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INFLUENCE OF RESOURCE DISTRIBUTION AND ABUNDANCE ON BUTTERFLY POPULATION STRUCTURE

A DISSERTATION

SUBMITTED TO THE DEPARTMENT OF BIOLOGICAL SCIENCES

AND THE COMMITTEE ON GRADUATE STUDIES

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

By

Lawrence Edmund Gilbert, Jr.

May 1971

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I certify that I have read this thesis and that in my opinion it is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Peter H. Raven

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Christine Gilbert typed and edited this dissertation in addition to taking care of me. For these and many other things I owe her my deepest gratitude.

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TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	iii
LIST OF TABLES	vi
LIST OF FIGURES	vii
INTRODUCTION	1
Chapter	
I. THE EFFECT OF RESOURCE DISTRIBUTION ON POPULATION STRUCTURE IN THE BUTTERFLY EUPHYDRYAS EDITHA: JASPER RIDGE VS. DEL PUERTO CANYON COLONIES	2
Introduction	2
Animal Dispersal	3
Butterflies and the Study of Dispersal	9
Euphydryas editha in the Bay Area	10
Methods	11
Results	14
Larval Food Plants at Del Puerto	14
Adult Nectar Plants at Del Puerto	19
Adult Dispersal and Resource Distribution, Del Puerto vs. Jasper Ridge	24
Discussion	29
II. THE DISTRIBUTION AND ABUNDANCE OF RESOURCES AS FACTORS WHICH DETERMINE POPULATION STRUCTURE IN A TROPICAL BUTTERFLY, HELICONIUS ETHILLA	44
Introduction	44
Population Structure of Tropical Butterflies	44
Heliconius ethilla in Trinidad	46
Andrew's Trace Study Area	47
The Resources of Heliconius ethilla at Andrew's Trace	52
Methods	53
Subareas at Andrew's Trace	54
Movements Among Subareas	55
Population Size and Stability	55
Age Structure of H. ethilla Populations	60

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TABLE OF CONTENTS--Continued

Chapter	Page
II. (Continued)	
Longevity and Reproductive Activity.	63
Reproductive Effort and Mortality.	69
Egg Production, and Pollen as an Adult Resource. . .	73
The Nature of Adult Resources and Home Range Behavior	75
Distribution and Abundance of Resources X Population Structure.	85
BIBLIOGRAPHY.	91

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LIST OF TABLES

Table		Page
1.	Population size and density versus percentage of butterflies estimated to leave home in two Jasper Ridge populations (G and H)	8
2.	*Euphydryas editha* density: Jasper Ridge H vs. Del Puerto.	38
3.	Summary of *H. ethilla* recapture data.	56
4.	Sex ratio and sex differences in probability of recapture at Andrew's Trace. Areas A and B are combined.	56
5.	Longevity of marked *H. ethilla*.	62
6.	Some representative data showing individual recapture patterns along Andrew's Trace (Stations 1-26)	82

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LIST OF FIGURES

Figure		Page
1.	Dispersal as a function of numbers and density in *E. editha* at Jasper Ridge.	7
2.	Map of serpentine islands in the San Francisco Bay Region.	13
3.	Map of Del Puerto Canyon study sight, located 15 miles WSW of Patterson, Stanislaus Co., Calif., along Del Puerto Creek.	16
4.	Larval resources of *E. editha* and *E. chalcedona* at Del Puerto Canyon.	18
5.	*E. editha* adult population at Del Puerto Canyon: spatial changes through time. (A) 12 April 1970 (B) 17 April 1970 (C) 1 May 1970 (D) 3 May 1970 (E) 14-15 May 1970	21
6.	(A) Distribution of *E. editha* larval and adult resources at Del Puerto Canyon. (B) Movements of adult *E. editha* at Del Puerto Canyon.	26
7.	(A) Distribution of *E. editha* larval and adult resources at Jasper Ridge superimposed to scale on the Del Puerto Canyon map (for comparative purposes). (B) Typical pattern of adult movements between capture events at Jasper Ridge (based on 8 years of mark-release-recapture data).	28
8.	Comparison of dispersal tendency in two *E. editha* populations.	31
9.	Aerial view of northern Arima Valley and surrounding ridges of the Northern Range, Trinidad, W. I.; scale is one mile.	49
10.	*Heliconius ethilla* study area, at Arima Pass, along Arima-Blanchisseuse Highway, Trinidad, W. I. . .	51
11.	*Heliconius ethilla* male population estimates with $\pm$ one S. E. limits, areas A and B of Andrew's Trace, December 1969 to December 1970	59

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LIST OF FIGURES--Continued

Figure		Page
12.	Relationship between known minimum age (days elapsed since initial marking of butterfly) and wing condition in H. ethilla.	65
13.	Minimum life expectancy curve for recaptured H. ethilla: males (N=210) versus females (N=77).	68
14.	Alteration of spatial pattern of H. ethilla adult movement with changing resource patterns.	78

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INTRODUCTION

Each of the two chapters of this dissertation describes a separate but related study designed primarly to answer the following question: How do the dispersion patterns of essential resources, such as larval food plant and adult nectar sources, affect the population structures of butterflies?

The first chapter asks this question (among others) with respect to the well studied, temperate zone butterfly Euphydryas editha. The experimental approach involves comparing different populations of this species with respect to the ways in which individuals and populations respond to differences in the dispersion patterns of resources from place to place and through time.

Chapter Two summarizes a similar investigation of a long-lived tropical American butterfly, Heliconius ethilla, in Trinidad, W.I. In this study, the same population was followed for more than one year in an attempt to learn (among other things) how the nature, abundance, and dispersion of resources through space and time determined the observed structural features of the population.

Since each of these studies is separately and fully introduced at the beginning of the appropriate chapter, no further introduction needs to be provided here.

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CHAPTER I

THE EFFECT OF RESOURCE DISTRIBUTION ON POPULATION STRUCTURE IN THE BUTTERFLY EUPHYDRYAS EDITHA: JASPER RIDGE VS. DEL PUERTO CANYON COLONIES

Introduction

This is the second in a series of studies devoted to comparative ecological studies on numerous populations of the butterfly Euphydryas editha Bdv. in California and adjacent states, the first being a comparison of adult oviposition preference (Singer,1971). This work was stimulated by the detailed study of population structure of the Jasper Ridge colony of E. editha by P.R. Ehrlich (1961) in which "intrinsic barriers" to dispersal were shown to divide the colony into three essentially isolated populations, which undergo independent fluctuation in numbers (Ehrlich,1965).

The presence of other E. editha populations in the San Francisco Bay Area which live in dry chaparral-covered canyons rather than open annual grassland has provided a natural experiment which has not only helped in attacking some previously raised questions about the population biology of E. editha (Ehrlich,1965) but also stimulated questions not obvious from the previous studies on the Jasper Ridge colony. In this chapter the nature of the structural differences between these different types of habitat are described, and the way these differences influence various aspects of local population

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structure, including the phenomenon of "intrinsic barriers" to dispersal at Jasper Ridge, will be examined. Throughout the chapter, comparisons with other kinds of animals will be stressed.

Animal Dispersal

Most terrestrial animals are highly mobile as adults and yet sufficiently sedentary to be organized into mosaics of local populations. Ecologists have long been interested in animal dispersal from the standpoint of its effects on population density. There has been considerable controversy over whether an animal is stimulated to move by epideictic displays from conspecifics, a tendency evolved by group selection to prevent overexploitation of resources (Wynne-Edwards, 1962), or whether it moves because natural selection has favored those individuals which disperse when some important resource becomes limiting (Lack, 1966).

Population geneticists, on the other hand, have been more concerned with the effects that animal movement have on the genetic integrity of local population units. (They also tend to use terms like "migration" in a way different from the ecologists' usage.) It has long been thought that gene flow, resulting from animal movements among populations, is the cohesive force holding populations of a species together. As such, it has been considered a negative factor in evolution by preventing local fine-tuning by a population to environmental patchiness (Mayr, 1963). In a slightly different vein, Soulé (1971) has recently argued that because central populations tend to receive gene flow from a greater variety of areas than do peripheral populations, gene flow, rather than adaptation to broader

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niches, explains the higher genetic diversity in the centers of range of species such as Drosophila willistoni. Gene flow has also been implicated as the major factor helping to maintain the lethal t-allele polymorphism in mice (Levin, et al., 1969).

Levins (1964) provides perhaps the most thoughtful and interesting ideas about the evolutionary importance of gene flow. He argues that whether gene flow between adjacent populations reduces population fitness depends upon the temporal and spatial aspects of environmental variation. For instance, two populations in environments which are constant in time, variable in space, and permanently different (e.g., edaphic features) will suffer reduced fitness if gene flow occurs. On the other hand, two populations will benefit from gene flow if their respective environments fluctuate independently about the same mean. Levins suggests that optimal levels of gene flow are established by natural selection and implies that gene flow rates are species characteristics.

Recently Ehrlich and Raven (1969) have summarized numerous field studies (such as those of E. B. Ford and co-workers) which indicate that natural selection is sufficiently intense to override the influence of gene flow. They question the role of gene flow in preventing the differentiation of populations and challenge its evolutionary importance. Ehrlich and Raven, like Levins (1964), tend to speak of the levels of gene flow and dispersal tendency as species characteristics for the purpose of making general statements (for example, their reference to the sedentary nature of the "species" E. editha in California, p. 1229).

There has been little explicit recognition of the fact that

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within a species extensive interpopulation variation might exist with respect to the innate tendency of individuals to disperse under a given set of conditions. More often dispersal tendency is thought to be a flexible character which varies with resource abundance or population density. For example, bird ecologists have recognized that the spacing patterns and dispersal tendency of a bird species can vary within the species from area to area depending on food supply (Lack, 1966). Evolutionists have suggested with little evidence that gene flow rates may vary with the density of a population, dense central populations applying gene flow pressure on peripheral populations (Mayr, 1963). There is reason to believe, however, that this latter generality does not hold for many terrestrial animal groups. For instance, in both thrips (Davidson and Andrewartha, 1948) and Drosophila (Dobzhansky and Wright, 1943) dispersal is not a function of density over the values observed. More appropriate is the example of Jasper Ridge Euphydryas editha in which studies of population structure show that movements among local semi-isolated populations do not increase with density. In fact, for one population (G) the reverse seems to hold. I have summarized seven years of data for two adjacent E. editha populations in Figure 1. In contrast, long term studies on another melitaeine butterfly, Melitaea harrisii, by Dethier (Dethier and MacArthur, 1964) indicate that high density increases emigration. The same is true for at least some pierid butterflies (Shapiro, 1970).

There are several reasons why the subject of animal dispersal is confusing. First, most workers tend to study dispersal from a somewhat narrow point of view. Theoretical population geneticists

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Figure 1

Dispersal as a function of numbers and density in E. editha at Jasper Ridge. Each value for "percent known to leave home" represents the percentage of recaptured individuals which have been observed to move from an area (G or H) of original capture during a flight season. In the case of large areas or large populations or both, the actual recapture of immigrants in another area is required. However, in the case of a very small area such as G, when the population size is very small, direct census is possible (e.g., the years 1963, 1971 in Table 1). These graphs are based on the data of Table 1.

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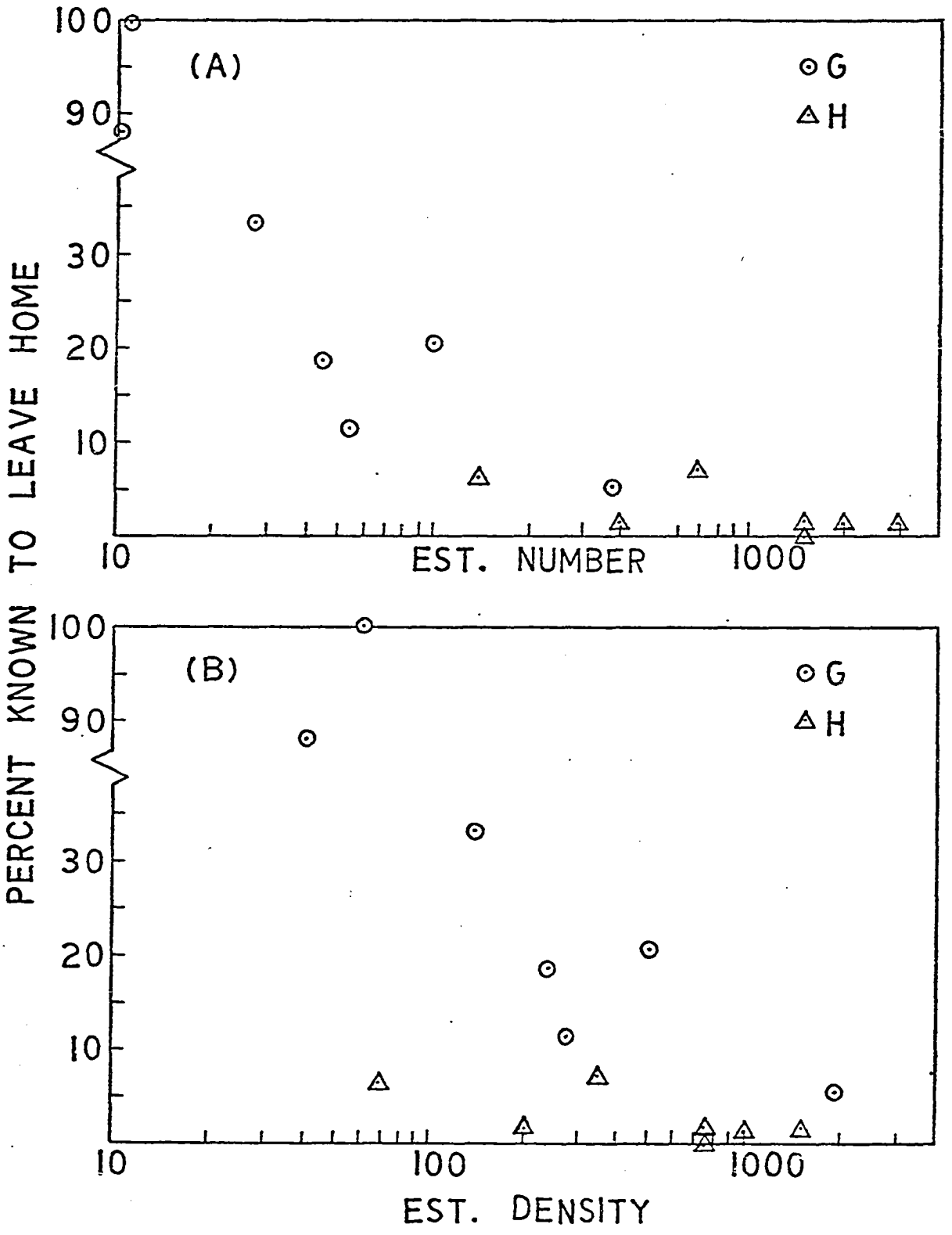

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TABLE 1

POPULATION SIZE AND DENSITY VERSUS PERCENTAGE OF BUTTERFLIES ESTIMATED TO LEAVE HOME IN TWO JASPER RIDGE POPULATIONS (G AND H). THE DATA FOR THE YEARS 1960 TO 1963 WERE GATHERED BY P.R. EHRLICH (1965 AND UNPUBLISHED). THE DATA FOR 1969 TO 1971 WERE GATHERED BY M.C. SINGER AND L.E. GILBERT. I THANK P.R. EHRLICH FOR MAKING HIS EARLY RECORDS AVAILABLE.

