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Field boundaries restrict dispersal of a tropical tiger beetle, *Megacephala angustata* Chevrolat 1841 (Coleoptera: Cicindelidae)

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Abstract

Horgan FG, Chávez JC. 2004. Field boundaries restrict dispersal of a tropical tiger beetle, *Megacephala angustata* Chevrolat 1841 (Coleoptera; Cicindelidae). Entomotropica 19(3): 147-152.

Field boundaries may divide populations of predatory invertebrates into local populations at the field scale by restricting between-field dispersal. This could reduce recolonisation rates after pesticide use or decrease the efficiency of numerical responses by natural enemies to pest outbreaks. The present study examines the impact of field boundaries on dispersal of the predatory tiger beetle, *Megacephala angustata* Chevrolat 1841 at a farm in coastal El Salvador. Pitfall trapping indicated that beetles occurred in most habitats on the farm. In pastures, captures were higher in open, unshaded areas than under field boundaries. Beetle dispersal was examined in a capture-mark-recapture study at the site. Movement between fields was very rare as indicated by a linear relationship between the accumulated number of marked beetles and the proportion of recaptures in each of three fields. In spite of frequent recaptures, three weeks after marking, only 2 of 401 beetles were found outside the fields where they had been originally captured and marked.

Aditional key words: *Bursera simoruba* (L.) Sargent, capture-mark-recapture, El Salvador, predation, Schnable method, tropical pastures.

Resumen

Horgan FG, Chávez JC. 2004. Barreras vivas como agente de restricción para la dispersión de un cicindélido tropical, *Megacephala angustata* Chevrolat 1841 (Coleoptera: Cicindelidae). Entomotropica 19(3): 147-152.

Las barreras vivas pueden restringir la dispersión de invertebrados depredadores en tierra agrícola y dividir sus poblaciones en poblaciones locales a nivel de campo con consecuencias tanto para la recolonización después del uso de plaguicidas como el control natural de plagas. En el estudio presente se investiga el efecto de barreras vivas sobre la dispersión de *Megacephala angustata* Chevrolat 1841 en una granja en la costa de El Salvador. Trampas de caída indicaron una aversión a los habitat sombreados, incluso a la sombra de barreras vivas, por la especie. Un estudio captura-marca-recaptura indicó que el movimiento entre potreros es poco común. Tres semanas después de marcar los escarabajos y a pesar de frecuentes recapturas, solamente 2 de 401 individuos se encontraron afuera de los potreros donde se les habían marcado.

Palabras clave adicionales: *Bursera simoruba* (L.) Sargent, captura-marca-recaptura, depredación, el método Schnable, El Salvador, pastizales tropicales

Introduction

Shady field boundaries, hedgerows, ditches and grassy banks continue to be a prominent feature of rural landscapes due to cultural practices relating to property delimitation and farm division (Schroth et al. 2000; Le Coeur et al. 2002). However, a number of studies have indicated that the modernization and intensification of agriculture has caused notable reductions in their prominence (Le Coeur et al. 2002). Research interest in field boundaries has stemmed from their benefits in conservation, pest management and soil improvement (Pattanayak and Mercer 1998; Thomas et al. 2001; Le Coeur et al. 2002). They can act as important refuges for flora and fauna, including both pest and beneficial species and can promote or inhibit the dispersal of species through agricultural land (Mauremooto et al. 1995; Girma et al. 2000; Horgan 2002; Wratten et al. 2003). As noted by Girma et al. (2000), the effects of such linear landscape features cannot be generalised but depend on the species in question (including the crop and boundary-associated fauna). However, as more information is gathered on specific cases, design and management of field boundaries can be directed towards optimising for the majority of beneficial effects.

