

*Short communication***Population Structure of a Monophagous Chrysomelid Beetle in a Mexican Lowland Rain Forest**

Ken OYAMA Centro de Ecología, U. N. A. M. Apartado Postal 70-275, México, 04510, D. F.

Rodolfo DIRZO Centro de Ecología, U. N. A. M. Apartado Postal 70-275, México, 04510, D. F.

ABSTRACT The population structure of the chrysomelid, *Calyptocephala marginipennis* was examined in a Mexican lowland rain forest. This species is a monophagous beetle that feeds exclusively on leaves of the dioecious palm, *Chamaedorea tepejilote*, making specific ruptures along the leaf veins, which are easily recognized in the field. In order to know the population structure, survivorship and migration rates of this insect, a capture-recapture study was done during 24 consecutive days. Two hundred nineteen beetles were marked in total and, on average, 72 % were recaptured. Daily recaptures varied from 31.4 % to 93.1 %. The estimated mean number of beetles per day was 927.7 individuals, and the estimated mean of survivorship per day was 0.88. These results together with previous studies on the effects of this herbivore on the survivorship and reproduction of *C. tepejilote*, support that *C. marginipennis* beetles have a close relationship with this palm at Los Tuxtlas, Mexico.

One way to understand the distribution and abundance of mobile insects is to carry out mark-recapture studies on a species population within its environment. Different aspects of insect population dynamics have been elucidated with this approach, for example contrasting behavioral regimens among local populations of butterflies (Ehrlich, 1965; Ehrlich *et al.*, 1975) or the status of local rare species of dragonflies (Garrison & Hafernik, 1981). Capture-recapture methods have been used extensively with insects of relatively large body size, thus making hand manipulation easy (e. g. butterflies or dragonflies); however a few studies exist with smaller insects in tropical communities. *Calyptocephala marginipennis* Bohem. (Chrysomelidae) is a small beetle (ca. 6 mm long), which is easy to distinguish accurately in the field due to its pale brown elitrae with a dark line at the margin. At the Los Tuxtlas rain forest, this herbivore feeds exclusively on the leaves of the understory dioecious palm, *Chamaedorea tepejilote* Liebm. ex Mart., making specific longitudinal ruptures along the leaf veins, which are easily recognized in the field (Oyama, 1984; Oyama & Dirzo, 1991). The cumulative damage by this herbivorous insect, together with the fall of branches or other debris from the canopy negatively affect the leaf dynamics and reproduction (Oyama, 1987; Oyama & Mendoza, 1990), resource allocation (Oyama & Dirzo, 1988) and, in some cases, the mortality of plants of *C. tepejilote* (Oyama, 1987; 1990). Eight species of *Calyptocephala* have been reported in Neotropical forests from Mexico to Brazil (Baly & Champion, 1885-1894) paralleling the geographic distribution of the *Chamaedorea* species. However, many

aspects of the biology of this beetle are still unknown due to its small size and therefore difficulties to find it in the field. In this study, the population structure of *C. marginipennis* was estimated using field data obtained from mark-recapture methods. This study was conducted at the Estación de Biología Tropical Los Tuxtlas of the Universidad Nacional Autónoma de México. This 700 ha reserve is located in south east Mexico (95°04' - 95°09' W; 18°09' - 18°36' N); annual rainfall is about 4500 mm and the mean annual temperature is 24°C (Lot-Helgueras, 1976; Ibarra-Manríquez & Sinaca Colín, 1987).

