HABITAT SELECTION AND POPULATION STRUCTURE IN *PLEBEJUS SAEPIOLUS* BOISDUVAL (LYCAENIDAE)

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The importance of resource distribution has been demonstrated for the survival of both the larvae and adults of butterflies (Dethier, 1959; Gilbert, 1971; Singer, 1971). Nearly all butterfly larvae feed on the leaves and flowers of angiosperms, and most temperate zone adults depend on nectar for food. Furthermore, the relationships of butterflies and their larval food-plants may be quite specific and complex (Breedlove & Ehrlich, 1968, 1972; Downey & Fuller, 1961; Ehrlich & Raven, 1964). It is therefore reasonable to suppose that the distribution of specific plant resources may have great influence on the habitat selection of the mobile adult butterflies.

During the summer of 1971, a study was made of the structure of a population of the lycaenid butterfly *Plebejus saepiolus* Boisduval and the distribution of its resources in a subalpine meadow in Gunnison Co., Colorado. The females of this species oviposit singly on the flowers and developing fruits of the alsike clover, *Trifolium hybridum* L., and probably also on other species of *Trifolium*. It is noteworthy that *Trifolium* was found to be by far the most important adult nectar source for *P. saepiolus*.

The objectives of the study were to investigate how *P. saepiolus* distribute themselves with respect to the *Trifolium* resource and to discover how frequently individuals move within and between areas of favorable habitat. A capture-recapture technique involving a number of discrete areas was chosen in order to obtain this information.

The study site was a gently sloping meadow at 2708 m. elevation, just east of the Crested Butte, Colorado, Town Cemetery. Located in a valley, the site was not noticeably affected by any constant prevailing winds. The vegetation of the meadow was dominated by *Artemisia tridentata* Nutt. and grasses, with other plant associations occurring locally, particularly in wetter regions. The distribution of *Trifolium* was mapped over the site, and on this basis six 30 × 60 meter areas, designated "a" through "f," were selected for the study (Fig. 1). Three of these (*a*, *e*, and *f*)

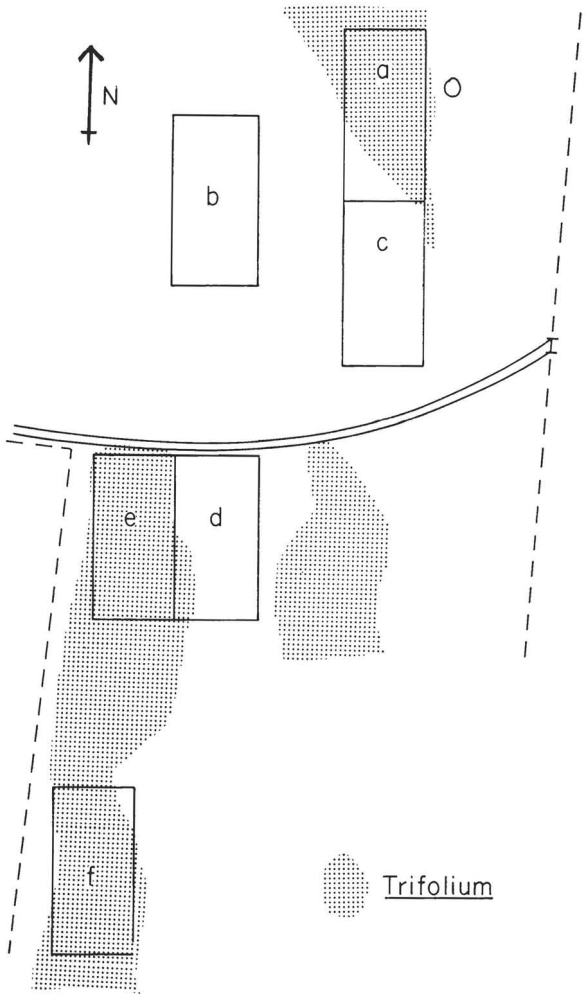

Fig. 1. *Plebejus saepiolus* study areas.

were in relatively wet regions of high *Trifolium* density, while the others (*b, c,* and *d*) were drier and contained little or no *Trifolium.*

On each day of the study, two people spent ten minutes in each of the six areas collecting all *P. saepiolus* found. At the end of ten minutes, all individual butterflies were sexed, marked with an individual number (except for recaptures for which the number was recorded), and released from the center of the area. Less than 1% of the insects were unable to fly when released. The marks were not conspicuous and thus were un-

TABLE 1. Total captures of *Plebejus saepiolus* in study areas (1971).

Date*	Study Areas					
	a	*b*	*c*	*d*	*e*	*f*
6/24	10	0	1	7	17	23
6/25	15	3	0	2	22	24
6/26	12	1	1	3	22	28
6/27	12	0	0	1	22	19
6/28	12	2	2	1	28	28
6/29	10	0	0	0	19	20
6/30	15	1	0	1	22	21
7/2	15	0	0	0	26	20
7/4	10	0	0	0	20	22
Mean	12.33	.78	.44	1.67	22.00	22.78
Variance	4.75	1.19	.53	5.00	11.25	11.19
Std. Dev.	2.18	1.09	.73	2.24	3.35	3.35
Std. Dev. of Mean	.73	.36	.24	.75	1.12	1.12

* 7/1 and 7/5 were omitted due to cloudy weather conditions which caused unusually low butterfly captures.

likely to affect either the survival of marked individuals or their probability of being captured.