Year	Area G (.2 Hectares)			Area H (2.0 Hectares)		
	Est. N	Density[a]	% Leaving[b]	Est. N	Density[a]	% Leaving[b]
1960	50-60	275	11.5 (3/26)	130-150	70	6.3 (2/32)
1961	40-50	235	18.8 (3/16)	600-800	350	7.3 (8/109)
1962	25-30	137	33.3 (1/3)	1200-1800	750	2.6 (3/112)
1963	10-12[c]	60	100.0 (0/0)[d]	1200-1800	750	0.0 (0/155)
1969	150-200	878	5.3 (1/19)	3000	1500	1.7 (4/231)
1970	100[e]	500	20.8 (5/24)	2000	1000	1.3 (1/77)
1971	8	30	88.0 (7/8)[f]	400	200	1.5 (1/64)

a. Estimated number per hectare.

b. Minimum percent known to leave area.

c. All 4 captures in 1963 were males. The lack of butterflies in G in 1964 (Ehrlich, 1965) suggests that there were no females in 1963.

d. It is reasonable to assume that all 4 of these males left G and were simply not recaptured in the other areas.

e. This estimate is 180-300 by Jolly's (1965) method if the 5 leaving are considered at risk in G.

f. Seven of the eight butterflies in G in 1971 left after brief residence. The last, a male, stayed one week, then transferred to Area H (18-21 April 1971). Therefore, it can be said that 100% left G in 1971.

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understandably stress empirical examples which fit workable diffusion theory models (e.g., Chapman, 1967) and neglect more messy situations in which animals do not behave purely randomly. Population ecologists likewise have not for the most part attempted to analyze the behavior of individual organisms with respect to the structure of the habitat, while ethologists have narrowed their scope to social interactions and have neglected entirely ecological considerations. In general, all of these approaches to animal populations have neglected detailed study of population structure broadly defined (Ehrlich and Holm, 1962). Equally serious is the biased sample of organisms from which generalities in evolutionary and behavioral ecology have emerged. While it has been suggested that certain fundamental polarities exist in nature which give rise to conceptual dichotomies (due to taxonomic or other biases) among population biologists (Orians, 1962; Horn, 1968; Pianka, 1970), this does not seem to be widely appreciated as yet. The influential works of Mayr, MacArthur, Lack, Wynne-Edwards, and Klopfer, for instance, all suffer from ornithological bias. On the whole, the major theoretical constructs of each of these are based heavily on bird examples and quite likely apply only to birds or other vertebrates.

Butterflies and the Study of Dispersal

Butterflies, because they are large, day-flying, and easily handled, are ideal animals for maximizing the levels and angles of approach to the problem of relating habitat structure, individual dispersal, and population structure. As phytophagous insects, butterflies are representatives of the most diverse group of

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terrestrial animals so that population studies of butterflies should provide the basis for at least a subset of realistic generalities about populations and communities. Because of funding considerations, most studies of insect dispersal and population structure deal with herbivorous pest species (see Johnson, 1969) which as a group are likely to differ in dispersal characteristics from other phytophagous insects such as E. editha (see discussion section). Thus, it is felt that this as well as other investigations of E. editha should complement similar studies on other kinds of animals and will allow reevaluation of some of the ecological generalities based on those studies.

The key questions have already been discussed but should be summarized once again.

1). What are the relative roles of population density, food supply, and other aspects of habitat structure in determining how far an animal will disperse from its birthplace?

2). What are the fundamental differences between different groups of animals (e.g., birds vs. phytophagous insects) in the way population structure responds to changes in habitat structure?

3). Are such individual attributes as dispersal tendency characteristic of species or populations?

4). How does dispersal relate to gene flow?

5). What are the evolutionary consequences of gene flow?

Euphydryas editha in the Bay Area

Euphydryas editha bayensis is a race of E. editha which is confined to a strip of California bounded on the north by San Francisco

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Bay, on the west by the Coast Range foothills, and on the east by the Central Valley. It is usually associated with serpentine rock outcroppings at least as far south as San Luis Obispo. All populations except two examined in the Bay Area fly between late February and late April on open serpentine annual grasslands. One exception mentioned above is the Del Puerto Canyon population, which, while only 40 miles from Jasper Ridge and only 20 miles from the nearest "Jasper Ridge type" population near San Jose, flies two months later (late April and May-June). Fig. 2 shows the serpentine islands of the Bay Area along with populations which we have had under surveillance since 1968. In most of these populations larvae feed on Plantago erecta and Orthocarpus except the Del Puerto Canyon (DP) population which feeds on Pedicularis densiflora.

Methods

Because of the steep terrain at Del Puerto Canyon, the mapping of plants and butterfly captures there requires some special techniques. An observation station was established on the south wall of the canyon while several collectors proceeded up the north wall where the population was situated. By means of a large map of the opposite slope, the spotter was able to plot the positions of food plants, larvae, and adults. Communication between the spotter and collector was made with small transceivers and by shouting. Movements were studied by marking butterflies and mapping their recovery points. In addition to E. editha, two other species, E. chalcedona and C. leanira, were studied and the E. chalcedona results will be mentioned briefly in discussing the Del Puerto E. editha.

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Figure 2

Map of serpentine islands in the San Francisco Bay Region. *E. editha* colonies under study in this areas are as follows: EW, Edgewood Road; WS, Woodside; JR, Jasper Ridge; SJ, San Jose; CR, Coyote Reservoir; MD, Mount Diablo; DP, Del Puerto Canyon. Scale division is five miles.

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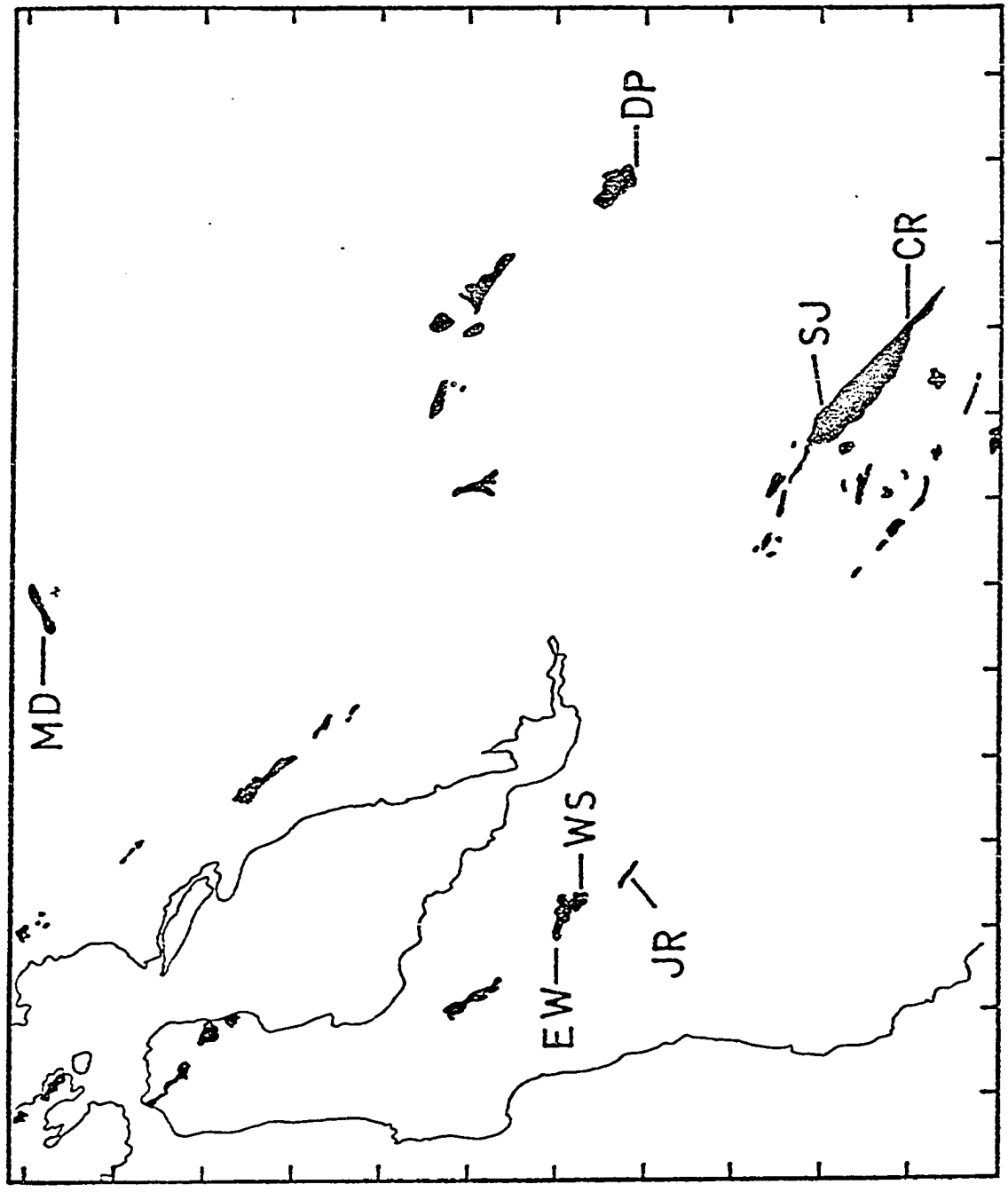

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The topographic map of the area (Fig. 3) was made with the simple equipment of pocket compass, graph paper, and altimeter. Photographs of various parts of the area helped in checking the accuracy of this map, which is sufficient to resolve movements of marked animals of 50 meters and more. Many numbered stations (marked with plastic flagging) aided in establishing exact positions of marked and recaptured butterflies. Most of the work reported here took place between 12 April and 19 May 1970. Preliminary observations of the area were carried out in May and June of 1968 and 1969.

Results

Larval Food Plants at Del Puerto

An intensive survey of the Del Puerto habitat in April 1970 revealed E. editha larvae on four different but related food plants: Collinsia sp., Castilleja foliolosa, C. affinis, and Pedicularis densiflora (all Scrophulariaceae). However, a detailed study to be reported elsewhere indicated that Pedicularis densiflora is the only important food plant and E. editha appear on others only in the region of Pedicularis defoliation. Pedicularis, a hemiparasite, is distributed along the ridge tops of north facing slopes and is almost always associated with Manzanita (Arctostaphylos sp.). Likewise E. editha larvae are clumped along a narrow band which coincides with the Pedicularis distribution. This was a surprising result since adults in previous years (1968, 1969) had been found along the creek 500 feet below the larval population. E. chalcedona and Closyne leanira are associated with both Castilleja species, and their larvae are found wherever Castilleja is found, from the bottom to the top of the canyon face. Figure 4 summarizes

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Figure 3

Map of Del Puerto Canyon study site, located 15 miles WSW of Patterson, Stanislaus County, California, along Del Puerto Creek (heavy line). San Jose-Patterson Road is double line. Contour lines represent 100 foot intervals and are approximate. Elevation ranges from 1,400 feet on road to 2,200 feet at top of map.

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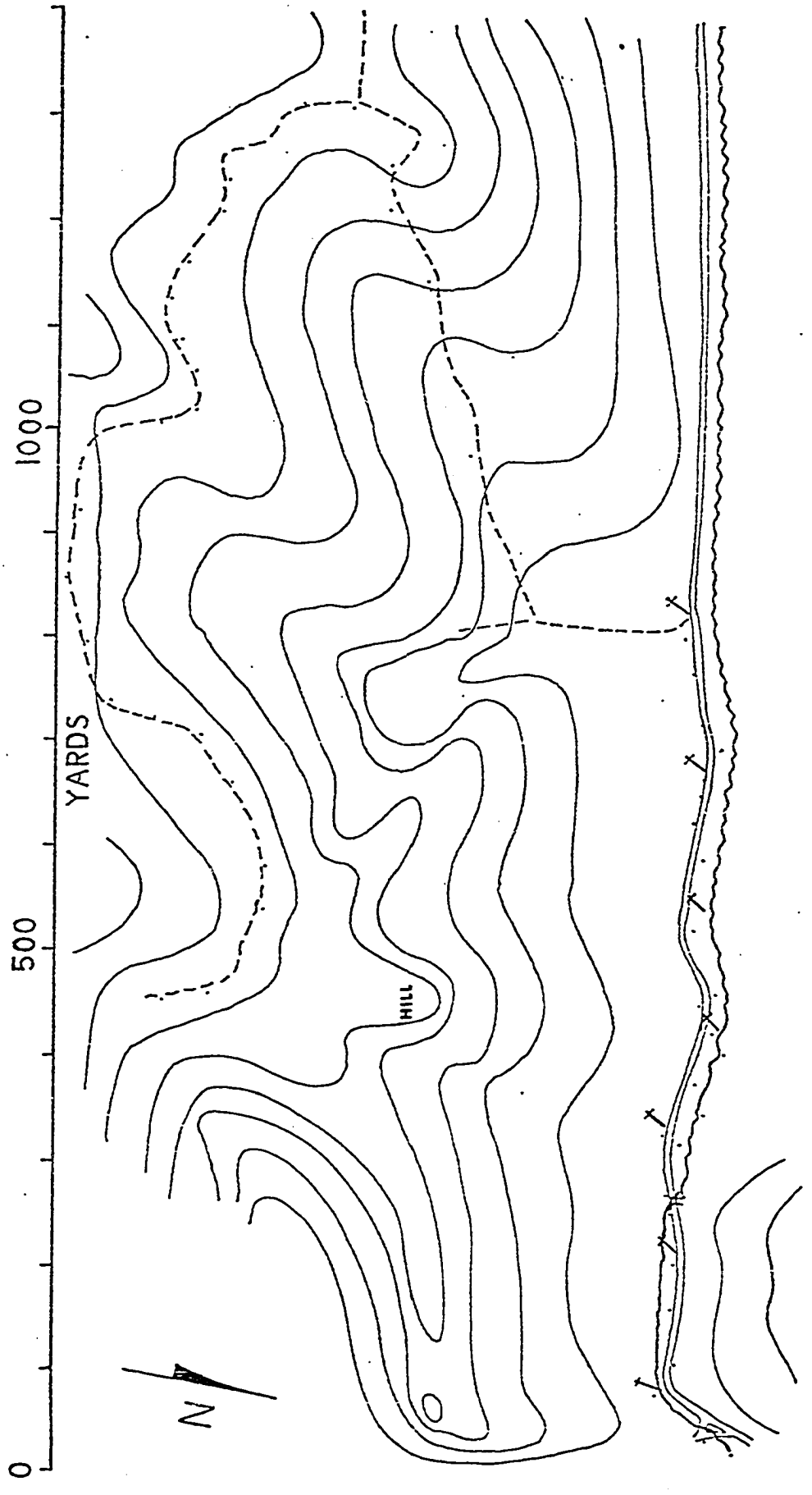

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Figure 4

Larval resources of E. editha and E. chalcedona at Del Puerto Canyon. Stippled areas represent Pedicularis densiflora (E. editha, occasionally E. chalcedona); large dots represent Castelleja foliolosa (E. chalcedona); small dots represent Castelleja affinis (E. chalcedona). Collinsia heterophylla (not shown) is scattered widely over the area but is not an important food plant for E. editha in this area.

