Estimating Populations of *Idiarthron subquadratum* (Orthoptera: Tettigoniidae) Using Mark-Recapture Methods in Coffee Plantations in Chiapas, Mexico

JOSÉ A. ZÚÑIGA,[1,2] JUAN F. BARRERA,[1,3] JAVIER VALLE,[1] and TREVOR WILLIAMS[1]

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ABSTRACT *Idiarthron subquadratum* (Orthoptera: Tettigoniidae) is a sporadic pest of coffee in parts of Mesoamerica. Mark-recapture techniques were employed to determine the adult population size in coffee plantations in the municipality of Siltepec, Chiapas, Mexico, where the insect has caused crop losses of around 50% over the past decade. Eight experimental blocks 50 by 50 m were defined in an area of 2,500 m^2. A trap was designed consisting of a bamboo tube 30 cm in length and closed at one end. Trials indicated that insect trapping efficiency was not improved by the presence of baits. Traps placed above the ground in coffee bushes or as banana leaves placed on the side of an experimental gauze cage captured significantly more *I. subquadratum* individuals than traps placed on the ground. Tests with different types of paint combinations for marking insects revealed that nitrocellulose paint was durable, water-resistant and nontoxic to *I. subquadratum.* Mark-recapture experiments were performed at 48-h intervals over a 1-mo period. Concurrently, direct nocturnal observations of *I. subquadratum* individuals feeding on coffee leaves and berries were made on four occasions during the study period. The prevalence of *I. subquadratum* feeding damage was also quantified at three sample dates during the study. Jackson's negative and positive index, Fisher-Ford model, Lincoln-Petersen index, and Jolly-Seber's stochastic model gave statistically similar mean population estimates. All of these mark-recapture models were also statistically similar to estimates generated by direct nocturnal counts of insects observed feeding on coffee bushes. In contrast, Bailey's triple capture model gave a population estimate significantly lower than the other models. *I. subquadratum* feeding damage to coffee berries was significantly greater in blocks interplanted with banana. We conclude that mark-recapture methods combined with analysis using the Lincoln-Petersen model are simpler and less time consuming than direct nocturnal observations and give quantitatively similar population estimates.

RESUMEN *Idiarthron subquadratum* (Orthoptera: Tettigoniidae) es una plaga esporádica del café en algunas partes de Mesoamérica. Técnicas de marca-recaptura se usaron para determinar el tamaño de población del adulto en cafetales del municipio de Siltepec, Chiapas, México donde el insecto ha causado pérdidas al cultivo de alrededor de 50% durante la década pasada. Ocho parcelas experimentales de 50 por 50 m fueron definidos en un área de 2,500 m^2. Se diseñó una trampa consistente en un canuto de bambú de 30 cm de longitud y cerrado por uno de sus extremos. Pruebas indicaron que la eficiencia del trampeo del insecto no fue mejorada por la presencia de cebos. Las trampas puestas sobre plantas de café u hojas de plátano puestas sobre un lado de una caja experimental de tela fina capturaron significativamente más individuos de *I. subquadratum* que trampas puestas sobre el suelo. Pruebas con diferentes tipos de combinación de pinturas para marcar insectos revelaron que la pintura de nitrocelulosa fue más durable, resistente al agua y no tóxica a *I. subquadratum.* Los experimentos de marca-recaptura se realizaron a intervalos de 48-h durante un mes. Al mismo tiempo, se hicieron observaciones en la noche cuando los individuos de *I. subquadratum* se alimentaban de hojas y frutos del café en cuatro ocasiones durante el periodo de estudio. La prevalencia del daño de la alimentación de *I. subquadratum* también fue cuantificada en tres fechas de muestreo durante el estudio. Los índices positivo y negativo de Jackson, el modelo de Fisher-Ford, el índice de Lincoln-Petersen, y el modelo estocástico de Jolly-Seber dieron estimaciones de las medias de la población estadísticamente similares. Todos estos modelos de marca-recaptura fueron también estadísticamente similares a las estimaciones obtenidas con los conteos nocturnos de los insectos observados alimentándose de las plantas de café. En contraste, el modelo de la triple captura de Bailey dio una estimación de la población significativamente más baja que los otros modelos. El daño de la alimentación de *I.*

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[1] El Colegio de la Frontera Sur, Apartado Postal 36, Tapachula 30700, Chiapas, Mexico.
[2] Universidad de San Carlos de Guatemala, Guatemala, C.A.
[3] E-mail: jbarrera@tap-ecosur.edu.mx.

subquadratum a los frutos del café fue significativamente más grande en las parcelas intercaladas con plátano. Concluimos que los métodos de marca-recaptura combinados con el análisis del modelo de Lincoln-Petersen son más simples y consumen menos tiempo que las observaciones nocturnas y dan estimaciones de la población cuantitativamente similares.