We chose 136 palms of *C. tepejilote* as sample units because it is impossible to look for and capture this insect at flight in the forest. The beetle usually stays in the abaxial surface of leaves of *C. tepejilote* eating or resting for several hours and in a few cases for more than one day. Palms therefore constituted good sample units because of the close relationship between this beetle and the leaves of *C. tepejilote*. All 136 palms were tagged and mapped in a 600 m² (30×20m) permanent plot used for a long-term demographic study (Oyama, 1987; 1990) and their leaves were revised every day following the same order. Multiple censuses were carried out during 24 consecutive days. Individuals captured in the same day were marked on the elitrae with a unique combination of paints and colors using a commercial "high adherence" paint and released at the same place of capture (e. g. on the same palm leaf, in the same position). We did not distinguish between sexes or stages of development although all beetles marked were adults. The Jolly method (1965) was used to compute daily population numbers (N_i), survival rates (ϕ_i), proportion of marked animals in the population (α_i), and number of animals marked at risk (M_i) (Table 1). Because biases were produced in the estimation of survival rates (values higher than 1), average of survival rates were calculated using a modification of the method depicted by Scott (1973). Survival rates greater than one were averaged with the values obtained one day before and one day after. This average was converted to one day rate by the following formula: one day rate = (average survival rate)^{1/d}, where d = number of days considered for the estimation of the average (3 days in all cases except the first day), and this value was used in substitution of the greater-than-one survival rate. This formula yields values nearer to 1.0. Overall survival rates were converted to longevity in days using the formula of Cook *et al.* (1967): expected life span in days = -1 / ln (ϕ_{avg}). Dispersion patterns of *C. marginipennis* were assessed using Morisita's (1959) index:

$$I = \frac{\sum_{i=1}^q n_i (n_i - 1)}{N(N - 1)}$$

where q = total samples, n_i = numbers in the *i*th sample, and N = number of individuals found in all the samples. Values <1 indicate uniformity, values = 1 indicate randomness, and values > 1 indicate aggregation.

Two hundred and nineteen beetles were marked in total and, on average, 72% were recaptured. Daily recaptures varied from 31.4 % to 93.1 % (Table 1). The estimated mean number of beetles per day was 927.7 individuals with a broad range, from 138 to 2246

Table 1. Population parameters estimated from Jolly's multiple recapture data for *Calyptocephala marginipennis* for 24 days. α_1 = proportion of recaptures (%), M = number of marked beetles at risk, N_1 = total population estimates, ϕ_1 = daily survival rate, S. E. = standard error.

| Day(i) | α_1 | M _i | N _i | S. E. | ϕ_1 | S. E. |
|--------|------------|----------------|----------------|--------|----------|-------|
| July 9 | — | 0 | — | — | 1.15 | — |
| 10 | 31.4 | 42.7 | 137.9 | 23.3 | 1.21 | 0.51 |
| 11 | 67.6 | 197.1 | 289.9 | 277.9 | 0.86 | 0.12 |
| 12 | 77.4 | 179.0 | 232.5 | 219.9 | 1.29 | 0.00 |
| 13 | 62.5 | 421.9 | 669.7 | 105.1 | 1.29 | 1.38 |
| 14 | 85.7 | 1474.4 | 1714.4 | 688.5 | 0.81 | 0.41 |
| 15 | 79.5 | 1201.0 | 1520.25 | 596.9 | 0.89 | 0.42 |
| 16 | 93.1 | 1075.8 | 1156.8 | 435.0 | 0.47 | 0.20 |
| 17 | 66.7 | 510.0 | 761.2 | 370.3 | 0.84 | 0.27 |
| 18 | 90.0 | 435.8 | 484.2 | 299.9 | 1.08 | 0.99 |
| 19 | 69.2 | 949.8 | 1301.1 | 376.9 | 0.82 | 0.52 |
| 20 | 71.4 | 780.0 | 1098.6 | 489.7 | 1.06 | 2.84 |
| 21 | 92.3 | 2066.0 | 2245.7 | 2078.2 | 0.18 | 0.17 |
| 22 | 79.2 | 371.8 | 470.6 | 828.2 | 0.93 | 0.26 |
| 23 | 54.6 | 349.3 | 635.2 | 815.1 | 1.10 | 1.24 |
| 24 | 74.1 | 931.3 | 1258.5 | 762.1 | 0.47 | 0.24 |
| 25 | 71.4 | 436.5 | 614.8 | 721.9 | 0.87 | 0.35 |
| 26 | 75.0 | 384.9 | 513.2 | 945.2 | 1.18 | 2.35 |
| 27 | 76.9 | 1268.0 | 1646.8 | 926.2 | 0.84 | 0.59 |
| 28 | 66.7 | 1071.0 | 1598.5 | 1527.9 | 0.56 | 0.52 |
| 29 | 84.2 | 605.0 | 720.2 | 968.5 | 0.55 | 0.45 |
| 30 | 65.0 | 333.0 | 512.3 | 860.1 | 1.00 | 1.46 |
| 31 | 51.6 | 605.0 | 1163.5 | 1152.2 | 0.68 | — |
| Aug. 1 | 70.6 | 420.0 | 591.6 | — | — | — |