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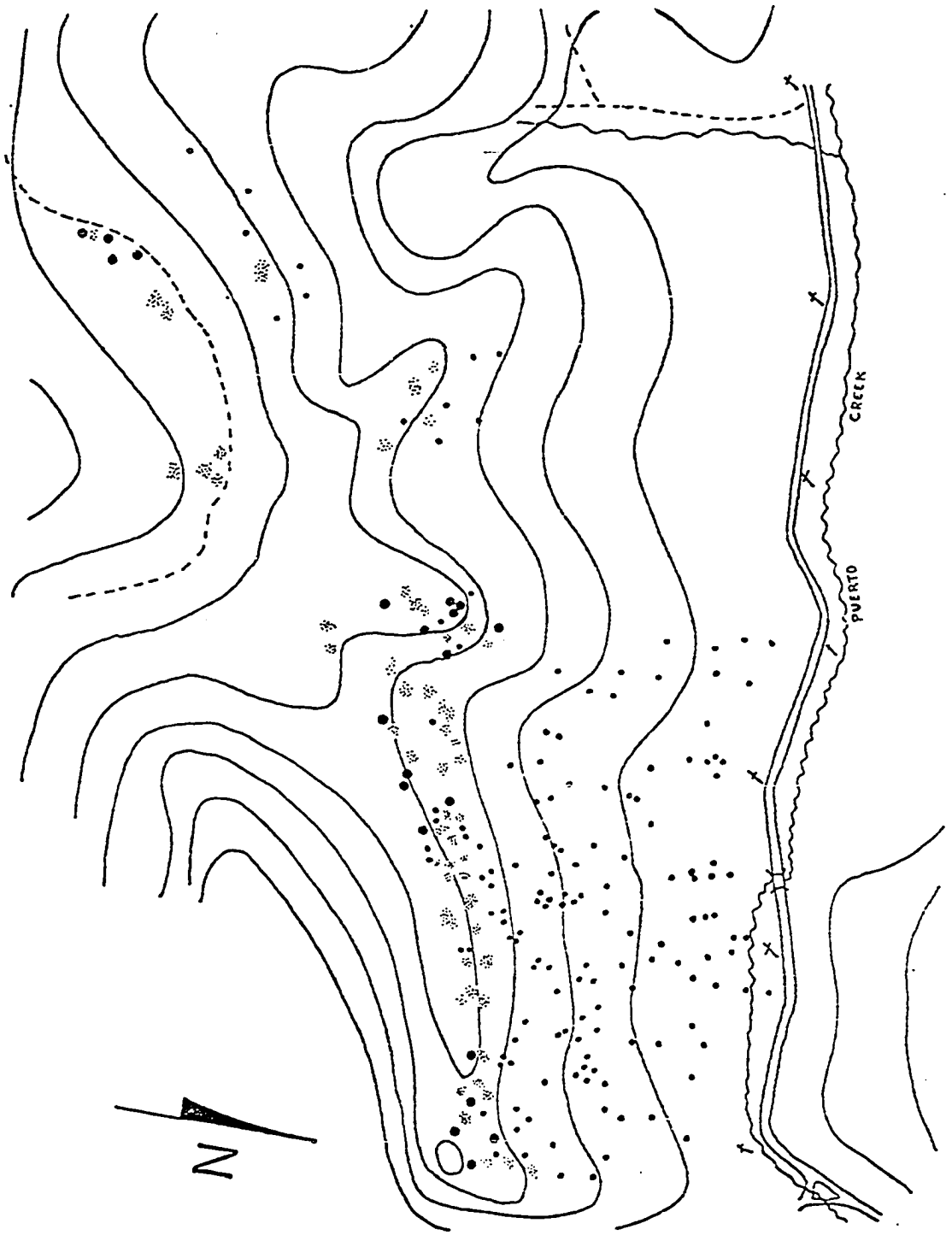

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the distribution of E. editha and E. chalcedona food plants at the Del Puerto Canyon locality.

Adult Nectar Plants at Del Puerto

Two plants, Eriodictyon californicum (Hydrophyllaceae) and Achillea millefolium (Compositae), are of particular importance as nectar sources for adult butterflies at Del Puerto. Both of these plants seem to grow in areas where the natural vegetation has been disturbed. Eriodictyon in particular has apparently extended its distribution rather widely along mining trails cut through this large block of serpentine mountains. Eriodictyon has a deeper corolla tube than other nectar plants for E. editha in the Bay Area. However, no difference in proboscis length exists between Jasper Ridge and Del Puerto E. editha. Instead, Del Puerto adults are just more persistent at prying into the flower. Whether this behavior can be learned by Jasper Ridge animals is currently under study.

The nectar plants at Del Puerto are widely scattered about the area and bear no relation to larval food plant distribution. In addition, there was a shift through the 1970 flight season in the pattern of available nectar. Early in the season (mid to late April) only plants on the hill top were in bloom, and later (1-3 May) when plants along Del Puerto Creek came into flower, the editha population shifted down the hill, Fig. 5 A-E. Whereas early changes in adult distribution could be explained by an emergence pattern (the first adults appearing where the largest larvae had been found) the later changes such as the shift down the hill are explained nicely by the changing nectar patterns.

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Figure 5

E. editha adult population at Del Puerto Canyon: spatial changes through time.

(A) 12 April 1970
(B) 17 April 1970
(C) 1 May 1970
(D) 3 May 1970
(E) 14-15 May 1970

Dots represent male capture points, solid triangles, mated females, open triangles, virgin females.

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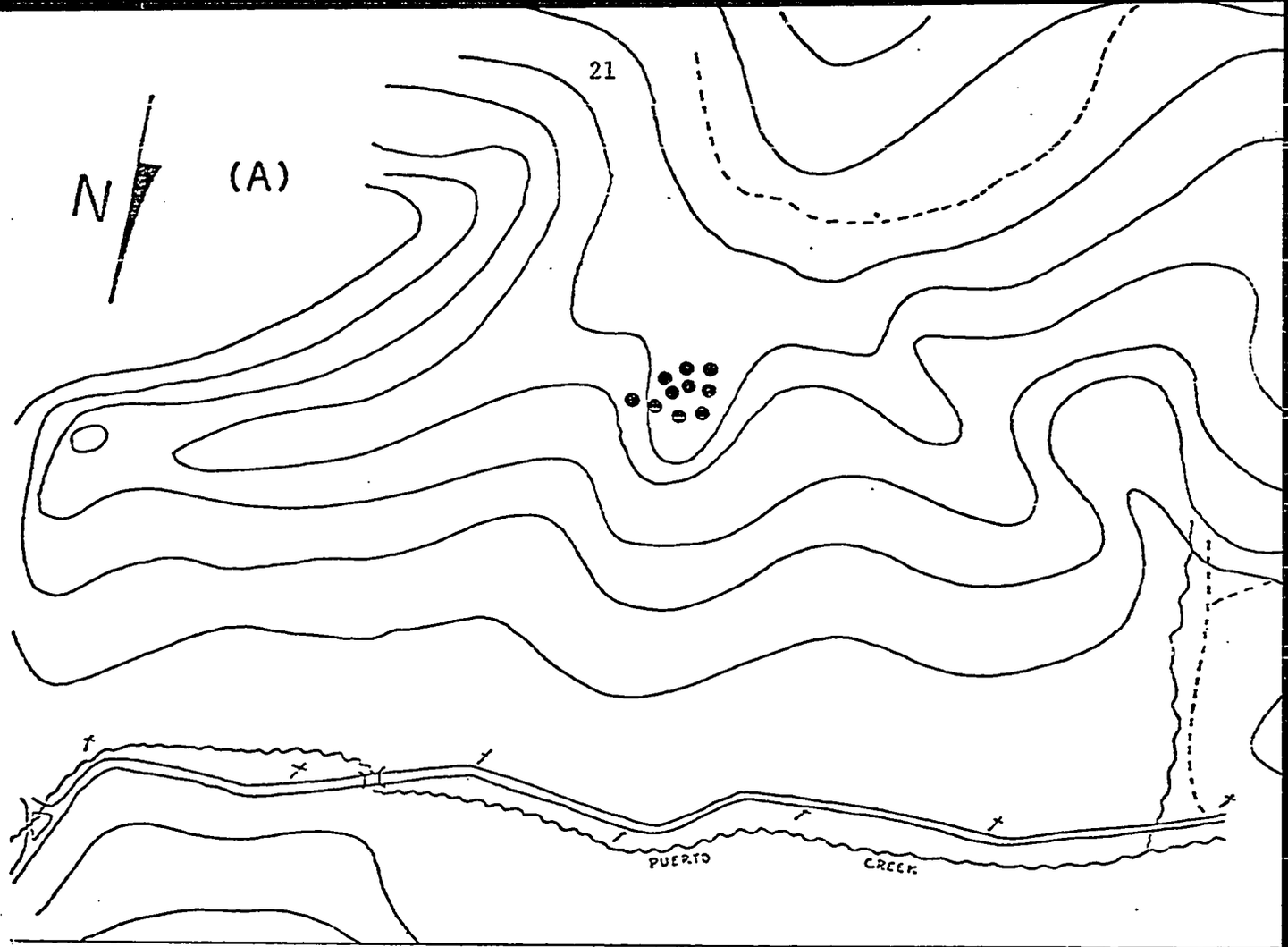