KEY WORDS *Idiarthron subquadratum,* population estimation, sampling, trapping, mark-recapture, coffee pest

Idiarthron subquadratum Saussure & Pictet, commonly known in Mesoamerica as the "Chacuatete," is a univoltine insect that feeds nocturnally on coffee plants (*Coffea* spp.) (Le Pelley 1968). A number of other plants found in coffee plantations including banana (*Musa* spp.), orange (*Citrus* spp.), chayote (*Sechium edule* Sw.), and squashes (*Cucurbita* spp.) may also be attacked. The females are large, measuring some 50 mm from head to the tip of the saber-shaped ovipositor. During the day, the nymph and adult *I. subquadratum* hide in tree holes or beneath fallen leaves, especially those of banana. Eggs are laid in the soil in groups of several dozen at the beginning of the dry season, between November and December each year. The nymphs begin to emerge at the start of the following rainy season between May and June. Adults appear in October and mating is observed to occur in the same month. By January, the majority of adults are dead from the cool temperatures that descend over the upland coffee-growing areas at that time (Reyes de Romero 1986; J.F.B., unpublished data).

Nymph and adult *I. subquadratum* feed on buds, leaves, and berries of the coffee bush; but in general this insect is not considered an economically important pest. However, in certain coffee-growing regions including El Salvador (ISIC 1989), Guatemala (ANACAFE 1998) and Mexico (INMECAFE 1990) there have been reports of sporadic outbreaks of this insect causing serious crop losses. For example, in the municipality of Siltepec, Chiapas, Mexico, *I. subquadratum* has been causing losses in the yield of coffee beans often exceeding 50% during most of the past decade (1990–2000) (Barrera 1998). Approximately 1,000 ha of coffee plantation and surrounding woodlands are currently infested by this pest in Siltepec (J.F.B., unpublished data).

Due to the paucity of information concerning the pest status of *I. subquadratum* in coffee plantations and the lack of studies on the ecology and control of this insect, a project was initiated to obtain information on the behavior, habits, and possible methods of biorational control in the coffee plantations of Chiapas, Mexico (Barrera 1998). The current study represents part of this project with the objective of estimating the size of the *I. subquadratum* population in the plantations of small-scale coffee producers in Siltepec, using mark-recapture techniques.

Mark-recapture seemed to be appropriate for this study because insects are inactive during the day making direct counts difficult, adult insects are large and can be marked with relative ease, and because insects can be captured by placing traps under fallen leaves or in the dark interior canopy of coffee bushes. Moreover, a number of different mark-recapture models were applied to the data to determine the relative precision of each compared with a direct counting method.

Materials and Methods

Study Area. The coffee plantations used in this study were between the communities of Vega de Guerrero (15° 34′ 12.4″ N, 92° 20′ 45.9″ W) and Vicente Guerrero (15° 34′ 35.2″ N, 92° 20′ 54.8″ W) at an altitude of ≈1000 m a.s.l. in the municipality of Siltepec, Chiapas, Mexico. The climate in Siltepec is warm and humid with a mean annual temperature of 21.8°C and an annual rainfall of 2,637 mm, most of which falls in the rainy season from May to November (INEGI 1994). Coffee (*Coffea arabica*) is grown along the fertile river valleys that descend from the mountains. A diversity of shade trees are also planted among the coffee bushes to provide wood and fruits, mainly banana, plantain and citrus. Maize and beans are grown at higher altitudes.

Selection of a Suitable Marker Substance. A number of easily available paints were tested for their toxicity and their ability to persist on the cuticle of the insect. These were fluorescent acrylic paint (Química Mexicana Gama Color), a water-based white typewriter correcting fluid, (Industrias Kores, Mexico City), a 1:1 mixture of fluorescent acrylic paint and typewriter correcting fluid, a 1:1 mixture of typewriter correcting fluid and artificial food color (McCormick-Herdez, Mexico City), nitrocellulose lacquer (Acuario S.A. de C.V., Mexico City) and a cellulose paint (Hansa Lloyd, Mexico City). Field-collected adult insects were marked on the pronotum with a drop of paint applied with a toothpick ($N = 25$ for each type of paint). A control group of 25 insects were handled but not marked. Each marked insect was placed individually in a plastic cup (125 ml capacity) and sealed with a muslin gauze and held at 27°C, 70% RH, and a photoperiod of 12:12 (L:D) h. Insects were offered leaves of *Commelina* sp. daily. The number of dead insects or insects that had lost their paint mark was recorded each day until death. Dead insects were immediately placed in a cup containing water for a period of 24 h to determine the water-resistance of the paint mark. Insect longevity in each treatment was compared by Kruskall-Wallis test with a critical P value of 0.05.

