Estimation of abundance and dispersal distance of the sugarcane click beetle
Melanotus sakishimensis Ohira (Coleoptera: Elateridae) on Kurima Island,
Okinawa, by mark-recapture experiments

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Abstract
The absolute population density and natural mean dispersal distance of the sugarcane click beetle Melanotus sakishimensis Ohira (Coleoptera: Elateridae) were estimated by using mark-recapture experiments in an agricultural area (180 ha) on Kurima Island, Miyakojima, Okinawa in mid-February, from 2002 to 2006. Funnel-vane traps with synthetic sex pheromone were uniformly placed along field roads at 100 points to capture adult males. Estimates of population densities of males that were obtained by the Jolly-Seber and Yamamura methods from 2002 to 2006 were 33,761, 29,727, 14,960, 11,360 and 8,634, respectively. The Yamamura method was adopted in 2004 and 2005 when the survival rates estimated by Jolly-Seber method became larger than 1. The estimate of lifetime natural mean dispersal distance (±SE) that was calculated by eliminating the influence of artificial trap removal was 193.8±11.0 m. The estimate of the male removal rate (and the 95% profile likelihood confidence interval) was 0.131 (0.117–0.147), indicating that the amount of male removal was not sufficient for the population control in this experiment.

Key words: Funnel trap; mass trapping; monitoring trap; male removal; population estimate

INTRODUCTION
Two species of the sugarcane click beetle Melanotus sakishimensis Ohira and Melanotus okinawensis Ohira (Coleoptera: Elateridae) are serious pests of sugarcane in Okinawa and Kagoshima, Japan (Ohira, 1988). M. sakishimensis occurs on Miyako Islands and Ishigaki Islands, the northern part of Okinawa Island, Yoron and Okinoerabu Islands, Tokuno-shima, and Amami-Oshima Islands, whereas M. okinawensis occurs on Okinawa, Kume, Minami-Daito, Kikai-jima, Tokuno-shima and Amami-Oshima Islands (Ohira, 1988; Setokuchi et al., 1990). The population of these two click beetle species comprises two- and three-year cycles at certain ratios (Nagamine and Kinjo, 1981; Setokuchi et al., 1990; Nakamori, 2000; Arakaki et al., 2008). Adult emergence occurs in the autumn, and adults remain underground until the following February or March (Nagamine and Kinjo, 1981). All dissected females of these two click beetle species had fully matured eggs in their abdomen in the early period of emergence from the ground (Arakaki, unpublished data), thus were sexually mature at that time. Larvae (wireworms) of these species injure underground buds of sugarcane, and impede continuous growth after the harvest (Hokyo, 1980; Nagamine and Kinjo, 1981). Ratooning rates in Miyako Island were above 60% in the 1960’s and 1970’s. However, the use of

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409
organochloride insecticide, which was a very effective control of soil dwelling pests, was prohibited in 1971. Since then, the ratooning rates decreased year by year, dropped below 10% in the early 1980’s, and attained only 2–3% after 2000 (Tokeshi, 2006). This decrease was caused by the increases in the populations of soil dwelling pests such as wireworms and white grubs (Hokyo, 1980; Nagamine and Kinjo, 1981). Large amounts of non-organochloride insecticide had been applied before planting or during the early growth period of the sugarcanes to control these larvae (Yasuda and Hokyo, 1983). However, rain immediately penetrates underground through limestone in these coral originated islands, and application of insecticides poses a risk of groundwater pollution. This is unacceptable because people rely on groundwater for drinking water. Therefore, alternative tools for controlling this pest are urgently required.

Dodecyl acetate was identified as a female sex pheromone in *M. okinawensis* (Tamaki et al., 1986). Subsequently, female sex pheromone was identified as (E)-9,11-dodecadienyl butyrate and (E)-9,11-dodecadienyl hexanoate in *M. sakishimensis* (Tamaki et al., 1990). Nagamine and Kinjo (1990) first reported the effectiveness of mass trapping from 1985 to 1989 (4.4 traps/ha) to control the other sugarcane click beetle *M. okinawensis* in sugarcane fields (24.75 ha) at Yomitan-village, Okinawa Island. Since then, mass trapping has been conducted to control both species in various regions, with a trap density of 1 trap/1–1.5 ha. Despite more than ten years of control by mass trapping on several Islands, the ratooning failure of sugarcane from wireworm attack continued to be a big problem (e.g. Nakamori and Kawamura, 1997). The effectiveness of mass trapping has not previously been evaluated except through the total number of male trap catches.