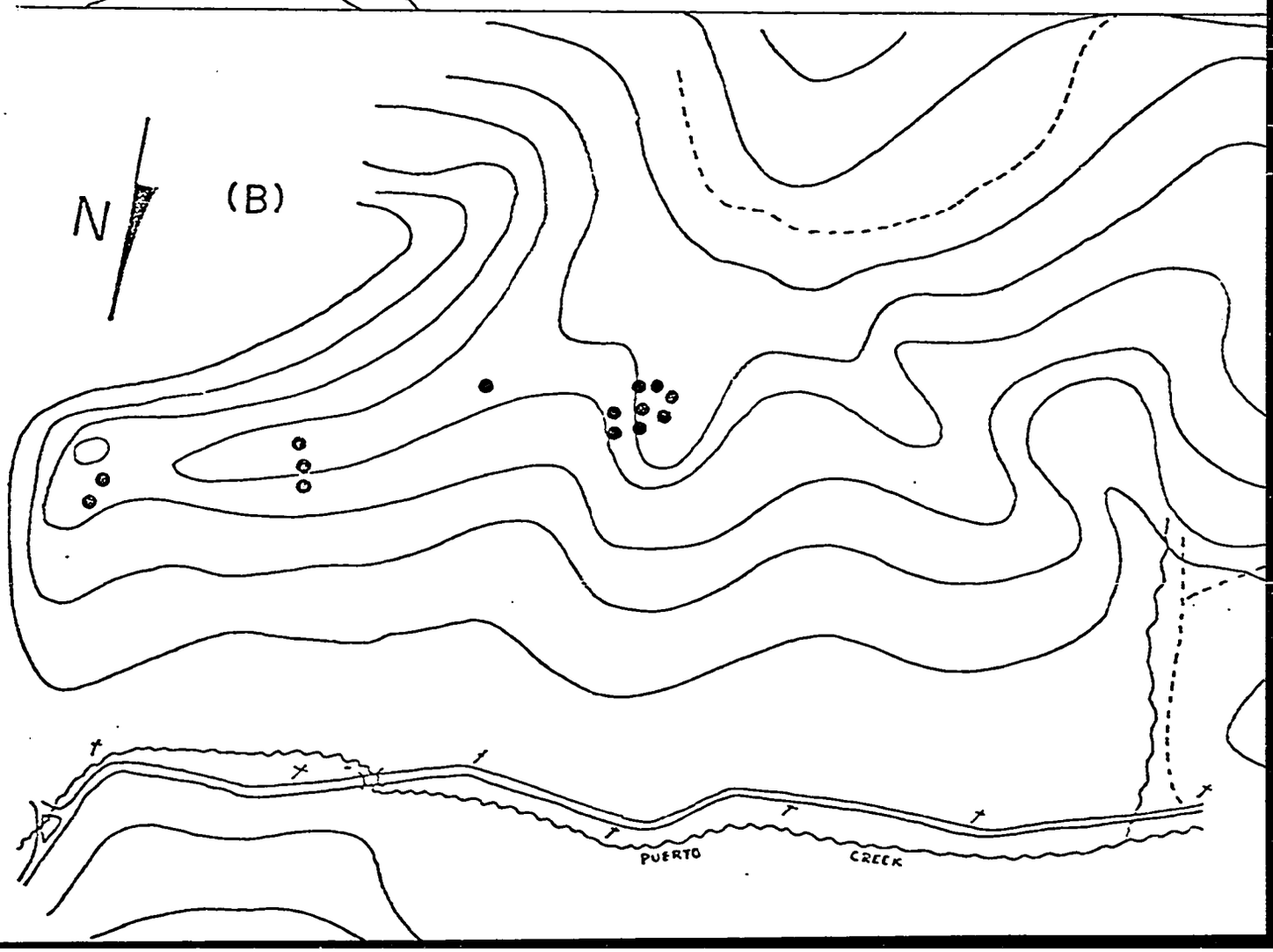

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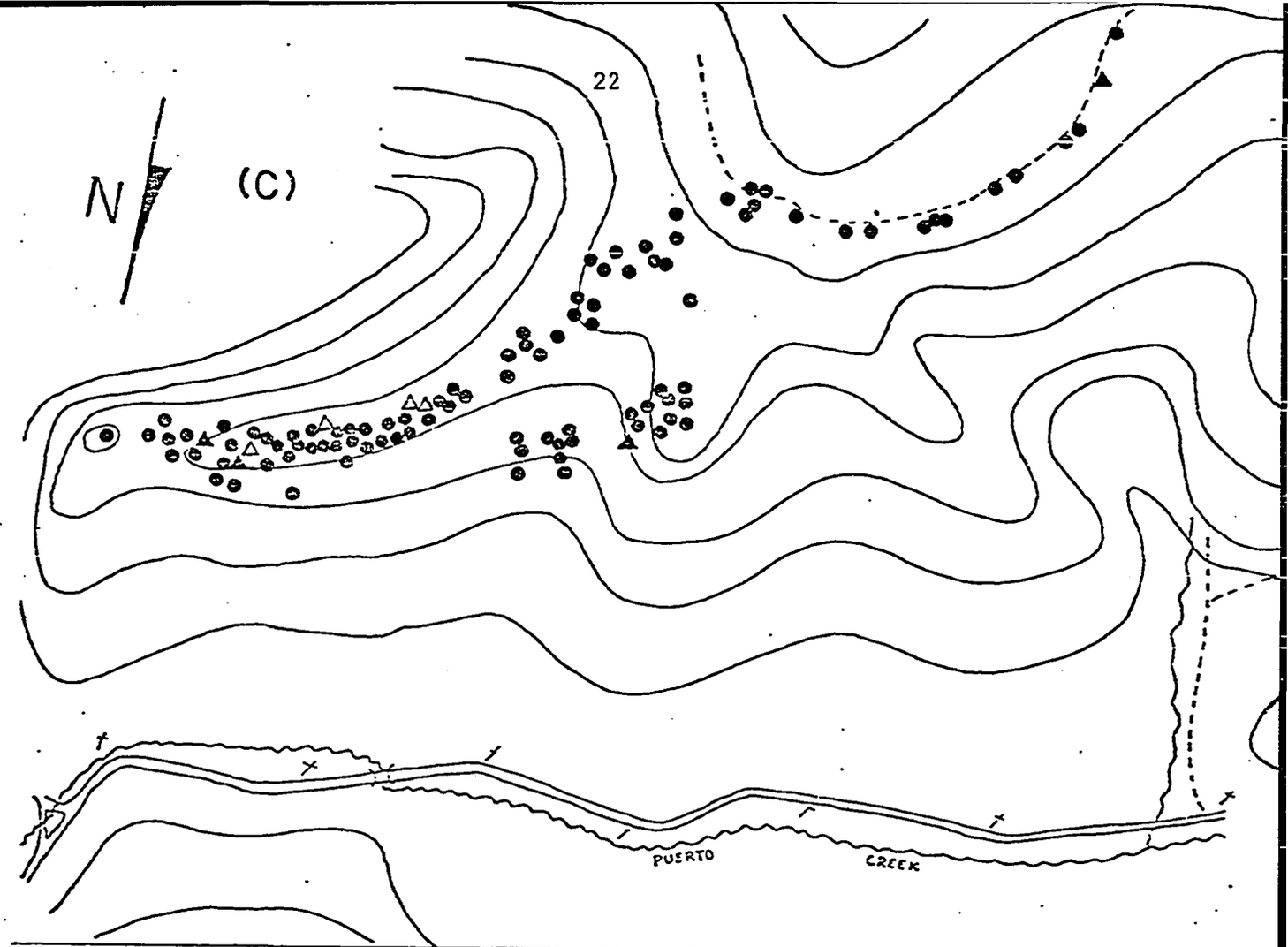

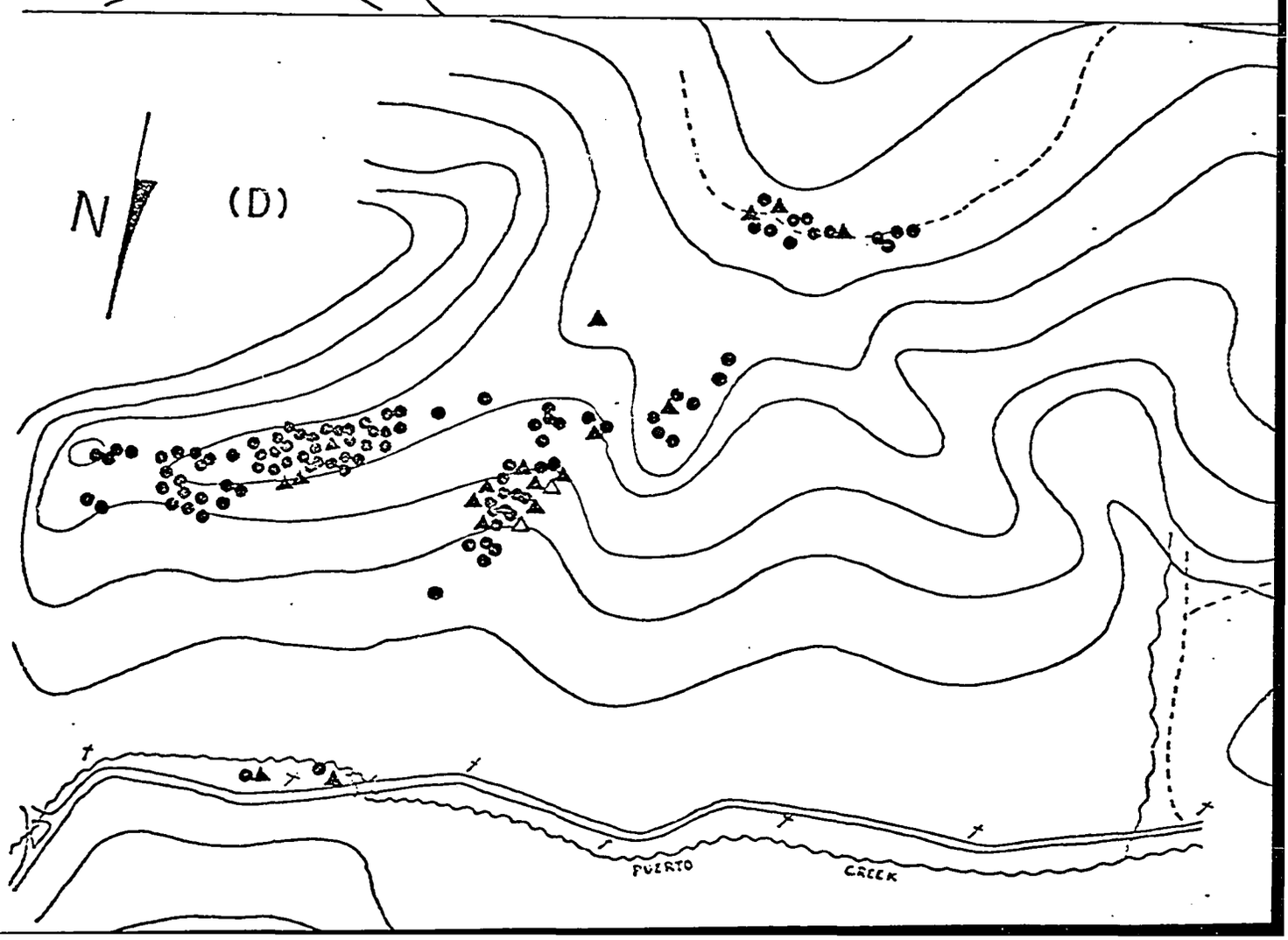

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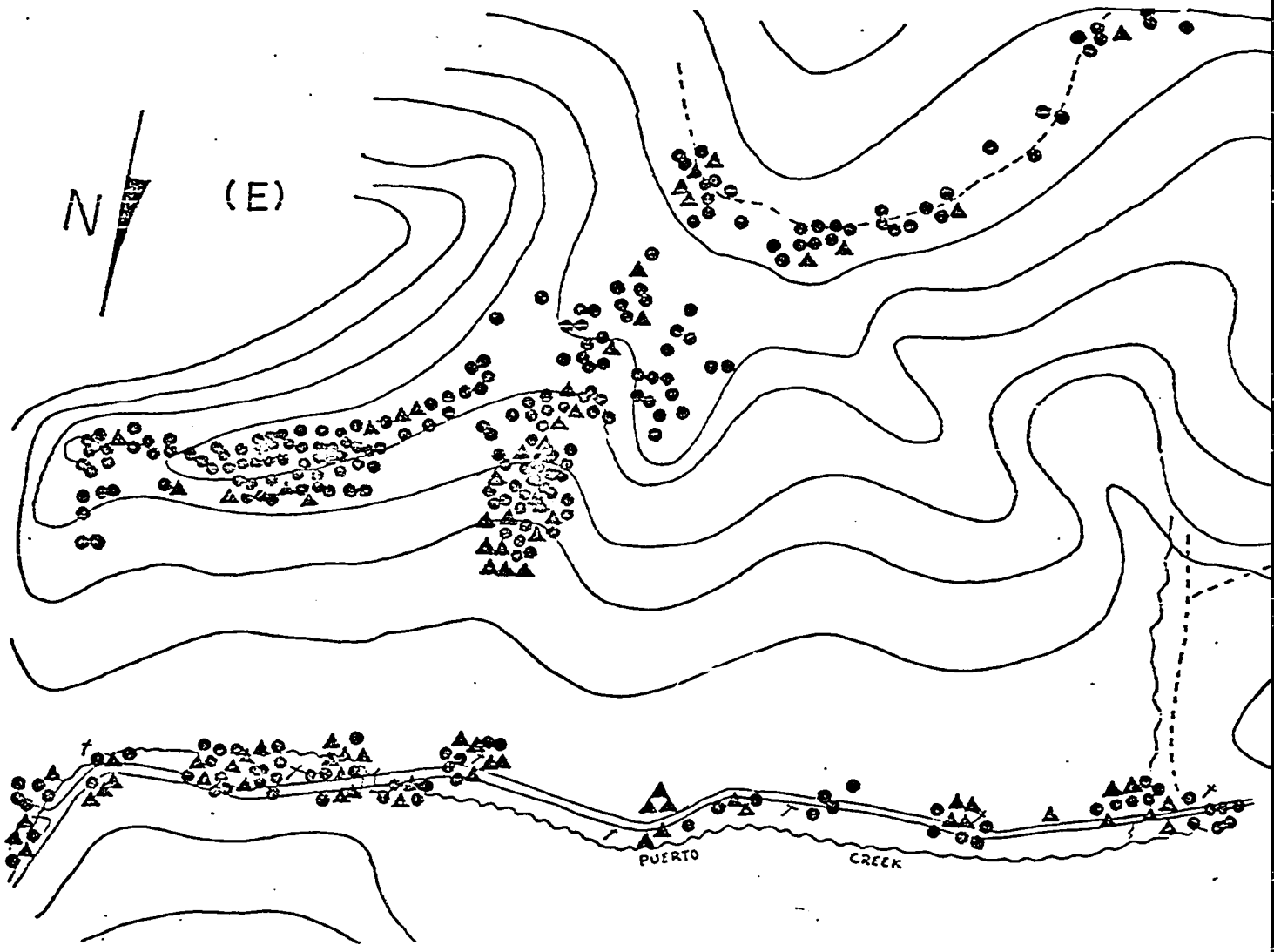

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The analysis of adult recapture data indicates that the adults which begin to appear along the creek in early May do not emerge there but are transfers from the ridge above. Canyon dwelling races of E. editha such as E. e. baroni are regarded as "rare" or low density animals (Tilden, 1965). The Del Puerto study shows that one reason for this may be the fact that collectors are usually operating on the fringe of adult distribution rather than being in the center of the population. Pope Creek Canyon, Napa Co., a well known locality for E. e. baroni, may seem denser than others because the ridge top food plants, adult nectar, and access roads all coincide. This may also explain why it is an "early flying" population relative to other canyon dwelling E. editha.

Adult Dispersal and Resource Distribution, Del Puerto vs. Jasper Ridge

If we consider individual movements at Del Puerto in relation to the pattern of larval and adult resources there, (Fig. 6 A,B), it is quite obvious that adult population structure is largely defined by the pattern of nectar plants in the area. As a result there is no subdivision of this colony into restricted populations as is the case on Jasper Ridge.

On the other hand, at Jasper Ridge the major food plant, Plantago erecta, is distributed in a continuous band between populations H,G, and C. In contrast, suitable nectar plants, primarily Lomatium (Umbelliferae), Layia, and less important Baeria (both Compositae), occur only within certain parts of the larval food plant patch. It is possible that small yellow composites such as Baeria provide no more than important visual stimuli which are correlated with the

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Figure 6

(A) Distribution of E. editha larval and adult resources at Del Puerto Canyon. Larval food plant, Pedicularis densiflora, is represented by stippling; adult nectar plants, Eriodictyon and Achillea, are represented by bold circles.

(B) Movements of adult E. editha at Del Puerto Canyon. Solid arrows represent movements with one or more days between capture events; the dashed arrow represents a same day transfer. Large dots represent individuals marked on some previous day and recaptured at original point of marking.

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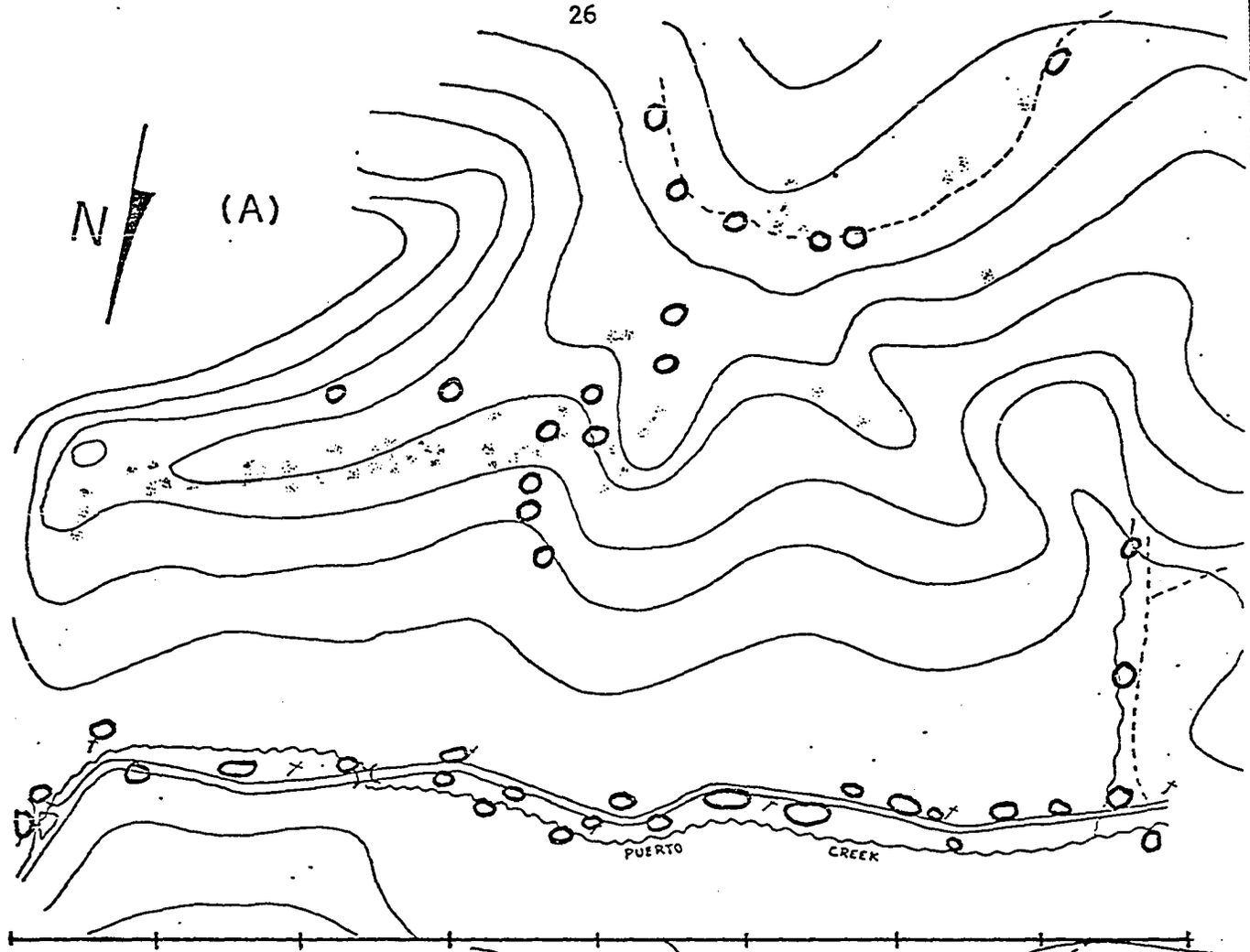