Design and Placement of a Suitable Trap. Given the behavior of hiding in dark places during the day, a trap was designed consisting of a 30-cm piece of bamboo closed at one end. Similar traps had been tested previously in El Salvador (ISIC 1990). Tests comparing unbaited traps with traps baited with maize grain and natural vegetation revealed no significant difference in the prevalence of capture (J.F.B., unpublished data). A study was performed to determine the most suitable location for traps placed in coffee bushes. Nine bushes bearing coffee berries were individually covered with fine nylon gauze cages and at 1000 hours, 20 *I. subquadratum* adults were introduced into each cage. Five hiding places were offered in each cage: (1) a bamboo tube placed at the top of the coffee plant, (2) a bamboo tube placed in the center of the coffee plant, (3) a bamboo tube placed on the soil under the coffee plant, (4) a banana leaf placed against the side of the cage, (5) a banana leaf placed on the ground. Two days later, the percentage of *I. subquadratum* adults observed in each of the hiding places was recorded. Percent data were arcsine transformed and subjected to analysis of variance (ANOVA) followed by mean separation using the Tukey test ($P = 0.05$).

Response of *I. subquadratum* to Previously Inhabited Traps. This study was performed to determine whether traps previously inhabited by *I. subquadratum* were more or less attractive to unrelated *I. subquadratum* adults. This test was necessary to determine whether or not traps could be reused during the study period. Consequently, nine fruiting coffee bushes were covered with fine nylon gauze cages. Two bamboo traps were placed within each cage, one of which had been inhabited by 10 *I. subquadratum* adults the previous night and another that had not been inhabited and moreover had been washed repeatedly with water and left to dry in the sun before being placed inside the cage. Ten recently captured *I. subquadratum* adults were introduced into each cage at 0800 hours; the location of each insect was recorded the following day. The study was repeated 60 times.

Field Experiment to Estimate the *I. subquadratum* Population. Eight blocks of coffee were selected within a 2-ha area close to Siltepec during the period of ripening and harvesting from 4 to 30 October 2000. Experimental blocks were 50 by 50 m in area with a distance of 100–1,000 m between blocks. Four of these areas were manually cleared of banana plants while banana plants were conserved in the remaining four blocks. Information on the *I. subquadratum* population size was collected by direct counting and mark-recapture studies.

Direct Counting. Nocturnal counts of *I. subquadratum* were performed using flashlights by recording the number of individuals observed feeding on coffee bushes. The number of insects of each sex and development stage (adults and nymphs) was noted for 100 randomly selected coffee bushes in each of the eight experimental blocks. Direct observations began at 2100 hours and ended around 0200 hours. Counts were made once a week for 4 wk (6, 13, 21, and 29 October). Mean number of insects per plant from each sample date were subjected to ANOVA and Tukey test. The mean (m) and variance (s^2) of insects per plant in each block and in each treatment (with or without banana plants) were calculated to give a series of 32 data pairs which were used to calculate the coefficients a and b from Taylor's power law: $\log s^2 = \log a + b \log (m)$, where b represents the index of aggregation ranging from zero for a completely uniform distribution to infinity for a completely aggregated distribution. When the distribution is random, $a = b = 1$ (Taylor 1961). The significance of the b value and its associated 95% CL was performed following the procedure described in Sokal and Rohlf (1987). To compare direct counting population estimates with mark-recapture models results, the mean insect density for each sample date was calculated as mean number of insects per plant multiplied by the number of coffee bushes per area; the study area of 2 ha contained an estimated density of 1,800 coffee bushes/ha or 3,600 bushes in total.

Mark-Recapture Study. Nine bamboo traps were placed in the interior of individual coffee bushes at equidistant intervals of 14.3 m in a 3 × 3 grid within each of the eight blocks. Total number of traps was 56. Traps were not moved during the course of the study. Forty-eight hours later, traps were checked and the number and sex of adults and nymphs was registered. All the captured insects were marked on the pronotum with nitrocellulose lacquer and immediately released onto a coffee bush, 3–5 m away from the trap in which the insect was found. In total, 13 subsequent samples at 48-h intervals between 6 and 30 October were marked with different colors (while, red, blue, or yellow) or combinations of these colors. Population estimations and additional parameters were obtained using the Lincoln-Petersen index, Jackson's positive and negative models, Bailey's triple capture model, the Fisher-Ford model and the stochastic Jolly-Seber model. Detailed principles and analytical procedures for each of these models are given in Southwood (1978), Blower et al. (1981), Service (1993), Vera et al. (1997). To compare the different models, population estimates from each model were averaged to calculate the mean, which was subsequently transformed by $\sqrt{x}$ and subjected to ANOVA followed by mean separation using Tukey test at the 5% level.