The present study examines the permeability of field boundaries in agricultural land in El Salvador to dispersal by a potentially important predatory beetle, *Megacephala angustata* Chevrolat 1841. Although field boundaries vary between farms and regions, the boundaries studied here are typical of many from dry coastal regions of Central America. Following forest clearing, fields are initially delimited by barbed wire fencing connected by posts of *Bursera simoruba* (L.) Sargent and occasional shade trees. Because of rapid growth rates in margins left close to the fences, the boundaries rapidly gain volume and height. Posts of *B. simoruba* take root and branch, and weedy plants entangle the wires (see Martin 1991). In older boundaries, the original wire fencing is often indistinguishable (personal observation). *Megacephala angustata* was chosen as a model species because it is relatively common in Salvadoran farmland and tiger beetles in general are noted as highly active cursorial species whose dispersal and predatory behaviours have been well documented (Dreisig 1981; Pearson 1988). However, to our knowledge, average displacement by tiger beetles in farmland and the effects of landscape features on this displacement have not been previously studied, and there are very few studies on the effects of field boundaries on tropical fauna in general. Through an extensive program of pitfall trapping, we determine habitat use and seasonality of adult *M. angustata* in Salvadoran pastures. Using a capture-mark-recapture technique, we examine the permeability of field boundaries for the species and, therefore, determine the extent of movement between fields and crops. Interactions between *M. angustata* and field boundaries are discussed in the context of natural control of pasture pests.

Materials and methods

Study site and field boundaries

Studies were carried out at the Experimental Field Station "La Providencia" of the University of El Salvador in San Luis Talpa, El Salvador (13°20'N, 87°05'W). The climate of La Paz is typical of the hot tropical plateau of the Central American Pacific coast with mean daily temperatures oscillating between 23 and 28°C and an average annual rainfall of 1,720mm. The field-station, at an altitude of 50 m.a.s.l., has an area of 32.7ha. Pastures at the site were mainly of pangolagrass *Digitaria decumbens* Stent. The fields were generally small (0.5ha) and separated by field boundaries, which were often overgrown. Field boundaries were barbed wire fences connected to *B. simoruba* posts and shade trees. Trees included *Ficus glabrata* H.B.K., *Enterolobium cyclocarpum* (Jacquin) Grisebach Schultes and *Cordia alba* (Jaquin) Roem and Schultes. The boundaries, including field margins, were about 1-2m wide at the base with most trees reaching a height of 5-10m and a canopy width of about 5m.

Pitfall trapping

In 1996, pitfall traps were operated throughout the year and examined weekly. Traps were set out in five pastures. In each pasture, five traps were located in the centre of the field and five along the field boundary in areas that did not receive direct sunlight throughout the study. Traps were separated by about 20m. Each pitfall consisted of a circular metal container, 30cm deep, dug into the ground and level with the ground surface. A tightly fitting funnel, 15cm in diameter, was placed at the mouth of the container. An empty collecting jar was placed beneath the funnel in the metal container. No killing agent was used and beetles were released at about 10m from the nearest trap.

In 1997, traps were set out at seven locations including two pastures that differed in grazing intensity and drainage, a citrus grove, a cornfield, a lakeshore dominated by weedy shrubs, and two woodland sites (woodland and riverbank). The grove, of young lemon (*Citrus limon* [L.] Burm.) and orange trees (*Citrus sinensis* [L.] Osbeck) with a grassy undergrowth and patches of bare soil, was generally open with little shade. The woodland site was dominated by *Ficus benjamina* L. and *F. glabrata* with a thick canopy, whereas the riverbank was dominated by *B. simoruba* and *C. alba* with a lower canopy. Traps consisted of 0.5 litre plastic cups, with slits for water drainage, placed in the ground without any killing agent. Traps were activated between 26 May and 21 September. Twenty traps were set out at each location in two transects of ten, and trap catches were noted every two days. Beetles were released back to the sites at a distance of about 10m from the nearest trap.

Capture-mark-recapture

In 1997, an experiment was set up to examine beetle movement in pastures and between crops. Pitfall traps (as described above for 1997) were set out in three pastures including two adjacent pastures (B & C) and a third pasture (A) separated from 'B' by an intermediate pasture without traps. In each of the pastures, traps were arranged in three sectors that consisted of circles of seven traps, each with an inner circle of three traps. The full radius of each outer circle was 5m with 4m to the inner circle. The centres of adjacent circles were separated by a distance of 18m and were 15-25m from the nearest field boundary. Beetles trapped in each of the three sectors were marked according to the sector (left elytra, right elytra or both) and beetles trapped in the different fields were marked using differently coloured paints (brown, dull blue or dull green). An acrylic paint was used for marking and marks were applied using a light straw. After marking, the beetles were released 1m from the trap where they were captured,

Table 1. Population estimates and movement of marked *M. angustata* in three enclosed pastures on a farm in El Salvador.