RESULTS

Before considering in detail the results of this experiment, the sex ratio of the captured butterflies should be examined. The female to male ratio was 0.19 whereas the ratio for laboratory-reared butterflies of various species is normally about 1.0 (Brussard & Ehrlich, 1970). The hypothesis that males are much more likely to be captured is supported by the recapture data in which 13% of the males marked were recaptured at least once, while only 4% of the females were recaptured. Since the two sexes are quite similar in appearance, the disparity should be due largely to behavioral differences, including greater flight activity by males. The recapture data therefore refer principally to males; females are expected to be more sedentary than the data for males would suggest. If this were true, we might expect males to be found more often in less favorable areas because of their greater mobility. The sex ratio for areas *a*, *e*, and *f* (0.20) versus that for *b*, *c*, and *d* (0.12) support this, but the data are based upon too few captures to be relied upon.

Table 1 presents information on total captures of *P. saepiolus* in the study areas. The difference between the numbers captured in the *Trifolium* areas (*a*, *e*, and *f*) and the non-*Trifolium* areas (*b*, *c*, and *d*) is highly significant ($p < 001$; modified T-test). The scarcity of captures in non-*Trifolium* areas indicates that individuals are seldom found more

Area of Capture	Area of Recapture a	b	c	d	e	f	Tot.
a	13						13
b		1					1
c			1				1
d					1		1
e	2				23	2	27
f	1				8	14	23
Tot.	16	1	1	0	32	16	(66)

Fig. 2. Matrix of capture-recapture data arranged by location.

than a few meters from *Trifolium*. This is emphasized by the low yield from area *d*, whose east and west edges follow the borders of *Trifolium* regions containing many *Plebejus saepiolus*. The data strongly suggest that habitat selection involving the oviposition plant is occurring for *P. saepiolus*.

One valuable feature of mark-release-recapture techniques is that they provide information about the movements of individuals. Fig. 2 presents in matrix form the locations of all recapture events; entries on the main diagonal represent recaptures in the same areas as the original capture and off-diagonal entries represent transfer recaptures. It is clear that most recaptures occurred in the original capture area and that most of the transfers were between areas *e* and *f* which are separated by 60 m. of favorable habitat. The ratio of transfers to same-area recaptures is 0.27 for all areas together and 0.27 for areas *e* and *f* alone. If the positions of individuals were randomized while retaining the observed number of individuals in each area, these ratios would be 2.12 and 1.00, respectively. Thus, even male *Plebejus saepiolus* do not travel freely over the 60 m. between areas *e* and *f*. An additional indication of the sedentary nature of these butterflies comes from observations of *P. saepiolus* concurrent with this study in which only 2 of the 37 individuals observed in the 30 × 60 meter region just east of area *d* were marked, while 7 of the 27 in area *e* were marked. These favorable areas are separated by 30–40 meters of drier ground not supporting *Trifolium*.

In the course of this study, male-male encounters were frequently observed. A possible effect of such encounters would be to encourage the even distribution of males over favorable habitat. The mean and variance data of Table 1 indicate that this is occurring. If the captures were totally independent events and the average population constant through time, the number of captures would follow a Poisson distribution (variance equal to the mean). Butterfly responses to weather or changes in population would increase the variance. For areas *a*, *e*, and *f*, however, the variances are about half the means. The captures are therefore not independent events, and the number of butterflies in an area is more uniform than would be expected if they did not interact.

CONCLUSIONS

Plebejus saepiolus, in contrast to other species of butterflies found in subalpine Colorado (Sharp, Parks & Ehrlich, MS in prep.), shows a striking degree of correlation with the micro-distribution of its oviposition plant *Trifolium*, which itself has a patchy distribution. *P. saepiolus* appears to be quite sedentary and, as with its relative *Plebejus icarioides* Boisduval, its populations are localized. Other butterfly species in the area, notably *Erebia epipsodea* Butler (Brussard & Ehrlich, 1970) and *Colias alexandra* Edwards (Ward B. Watt, pers. comm.), range widely and have large populations. The distributions of individuals in these populations do not correlate strongly with that of their oviposition plants, and the plants themselves are widely distributed.

It seems likely that *P. saepiolus* distributions represent one strategy available to a small, weakly-flying butterfly in a seasonally unpredictable environment such as subalpine Colorado. By maintaining sedentary populations closely associated with the perennial plant which provides both larval food and nectar for the adults, *Plebejus saepiolus* can minimize uncertainties in finding a source of food.

ACKNOWLEDGMENTS

Support for this work was provided by the National Science Foundation Graduate Fellowship Program and by NSF Grants #GB 19686 and #GB 22853X. The authors are grateful to the Rocky Mountain Biological Laboratory for the use of their facilities, and to M. C. Singer and Ward B. Watt for much valuable information. Thanks are due to Paul R. Ehrlich and Richard W. Holm, who read and criticized the manuscript.

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FOODPLANT ECOLOGY OF THE BUTTERFLY *CHLOSYNE LACINIA* (GEYER) (NYMPHALIDAE). I. LARVAL FOODPLANTS

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For several years I have studied field populations of *Chlosyne lacinia* (Geyer) (Nymphalidae: Melitaeini) in central and south Texas for genetic (Neck et al., 1971) and ecological genetic data. A considerable amount of information concerning foodplants of this species has been collected. Foodplant utilization information is an important base from which ecological studies may emerge. Such information is also invaluable in evaluating the significance of tested foodplant preferences of larvae and adults. Such studies have been under way by other investigators and will be available for comparison with natural population observations.

In addition to personal observations (which cover a four-year period encompassing some 20 generations), an extensive search of the literature reveals numerous, though scattered, previous reports of foodplants. Literature references to populations in central and south Texas are integrated into Table 1 with personal observations. All reports of foodplants outside the study area are discussed separately at the end of the study area foodplant discussion.

Foodplants (see Table 1) are arranged into three basic categories ac-