beetles. This variation may be explained based on the beetle's behavior. This insect stays for a long time feeding or resting on an individual plant. After some hours, the beetle moves on to a different palm, stays there for some time, and then moves again to another palm. The direction of these movements apparently does not follow any particular direction, but the spatial distribution of the palms. Thus the insect's behavior is closely related to the palm's density and spatial distribution; regularly, *C. tepejilote* occurs at a high density, more than 1300 mature plants per ha or more than 4000 plants per ha including seedlings and juveniles at Los Tuxtlas forest (Oyama, 1987, 1990) with an aggregated spatial pattern (Oyama, 1994; Bongers *et al.*, 1988). In a few days or even in one day, one beetle may leave the permanent plot and return several days later. Then, we have recaptured beetles both in the next following days or after several days. This may be responsible for the relatively high, yet variable α_1 values and, consequently, the high and variable number of individuals per day (Table 1). In other parts of the Los Tuxtlas forest, as well as in other tropical sites of Mexico where *C. tepejilote* occurs at low densities (and / or is not clumped) the beetle is also very rare (R. Dirzo pers. obs.; S. Sinaca pers. com.).

The estimated survival rates ranged from 0.18 to 1.29. Most of the "mortality" may be attributed to local emigration of the beetles off the permanent plots we used. The estimated longevity of 7.7 days should be interpreted as the number of days that a single beetle stays, on average, active within the permanent plot. One individual beetle lived for at least 24 days, the duration of the study period. The pattern of dispersion was uniform ($I = 0.04$) suggesting that, at the scale of *C. tepejilote* leaves, beetles are distributed regularly.

A rough estimate of 6.82 beetles per palm per day (mean number of beetles 927.7 / 136 palms), and an estimated consumption rate of 0.28 cm² of leaf area / hour / individual beetle obtained from experimental studies on the feeding behavior of *C. marginipennis* on leaves of *C. tepejilote* (Oyama, 1984; Oyama & Dirzo, 1991) support previous indications that the effect of *C. marginipennis* on the leaf dynamics, growth, reproduction and survivorship of *C. tepejilote* is considerable (Oyama, 1987, 1990; Oyama & Mendoza, 1990). Detailed studies on the population dynamics of phytophagous insects are much relevant and necessary in the investigations of tropical plant-herbivore interactions not only to understand how insects affect plants, but also to understand how, in some cases, plant limiting factors (e. g. plant density, plant defenses, quality of food, etc.) may be determining the numbers of insects in a certain environment. These studies may also be relevant for the management of plants, such as *C. tepejilote*, with considerable economic potential.