The following three factors related to mass-trapping methods were evaluated by using mark-recapture methods for the isolated population of *M. sakishimensis* on Kurima Island: 1) dispersal distance, 2) absolute density of male beetles, and 3) removal rate of male beetles. We also examined annual trends of total trap catches to evaluate the control effect of mass trapping through a 5-year test from 2002 to 2006.

**MATERIALS AND METHODS**

**Experimental area.** Experiments were conducted on Kurima Island (about 286 ha), Miyakojima, Okinawa, Japan from 2002 to 2006. Kurima Island is located 1.6 km southwest of Miyako Island, and is connected to Miyako Island by a bridge. The agricultural area on Kurima Island covers 180 ha. Sugarcane (56.7 ha), tobacco (38.9 ha) and pasture (4.3 ha) are the main cultivated crops. During the experiment, the area of sugarcane cultivation was generally constant on Kurima Island. A village is located on the northeast part of the island. A shelterbelt forest (about 74 ha) covers the periphery of the island.

**Sex pheromone trap.** The pheromone lure used for *M. sakishimensis* was Sakimelanolure (Sankei Chem. Co., Kagoshima). This is a polyethylene tube (140 cm length) containing 500 mg of a mixture of (E)-9,11-dodecadienyl butyrate (73%), (E)-9,11-dodecadienyl hexanoate (2.5%) and antioxidant (24.5%). The tube lure was bent into a ring shape (8.5 cm dia.). The life of the pheromone lure is more than four months, which covers the adult emergence period (Nakamori, 2000). A pheromone tube was attached to a funnel trap with crossed vanes (15 cm dia.×38.5 cm ht., Trécé Inc., Salinas, Calif., USA). The traps were anchored with wire to a stick (about 1 cm dia.×60 cm) in the ground (Fig. 1).
Insects. The male beetles used for the mark-re-capture experiments were collected using sex pheromone traps at Gusukube, Miyako Island, three to four days before the experiments. The insects were stored in semitransparent plastic boxes (34×27×11.5 cm) and provided with pieces of split sugarcane stalks (30 cm long) as food and shelter. One day before the experiments, the pronota and/or elytra of beetles were marked with an oily fine-tip marker (Paint Marker, Mitsubishi Pencil Co., Ltd., Tokyo). Markings signified different release dates and sites. The marks were not removed even after insects were caught in traps.

Trap arrangements on Kurima Island. Funnel-vane traps were set on the ground along a road at 100 sites evenly in the agricultural area in early February for the density estimation and mass trapping experiment (Fig. 2). They were removed in mid-May in the years 2002–2006.

Estimation of population density. Population density and survival rate were estimated by the Petersen method, Jolly-Seber method (Seber, 1982), Yamamura method (Yamamura et al., 1992), and Yamamura B method (Yamamura, 2003). We used these methods simultaneously because they have complementary characteristics (Arakaki et al., 2008).

One thousand marked beetles were released twice at two-day intervals in mid-February from 2002 to 2006. The first release of 2005 was an exception with a release of 500 insects. Insects were released uniformly along the road so that the marked individuals mixed well with wild ones. The numbers of marked and wild beetles captured in 100 traps were counted at two-day intervals.

Estimation of dispersal distance. To estimate the dispersal distance, 600 marked beetles were released twice at two-day intervals at the same date as the estimation of population density at the center of the island (Fig. 2). Estimation for dispersal distance was not conducted in 2004, because trap catches for marking were too low to conduct both estimations (density and dispersal). The low catches were due to the low temperatures in the three days before the experiment.