Feeding Damage. *I. subquadratum* causes characteristic feeding damage to leaves and coffee berries. In total, 90 coffee bushes in each of eight experimental block were randomly selected. From each bush, one branch from the central third of the bush was randomly selected and the number of damaged and undamaged leaves and berries was recorded. A total of three such evaluations was performed on 5, 17, and 29 October. The proportion of damaged leaves and berries in blocks with or without banana plants was arcsine transformed and compared by *t*-test.

Climatological data were gathered during the field experiment including rainfall, mean temperature and relative humidity on a daily basis.

Idiarthron subquadratum voucher specimens were deposited in USDA Systematic Entomology Laboratory, Washington, DC, and in the Insect Collection held at El Colegio de la Frontera Sur, Tapachula, Chiapas, Mexico.

Table 1. Abundance of *I. subquadratum* adults found in five different types of refuges in caged experiments under field conditions

Refuge	Mean % of insects
Bamboo tube at top of coffee bush	15.0 ± 4.1a
Bamboo tube in centre of coffee bush	13.8 ± 3.1a
Bamboo tube on soil under coffee bush	1.1 ± 0.7b
Banana leaf resting against cage wall	8.3 ± 2.2a
Banana leaf on soil surface	0.00b

Means ± SEM followed by the same letter were not significantly different, Tukey test ($P < 0.05$). $n = 9$ replicates, 20 insects per replicate.

Results

Selection of a Suitable Marker Substance. There were no significant differences in longevity of *I. subquadratum* treated with different types of paints ($H = 5.6$, $P = 0.47$), indicating that none of the paint marks were toxic to this insect. Fifty percent mortality occurred at 18–36 d after marking. Between 92 and 80% of the insects marked with acrylic paint, with or without typewriter correcting fluid, respectively, lost their marks by the time they died. In contrast, all the other types of paint were retained by insects until their death. Paint marking caused no obvious changes in the behavior or activity of marked insects compared with unmarked controls. Finally, nitrocellulose lacquer was selected as the paint mark of choice as it dried rapidly and was the only mark that did not disappear after 24 h of being submerged in water.

Design and Placement of a Suitable Trap. A significantly greater proportion of insects were found in refuges above the ground, be it in the bamboo traps at the top or in the middle of the coffee bush (13.8–15%) or on the banana leaf resting against the side of the cage (8.3%), compared with hiding places on the ground (0–1.1%) ($F = 11.4$; df = 4, 40; $P < 0.001$) (Table 1). Consequently, it was decided to adopt the bamboo trap at the center of the coffee bush as the experimental standard, given that it was durable, easy to place and check, and structurally more uniform than a banana leaf.

Response of *I. subquadratum* to Previously Inhabited Traps. Of the 600 insects used in this experiment, only 56 (9%) were found 24 h later inside a bamboo trap. Of these, 28 insects were in traps previously inhabited by *I. subquadratum* and 28 were found in clean, uninhabited traps, indicating that previous occupation by conspecifics did not render a trap more or less attractive to this insect.

Field Experiment to Estimate the *I. subquadratum* Population. *Direct Counting.* Of the 1,801 insects recorded by direct nocturnal counting, 98.4% were adults. Due to their low numbers, nymphs were excluded from the statistical analyses (Fig. 1). The adult sex ratio was ≈1:1 (51.4% male). The mean number of adults per plant increased significantly over the study period ($F = 21.2$; df = 3, 3,192; $P < 0.001$). Overall, the density of *I. subquadratum* adults was higher in blocks containing banana plants compared with blocks cleared of banana ($F = 32.3$; df = 1, 3,192; $P < 0.001$) This difference was most evident in the first (6 October) and last (29 October) counts. Estimates of b from Taylor's power law ranged between 0.699 and 0.999 for females and 0.533 and 0.746 for males, indicating that the distribution of these insects tended to be uniform rather than random (Table 2).

