-h experimental period. Twenty percent (2001 line) or 26% (2003 line) of the beetles, however, flew for >60 min, and some beetles flew for >300 min. Selection for flyers with a flight time >60 min and nonflyers with no flight shifted the frequency distributions of flight time after eight generations (Fig. 2). The bidirectional selection had significant effects on flight time (Table 2). These results show that the flight activity of \( O. \) communa is clearly under genetic control.

To determine whether the increased flight time of the flyers was due to an increase in the number of flights during the 23-h period or to an increase in flight duration of single flights, I compared these traits between \( F_1 \) (before selection) and FL8 (flyers selected for eight generations) beetles from the 2001 and 2003 lines (Table 3). Origin and flyer selection had significant effects on both traits; in particular, flyer selection increased the duration of single flights. The interaction of origin × selection also had significant effect on the number of flights, probably because effect of selection was smaller on the 2003 line than the 2001 line, especially on females.

Adult age did not affect the flight of the nonflyers; their flight activity was as low at age 14 d as at 7 d (\( N = 24 \) at each age; for flight time, \( F = 0.419, \quad P > 0.5 \) by ANOVA; for percentage of beetles flying, \( \chi^2 = 1.42, \quad P > 0.2 \) by logistic fit model). Starvation also had no significant effect on the flight of the nonflyers, whose flight activity was low after both 1 and 2 d of starvation (\( N = 24 \) at each of 0-, 1-, and 2-d starvation; for flight

<table>
<thead>
<tr>
<th>Flight component</th>
<th>Repeatability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total flight time (min)</td>
<td>0.648 ± 0.064</td>
</tr>
<tr>
<td>Longest single flight (min)</td>
<td>0.571 ± 0.075</td>
</tr>
<tr>
<td>No. of single flight</td>
<td>0.437 ± 0.090</td>
</tr>
<tr>
<td>Mean single flight (min)*</td>
<td>0.389 ± 0.122</td>
</tr>
<tr>
<td>Fly (1) or not (0)</td>
<td>0.797 ± 0.040</td>
</tr>
</tbody>
</table>

*Mean value of single flights within individuals.
time, $F = 0.694, P > 0.5$; for percentage of beetles flying, $\chi^2 = 2.15, P > 0.1$).

**Adult Morphology of Selected Lines.** Artificial selection for eight generations had no significant effect on body size, wing size, and relative wing size, but 17 generations of selection did have a significant effect on wing size and relative wing size (Table 4). The flyer line FL17 had larger wings, both in size per se and relative size, than the nonflyer line NF17, although these differences were not large (Table 4).

**Estimates of Heritability of Flight Activity.** Heritability of flight activity of *O. communa* was estimated on the basis of two traits exhibiting high repeatabilities, i.e., the percentage of beetles flying (a fly-or-not criterion) and total flight time. Bidirectional artificial selection shifted the percentage of beetles flying and total flight time in opposite directions (Figs. 3 and 4). The percentage of beetles flying approached 100% after five generations of selection or 0% after five to eight generations. In the 2001 flyer line, the mean flight time also approached a plateau during these generations, whereas in the 2003 flyer line, it gradually increased after these generations and reached a plateau around 10 generations. I estimated the realized heritability of flight activity by the linear regression described in Materials and Methods by using the changes in the two traits during these generations (Table 5). The estimates were $0.440–0.864$ for flyer selection and $0.206–0.413$ for nonflyer selection based on the percentage of beetles flying (assuming a threshold trait). However, based on total flight time, the estimates were $0.125–0.247$ for flyer selection and $0.334–0.531$ for nonflyer selection.

**Discussion**

**Genetic Variation in Flight Activity.** The *O. communa* population exhibited substantial variation in flight activity among individuals; $>30\%$ of the beetles did not fly at all during the 23-h experimental period, whereas 20–26% of the beetles flew for over 60 min. Bidirectional artificial selection based on total flight time (0 or $>60$ min) significantly shifted the distributions of flight time and percentage of beetles flying after several generations. The selected nonflyer line retained low flight activity, regardless of adult age or

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**Fig. 1.** Frequency distributions of flight time during 23 h in the F1 progeny of the 2001 and 2003 lines of *O. communa*.

**Fig. 2.** Frequency distributions of flight time in selected flyer and nonflyer lines of *O. communa* after eight generations.
starvation. The observed responses of the *O. commun*na lines to the artificial selection reveal that this beetle has genetic variation in flight activity. The artificial selection also affected the wing size. However, more generations of selection were required to have an effect on wing size than on flight activity.