We are liable to underestimate dispersal distance when we use traps to record the dispersal distance of released insects. Turchin (1998) referred to this as a Heisenberg effect. A large number of traps should be placed to yield a precise estimate of mean dispersal distance, but these traps shorten the mean dispersal distance itself by intercepting organisms that would have dispersed further. Yamamura et al. (2003) proposed a procedure to solve this dilemma by placing traps uniformly in a lattice pattern, and by assuming a random movement and

Fig. 2. Arrangement of 100 traps (open circles with numbers) for the evaluation of density and natural mean dispersal distance of male beetles and for mass trapping experiment. The arrow shows the release point for evaluating the dispersal distance of beetles. Dotted area indicates the shelterbelt vegetations. Hatched area indicates the village region.
a constant rate of settlement for organisms. Their method used in the current experiment is summarized as follows.

Let us assume that the traveling individuals settle at a position at a rate $\lambda$, which is independent of time, space, and the density of individuals. If traps are placed uniformly in a lattice pattern, the instantaneous mortality caused by traps is nearly constant, and hence we can assume that moving individuals are removed by traps at an approximate constant rate $\delta$. Let $D$ be the diffusion coefficient of the random movement. We define $\lambda_D$ and $\delta_D$ by $\lambda/D$ and $\delta/D$, respectively. We refer to these quantities as “rate of settlement scaled by diffusion coefficient”. Then, the expected cumulative number of individuals captured by the $i$th trap placed at a distance $r_i$ is approximately given by

$$g(r_i) = \frac{N_0}{2\pi d} \delta_D K_0\left(\frac{r_i}{\sqrt{\lambda_D + \delta_D}}\right),$$

where $N_0$ is the number of released insects and $d$ is the density of traps per m$^2$. $K_0(\cdot)$ is a modified Bessel function of the second kind of order zero. We can obtain the maximum likelihood estimates of $\lambda_D$ and $\delta_D$ by using a multiplicative Poisson distribution (Yamamura et al., 2003). The Microsoft Excel spreadsheet for this estimation is available at (http://cse.niaes.affrc.go.jp/yamamura/Yamamura_et_al_2003_estimation.xls). The estimation requires the cumulative number of catches in each trap. However, we recorded the number of captured insects only 2 and 4 days after the release. Hence, some bias in estimates should be suspected.

Let a hat (\hat{\cdot}) indicate an estimate. Then, the mean dispersal distance in Eq. (1) is estimated by $\pi/(2\sqrt{\lambda_D + \delta_D})$. The mean dispersal distance when there is no trap estimated is $\pi/(2\sqrt{\lambda_D})$, by substituting $\delta_D=0$. The quantity of $\pi/(2\sqrt{\lambda_D})$ indicates the estimate of natural mean dispersal distance. The standard error (SE) is estimated by using the delta method: $SE(\hat{\lambda_D}) \equiv \pi/(4\lambda_D^{1/4})$, where $SE(\hat{\lambda_D})$ indicates the SE of $\hat{\lambda_D}$. The proportion of artificial reduction of mean dispersal distance by traps is estimated by

$$1 - \left(\frac{\hat{\lambda_D}}{\lambda_D + \delta_D}\right).$$

If this quantity is not large, we can consider that the influence of removal by traps is sufficiently small. Then, we can proceed to more sophisticated analyses of dispersal curves such as those assuming a heterogeneous population or those using the gamma model (Skellam, 1951; Clark et al., 1999; Yamamura, 2002, 2004; Yamamura et al., 2007).

### Estimation of male removal rate

Arakaki et al. (2008) proposed two methods to estimate the male removal rate by pheromone traps. One method is available for experiments using mark-recapture procedure. The other method is available for experiments where sex ratio of insects is examined in both pheromone-treated plots and control plots. Arakaki et al. (2008) performed the estimation for the experiment of $M. okinawensis$, and indicated that the two methods may yield equivalent estimates, although the two methods use quite different information. In the current experiment for $M. sakishimensis$, we can only use the former method that can be described as follows.

We again define $\lambda$ as the instantaneous natural mortality and $\delta$ as the instantaneous mortality caused by traps. Let $N$ be the number of released insects alive in the field and $S$ be the cumulative number of released insects that are captured by monitoring traps. Let $w$ be the proportion of monitoring traps among all traps. In our current experiment, we have $w=1$. Then we have

$$\frac{\partial N}{\partial t} = - (\lambda + \delta) N,$$

$$\frac{\partial S}{\partial t} = w \delta N.$$

The solution is given by

$$N = N_0 e^{-(\lambda + \delta) t},$$

$$S = w N_0 \delta/(\lambda + \delta) \left(1 - e^{-(\lambda + \delta) t}\right),$$

where $N_0$ is the number of released insects. The average duration of survival time is given by $1/(\lambda + \delta)$. This quantity becomes $1/\lambda$ when there is no trap. Hence, the proportion of reduction of survival time by traps is given by $\delta/(\lambda + \delta)$. We define this quantity as the male removal rate, because the chance of mating will be approximately proportional to the sum of survival durations of males.