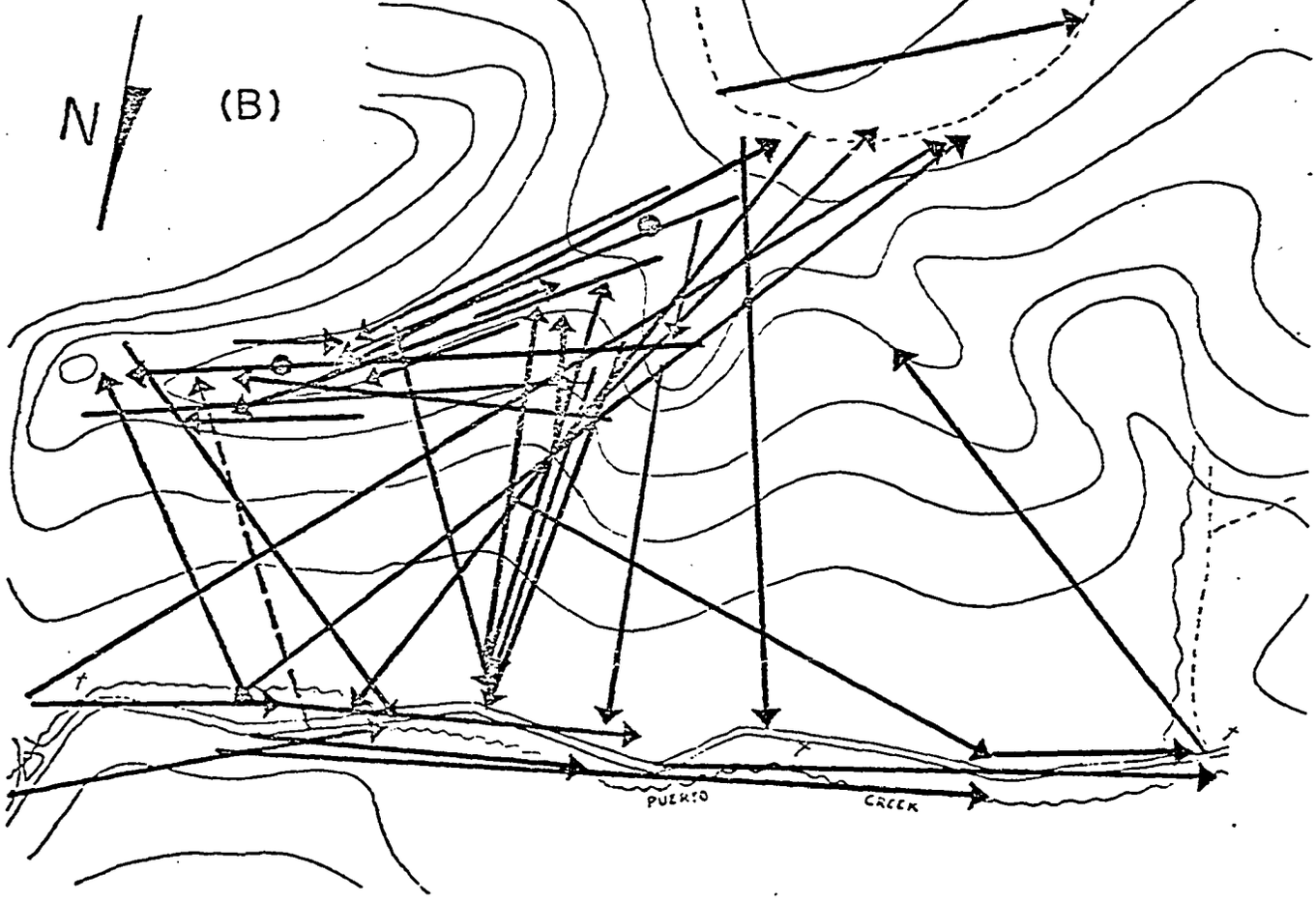

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Figure 7

(A) Distribution of E. editha larval and adult resources at Jasper Ridge superimposed to scale on the Del Puerto Canyon map (for comparative purposes). Stippled area represents larval food plants (Plantago erecta and/or Orthocarpus densiflora). Bold lines encircle areas of suitable adult nectar plants.

(B) Typical pattern of adult movements between capture events at Jasper Ridge (based on eight years of mark-release-recapture data).

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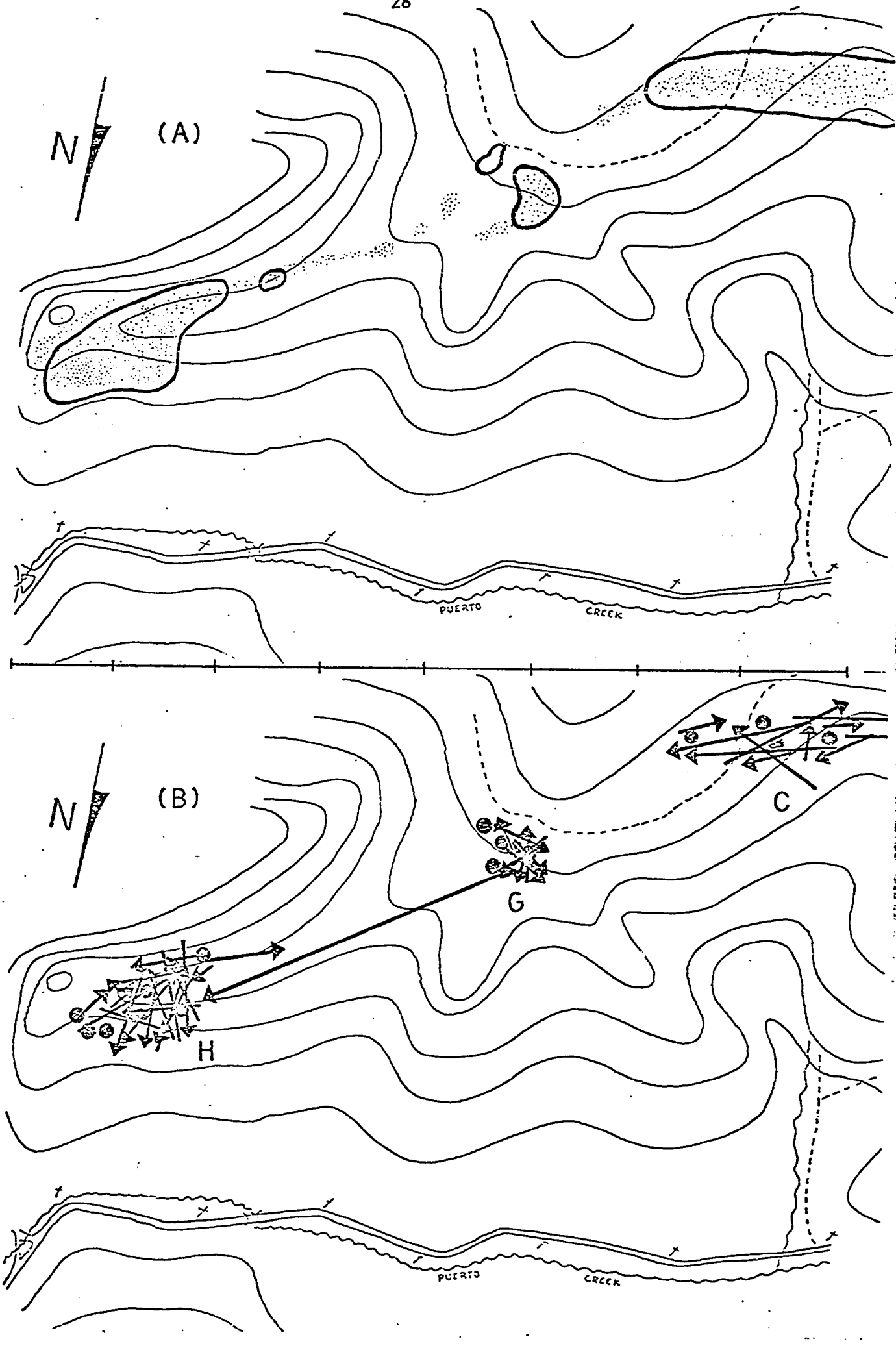

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presence of other more important but less conspicuous nectar sources, such as Lomatium. In Fig. 7, Jasper Ridge resource maps and transfer data are superimposed upon the Del Puerto map at the same scale for comparative purposes. In comparing maps A and B of Fig. 7 it can be seen that individual movements and consequently the described population units on Jasper Ridge are restricted to areas where adult nectar resources overlap suitable larval habitat. Thus, the "intrinsic barriers" to dispersal at Jasper Ridge quite likely include adult response to patches of flowers. Nectar manipulation experiments planned for Jasper Ridge after the 1970 season were unfortunately not possible in 1971 because of low adult numbers on Jasper Ridge in that year.

A graphic comparison of dispersal tendency of individuals within each of these two habitats is shown in Fig. 8 where the frequency distribution of transfer distances within Jasper Ridge's area H is plotted next to that of the Del Puerto population. The reason for the choice of JRH is the similarity in size between these two populations and the fact that transfer data within area H was gathered in 1970 (25 March-4 April) by M.C. Singer.

Discussion

Let us return to the questions about dispersal and population structure posed earlier in this chapter, to see whether the example of E. editha can be of more general use to population theory. First, what of the relative importance of density versus food supply in affecting the dispersal tendencies of animals?

In at least some E. editha populations high density either

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Figure 8

Comparison of dispersal tendency in two E. editha populations. The percentage (ordinate) of total recaptures moving a given distance (abcissa) is plotted in histogram form. Jasper Ridge Area H 1970 data is represented by solid bars (N=62); that of Del Puerto Canyon (1970) is represented by stippled bars (N=40). The single long transfer for JRH shown in the figure was an H to G transfer.

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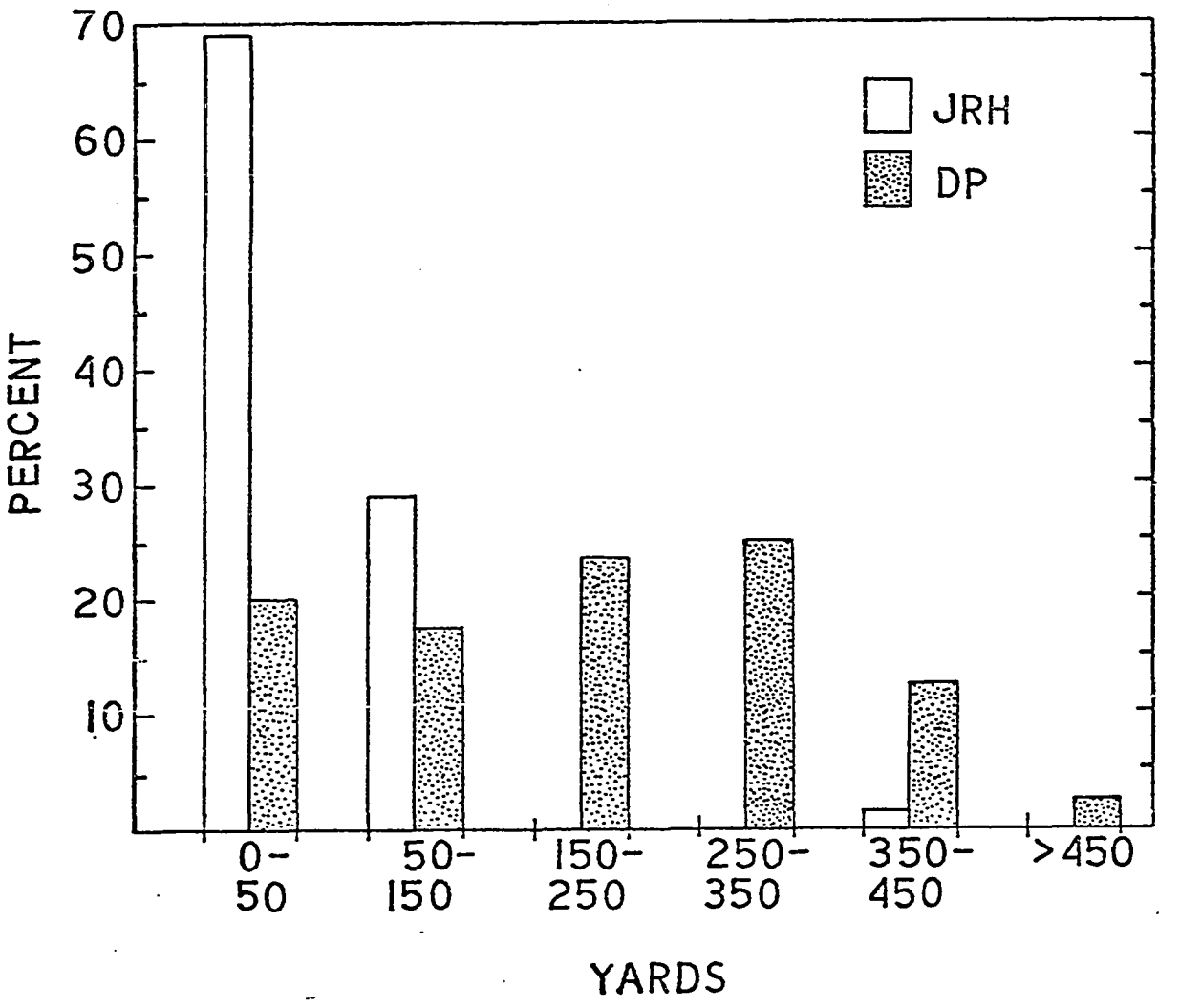

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decreases or does not alter the dispersal tendency of component individuals. Consider for instance the relative densities of E. editha at Del Puerto vs. Jasper Ridge area H. As seen in Table 2, adult density in space is an order of magnitude greater in the population (JRH) which has on the average more sedentary individuals (Fig. 8). Further indication that rate of emigration does not increase with density but may even decrease is provided by the data in Figure 1, Table 1. This shows that in JRH a twenty-fold increase in adult density over the years has not resulted in an increase in the precent of individuals known to transfer from H to other areas of JR. Similar data for JRG (Fig. 1) provides a much stronger case for the negative correlation between dispersal and density.