Field	Number marked	Estimated population size	Estimated dispersal rate (m/day)*	% recaptured at adjacent circle of traps	% recaptured at distant circle of traps	Number crossing boundaries (τ [days] /distance[m])	Number entering new crop (τ [days] /distance[m])
A	149	233	6.08	8.05	4.03	0	0
B	122	217	7.44	16.39	4.91	1 (12.66/80)	0
C	130	286	6.92	15.38	2.31	0	1 (>21/150)

* Calculated for dispersing beetles, i.e., beetles that travelled between sectors within fields.

perpendicular to and outside the circle to which the trap belonged. Using this trap layout, movement of beetles within sectors (i.e. circles of traps), between sectors within fields (i.e. between circles of traps), across boundaries, and across fields, could be determined. Beetles were collected and marked daily between 24 June and 2 July. Traps were examined every day until 15 July.

Data analysis

Habitat preferences were examined using ANOVA on *log*(*x*+0.1) transformed data. Pair-wise post-hoc comparisons were made using Tukey tests. The occurrence of beetles in shaded and open areas within pastures were compared using a paired-sample t-test on *log*(*x*+0.1) transformed data. The Schnable-method was used to estimate population sizes. The method estimates total populations based upon the ratio of recaptured individuals to total beetles trapped at a given site (Krebs 1998). The advantage of the Schnable-method is that it allows one to detect changes in abundance-activity within the population (Krebs 1998) where a linear relationship between the accumulated number of marked beetles and the proportion of recaptures indicates a lack of immigration from, or emigration to the population. Data residuals were plotted following all parametric analyses to check for homogeneity and normality.

Because beetles were continually marked throughout the dispersal experiments, the 'average-time-marked', τ, was used to determine dispersal rates, where

$$\tau_t = \frac{\left(\sum_{i=1}^{t-1}\left(X_i T_i\right)\right)}{\sum X}$$

and τ_t is the average-time-marked on day t, X is the number of beetles marked on the ith day, T is the time lapsed between each marking day and day t, and $\sum X$ is the accumulated total number of marked beetles in the population on day t. The average-time-marked is the average time that beetles in a population on a given day had spent freely moving since first marked. Because of the large number of beetles marked in the experiments, we assume that the average-time-marked permits a good approximation of individual dispersal rates; however, the approximation deteriorates with increasing periods of new marking.

Results

Habitat use and seasonality

Adult *M. angustata* were active from early June until mid-August at pastures in 1996. Activity commenced in late April albeit with low numbers of beetles (Figure 1). Within pastures, beetles were less abundant along field boundaries (t=-3.184, d.f.=4, P=0.033) (Figure 1 inset).

The species occurred in all habitats where pitfall trapping was conducted in 1997. Abundance-activity varied between habitat-types on the farm (ANOVA: $F_{6,149}$= 42.05, P<0.001) (Figure 2). Beetles were most abundant-active in the citrus grove and pastures with significantly less abundance-activity in the remaining habitats.

Dispersal

A total of 401 beetles were marked throughout the study. The numbers, and, therefore, densities of beetles in each field were very similar (Table 1). Recaptures were frequent in all fields (about 70% of captures). About 80% of recaptures in each field were within a 10m radius of the original release sites. Few beetles moved further than 18m and only 2 individuals were encountered outside the fields where they had been originally captured (Table 1). Beetle moved an average of 6.81 ± 0.40m per day (n = 3), but at least one individual moved about 24m per day. Within each field, populations remained stable as indicated in Figure 3. The linear relationship between the accumulated number of marked beetles and the proportion recaptured suggests that mortality and between-field dispersal were minimal and activity was largely constant.

Discussion

Megacephala angustata is an active predatory beetle common in Salvadoran farmland. Our results indicate that the species occurs across a variety of typical farmland habitats

Figure 1. Abundance-activity of *M. angustata* in cattle pastures during 1996 with (inset) mean captures in the open and along shady field boundaries. Bars indicate standard errors (*n* = 5 fields).