Equation (6) indicates that, if we examine the trap catches for sufficient duration after the release of marked individuals, an estimate of male removal rate is given by the quantity $S_e/(wN_0)$, where $S_e$ is...
the cumulative number of recaptured individuals. The variance of estimate is given by the delta method using the variance for the binomial variables. However, in several years, we examined the trap catches only at two and four days after the release of insects. Hence, we estimate the parameters, \( \lambda \) and \( \delta \), by using the maximum likelihood method, by assuming that the number of captured individuals follows the Poisson distribution of the predicted mean. We used statistical software, JMP, for performing the nonlinear maximum likelihood estimation (SAS Institute, 2005). We assume that \( \lambda \) and \( \delta \) are kept constant across years, for convenience.

**Seasonal fluctuation of trap catches by monitoring traps.** Seasonal trends in captures of the click beetle were recorded by using the same funnel-vane traps with synthetic sex pheromone at four sites (Nobarugoshi, Sugama, Nakayama and Bora) on Miyako Island from mid-January to late-May in the years 2002–2006 by the Miyako Branch of the Okinawa Prefectural Plant Disease and Insect Control Station, Miyakojima, Japan. Miyako Island and Kurima Island are located at a short distance (1.6 km in distance). Hence, the seasonal population trends will be expected to be similar.

**Meteorological data.** Weather data during the survey periods were obtained from the Miyako Branch of the Okinawa Meteorological Station (Table 1).

### RESULTS

**Seasonal fluctuation of trap catches by monitoring traps**

In the seasonal male trap catches by monitoring traps on Miyako Island, the peaks of occurrence fluctuated somewhat year by year (Fig. 3). The most early peak of occurrence was observed mid-February 2005, and late occurrence was observed in early March 2004. Generally male catches started from mid- to late January, peaked from

<table>
<thead>
<tr>
<th>Days from the 1st release</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
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<tr>
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<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>18–22 Feb. 2002</td>
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<tr>
<td>Mean temperature (°C)</td>
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<td>16.8</td>
<td>16.6</td>
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<td>20.5</td>
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<td>NE</td>
<td>NE</td>
<td>SE</td>
<td>SE</td>
</tr>
<tr>
<td>Mean wind velocity (m/s)</td>
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<td>4.9</td>
<td>3.8</td>
<td>2.8</td>
</tr>
<tr>
<td>Rainfall (mm/d)</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>17–21 Feb. 2003</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean temperature (°C)</td>
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<td>18.7</td>
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<td>NE</td>
<td>NNE</td>
<td>NNE</td>
<td>SSE</td>
</tr>
<tr>
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<td>2.1</td>
<td>4.3</td>
<td>6.4</td>
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<td>0</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>16–20 Feb. 2004</td>
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<tr>
<td>Mean temperature (°C)</td>
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<td>18.3</td>
<td>19.3</td>
<td>20.0</td>
<td>21.0</td>
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<tr>
<td>Dominant wind direction</td>
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<td>NE</td>
<td>ESE</td>
<td>SSE</td>
<td>E</td>
</tr>
<tr>
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<td>2.4</td>
<td>3.1</td>
<td>3.5</td>
<td>4.9</td>
</tr>
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<td>0</td>
<td>12.5</td>
<td>0</td>
<td>0</td>
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<td>14–18 Feb. 2005</td>
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<tr>
<td>Mean temperature (°C)</td>
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<td>22.5</td>
<td>23.8</td>
<td>22.5</td>
<td>19.7</td>
</tr>
<tr>
<td>Dominant wind direction</td>
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<td>SSE</td>
<td>S</td>
<td>S</td>
<td>WSW</td>
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<tr>
<td>Mean wind velocity (m/s)</td>
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<td>4.9</td>
<td>4.9</td>
<td>4.1</td>
<td>4.7</td>
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<td>Rainfall (mm/d)</td>
<td>18</td>
<td>41</td>
<td>—</td>
<td>0</td>
<td>36</td>
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<tr>
<td>21–25 Feb. 2006</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Mean temperature (°C)</td>
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<td>22.5</td>
<td>20.0</td>
<td>20.0</td>
<td>22.3</td>
</tr>
<tr>
<td>Dominant wind direction</td>
<td>NE</td>
<td>NNE</td>
<td>N</td>
<td>NE</td>
<td>ENE</td>
</tr>
<tr>
<td>Mean wind velocity (m/s)</td>
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<td>3</td>
<td>5.4</td>
<td>5.4</td>
<td>5.4</td>
</tr>
<tr>
<td>Rainfall (mm/d)</td>
<td>0</td>
<td>0</td>
<td>4.5</td>
<td>45</td>
<td>18</td>
</tr>
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</table>
mid-February to early March and approached termination around early April.