On the other hand, shifts in adult population structure observed at DP resulting from changing nectar distribution (between 3 and 14 May 1970; Fig. 5 D,E) indicate that for this E. editha population, the number of butterflies per unit volume of nectar is perhaps closer to what most biologists (e.g. Tanner, 1966) think of as "density". Thus, increasing the number of butterflies in a small area while holding nectar supply constant will cause increased emigration mainly because less nectar, rather than less space, is available per individual.

Making this distinction helps to explain the apparent positive correlation between "density" and emigration observed for Melitaea harrisii (Dethier and MacArthur, 1964). They observed that artificially increasing by five-fold the number of adults in a small field caused a reduction in the number of eggs laid in the field. However, food plants bordering the field received more eggs than usual, indicating that emigration from the field had reduced the number of egg masses

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deposited there. Dethier and MacArthur observed that the carrying capacity of the field was reached before larval food became limiting and concluded that emigration was the main density dependent factor operating within a separate field. There is little doubt that "density" in this case actually means "butterflies per unit adult resource", since there is little reason to expect positive correlation between density and dispersal for most butterfly populations (see below).

Thus, for E. editha and probably for M. harrisii, increasing the density of adults is not as important in causing emigration as is limitation of nectar supply. That nectar is an important resource for butterfly populations has not been widely emphasized. Stern and Smith (1960) have demonstrated that transfer of stored energy and nutrients from fat body to developing eggs is inhibited by insufficient carbohydrate in the adult diet of Colias. It also has been found that E. editha females kept on water diets will lay the eggs which were mature at hatching but will mature no further eggs. Moreover, the fat body is apparently unavailable for adult maintenance as these females die much sooner than normal (unpublished data of L.E. Gilbert and M.C. Singer). Therefore, the generality that an emigrant E. editha stands a lower chance of leaving offspring than a stay-at-home (Ehrlich and Raven, 1969) depends greatly upon the nectar availability of "home".

Density is important as a factor affecting adult dispersal in those animals for which the amount of area reflects the amount of resource it contains (contrast this with nectar availability vs. area at DP vs. JRH, Table 2). In the most extreme cases space itself

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becomes a resource. This is true when a given area predicts the future availability of some important resource. For example, territorial males of the butterfly P. zelicaon defend hill top courtship areas where the appearance of virgin females is highly predictable. However, a given male may never encounter a virgin female during its tenure in the area (Gilbert, 1971a). Likewise, breeding pairs of the Tawny Owl in English woods defend approximately the same size of territory year after year in spite of fluctuations in prey abundance (Southern, 1954; 1959), indicating that the defended area is a measure of potential or predicted resource. For these organisms it can be said that dispersal from areas of high density would be due to increased intraspecific interaction rather than a decreased amount of resource.

However, most examples of animal dispersal resulting from "high population densities" can be directly attributed to some food resource becoming limited in an area (Lack, 1966).

This brings up the second question: What are the fundamental differences between different groups of animals (e.g. birds vs. phytophagous insects) in the way population structure responds to changes in habitat structure (i.e. resource distribution)? Perhaps the most fundamental comparison to be made appropriate to this question is that between animals in which all food gathering occurs in the adult phase (birds, mammals, social insects) and those in which the larval stages are independent of the adult. This latter group should be subdivided into animals in which larval food and adult food are the same (e.g. Homoptera) versus those in which larval feeding and adult feeding are completely different (e.g. Lepidoptera).

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At the outset, a fundamental difference between the population structures of birds versus phytophagous insects like butterflies should be mentioned. In the case of many birds, the distribution and abundance of resources in the habitat at the time when breeding pairs are establishing territories determines just how many birds are able to breed in a given area, with juvenile birds often unable to find suitable breeding territory for their first year (Lack, 1966). Thus, population structure* in birds is established before the feeding of babies has started. Consequently, any changes in the availability or distribution of resources changes only adult foraging patterns (see Horn, 1968a) and perhaps fledgling success, but not population structure (at least in a proximate sense).

In contrast, most butterflies and other phytophagous insects carry on courtship, mating, and reproductive activities throughout their adult life so that altering the pattern of adult (and for some insects, juvenile) movements in space can drastically alter population structure.

Another major distinction between birds and butterflies is important to this discussion. Parent birds attempt to select habitats which will provide sufficient food for their offspring. The flexibility of adult foraging behavior tends to buffer minor alterations in local resource patterns. In butterflies, on the other hand, the larval stage is completely independent once the egg is deposited.

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*In this dissertation, population structure is defined as the sum of all the factors that govern the pattern in which gametes from various individuals unite with each other (Ehrlich and Holm, 1963).

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A female butterfly ovipositing on a plant cannot anticipate its condition at some future time. For example, in at least two species of butterflies, the eggs are laid without respect to suitability of food plant patch so that much wastage occurs (Dethier, 1959; Singer, 1971b).

Insects of this latter type can be said to be "habitat correlated" organisms (Klopfer, 1969) since adult populations occur in areas where for some reason (not entirely predictable to the adult) the larval stages are able to survive. Insects become less habitat correlated and more habitat selecting as the cues available to the adult stage predict more accurately the location and state of larval resource in a habitat (i.e. as the correlation between adult and larval resources is strengthened).

It may be of general significance that those insects for which the correlation between adult and larval food habits is high (so that adults choose the larval habitat more accurately) tend to be a) widely dispersing, and b) important pests of crops. Correlation between adult and larval resource may come about in three ways. These are listed in the order of the strength of the correlation.

1.) Both larvae and adult may feed on the same plant (locusts, aphids, etc.).

2.) Adult food is correlated directly with larval food, by being another part of the same plant. (For instance, widely dispersing or migratory butterflies such as the Danaus, for which nectar and larval food are provided by the same milkweed plant; also Pieris, Colias, etc.)

3.) Adult and larval food plants are always found together

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in the same community, and the larval food plant is "non-cryptic" (see below).

Minimizing the complexity of feeding habits by utilizing the same food resources throughout larval and adult life increases environmental predictability for an insect. For one thing, an adult choosing a place to lay eggs can directly monitor the density of conspecific competitors. Therefore, increased emigration with increasing density is to be expected. Aphids, for instance, enter a dispersal phase in response to density. For such insects measurements of adult density in terms of space over a pure stand of "larval" food plant may have some meaning, in contrast to the situation in E. editha discussed above.

From these considerations one should be able to predict which species are likely to have intrinsic barriers to dispersal. Intrinsic barriers can be expected to be strongest in those animals which have a more complex and cryptic set of resource requirements. For instance, in many populations of E. editha several possible larval food plants are available within the range of adult movements. However, larval survival may tend to be correlated with one or two of these plants but not the others for complex reasons (Singer, 1971b). This means that an E. editha female dispersing from one kind of habitat to another (each with the same set of food plants) may be unable to select the proper food plant in the new habitat because her oviposition preference may be irrelevant (Singer, 1971a). In other words, there are no external cues which will allow an immigrant female to judge which of the several possible food plants, if any, is suitable in a strange area; i.e., the appropriate resource is "cryptic". For

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TABLE 2

EUPHYDRYAS EDITHA DENSITY:

JASPER RIDGE H VS. DEL PUERTO

Population	Date	Area Occupied (Hectares) Larvae[a]	Adults[b]	Est. # Males	Density Males[c]
JRH	1970	2.0	2.0	2000	1/10 m^2
DP	1970	2.6	25.0	2500	1/100 m^2

[a]Larval density

In terms of area: JRH ≅ DP

In terms of food plant: DP > JRH

[b]Adult density

In terms of area: JRH > DP (by factor of 10)

In terms of nectar resource: DP ≅ JRH

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species like E. editha there is strong selection for the evolution of respect for intrinsic barriers or perhaps better stated, intrinsic attraction to places to which a population has become genetically adjusted by staying put. This says that the more complex and unique each habitat patch of a species tends to be, the more tendency there will be for individuals on that patch to be sedentary and recognize those cues which indicate the presence of suitable habitat. In the case of E. editha the most reliable cues would seem to be the presence of hatching adults since these are almost always closely correlated with suitable habitat.

The third question in essence asks whether it is possible to generalize meaningfully about dispersal in the "species" Euphydryas editha (e.g. Ehrlich and Raven, 1969; and the previous section of this chapter). The answer which emerges from comparison of different E. editha populations is that adult dispersal tendencies are quite likely evolved to fit local or regional situations. For instance, the Jasper Ridge colony may well be exceptional in the extremely local subdivision of its populations. In regions where suitable habitat is continuous and extensive, panmixis over much greater area is to be expected. It is known for instance that in the Santa Maria area (and also in the vicinity of San Diego) E. editha is a wide ranging fugitive species which colonizes areas recently disturbed by agriculture or burning (Singer, 1971b). Thus, it may only be possible to make general statements about the levels of dispersal and gene flow between populations in areas of similar habitat structure. Certainly, however, no one situation characterizes adult dispersal or population structure for this species or, for that matter,

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any race of the species (since DP and JR are both E. e. bayensis).

Euphydryas chalcedona, on the other hand, because of its shrubby usually perennial ("non-cryptic") larval food plants and nectar plants (Eriodictyon, etc.) may have less complexity, uniqueness, and a more predictable pattern of resources from place to place and through time. Its higher vagility (unpublished data of I. Brown) fits the idea that correlation between widespread larval and adult food plants leads to higher adult dispersal (and perhaps less race formation) since the chance of emigrant E. chalcedona surviving in a new habitat is much higher than for E. editha. For instance, suitable E. chalcedona adult and larval food plants are available simultaneously at JR and DP in contrast to the situation described above for E. editha. A similar pair of species, Lincoln vs. song sparrows, has been described by Miller (1942).

As to question four, the meaning of dispersal in terms of gene flow is another problem which is poorly understood. It is safe to say that dispersal results in gene flow only between E. editha populations with very similar food plant requirements. For instance, although dispersal from Del Puerto Canyon to Jasper Ridge is possible, the chances of gene flow are vanishingly small. For one thing, the immigrant will arrive too late to mate with virgin females if it is a male, too late to oviposit on Plantago if female (Singer, 1971b). On the other hand, Pedicularis and Eriodictyon, key resources at Del Puerto, are abundant at Jasper Ridge so that an immigrant from DP would appear to have suitable plants to oviposit upon. Unfortunately, the survival of the eggs and young larvae on JR Pedicularis is very poor owing to litter

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predators where Pedicularis happens to grow on Jasper Ridge (unpublished data of M.C. Singer and L.E. Gilbert).

Finally, consider the evolutionary consequences of gene flow in E. editha. It should be possible to predict these consequences on the basis of what is now known of population structures in this species. First, it should be pointed out that there are two different levels at which gene flow may be occurring in E. editha (recall that gene exchange is impossible among many E. editha populations). These are:

1.) Within Habitat (i.e. within an area of continuous, suitable substrate unbroken by extrinsic barriers).

2.) Between Habitat (i.e. between suitable areas where the areas are separated by unsuitable terrain).

Within Habitat Gene Flow. The significance of "within habitat" gene dispersal depends upon the degree of patchiness within the habitat, while the nature of these patches depends on the life stage of the butterfly concerned. Assume several microclimate patches in a habitat (described by Singer, 1971b), one of which selects for one larval genotype A, the other for genotype B, another for C. Assume further that those patches are of sufficient size such that a larva lives its whole life in one patch -- i.e. the differences between patches are "coarse grained". Assume, too, that the differences between patches are of no immediate concern to the mobile adult which travels among many such patches during its adult life span -- i.e. the differences are treated as "fine grained" (Levins, 1968).

Adult females which carry larval genotype A will therefore mate with males of all other genotypes and will (in the case of E. editha)

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oviposit randomly with respect to the larval patches. Therefore, since the adult does not choose the proper substrate for its offspring and because the larvae are sedentary, polymorphism will constitute an optimum response to environmental diversity by such habitat correlated animals. The greater the temporal stability of a patch and the more that adults tend to be restricted to that patch, the higher the probability that the genotypes of a local larval population will be adjusted to the local environment where eggs are laid. In this case, restriction of adult movements (and thus, gene dispersal) allows local differentiation. It is possible that such differentiation has occurred on Jasper Ridge as a result of the peculiar restriction of adult movements there (as discussed above). Since adult numbers in these areas fluctuate independently (Ehrlich, 1965), and since ecological differences between the areas are known to be important to E. editha (Singer, 1971b), there is ample reason to predict genetic differentiation with respect to certain features of larval biology.

In contrast, positioning of adult resources around larval resources at DP prevents the kind of restriction of adult movement relative to larval food patches found at JR. Thus, the population's genetic response to patchiness in the larval environment at Del Puerto will be different from that at Jasper Ridge largely because of the way in which adult nectar resources are arrayed in space.

Between Habitat Gene Flow. For Bay Area E. editha populations movement between habitats separated by even a mile of nonhabitat seem highly unlikely. In three years of marking individuals at both Woodside and Jasper Ridge (Fig. 2) no transfers have been

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detected. However, because of the greater tendency of adults to move long distances within habitats such as Del Puerto, movements between such habitats may be more likely.

To the south near Santa Maria and in San Diego County, E. editha colonizes disturbed areas as has been previously pointed out. Higher intrinsic dispersal tendency by individuals of those populations compared to individuals of Bay Area populations seems likely judging from the apparent remoteness of recently colonized areas from other populations. One possible explanation for this difference is that Bay Region populations live in habitats of climax vegetation which vary in suitability depending largely on the weather within a season. Overall climatic patterns in the Bay region tend to be highly predictable between years compared to San Diego County where the Mediterranean pattern is breaking down. Selection would not be predicted to favor high dispersal tendency under the relatively stable conditions of the Bay Area. Many habitats occupied by E. editha along the southern California coast, because they are disturbance areas, will tend to undergo directional change due to succession and may completely disappear. This pattern coupled with greater climatic uncertainty and the noncryptic nature of larval resources in these southerly habitats (Singer, 1971b), makes greater dispersal tendency an optimum strategy.

If this increased dispersal results in substantial gene exchange between populations, one might predict less genetic differentiation between ecologically similar populations in the San Diego Region than in the San Francisco Bay Area (e.g. between WS and JR).