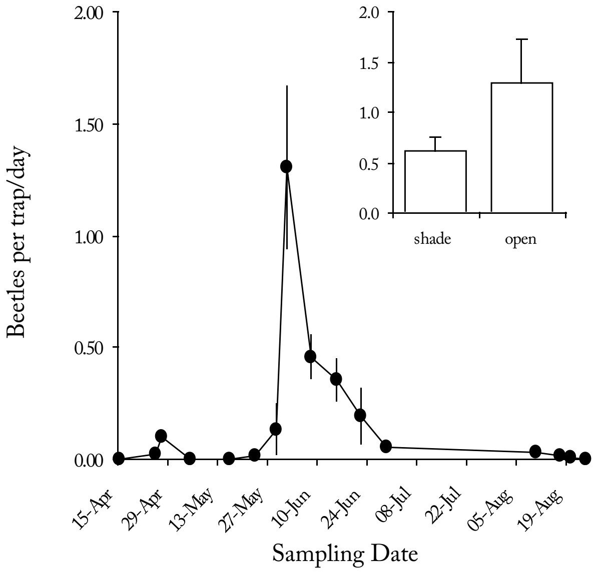
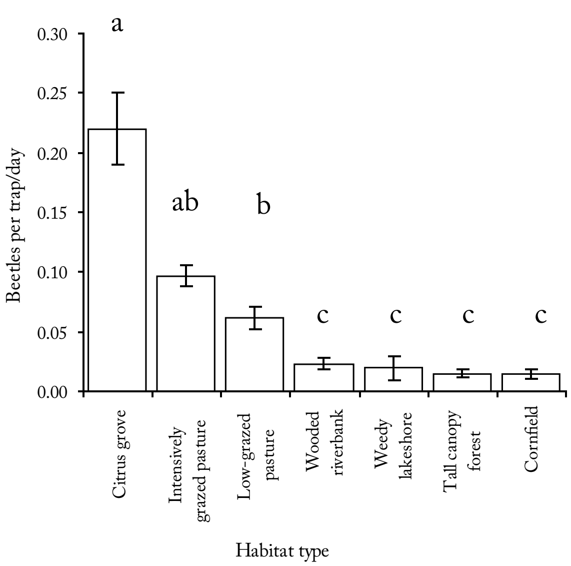
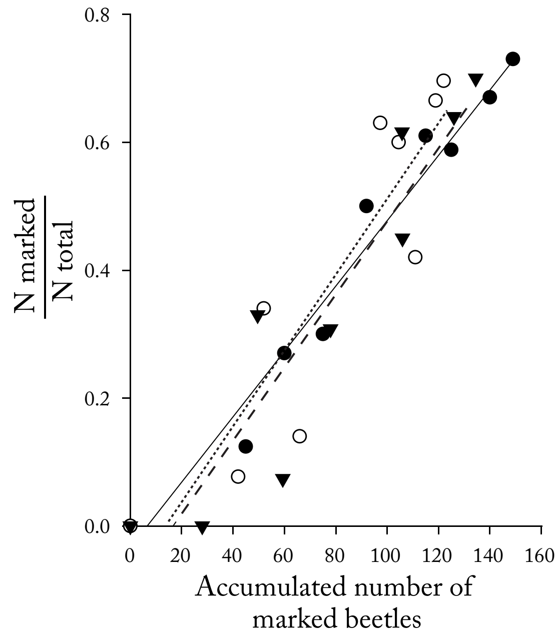


Figure 2. Abundance-activity of *M. angustata* at seven locations of different habitat-type at La Providencia. Letters indicate homogenous groups. Standard errors are indicated (n = 20 traps).



including woodland. The species was common in pastures and as such may constitute an important natural enemy of pasture pests. However, within pastures, fewer beetles were captured in traps placed under field boundaries than in traps at the centre of the fields. Furthermore, in spite of a high number of recaptures, only 2 of 401 beetles crossed field boundaries. These results suggest that field boundaries

Figure 3. Relationship between the accumulated number of beetles marked and the proportion recaptured in three cattle pastures. Solid circles, solid line = field A, y = 0.006x – 0.093, R^2 = 0.71, P = 0.004; open circles, dotted line = field B, y = 0.005x – 0.056, R^2 = 0.97, P < 0.001; solid triangles, dashed line = field C, y = 0.006x – 0.094, R^2 = 0.83, P = 0.001.



represent a barrier to the dispersal of *M. angustata* and largely confine individuals to certain fields.