Estimations of population density

Estimates of the density ranges per unit agricultural area (180 ha) from 2002 to 2006 were 8,634–33,761 males by Jolly-Seber method, 11,360–72,939 males by Yamamura method, 6,452–71,515 males by Yamamura B method, and 43,406–64,301 males by Petersen method (Table 2). In the survival rates, those exceeding 1 were omitted from the discussion. Estimates of the two-day survival rates from 2002 to 2006 were 0.144–0.700 by Jolly-Seber method, 0.218–0.534 by Yamamura method, and 0.110–0.648 by Yamamura B method in range (Table 3).

Mean dispersal distance

The arithmetic mean distances (m) of recaptured beetles during two days after the release were 264.8, 222.4, 234.7, and 262.6 in 2002, 2003, 2005, and 2006, respectively (Table 4). The maximum observations (m) of dispersal distance were 984.4, 775.7, 809.9, and 715.3 in 2002, 2003, 2005, and 2006, respectively. Several meteorological factors such as temperature, rainfall, and wind velocity, may influence the mean dispersal distance, but we could not find clear influence of these factors that are listed in Table 1. The estimates of parameters ($\hat{D}$/SE) obtained by using all data were $\hat{D} = 6.57 \times 10^{-5} \pm 0.75 \times 10^{-5}$ and $\delta = 0.34 \times 10^{-5} \pm 0.06 \times 10^{-5}$. The estimate of the natural mean dispersal distance ($\pm$SE) was 193.8 ± 11.0 m. The proportion of underestimation that is given by Eq. (2) was 0.025.

Estimation of male removal rate

Maximum likelihood estimates (and their 95% profile likelihood confidence intervals) of instantaneous mortality that were obtained from Eq. (6) were as follows: $\hat{\lambda} = 0.259$ (0.210–0.325) and $\delta = 0.039$ (0.035–0.044). The maximum likelihood es-

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Table 2. Estimations of absolute population ($\pm$SE) of *M. sakishimensis* males on Kurima Island (agricultural area: 180 ha) by the Jolly-Seber, Yamamura, Yamamura B and Petersen methods. The column of $\mu$ indicates the average number of captured wild individuals per day during the two days' recapture.

<table>
<thead>
<tr>
<th></th>
<th>Jolly-Seber</th>
<th>Yamamura</th>
<th>Yamamura B</th>
<th>Petersen</th>
<th>$\mu$</th>
</tr>
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<tbody>
<tr>
<td>2002</td>
<td>33,761 ± 11,372</td>
<td>20,591 ± 10,102</td>
<td>67,955 ± 32,610</td>
<td>64,301 ± 8,519</td>
<td>2,058</td>
</tr>
<tr>
<td>2003</td>
<td>29,727 ± 11,686</td>
<td>72,939 ± 33,419</td>
<td>11,268 ± 950</td>
<td>43,406 ± 3,912</td>
<td>4,875</td>
</tr>
<tr>
<td>2004</td>
<td>33,494 ± 8,406</td>
<td>14,960 ± 5,603</td>
<td>71,515 ± 27,180</td>
<td>46,269 ± 4,746</td>
<td>2,478</td>
</tr>
<tr>
<td>2005</td>
<td>33,127 ± 6,637</td>
<td>11,360 ± 1,561</td>
<td>14,965 ± 2,958</td>
<td>58,489 ± 5,749</td>
<td>5,000</td>
</tr>
<tr>
<td>2006</td>
<td>8,634 ± 3,061</td>
<td>13,033 ± 5,577</td>
<td>6,452 ± 1,766</td>
<td>45,799 ± 4,580</td>
<td>2,397</td>
</tr>
</tbody>
</table>
The estimated male removal rate was \( \hat{\delta}(\hat{\lambda} + \hat{\delta}) = 0.131 \) (0.117–0.147).