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CHAPTER II

THE DISTRIBUTION AND ABUNDANCE OF RESOURCES AS FACTORS WHICH DETERMINE POPULATION STRUCTURE IN A TROPICAL BUTTERFLY, HELICONIUS ETHILLA

Introduction

In the preceding chapter an attempt was made to answer questions concerning the role of resource patterns in determining the population structure of an annual temperate-zone butterfly, Euphydryas editha. Similar questions may be framed with respect to butterfly species which, because they inhabit humid tropical environments with adequate resources available throughout the year, exist as continuously breeding adult populations. This chapter discusses studies of such a species, the butterfly Heliconius ethilla Godt., in Trinidad.

Population Structure of Tropical Butterflies

Those tropical species for which careful population studies have been undertaken fall into two basic categories. First, there are species whose population structures appear to resemble those described for a number of temperate zone lepidopterans. Second, there are species which differ in a number of striking ways from any temperate zone butterfly which has been investigated.

Butterflies in the first group are "weedy" species, typically found at high density along roadsides and in pastures. Populations

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of one of these, the satyrine butterfly Euptychia hermes, have been studied in Costa Rica by Emmel (1970). Both the population density (1800/ha. est.) and the sedentary behavior of individuals of E. hermes are reminiscent of E. editha populations (Chapter I). Another "weedy" species, Anartia fatima, was studied in Costa Rica by Andersen (1969). During an 8 day study Andersen caught and marked a total of 539 adult A. fatima in a 2 hectare pasture near Finca La Selva. The recapture rate during this study was less than 10% indicating a very large population, high rates of adult turnover, or both.

Butterflies of the second group include Heliconius erato (Benson, 1970; Turner, 1971) and Marpesia berania (Benson, 1971). These species, as well as others observed by early naturalists in the American tropics, share a number of interesting features not typical of temperate zone butterflies. The first of these is the extreme longevity (up to six months) of active adults (Turner, 1971; Benson, 1970, 1971); the second is the constant day to day pattern of individual movements ranging from daily promenade areas (Seitz, 1913) to regular feeding stations over a number of months (Michael, 1894); and the third is the fidelity shown by individuals or groups to nocturnal roosting sites (Turner, 1971; Benson, 1971). Anecdotally, most species in some of the characteristic tropical American butterfly groups, such as the Riodinidae, are considered to exist as highly localized, low density populations. It is likely that this description fits many canopy species which, because of their inaccessible habitat, are rarely collected. On the other hand, the hyperdispersion and low density of tropical forest trees

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(Janzen, 1970) could possibly lead to localization of the population of any phytophagous insect which specializes on a certain tree species.

The details of adult population structure, however, have not been adequately analyzed for any tropical butterfly species to date. For one thing, the long adult life spans of the species studied require extensive and long term observation of individual movements in order to describe local population units fully. Moreover, because in the tropics the adult populations experience each season of the year (dry vs. wet), any direct comparisons with well studied temperate zone lepidopteran populations (Sheppard, 1951; Turner, 1963; Ehrlich, 1965; Brussard and Ehrlich, 1970) requires that the tropical study extends for at least one year, a criterion which no study prior to this one has fulfilled.

One major goal of the H. ethilla study, then, was to provide basic information concerning population structure and dynamics of a tropical butterfly over a long period of time. In the course of the study, questions arose concerning the role of adult longevity and home range behavior in influencing observed population phenomena. Another question concerned the nature and importance of adult resources in determining the observed patterns of dispersal and longevity. An attempt was made to identify important resources and to collect data on adult movements and resource patterns such that direct comparison with the E. editha study (Chapter I) would be possible.

Heliconius ethilla in Trinidad

Heliconius ethilla is a widespread tropical American species for which several distinctive races have been described. The taxonomy of

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this section of the genus Heliconius is somewhat confused (Emsley, 1965) and recently H. ethilla has been referred to as H. numata (Turner, 1968). In Trinidad this species is restricted to the forested ridges of the northern range where it is the primary model in the "tiger stripe" mimicry complex (Moulton, 1909). The Trinidad populations have been of particular interest in that they show a color polymorphism while most mainland populations are monomorphic (Sheppard, 1963; Turner, 1968).

The selection of this species for study was based on the easy access of forest reserves where the species is found, and the proximity of these areas to the excellent butterfly research facilities of the Beebe Tropical Research Station at Simla, Arima Valley. That the general biology of the genus Heliconius has been intensively studied (Alexander, 1961; Beebe et al., 1960; Brower et al, 1963; Crane, 1957; Emsley, 1963, 1965; Swihart, 1967; Turner and Crane, 1962) was also significant in the choice of H. ethilla.

The H. ethilla populations under study for the past one and one half years live in the vicinity of ridge top "traces" (narrow roads) on opposite sides of the Arima Valley (Fig. 9). Andrew's Trace which runs south from Arima Pass (Figs. 9; 10) is the primary study area while La Laja Trace on the other side of Arima Valley is periodically sampled for comparative purposes. In this chapter, I will only be concerned with the studies of population structure at Andrew's Trace.

Andrew's Trace Study Area

Andrew's Trace is little more than a jeep trail running through heavy mature second growth forest. The area under study has expanded

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Figure 9

Aerial view of Northern Arima Valley and surrounding ridges of the Northern Range, Trinidad, W.I.; scale is one mile. H. ethilla study areas are dotted lines, the Arima-Blanchisseuse Road is solid line. The structure on the horizon is the Trinidad Microwave Relay Station, a prominent landmark in the area. The inset map of Trinidad shows Northern Range (stippled area) and location of Arima Pass (circled). Scale divisions are 5 miles each.

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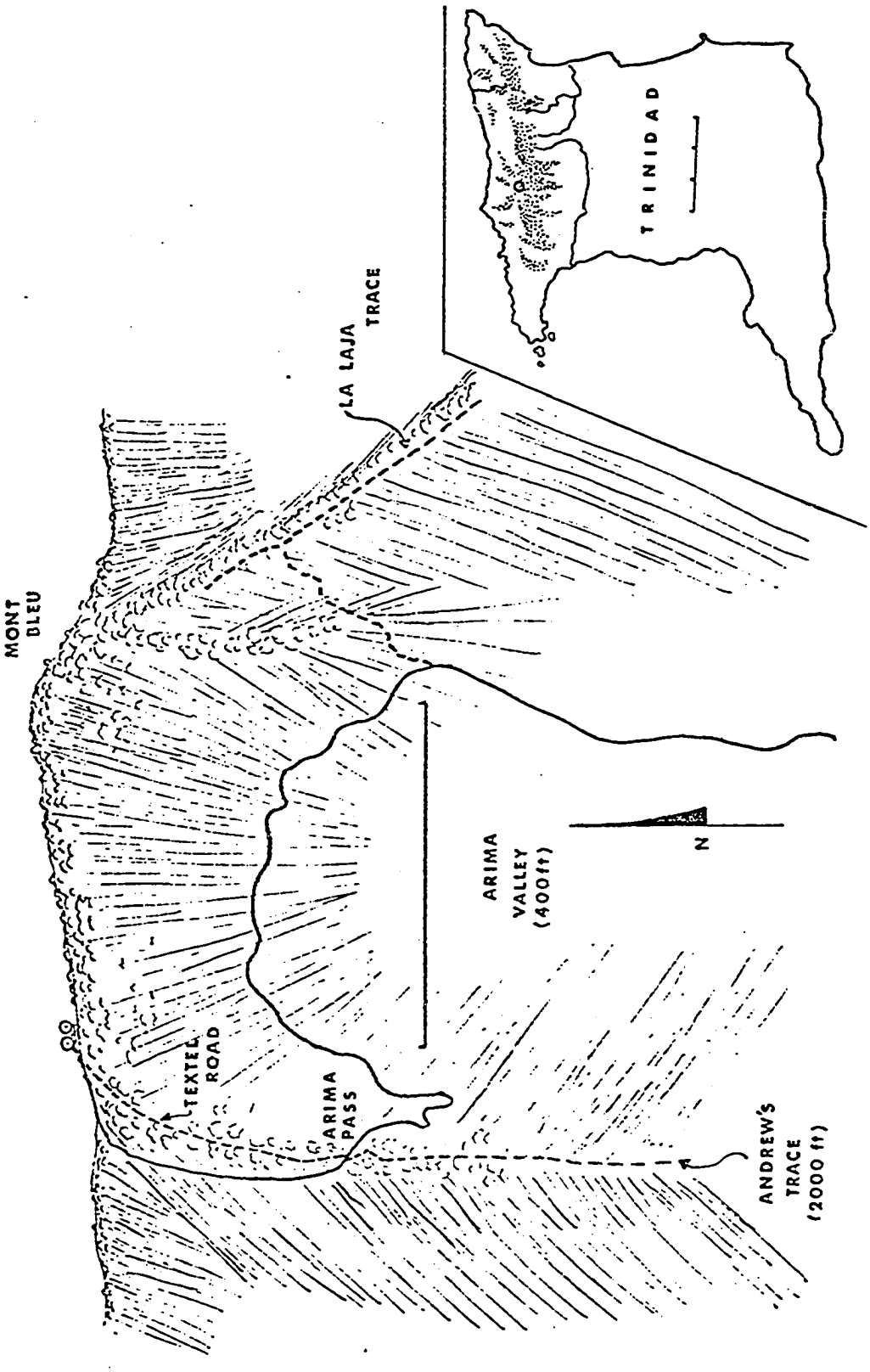

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Figure 10

Heliconius ethilla study area, at Arima Pass, along Arima-Blanchisseuse Highway, Trinidad, W.I. Black dots show positions of numbered reference stations, which are spaced at 50 yard intervals (1-26) or 50-70 yard intervals (remainder of stations). The stations which correspond to permanent milepost markers are as follows: Sta. 70 = milepost 8 3/4; Sta. 61 = milepost 9; Sta. 52 = milepost 9 1/4; Sta. 44 = milepost 9 1/2; Arima Pass = milepost 9 3/4. Elevations range from 1500 ft. (Sta. 71) to 2100 ft. (Sta. 23). Contour lines are very approximate and represent 100 ft. intervals. Scale divisions are 100 yards.

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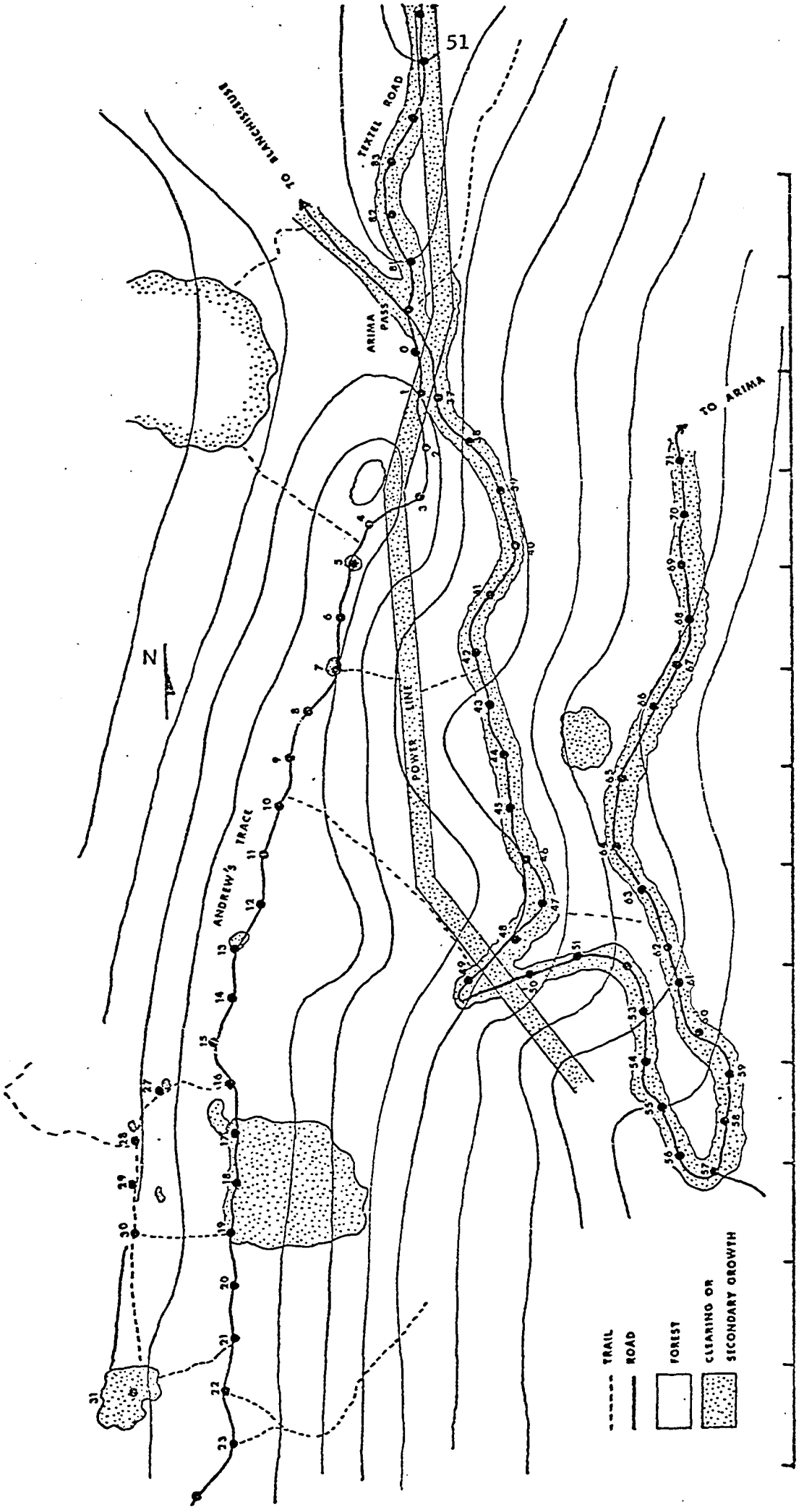

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steadily as the limits of adult movement are investigated. At the present time the principal study area extends from Arima Pass on the Arima-Blanchisseuse Highway along Andrew's Trace for about one mile at which point the forest has been removed and H. ethilla do not occur. This area also includes the slopes above a section of highway between mile post 8 3/4 and Arima Pass, a vertical distance of about 500 feet. Steep slopes and heavy forest have prevented much exploration of the area further than that indicated by roads and trails in Figure 10. The elevation of Andrew's Trace averages about 2000 feet and the study area extends down to 1500 feet in some areas.

The Resources of Heliconius ethilla at Andrew's Trace

Passiflora cyanea, the larval food plant of H. ethilla, is abundant in the second growth and along forest traces near Andrew's Trace. During the study (February 1970) a large clearing was created illegally in the forest by local residents, between stations 17 and 19 (Fig. 10); by August 1970 this field was dense with seedlings of the P. cyanea vine. This plant occurs in virtually all tree-fall clearings as well as man-made forest edges such as a power line right of way which runs through the area (Fig. 10).

Adults visit flowers of the lianas Gurania spinulosa Poepp. et Endl. and Anguria triphylla Miq. (both Cucurbitaceae) and the shrub Palicourea crocea (Rubiaceae). The cucurbit vines tend to occur both in the canopy and in man-made second growth along forest margins and in small tree-fall clearings. Palicourea is found primarily along the ridge top in more shaded but obviously disturbed situations.