REFERENCES

- Baly, J. S. & Champion, G. C. 1885-1894. *Biologia Centrali-Americana. Insecta. Coleoptera.* Vol. IV. Part 2. p. 129.
- Bongers, F., Popma, J., Meave del Castillo, J. & Carabias, J. 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* **74** : 55-80.
- Cook, L. M., Brower, P. P. & Croze, H. J. 1967. The accuracy of a population estimation from multiple recapture data. *J. Animal Ecol.* **21**: 57-60.
- Ehrlich, P. R. 1965. The population biology of the butterfly, *Euphydryas editha* II. The structure of the Jasper Ridge colony. *Evolution* **19**: 327-336.
- , White, R. R., Singer, M. C., McKechnie, S. W. & Gilbert, L. E. 1975. Checkerspot butterflies: a historical perspective. *Science* **188**: 221-228.
- Garrison, R. W. & Hafernik, J. E. Jr. 1981. Population structure of the rare damselfly, *Ischnura gemina* (Kennedy) (Odonata: Coenagrionidae). *Oecologia* **48**: 377-384.
- Ibarra-Manríquez, G. & Sinaca-Colín, S. 1987. Listados florísticos de México. VII. Estación de Biología Tropical Los Tuxtlas, Veracruz. Instituto de Biología, Universidad Nacional Autónoma de México, México.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* **52**: 225-247.
- Lot Helgueras, A. 1976. La Estación de Biología Tropical Los Tuxtlas: pasado, presente y futuro. In: Gómez-Pompa, A., del Amo, S. Vázquez-Yanes, C. & Butanda, A. (eds.)

- Investigaciones sobre la regeneración de selvas altas en Veracruz, México, 31-69. CECSA, México.
- Morisita, M. 1959. Measuring the dispersion of individuals and analysis of the distributional patterns. *Mem. Fac. Sci. Kyushu Univ.* **2**: 215-235.
- Oyama, K. 1984. Biología comparativa entre individuos masculinos y femeninos de *Chamaedorea tepejilote* Liebm. Tesis profesional, Facultad de Ciencias, Universidad Nacional Autónoma de México, México.
- 1987. Demografía y dinámica poblacional de *Chamaedorea tepejilote* Liebm. en la selva de Los Tuxtlas, Veracruz (México). Tesis de maestría, Universidad Nacional Autónoma de México, México.
- 1990. Variation in growth and reproduction in a Neotropical dioecious palm, *Chamaedorea tepejilote*. *J. Ecol.* **78**: 648-663.
- & Dirzo, R. 1988. Biomass allocation in the dioecious tropical palm *Chamaedorea tepejilote* and its life history consequences. *Pl. Sp. Biol.* **3**: 27-33
- & —— 1991. Ecological aspects of the interaction between *Chamaedorea tepejilote*, a dioecious palm and *Calyptocephala marginipennis*, a herbivorous beetle, in a Mexican rain forest. *Principes* **35**: 86-93.
- & Mendoza, A. 1990. Effects of defoliation on growth, reproduction and survival of a Neotropical dioecious palm *Chamaedorea tepejilote*. *Biotropica* **22**: 119-123.
- Scott, J. A. 1973. Convergence of population biology and adult behavior in two sympatric butterflies, *Neominois ridingsii* (Papilionoidea: Nymphalidae) and *Amblyscirtes simius* (Hesperioidea: Hesperidae). *J. Animal Ecol.* **42**: 663-672.

Accepted Aug. 12, 1993

Ken OYAMA, Rodolfo DIRZO メキシコ低地降雨林における単食性ハムシ科甲虫の集団構造

ハムシ科の1種 *Calyptocephala marginipennis* の集団構造をメキシコ低地降雨林において調査した。この種は単食性の甲虫であり、雌雄異株のヤシ科の *Chamaedorea tepejilote* の葉だけを食べる。葉脈に沿った割れ目状の特徴的な食痕は野外で容易に認識できる。この昆虫の集団構造・生存率・移住率を知るために、標識・再捕獲を24日間実施した。総計219個体を標識し、平均してその72%が再捕獲された。一日あたりの再捕獲率は31.4%から93.1%まで変異した。一日あたりの平均個体数は927.7個体、一日あたりの平均生存率は0.88と推定された。これらの結果は先行研究の結果とともに、*C. marginipennis* の食害がメキシコ、ロステュクストラスにおける *C. tepejilote* の生存・繁殖に少なからぬ影響を与えていることを示している。