Genetic variation in flight activity has been documented in various insect species that do not exhibit distinct morphological polymorphism of wing or flight muscle (Dingle 1968, Caldwell and Hegmann 1969, Parker and Gatehouse 1985, Gu and Danthanarayana 1997, Keil et al. 2001, Kent and Rankin 2001). In most or all of these species, the inheritance of flight activity is under polygenic control (Dingle 1986). Most of these reports analyzed the flight time or flight distance as a continuous trait. In the current study, however, two traits were chosen for analyses because of high repeatability; one was a threshold trait (flyer or nonflyer criterion or percentage of beetles flying), and the other was a continuous trait (total flight time). The flyer criterion had the highest repeatability among flight components analyzed. Thus, flight activity of *O. commun*na may be inherited greater as a threshold trait.

### Table 2. Factorial ANOVA to test the effects of origin (2001 and 2003 lines), selection (flyer and nonflyer selection for eight generations), and sex, and their interactions on flight time of *O. commun*na.

<table>
<thead>
<tr>
<th>Selection</th>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flyer</td>
<td>Origin</td>
<td>1</td>
<td>1.89</td>
<td>2.07</td>
<td>0.151</td>
</tr>
<tr>
<td>Selection</td>
<td>1</td>
<td>150.6</td>
<td>165.3</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>0.196</td>
<td>0.215</td>
<td>0.643</td>
<td></td>
</tr>
<tr>
<td>Origin × selection</td>
<td>1</td>
<td>0.252</td>
<td>0.309</td>
<td>0.578</td>
<td></td>
</tr>
<tr>
<td>Origin × sex</td>
<td>1</td>
<td>0.564</td>
<td>0.619</td>
<td>0.432</td>
<td></td>
</tr>
<tr>
<td>Selection × sex</td>
<td>1</td>
<td>0.098</td>
<td>0.108</td>
<td>0.743</td>
<td></td>
</tr>
<tr>
<td>Origin × selection × sex</td>
<td>1</td>
<td>4.65</td>
<td>5.11</td>
<td>0.024</td>
<td></td>
</tr>
</tbody>
</table>

### Table 3. Effects of origin (2001 and 2003 lines), flyer selection (before selection and after eight generations of selection), and sex on the number of flights and the duration of single flights in *O. commun*na.

<table>
<thead>
<tr>
<th>Original line</th>
<th>Sex</th>
<th>Selection</th>
<th>N</th>
<th>No. of flight (mean ± SE)</th>
<th>Duration of single flight (s, mean ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2001</td>
<td>Male</td>
<td>Before</td>
<td>43</td>
<td>31.7 ± 6.8</td>
<td>109.0 ± 21.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Flyer</td>
<td>42</td>
<td>52.4 ± 6.6</td>
<td>232.7 ± 36.7</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>Before</td>
<td>41</td>
<td>16.3 ± 3.0</td>
<td>134.0 ± 39.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Flyer</td>
<td>44</td>
<td>47.1 ± 7.1</td>
<td>309.3 ± 49.3</td>
</tr>
<tr>
<td>2003</td>
<td>Male</td>
<td>Before</td>
<td>40</td>
<td>20.2 ± 5.0</td>
<td>160.5 ± 41.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Flyer</td>
<td>42</td>
<td>30.5 ± 5.3</td>
<td>370.5 ± 56.4</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>Before</td>
<td>62</td>
<td>28.0 ± 4.2</td>
<td>129.8 ± 30.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Flyer</td>
<td>41</td>
<td>31.9 ± 4.1</td>
<td>317.8 ± 49.8</td>
</tr>
</tbody>
</table>

Factorial ANOVA shows significant effects of origin (*P* < 0.05), selection (*P* < 0.0001), and origin × selection (*P* < 0.05) on the number of flights and of selection (*P* < 0.0001) on the duration of single flights.

### Table 4. Body size, wing size, and relative wing size (mean and SE (in parentheses)) after two generations without selection (F2) and selected after eight and 17 generations (NF, nonflyer; FL, flyer).