Annual fluctuation of total trap catch

Cumulative number of beetles captured per trap in the agricultural area on Kurima Island was 333.1 in 2002 (Fig. 4). It was nearly doubled in 2005 (653.3). In 2006, however, it declined to a level similar to that in 2002 (392.1).

### DISCUSSION

Density estimation by multiple methods

We estimated the population by using four methods for mark-recapture data. The weather of Miyako Island in mid-February is highly variable. Temperatures fluctuated widely within a short period (Table 1). The survival rate of released insects and the probability of capture are influenced by meteorological factors such as air temperature as well as biological factors such as the viability of released insects, and hence the methods of estimation should be changed depending on the situations. The Petersen method is based on the assumption that there is no mortality. As is expected from the theoretical basis, the Petersen method produced generally higher estimates than other methods (Table 2). The Yamamura B method is based on the assumption that capture probability is constant during the experiment, and hence the estimate is not reliable under conditions with severe temperature fluctuations, because we empirically know that the efficiency of pheromone traps is much influenced by the temperature. The estimates from Yamamura B method in 2002 and 2004 were actually higher than those of other estimates (Table 2). More marked beetles (first release) were recaptured in the second survey than in the first survey in 2002 and 2004. The low temperatures on the days of first release and next day may have suppressed the flight activities of the beetles. The estimates of survival rate by Yamamura method are also not reliable (Table 3).

In contrast, Yamamura method is not influenced by the change in the probability of capture that may be caused by temperature fluctuation. However, the estimate becomes biased if the field population is increasing or decreasing. The estimate by Yamamura method in 2003 was higher than those of other estimates (Table 2). The survival rate in 2003 estimated by Yamamura method was larger than 1 (Table 3). The captured number of field individuals in 2003 at the first and second recaptures had an abrupt decrease from 9,477 to 273. The large estimate by Yamamura method in 2003 indicates that the population sharply decreased stochastically during the experimental period in that year, although the emergence of population may have continued after this period as suggested by the trap data in 2003 in Miyako Island in Fig. 3.
The estimate by Jolly-Sever method is influenced neither by the fluctuation of capture probability nor by the fluctuation of the field population, but influenced by the heterogeneity of released individuals. The estimates of survival rates by this method were larger than 1 in 2004 and 2005 (Table 3), suggesting that the survival rates of the individuals of the second releases were lower than those of the first releases in 2004 and 2005. Yamamura method is more reliable than Jolly-Seber method if the survival rates of released individuals are different depending on the date of release. Thus, we should tentatively adopt the estimates by Jolly-Seber method in 2002, 2003, and 2006, but use the estimates by Yamamura method in 2004 and 2005. Consequently, the estimates of male populations from 2002 to 2006 were 33,761, 29,727, 14,960, 11,360 and 8,634, respectively. The estimated population indicated a trend of decrease during the 5 years.

The column of $u$ in Table 2 indicates the average number of captured wild individuals per day during the two days’ recapture. Then, we can estimate the proportion of captured wild individuals per day of recapture, by dividing $u$ by the estimate of population. The estimates of the proportion from 2002 to 2006 were 0.061, 0.164, 0.165, 0.440 and 0.278, respectively. The trap efficiency fluctuated considerably. The efficiency will be influenced by meteorological factors. The correlation coefficient between the proportion of capture and meteorological factors in Table 1 (average of 5 days) were as follow: mean temperature, $r=0.925$ ($p=0.024$); mean wind velocity, $r=0.447$ ($p=0.541$); rainfall, $r=0.965$ ($p=0.008$). Thus, high correlation was detected for both mean temperature and rainfall. However, the direct influence of rainfall is uncertain because there is a high correlation between mean temperature and rainfall ($r=0.941$, $p=0.017$). The simple average of the proportion of captured individuals over 5 years was 0.222. This quantity will be much related to the male removal rate. However, this quantity will not be directly comparable to the estimate $\hat{\delta} = 0.131$, because the estimates of the proportion of captured individuals are based on the estimates of population; they were estimated by using the discrete approximation of a continuous removal process.