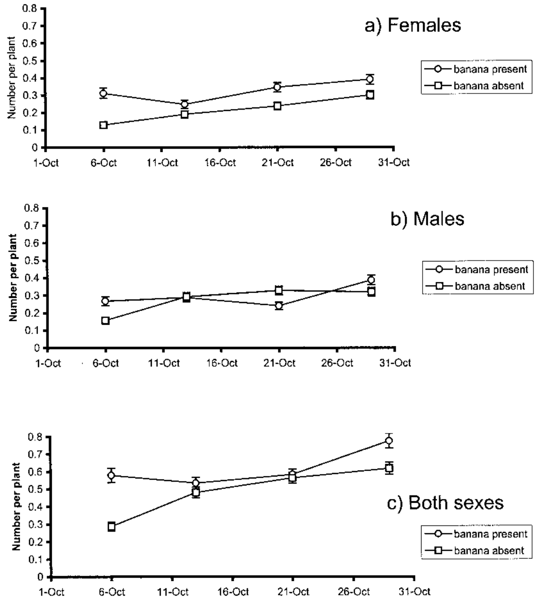

Fig. 1. Direct nocturnal counts (mean ± SE) on the number of *I. subquadratum* present on each coffee bush ($n = 400$) in plantations with or without banana plants in Siltepec, Chiapas, Mexico, during October 2000.

Mark-Recapture Study. The number of marked insects that were subsequently recaptured was low and therefore it was not possible to analyze data according to the presence or absence of banana plants. Consequently, data from each of the eight experimental blocks were pooled and sorted according to the procedures described by Jolly (1965) (Table 3). The

Table 2. Statistical results of an analysis of the distribution of *I. subquadratum* adults using Taylor's power law

Data category	Intercept (a)	Slope (b)	Range of CL95% of b	r^2	*n*
Females	1.017	0.850	0.699–0.999	0.81	32
Males	1.088	0.639	0.533–0.746	0.83	32
All adults, plantations with banana plants	0.849	0.991	0.568–1.413	0.64	16
All adults, plantations without banana plants	1.206	0.591	0.306–0.876	0.59	16
Overall totals	0.937	0.875	0.633–1.118	0.64	32

Data were obtained from direct nocturnal counts in coffee plantations with or without banana plants during October, 2000 in Siltepec, Chiapas. The coefficient b represents the index of population aggregation with 0 being uniform, and ∞ being highly clumped. When the population distribution is random $a = b = 1$. n is the number of samples; eight plantations (four with banana, four without) were each sampled four times.

Table 3. Jolly-Seber analysis of mark-recapture data on *I. subquadratum* in coffee plantations in Siltepec, Chiapas, Mexico, during October, 2000

Sample	Date	Proportion of captures	No. insects marked	Total population	Survival rate	No. new insects	Standard errors				Standard errors due to errors in the estimation of the parameter itself
i		$\hat{\alpha}_i$	$\hat{M}_i$	$\hat{N}_i$	$\hat{\phi}_i$	$\hat{B}_i$	$\sqrt{V(\hat{N}_i)}$	$\sqrt{V(\hat{\phi}_i)}$	$\sqrt{V(\hat{B}_i)}$	$\sqrt{V(\hat{N}_i\|N_i)}$	$\sqrt{V(\hat{\phi}_i) - \frac{\hat{\phi}_i^2(1-\hat{\phi}_i)}{\hat{M}_{i+1}}}$
1	6 Oct 2000	—	0.00	—	0.952	—	—	0.458	—	—	0.457
2	8 Oct 2000	0.0426	111.43	2,618.6	0.453	3,513.8	1,779.1	0.200	3,527.1	1,778.3	0.196
3	10 Oct 2000	0.0194	91.27	4,700.2	0.739	−2,777.1	3,631.6	0.312	2,718.0	3,631.4	0.310
4	12 Oct 2000	0.2037	142.14	697.8	1.060	2,268.9	326.8	0.582	1,979.8	324.5	0.582
5	14 Oct 2000	0.0652	196.20	3,008.4	0.646	−621.1	2,171.5	0.341	1,185.1	2,171.1	0.340
6	16 Oct 2000	0.1169	154.44	1,321.4	1.735	2,596.4	628.6	1.008	2,452.0	627.5	1.011
7	18 Oct 2000	0.0789	386.00	4,889.3	0.464	−191.3	3,193.7	0.288	1,078.7	3,193.3	0.287
8	20 Oct 2000	0.1019	211.57	2,077.2	0.207	102.5	1,064.3	0.091	211.2	1,063.5	0.088
9	22 Oct 2000	0.1200	64.00	533.3	0.479	69.0	225.4	0.104	97.2	224.5	0.094
10	24 Oct 2000	0.1919	62.31	324.7	0.513	73.9	110.1	0.228	66.0	109.0	0.224
11	26 Oct 2000	0.3036	73.00	240.5	1.205	677.6	109.9	0.904	630.5	109.3	0.905
12	28 Oct 2000	0.1395	135.00	967.5	—	—	819.6	—	—	819.5	—
13	30 Oct 2000	0.1778	—	—	—	—	—	—	—	—	—