<table>
<thead>
<tr>
<th>Sex</th>
<th>Beetle line</th>
<th>Head width (HW, mm)</th>
<th>Pronotum width (PW, mm)</th>
<th>Hindwing length (HwL, mm)</th>
<th>PW/HW</th>
<th>FwL/Hw</th>
<th>HwL/Hw</th>
<th>FwL/PW</th>
<th>HwL/PW</th>
<th>HwL/FwL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>F2 (N = 22)</td>
<td>1.473 (0.0073)</td>
<td>1.464 (0.0057)</td>
<td>3.575 (0.0157)</td>
<td>3.546 (0.0168)</td>
<td>1.82 (0.0159)</td>
<td>3.515 (0.0182)</td>
<td>2.14 (0.0164)</td>
<td>3.498 (0.0179)</td>
<td>1.393 (0.0052)</td>
</tr>
<tr>
<td></td>
<td>NF8 (N = 24)</td>
<td>1.46 (0.01)</td>
<td>1.45 (0.01)</td>
<td>3.56 (0.02)</td>
<td>3.54 (0.02)</td>
<td>1.82 (0.01)</td>
<td>3.51 (0.02)</td>
<td>2.14 (0.01)</td>
<td>3.498 (0.0179)</td>
<td>1.393 (0.0052)</td>
</tr>
<tr>
<td></td>
<td>FL8 (N = 25)</td>
<td>1.46 (0.01)</td>
<td>1.45 (0.01)</td>
<td>3.56 (0.02)</td>
<td>3.54 (0.02)</td>
<td>1.82 (0.01)</td>
<td>3.51 (0.02)</td>
<td>2.14 (0.01)</td>
<td>3.498 (0.0179)</td>
<td>1.393 (0.0052)</td>
</tr>
<tr>
<td>Female</td>
<td>F2 (N = 28)</td>
<td>1.47 (0.0075)</td>
<td>1.46 (0.0058)</td>
<td>3.58 (0.0162)</td>
<td>3.55 (0.0173)</td>
<td>1.82 (0.0164)</td>
<td>3.52 (0.0185)</td>
<td>2.14 (0.0164)</td>
<td>3.5 (0.0179)</td>
<td>1.393 (0.0052)</td>
</tr>
<tr>
<td></td>
<td>NF8 (N = 30)</td>
<td>1.46 (0.01)</td>
<td>1.45 (0.01)</td>
<td>3.56 (0.02)</td>
<td>3.54 (0.02)</td>
<td>1.82 (0.01)</td>
<td>3.51 (0.02)</td>
<td>2.14 (0.01)</td>
<td>3.498 (0.0179)</td>
<td>1.393 (0.0052)</td>
</tr>
<tr>
<td></td>
<td>FL8 (N = 31)</td>
<td>1.46 (0.01)</td>
<td>1.45 (0.01)</td>
<td>3.56 (0.02)</td>
<td>3.54 (0.02)</td>
<td>1.82 (0.01)</td>
<td>3.51 (0.02)</td>
<td>2.14 (0.01)</td>
<td>3.498 (0.0179)</td>
<td>1.393 (0.0052)</td>
</tr>
</tbody>
</table>

For statistical tests of relative wing length, the reciprocal was transformed by arcsine. Each category was compared among F2, NF8, and FL8 of the same generation and among F2, NF17, and FL17. There were no significant differences among F2, NF8, and FL8 (P > 0.05, ANOVA). Values followed by the same letter are not significantly different among F2, NF8, NF17, and FL17 (Tukey–Kramer method).
than a continuous trait, although both traits may be relevant to it. The results of artificial selection in *O. communa* were analyzed based on these traits, and the realized heritability of flight activity was estimated at 0.206–0.864 based on the threshold trait and 0.125–0.531 based on the continuous trait. The threshold trait showed higher heritabilities from response to upward selection than that to downward selection, whereas the continuous trait exhibited lower heritabilities from response to upward selection than that to downward selection. The estimated heritabilities for males and females do not show consistent differences. These estimated heritabilities indicate great genetic variation in the flight activity of *O. communa*.

Wing polymorphism is a threshold trait in many insect species, although it is controlled by a simple Mendelian inheritance in some species (Roff 1986, 1996). In insects exhibiting behavioral flight polymorphism, however, its genetics have not been analyzed as a threshold trait except in the grasshopper *Melanoplus sanguinipes* F. (Kent and Rankin 2001). These authors showed that the continuous flight time of *M. sanguinipes* had a bimodal distribution and estimated the heritability of its migratory tendency to be 0.567. Migratory tendency was assumed to be a threshold trait that exhibits two phenotypes, i.e., a migrant with a continuous flight time ≥60 min and a nonmigrant with a flight time <60 min. In several other insect species, the heritabilities of flight activity have been estimated under the assumption that the flight time and flight distance are continuous traits. Estimated heritabilities include 0.20 for male parents and 0.41 for female parents in the small milkweed bug, *Lygaeus kalmii* Stål (Caldwell and Hegmann 1969); 0.40 for the

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![Graph](image-url)  
**Fig. 3.** Changes in percentage of beetles flying and total flight time (mean ± SE) during 23 h for the flyer lines of *O. communa*.