Comparison of densities between congenerous species

Kishita et al. (2003) reported the density of a congenerous species, M. okinawensis, on Iki Island that is connected to Okinawa Island by bridges. We can compare the natural density of these species by using the mean density estimated by Jolly-Seber method in the first year of experiment. The estimate of mean density of M. sakishimensis on Kurima Island in 2002 (187.6 males/ha) was 1.6 times larger than that of M. okinawensis on Iki Island in 2000 (114.4 males/ha). The wireworms feed exclusively on sugarcane. Hence we should compare the density per unit area of sugarcane field. In this case, the estimate of mean density of M. sakishimensis in the Kurima Island (595.4 males/ha) was almost equivalent to that of M. okinawensis on Iki Island (557.9 males/ha). The ratooning rate was 2–3% in Miyako Island, 7.9% in Iki Island, while it was about 70% in Okinawa Island in 2000 (Tokeshi, 2006). The small ratooning rates in Miyako and Iki Islands may be due to the high densities of wireworms in these islands, although it may be partly due to the inferior quality of soil.

Interspecies comparison of dispersal distance

Yamamura et al. (2003) estimated the lifetime natural mean dispersal distance for M. okinawensis on Iki Island. The estimate ($\pm SE$) was 143.8 ± 7.6 m. The current estimate for M. sakishimensis on Kurima Island, 193.8 ± 11.0 m, is larger than that of M. okinawensis. If we use the asymptotic normality of estimates, the difference of the two estimates, 193.8 – 143.8 = 50.0 m, follows a normal distribution with a standard deviation that was estimated from two standard errors, $\sqrt{7.6^2 + 11.0^2} = 13.4$. Then, we can find that the natural mean dispersal distance of M. sakishimensis is significantly larger than that of M. okinawensis ($p<0.0002$). However, we should carefully use the estimate of natural mean dispersal distance, because the estimate is based on the assumption of normal diffusion with constant mortality. An increasing amount of literature indicates the importance of anomalous diffusion (Yamamura et al., 2007). Klafter and Sokolov (2005) described the current knowledge on dispersal as ‘anomalous is normal!’’ We used the cumulative number of recaptured insects within 2 or 4 days after release as the substitute of the total cumula-
tive recapture. This substitution may also cause some bias.

Nagayama et al. (unpublished) estimated the natural mean dispersal distance of another pest species living in the same fields on Kurima Island, the green chafer Anomala albopilosa sakishimana. The estimate of the average dispersal distance after one day was 1,200 m, much larger than those of the two click beetle species. The wireworms live in sugarcane fields and the adults remain to mate there (Nagamine and Kinjo, 1981). The click beetle may not need a strong flight capability because the habitats of larvae and adults are the same.

Comparison of male removal rate

The estimate of male removal rate (and the 95% profile likelihood confidence interval) in the mass-trapping experiment for M. okinawensis on Ikei Island was 0.345 (0.300–0.418) (Arakaki et al., 2008). The current estimate for M. sakishimensis on Kurima Island, 0.131 (0.117–0.147), is much smaller than that of M. okinawensis on Ikei Island. The density of traps was quite different between the two experiments for congeneric species, due to the difference in the cost of pheromone lures. On Ikei Island, 725 traps (in 2000) or 870 traps (from 2001 to 2005) were uniformly placed over an agricultural area of 81.4 ha. On Kurima, 100 traps were placed over an agricultural area of 180 ha. The densities of traps were 10.6/ha and 0.5/ha, respectively. The densities of traps are thus 20 times different between the two experiments, but the male removal rates are only about 2.5 times different. Obviously, trap efficiency was not proportional to trap density. It is currently not known whether this difference is due to the density-dependent efficiency of traps or behavioral differences in the species. Density-dependent efficiency of traps is likely to have at least some extent. Pheromone traps have two effects on field populations: disruption of the ability to locate pheromone, and the direct mortality by trapping. The latter effect occurs only when the insects can precisely locate the traps, but the ability to do this may be disrupted by the traps themselves if trap density is high.