—, Values could not be calculated.

number of captured insects fluctuated between 45 and 120 per sample occasion while the proportion of marked insects that were recaptured was variable but tended to increase during the study period with an average recapture prevalence of 13.0 ± 2.3% (Fig. 2). A decrease in the number of captured insects (n_i) and the concurrent increase in the proportion of recaptures ($\hat{\alpha}_i$) in the final 2–3 sample occasions had an important effect on the parameter estimates generated in the Jolly-Seber model and the population estimates (N_i) in the other models tested compared with the results of the direct counting studies (Table 4). Thus, all mark-recapture models resulted in a sub-estimation of population size after 22 October. To compare the different models, populations size estimate for each sampling date to 20 October (Table 4) were averaged to calculate the mean (Fig. 3). Considering each model in turn, the lowest estimate was obtained from Bailey's triple capture model (502 ± 226), followed by Jackson's negative model (1,167 ± 293) and then Jackson's positive model (1,300 ± 326). Direct nocturnal counts indicated a population size of 1821 ± 146 compared with 1,880 ± 578 from the Fisher-Ford model, 2,006 ± 361 from the Lincoln-Petersen model and 2,759 ± 601 from the Jolly-Seber stochastic model. All the models, except the Bailey triple capture, gave statistically similar populations estimates whereas the Bailey triple capture estimate was statistically similar to either of the Jackson models but significantly lower than the remaining models ($F = 4.82$; df = 6, 42; $P < 0.001$) (Fig. 3).

Feeding Damage. *Idiarthron subquadratum* feeding damage estimates indicated that leaves were generally more attacked (70% damage) than berries (15–45% damage). However, leaf damage remained relatively constant during the study period and was not affected by the presence or absence of banana (Fig. 4). In contrast, coffee berry damage was significantly greater in blocks with banana at the second ($t = 2.79$, df = 6, $P = 0.03$) and third sampling times ($t = 2.90$, df = 6, $P = 0.03$). The prevalence of coffee berry damage doubled during the 1-mo study period (Fig. 4b), and this increase was concomitant with an increase of about one-third of the size of the *I. subquadratum*

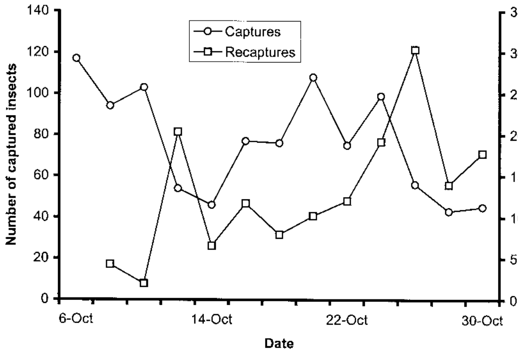

Fig. 2. Number of captured *I. subquadratum* and percentage of recaptures in an area of 2 ha of coffee plantations in Siltepec, Chiapas, Mexico, during October 2000.

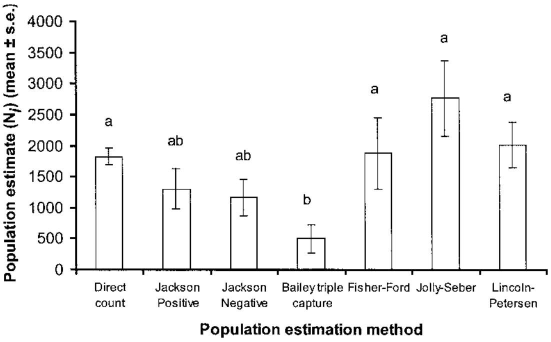

Fig. 3. Comparison of *I. subquadratum* population estimates (N ± SE) in 2 ha of coffee plantations in Siltepec, Chiapas, Mexico, using mark-recapture and direct nocturnal observations. Bars with the same letter are not significantly different (Tukey test, $P = 0.05$).

Table 4. A comparison of population estimates of *I. subquadratum* (N_i) in coffee plantations of Siltepec, Chiapas, Mexico derived from direct nocturnal counts and a selection of mark-recapture models during October, 2000