![Graph](image-url)  
**Fig. 4.** Changes in percentage of beetles flying and total flight time (mean ± SE) during 23 h for the nonflyer lines of *O. communa*.
African armyworm *Spodoptera exempta* (Walker) (Parker and Gatehouse 1985); 0.559 for male parents and 0.427 for female parents in the light brown apple moth, *Epiphyas postvittana* (Walker) (Gu and Danthanarayana 1992a); 0.27 for the Oriental armyworm *Mythimna separata* (Walker) (Han and Gatehouse 1993); and 0.57 for the field strain and 0.38 for the laboratory strain of the codling moth, *Cydia pomonella* (L.) (Schumacher et al. 1997) or 0.07–0.54 for *C. pomonella* (Keil et al. 2001). However, *S. exempta* showed a discrete bimodal distribution of flight time (Parker and Gatehouse 1985), suggesting this dimorphic phenotype may be a threshold trait. The estimated heritability of *O. commun* is within the range of the above estimates, although it was obtained on the basis of two different quantitative genetic models, i.e., a threshold and continuous trait models.

In most insects whose flight activity has been genetically analyzed to date, its considerable variation in flight activity has been observed between populations (e.g., Dingle 1968) or individuals (e.g., Schumacher et al. 1997). In *O. commun*, however, such variation has not been reported. This illustrates that genetic variation in flight activity may exist in insect species or populations that do not display obvious variation in flight activity, a situation that may be common in insects.

**Ecological Consideration of Variation in Flight Activity.** In this study, *O. commun* adults were classified into flyers and nonflyers; flyers were defined as individuals that flew at least once during the 23-h experimental period and nonflyers as those that did not fly at all. In other insects, however, several researchers have intuitively defined the critical flight time for determining long-flyers and short-flyers based on the frequency distribution of the flight times of the insects (cf. Kent and Rankin 2001), and these critical times are much longer than that of this study, e.g., continuous flight of 30 min in the milkweed bug, *Oncopeltus fasciatus* (Dallas) (Dingle 1968), a total flight time of 120 min or continuous flight time of 30 min in *S. exempta* (Parker and Gatehouse 1985), continuous flight of 30 min (Coats et al. 1986) or 20 min (Naranjo 1990) in the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, and continuous flight of 60 min in *M. san*ginipes (Kent and Rankin 2001). The shorter critical time in *O. commun* may be due to its lower flight activity than other insects. In fact, in two lines of *O. commun* before selection, >30% of the beetles did not fly at all on the flight mill. Yamanaka et al. (2007) performed autocorrelation analysis of the spatial pattern of host plant (*A. artemissifolia*) patches, and they suggested that the patches were distributed at average intervals of ≈100 m. Nonflyers (and possibly flyers with <1 min flight) may move within host patches, whereas other flyers can disperse between patches. *O. commun* increased its flight activity after 4 d posteclosion, which corresponded with increasing oviposition (Tanaka and Yamanaka, 2009). Thus, flyers will tend to disperse from patch to patch during reproduction, whereas nonflyers will tend to oviposit repeatedly within the same patch. In Japan, *O. commun* populations often increased rapidly due to the lack of effective natural enemies (Moriya et al. 2002) and defoliated host patches (Emura 2000, Yamazaki et al. 2000). The defoliation of host patches will be more of a disadvantage to the nonflyers that oviposit more eggs within the same patch than to the flyers. However, flyers also incur a risk, in that they may suffer higher mortality during dispersal and fail to find another host patch. The fact that flyers and nonflyers coexist within a population suggests that either may have an advantage depending on environmental and/or biological conditions; consequently, the genetic variation in flight activity is maintained within the population. In some insects, there is a trade-off between flight capacity and life-history traits, e.g., a greater fecundity in short-flyers (Gu and Danthanarayana 1992b, Gu et al. 2006). Such a trade-off in *O. commun* remains to be investigated in the future.

*O. commun* was accidentally introduced into Japan and has since rapidly expanded its distribution (Moriya and Shiyake 2001, Moriya et al. 2002). This rapid expansion despite a large proportion of non- or short-flyers in the population may be because the genetic variation in flight activity produces some individuals with very high flight activity. Thus, it is important to analyze genetic variation in the flight of exotic and invasive insects to help predict their expansion in colonized regions.

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### Table 5. Estimated realized heritabilities (± SE) of flight activity in *O. commun*.

<table>
<thead>
<tr>
<th>Line</th>
<th>Sex</th>
<th>Flyer</th>
<th>Nonfly</th>
</tr>
</thead>
<tbody>
<tr>
<td>2001</td>
<td>Male</td>
<td>0.864 ± 0.124***</td>
<td>0.413 ± 0.153***</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>0.675 ± 0.135***</td>
<td>0.305 ± 0.080***</td>
</tr>
<tr>
<td>2003</td>
<td>Male</td>
<td>0.440 ± 0.124***</td>
<td>0.206 ± 0.022*** ***</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>0.471 ± 0.126***</td>
<td>0.309 ± 0.005***</td>
</tr>
</tbody>
</table>

*P < 0.05, **P < 0.01, ***P < 0.001. The regression coefficient of response to selection (R) on cumulated selection differential (S) is significantly different from 0.*
References Cited


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