The scaled natural mortality and scaled artificial mortality that were estimated for obtaining the dispersal distance for M. okinawensis were $\hat{\lambda} = 0.348 (0.216–0.520)$ and $\hat{\delta} = 0.183 (0.153–0.227)$, respectively (Arakaki et al., 2008). The ratio, $\hat{\delta}_D/\hat{\lambda}_D$, is thus almost equivalent to the ratio $\hat{\delta}/\hat{\lambda}$, although they are calculated from much different (spatial and temporal) sets of information. In contrast, for M. sakishimensis, we have the estimates, $\hat{\lambda}_D = 6.57 \times 10^{-5} \pm 0.75 \times 10^{-5}$, $\hat{\delta}_D = 0.34 \times 10^{-5} \pm 0.06 \times 10^{-5}$, $\hat{\lambda} = 0.259 (0.210–0.325)$, and $\hat{\delta} = 0.039 (0.035–0.044)$. The ratio, $\hat{\delta}_D/\hat{\lambda}_D$, is fairly different from the ratio $\hat{\delta}/\hat{\lambda}$. The problem in the substitution in estimating $\lambda_D$ and $\delta_D$, which we mentioned above, may be a potential cause of this discrepancy.

Influence of male removal on the reduction of field population

If the removal of males by mass trapping was effective in suppressing the population of M. sakishimensis on Kurima Island, a decrease of trap catches will occur two or three years after the start of control. The cumulative catch per trap in 2006 (392.1) is rather slightly larger than that in the first year of control (Fig. 4). However, the dynamics of trap catches will not exactly indicate the dynamics of true population; the trap catches fluctuate due to the fluctuation of the efficiency of traps. The estimates of population, that were obtained by Jolly-Seber method and Yamamura method, indicated a trend of decrease from 2002 to 2006, although these estimates correspond to the population during a short period (i.e., during the 5 days experiment). A similar phenomenon was observed in the mass-trapping experiment for M. okinawensis conducted on Ikei Island (Arakaki et al., 2008); the population consistently decreased in Ikei Island through the experiment, although the proportion of male removal (0.345 or 0.319) and the proportion of mated females (73.9% in 2001 and 85.7% in 2002) seem not enough for causing the decrease. Another mechanism such as the suppression of oviposition behavior of females by pheromone substance should be considered to explain the decreases of population.

The density of traps is also critical in reducing the population. In Miyako Island and other islands, most people calculate the required trap density by using the manufacturer standard for Sakimeranure: 1 trap per 1 to 1.5 hectare (=0.67 to 1 trap
per hectare, Nakamori, 2000). However, the ‘density’ is not clearly defined in this ‘standard’. Two kinds of interpretation arise for the definition of trap density: (1) the number of traps divided by the area of sugarcane field, or (2) the number of traps divided by the total area of cultivation including all crops. Unfortunately, the former interpretation has been adopted by the local officers. In Miyako Island, half of the sugarcane fields are newly planted in summer every two years in turn (in two-year cyclic cultivation). To make matters worse, traps are applied only for the newly planted fields where the female adults aggregate for their oviposition (Yasuda and Hokyo, 1983). The same cultivation system has been used in Kurima Island, the total area of sugarcane fields in 2002 was 56.7 ha (newly planted fields 27.9 ha, and harvest fields 28.8 ha). Hence 0.67×27.9=19 traps had been used until the year before our experiment. However, this calculation seems not fully correct. The effectiveness of pheromone traps will be determined by the number of traps divided by the total area of activity of adult individuals. The area of mating activity of adults will be more appropriately given by the total area of cultivation including all crops than the area of sugarcane cultivation. It will be a clear difference between pheromone traps and pesticides: pesticides are usually applied only for the area where sugarcane plants are cultivated, because the pesticides usually attack the pests on the crops. The total area of cultivation is 180 ha in Kurima Island. Hence, the trap density per area of cultivation was only about 19/180=0.11 traps/ha until the year before our experiment. The meaning of trap density should be widely discussed and recognized.

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