The Schnable method used in this study proved successful in estimating population sizes. The method was also useful in gaining an insight into tiger beetle behaviour. The linear relationship between the accumulated number of marked beetles and the proportion of recaptures indicated that the populations were stable and that individual field populations were largely closed (i.e., immigration and emigration of beetles between fields were at very low levels). The relationship between the accumulated number of marked beetles and the proportion of recaptures would have been curvilinear had there been substantial immigration/emigration, or erratic had there been high mortality. Other studies that use mark-recapture techniques (with once-off marking) to investigate beetle dispersal are likely to confound the absence of recaptures at specific, distant traps, with death and emigration. Also, they may generally have lower recaptures than with the Schnable method because a lower proportion of the population is marked. Estimation of dispersal rates are difficult using the Schnable method. However, this can be overcome by using different marking patterns or colours on different days.

Whereas the present study indicates that field boundaries are largely impermeable to *M. angustata*, it does not explain the mechanisms involved in restricting beetle movement. In tropical landscapes, field boundaries offer very different habitat conditions to those of the open field. Boundaries influence temperatures, soil and air moisture levels, and light intensity in their immediate vicinity. In particular they lower temperature extremes and improve soil water status (Wilson 1996; Breshears et al. 1998). Shade also affects ecological processes such as organic matter breakdown and nitrogen cycling (Wilson 1996). The effects of shading on other species of tiger beetle vary according to species; however, even slight changes in moisture, salinity and light intensity can determine the local distribution of adult tiger beetles and the survival of their eggs and larvae (Gilbert 1997; Hoback et al. 2000; Romey and Knisley 2002). How these factors influence *M. angustata* or its prey is unknown. However, since the number of beetles caught in shaded pitfall traps was lower than in the open, then it seems that the beetles actively avoided the shade from tree canopies before reaching the physical barrier represented by tree-posts, dense tillers and weedy plants associated with the fence. Because a certain number of beetles did occur in the shade, then it is likely that the fence and its associated flora was the principal obstruction to between-field dispersal by beetles.

Our study indicated similar population densities of *M. angustata* in three different pastures. *Megacephala angustata* is aggressive on encountering conspecifics and cannibalism occurs where beetles are confined to arenas or traps (personal observation). Such aggression might be responsible for maintaining rather fixed densities of beetles in the fields. If this is the case, numerical responses to prey densities might be limited. At least in *Cicindela denekei* Brown, concentrated searches do not occur in areas of high prey densities, even though continued random searches in such areas will result in the beetles remaining for longer periods in areas of prey concentration (Kaulbars and Freitag 1993). However, high prey-density and satiation of beetles could also reduce beetle activity during outbreaks (i.e. activity is reduced in satiated carabids, see Frampton et al. 1995; Mauremooto et al. 1995). Because of the difficulties in interpreting pitfall data, mark-recapture techniques, such as those used here, are required to decipher the responses of tiger beetles to pest outbreaks.

Because of rapid movement during hunting, tiger beetles might be expected to travel large distances quickly. In this study, we noted dispersing individuals to move an average of about 7 m per day in pastures dominated by pangolagrass. This is similar to distances recorded for carabid beetles in temperate regions (Thomas *et al.* 1997; Zhang *et al.* 1997). Movement between fields is important for recolonisation after population depletion due to pesticide use. If field boundaries inhibit movement of predatory beetles but do not inhibit the movement of pest species, then pest outbreaks might be expected to occur following pesticide application and before effective recolonisation by the predators (see Raymond et al. 2002). In spite of this, field boundaries will still remain a beneficial feature of temperate and tropical landscapes (Schroth et al. 2000; Le Coeur et al. 2002). In a related paper, the same field boundaries as studied here were shown to enhance dung decomposition by coprophagous beetles (Horgan 2002). Field connectivity for predatory beetles could be enhanced by increasing the number and width of gaps in the boundaries. However, it is unknown how this might affect species that use field boundaries as dispersal corridors. There is a need for further studies on the impact of tropical field boundaries on the survival and dispersal of native flora and fauna in order to improve the design and management of these important landscape features.

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