Sample	Date	Direct count[a]	Lincoln-Peterson	Jackson		Bailey's triple capture	Fisher-Ford	Jolly-Seber
				Positive	Negative			
1	6 Oct 2000	1,584.0	2,223.0	1,474.6	1,323.2	0.0	1,695.1	2,618.6
2	8 Oct 2000		3,258.7	2,596.4	2,329.7	324.6	5,274.6	4,700.2
3	10 Oct 2000		515.0	298.3	267.7	0.0	1,185.8	697.8
4	12 Oct 2000		1,269.0	1,332.2	1,195.4	0.0	1,707.6	3,008.4
	13 Oct 2000	1,872.0						
5	14 Oct 2000		3,588.0	—	—	1,501.5	830.0	1,321.4
6	16 Oct 2000		1,482.3	633.2	568.2	1,097.3	1,358.9	4,889.3
7	18 Oct 2000		2,071.0	1,467.4	1,316.7	588.6	1,109.4	2,077.2
8	20 Oct 2000		1,641.6	1,086.1	974.5	81.4	1,135.3	533.3
	21 Oct 2000	2,088.0						
9	22 Oct 2000		535.7	334.2	299.9	54.4	678.6	324.7
10	24 Oct 2000		434.1	247.8	222.3	98.2	465.5	240.5
11	26 Oct 2000		492.8	322.9	289.7	252.3	871.8	967.5
12	28 Oct 2000		659.3	518.9	465.6	—	571.0	—
	29 Oct 2000	2,556.0						
13	30 Oct 2000		195			—		—

—, Not possible to calculate value.

[a] Calculated assuming a density of 3,600 coffee bushes in an area of 2 ha.

population, estimated by direct counting over the same period (Table 4). Such a trend was not observed between coffee berry damage and mark-recapture estimates because all models sub-estimated population size after 22 October. However, we can state that population size estimates on 20 October (for all models in Fig. 3 except the Bailey model), which ranged from 1,167 ± 293 to 2,759 ± 601 insects, corresponded to a prevalence of between 27 and 41% coffee berry damage observed at the second sampling time (Fig. 4b).

During the study period a total of 300 mm of rainfall was recorded, 95% of which fell in the first 15 d of the study. The mean temperature and relative humidity were 23.8 ± 0.4°C and 75 ± 0.9%, respectively. There was little fluctuation in these parameters during the study period. Temperature (y) and relative humidity (x) were negatively correlated ($y = -0.308x + 46.92$; $r = -0.7$; $P < 0.01$).

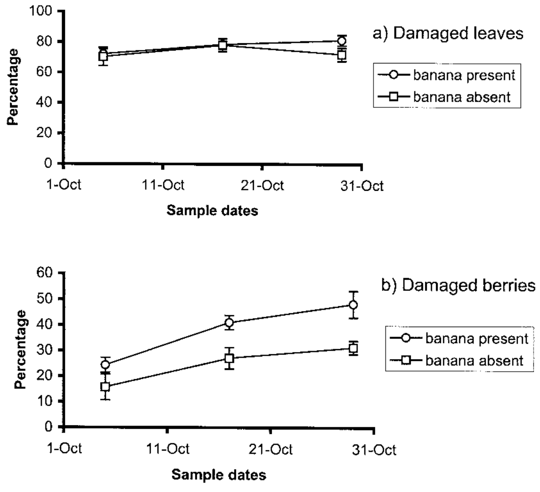

Fig. 4. Percentage feeding damage (mean ± SE) to coffee leaves and berries by *I. subquadratum* in plantations with or without banana plants in Siltepec, Chiapas, Mexico, during October 2000.

Discussion

Mark-recapture studies and direct nocturnal counts gave broadly similar estimates of the size of the *I. subquadratum* population in experimental coffee plantations in Siltepec, Chiapas, Mexico. Possibly, the most reliable of these methods was the direct count because *I. subquadratum* nymphs and adults are active at night and are relatively easy to observe with flashlight illumination when feeding from coffee leaves and berries. There exist a number of drawbacks to the direct counting method, however. These include the slow and labor intensive nature of the sampling and the undeniable risks to personal safety when walking through coffee plantations at night; plantation owners traditionally defend their properties by use of firearms, and are particularly vigilant during the coffee harvest season. Unfortunately this period coincides with the serious feeding damage caused by *I. subquadratum.* It was therefore necessary to carry out a community wide program of information related to the sampling program before the experimental period. The alternative option of performing daytime counts on *I. subquadratum* was not possible due to the logistic problems of checking all the possible hiding places in a given area. Given such problems, trap-based mark-recapture techniques seemed to be appropriate for a study of this nature.

In the selection of a suitable paint mark it was essential to choose a durable substance that would not affect the longevity or behavior of the marked individual (Southwood 1978). In all aspects, nitrocellulose lacquer was the most appropriate marker tested, being quick drying, water resistant and available in a diversity of colors. Similar findings were previously reported for grasshopper nymphs marked with cellulose paint (Blower et al. 1981). Such quick-drying paints reduce the time needed to handle the individual being marked and thus reduce the risk of physical injury to the insect.

The bamboo tube traps used in this study were originally described in El Salvador where they were baited with maize grains and natural vegetation (ISIC 1989). However, we found that these baits did not increase the probability of capture of *I. subquadratum* and tended to attract ants and rodents into the traps (J.F.B., unpublished data). The lack of captures of *I. subquadratum* in traps placed on the ground indicates that this insect is primarily arboreal. The placing of the traps in the central part of the coffee bushes was therefore suitable as an insect refuge and easy to check on each sample occasion.

Studies on the use of baited traps to monitor small mammal populations has clearly shown that certain individuals tend to become habituated to traps leading to erroneous trapping data (Poole 1974). The use of volatile chemical cues has also been reported that alter the behavior of the orthopteran *Schistocerca americana* (Bernays and Lee 1988). Consequently, great care was taken to ensure that the traps used in the current study were unchanged in their attractiveness to *I. subquadratum* through previous inhabitation by conspecific insects or vice versa. The finding that *I. subquadratum* did not respond to possible odors from previous conspecific occupants is supported by olfactometer studies in which *I. subquadratum* appeared unresponsive to odors from host and nonhost plants or conspecific individuals of either sex (Y. Henaut, unpublished data).

Direct observations indicated that the adult *I. subquadratum* population increased very slightly during the study period. The very low number of nymphs observed indicates that this population increase is likely to have occurred by immigration of adults into the study area rather than through metamorphosis of nymphs from the existing local population. Immigrating adults are likely to have arrived from surrounding woodland or from coffee plantations where food sources had been diminished by coffee harvesting.

All the mark-recapture models evaluated in our study gave statistically similar population estimates except that of Bailey's triple capture. Previous studies with mosquitoes also arrived at the conclusion that the Bailey triple capture model was a poor indicator of population size (Trpis and Hausermann 1986). The only unexpected variation in the pattern of recaptured insects occurred in the final week of the study when the number of captured insects declined and the proportion of marked insects found in traps overtly increased leading to a sub-estimation of the population size by all models.

This change in the pattern of captures could not be attributed to changes in climatic conditions as mean temperature and humidity were relatively constant and rainfall was almost nil. The phase of the lunar cycle, possibly an important factor for nocturnal organisms, also did not seem to be implicated given that the full moon occurred on 13 October and the new moon on 27 October. An alternative explanation is that the number of marked individuals was approaching saturation such that there were few unmarked insects remaining in the local population. If this is so, it suggests that *I. subquadratum* individuals tend to remain within a relatively small area presumably given the presence of an adequate supply of food. If this is so, mark-recapture studies of 2–3 wk should be sufficient to give accurate estimates of the *I. subquadratum* population rather than the month-long sampling period that we adopted. However, additional information is clearly desirable concerning the factors that affect the efficiency of the bamboo traps and the diurnal changes in the distribution of the insect that by day appears highly gregarious while hiding in leaf or tree hole refuges. In contrast, at night the insect is a clearly solitary feeder that tends to distribute itself in a uniform manner, suggesting competition for resources, be they food, space or mating opportunities (Rabinovich 1980).

It became apparent during this sampling program that to determine the effect of banana plants on the size of the *I. subquadratum* population, it would be necessary to double the density of traps in each experimental block. The low capture efficiency (≈13%) meant that few marked individuals were recaptured and therefore contributed to population size estimates. This is a recognized problem in mark-recapture studies (Hayes 1991).

Despite the limitations mentioned above, we consider mark-recapture methods to be a useful alternative to traditional population estimation techniques combined with the Lincoln-Petersen model that gave an accurate population estimate. This model has a number of advantages including analysis of samples in periods during which moderate changes occur in the total population size (Blower et al. 1981), and simplicity in data collection and in the calculation of parameter estimates (Poole 1974, Southwood 1978, Service 1993).

Feeding damage to coffee berries, but not leaves, increased during the study period, indicating that berries were more attractive to *I. subquadratum* adults. According to our estimates, a density of 0.78 *I. subquadratum* per coffee bush can result in damage to 48% of the berries. If these density and damage estimates are realistic, then the *I. subquadratum* population is likely to be the pest responsible for the ≈50% losses in yields reported by coffee growers in Siltepec.

Coffee interplanted with banana suffered more damage at the end of the study period than coffee grown in the absence of banana. This result confirmed the statements made by Reyes de Romero (1986) that banana plants represent the most important refuges for *I. subquadratum* populations. However, further studies are required to effectively demonstrate that *I. subquadratum* populations can be significantly reduced by eliminating banana plants from coffee plantations that suffer serious coffee crop losses from *I. subquadratum* infestations. For the moment, cutting and removing dead banana leaves and using tramps to capture and kill the insects could be the best strategy to manage this pest in Siltepec.

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