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Methods

Before initiation of mark-release-recapture studies permanent metal station markers were installed at 50 yard intervals on trees along Andrew's Trace. At the outset, in December 1969, the reference points were restricted to stations 1-26 (Fig. 10) along the ridge. Later, in August 1970 and December 1970, stations were added along the Arima-Blanchisseuse highway (stations 37 to 71), along the Textel Road (stations 81 to 96) and along trails and in small clearings on the west slope of the ridge. The area was mapped with compass and graph paper as was the case in the E. editha Del Puerto study.

Each 4 months an intensive mark-release-recapture program was carried out for approximately two weeks during which time about 120 unmarked butterflies would be given numbers. In the intervals between these "pulses" of marking, members of the Simla staff carried on the same program at a reduced level (one to two times per week). Unfortunately, between December 1969 and April 1970, no new marks were added although recapture information was collected on those marked during the previous December. For each capture event the location, time of day, sex, color morph, and condition of animal, as well as notes on behavior, were recorded.

Butterflies were marked with black magic markers only since this minimized the change in the appearance of the butterfly. Both coded spots and actual numbers were written on the wing at first, but when it was found that numbers written on both hind wings would suffice, the double marking system was abandoned.

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Subareas at Andrew's Trace

Since initiation of the study in December 1969, over 1000 individual H. ethilla have been marked and a total of 2600 capture events have been recorded. Individual butterflies have been recaptured as many as 10 times over periods of up to 162 days. Preliminary analysis of individual movement data indicates that along Andrew's Trace there exist two rather well defined subareas between which few adults move. Less extensive data indicates that the Textel Road (stations 81-96) forms a third effectively isolated subarea.

One of the subareas of Andrew's Trace will be referred to as area "A" and includes stations 1-10 (and occasionally 11, 12, 13) and all stations east of the ridge and south of Arima Pass (stations 37-71). This is to say that an individual marked at station 3 often turns up at station 5, 42, 65, or 49, but never at 14 to 31. The second subarea of Andrew's Trace, area "B", includes stations 14 to 31 and often station 13. The small clearing at station 13 occasionally is visited by individuals from area A but they almost always return to A. Many individuals of area B visit station 13. Whether this meeting point between the two populations is significant is not clear at this time.

No lower elevation boundaries have been set on the two areas short of the valley bottoms where ethilla does not occur. Individuals marked between stations 5 and 9 have been caught flying up and down the mountain along a small creek which crosses the road at station 65. On the other hand, the butterflies of area B seem to center their activities on the western slope of the main ridge where again lower limits have not been established.

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Movements Among the Subareas

Sheppard (1963) made the reasonable suggestion based upon the strong flight capabilities of the insect that substantial gene flow occurs between H. ethilla populations on Andrew's Trace and those in the mountains near Port of Spain some 14 miles away. However, as is obvious from the rather distinct subdivision of the colony at Andrew's Trace, extensive long range dispersal by H. ethilla can be discarded as a possibility as Turner (1968) suggests from his H. erato data. To illustrate the extent to which interarea movement does occur, I have summarized in Table 3 recapture and transfer data for butterfly numbers 1-960 (December 1969 to December 1970). An estimate of individuals leaving hime is calculated as the percent of butterflies recaptured at least once which have been observed to leave the area of initial marking. As can be seen in the Table, the overall estimate of 2.7% leaving is comparable to previous observations of Euphydryas editha in California (Ehrlich, 1965, and Chapter I of this thesis). It will be noticed that there is some variation in the percentage of interarea transfers through the year. The reason for this change is thought to be changing adult resource patterns and I will return to this point later in this chapter.

Population Size and Stability

Females are consistently at a lower frequency than males in all large population samples taken at Andrew's Trace. In addition, the percentage of all individuals being recaptured at least once is lower for females than for males (Table 4). Since the sex ratio of

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TABLE 3

SUMMARY OF H. ETHILLA RECAPTURE DATA

Marking Period	Recapture Period	Code Nos.	Total Marks	N[a]	%	N[b]	%
A. 13-XII-69-30-XII-70	15-XII-70-30-IV-70	1-115	111	59	56.5	3	5.1
B. 23-IV-70-18-VI-70	24-VI-70-13-XI-70	116-355	239	136	58.0	5	3.7
C. 18-VI-70-9-X-70	25-VI-70-16-I-71	356-679	322	132	41.0	4[c]	3.1
D. 9-X-70-18-XII-70	15-X-70-12-III-71	680-1018	288	122	42.4	0	0.0
Totals for year:		1-1018	960	449	46.8	12	2.7

a. Number recaptured at least once.

b. Number of recaptured individuals known to change areas.

c. One additional individual changed areas during period C but returned to its original area after several weeks.

TABLE 4

SEX RATIO AND SEX DIFFERENCES IN PROBABILITY OF RECAPTURE AT ANDREW'S TRACE. AREAS A AND B ARE COMBINED.

DATE	Percent Recaptured At Least Once (Areas A and B) FEMALES %	FEMALES N	MALES %	MALES N	Sex Ratio (Both Areas) FEMALE:MALE
Dec. 1969	38	29	61	77	26:74
April 1970	40	53	65	102	33:67
August 1970	42	80	51	129	36:64
Dec. 1970	34	71	51	103	41:59

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lab reared H. ethilla is not significantly different from unity (103 of 221 lab reared ethilla were female), it is likely that behavioral and perhaps survivorship characteristics are different for the sexes. The population estimates for areas A and B were therefore based on males only.

Figure 11 shows the estimated number of males (± one Standard Error) for each subarea during the four intensive sample periods. Since the estimates are based on the Simple Lincoln Index, they should be considered preliminary. A more refined approach yielding continuous weekly estimates through the year is in progress employing the procedures of Jolly (1965), Manly and Parr (1968), and Manly (1969). The overall patterns do not seem to be altered by these more sophisticated methods.

The total estimated male population for Andrew's Trace as seen in Fig. 11 was 139, 133, 223, and 156 during December 1969, April, August, and December 1970 respectively. These figures are remarkably stable through the period which included a substantial dry season January-April. The only significant size change obvious at this level of resolution is that of area A (and possibly area B) between April (dry season) and August (wet season). Whether size fluctuations occurred during the intervals between the four intensive study periods will not be known until further analysis is completed. However, superficial examination of the weekly data collected during the intervals indicates that no substantial changes took place.

While the population size estimates for H. ethilla at Andrew's Trace seem low by most temperate zone standards, two other Heliconius species, erato Linn. and melpomene Linn., which are constant members

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Figure 11

Heliconius ethilla male population estimates with ± one S.E. limits, areas A and B of Andrew's Trace, December 1969 to December 1970. (Area A = Sta. 1-12, area B = Sta. 13-26.)

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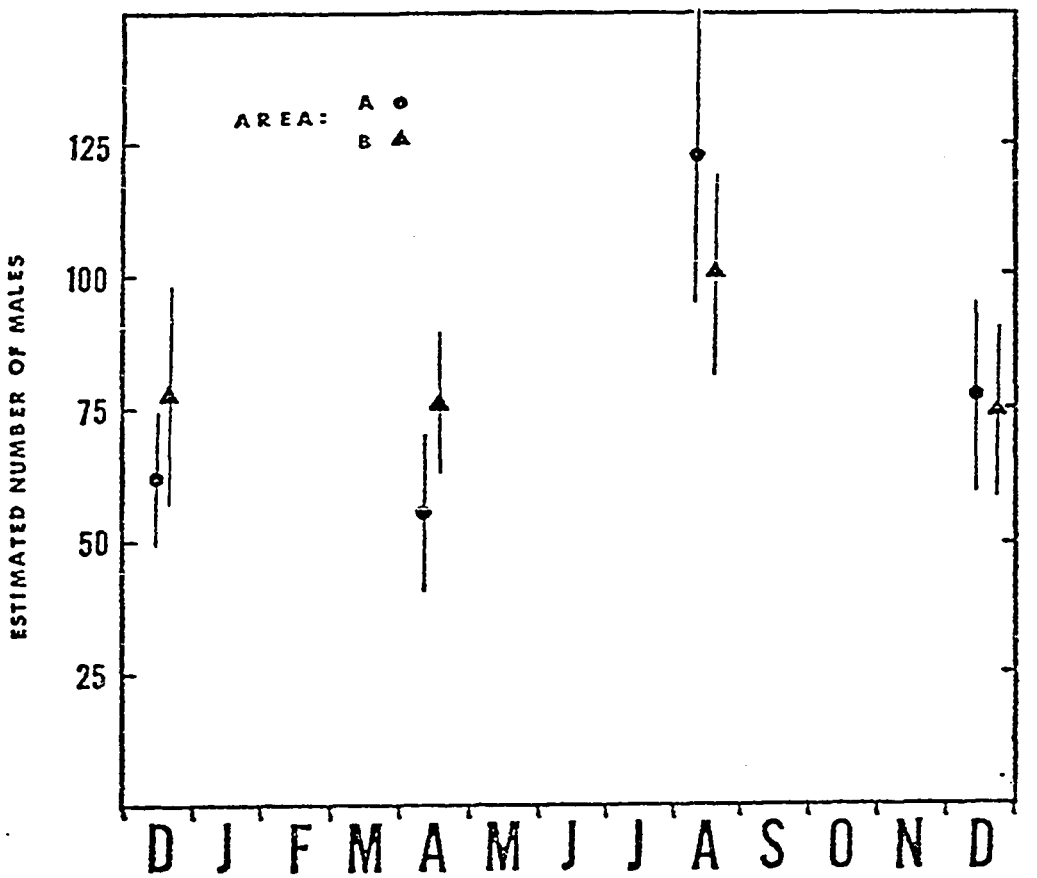

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of the Andrew's Trace butterfly community, are none the less always at much lower density than ethilla. For instance, out of 305 individuals of the three species caught and marked between August 14 and October 19, 1970, 272 (89%) were ethilla, 31 (10%) were erato, and 2 (<1%) were melpomene.

Moreover, other Heliconius species ecologically similar to ethilla which I have observed in Panama (H. ethilla melicerta Bates, H. cyndo Doubleday, H. sapho Drury) and in Costa Rica (H. ethilla zuleika Hew., H. pachinus Salvin) appear to exist at much lower densities than the Andrew's Trace ethilla populations. The most H. ethilla taken by one person in one day's collections at Andrew's Trace were 40 individuals caught over a period of 5 hours on 28 April 1970 and taking of 20 individuals in a like period was not unusual. I have seen no large forest Heliconius species with this kind of density anywhere in Costa Rica, with the possible exception of H. ethilla zuleika along river bottoms in Guanacaste Province.

Age Structure of H. ethilla Populations

The age structure of adult butterfly populations has not received much attention either because it is of minor importance in many instances, or because attempts at assigning age categories on the basis of wing condition have been unsuccessful (Ford, 1945; Turner, 1963). Of course, the longer adults of a species are capable of surviving the more interesting adult age structure becomes. Fortunately, in H. ethilla it has been possible to check several methods of determining age on the basis of wing condition by following the change in condition of individuals through time.

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Wing tear or tattering as used by some workers (Southwood, 1966, p. 315) is not correlated with age in this species. On the other hand, it has been found that the degree of scale loss is a reasonable predictor of the age of an adult ethilla. This is indicated by Figure 12 where the wing condition (expressed as arbitrary scale-loss categories) of a sample of multiply recaptured animals shows a regular pattern of change through time. Individuals whose records appear in the figure were all in fresh (F) condition at capture and most were recaptured over long time intervals. The data in this figure plus the records of several hundred multiply recaptured individuals make it possible to calibrate the wing scoring system.

Seven arbitrary wing condition categories have been sunk (for purposes of discussion) into the three shown at the bottom of Fig. 12. These are Fresh (F), Intermediate (I), and Worn (W). The approximate number of days of an individual's life covered by each category are 30 (F), 90 (I), and 40 (W). Thus, in the case of constant high adult survivorship until old age (Type I survivorship curve of Slobodkin, 1962), the age structure of the population as measured by wing condition would reflect the percentage of time that each individual spends in a wing condition category. Assuming the time sequence of condition change to be constant among individuals, the ratio of F:I:W individuals would approximate 30:90:40 or 19:56:25 if all adults were to have a life expectancy approaching 160 days.

Using this set of ratios as a base line for comparison, it should be possible to interpret population size changes on the basis of how the observed population size structure departs from "expected" through time. Thus, an excess of "Fresh" individuals might be caused

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TABLE 5

LONGEVITY OF MARKED H. ETHILLA

Minimum Days Surviving*	MALES	FEMALES	TOTAL
1- 20	61	30	91
21- 40	44	8	52
41- 60	24	14	38
61- 80	26	12	38
81-100	26	4	30
101-120	14	6	20
121-140	11	1	12
141-160	3	2	5
161	1	0	1
TOTAL	210	77	287
Mean Minimum Life Span	52 days	46 days	50 days

*The days elapsed between marking and final capture establishes a minimum age for each individual. The number of males and females in each category (20 day intervals) is summarized from the data for butterflies 1 to 576 (December 1969 to August 1970). Individuals not recaptured are eliminated from the table. Though the data presented in this table should give a reasonable picture of maximum life expectancy, it necessarily underestimates average life span due to sampling error.

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by an increase in recruitment (due to a drop in larval mortality) or to a drop in adult life expectancy, or both. Because ethilla adults can live so long, a short burst of increased adult recruitment followed by a return to normal will not affect the numbers entering the other age classes for one (in the case of I) to three months (in the case of W). Long term monitoring of age structure information is therefore a necessity.

Another application of this kind of age structure information will be in the interpretation of microevolutionary changes occurring in the populations. By comparing the age structure of the two color morphs through time it should be possible to pin down the season of the year and the stage of the butterfly where the important selection pressures are operative.

Longevity and Reproductive Activity

The maximum life span recorded for an individual H. ethilla was that of #318, a male. This individual was marked on 4 June 1970 and was last recaptured on 13 November 1970, 162 days later. It is quite likely that #318 was alive for a few days both before it was marked and after its last recapture. Thus, a maximum life span for H. ethilla of 180 days or 6 months is entirely possible and would match data collected for H. erato by Benson (1970) in Costa Rica.

Table 5 provides a summary of the minimum number of days survived by those individuals marked December 1969 to August 1970 (Nos. 1-569) and recaptured at least once. The mean minimum life span for the males of this group is 52 days, for females 46 days, and

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Figure 12

Relationship between known minimum age (days elapsed since initial marking of butterfly) and wing condition in H. ethilla. Degree of scale wear is arbitrarily assigned to six categories: VF (freshly emerged, or very fresh), F (fresh), I/F (between intermediate and fresh), I (intermediate in condition), I/W (between intermediate and worn), W (worn and faded); VW (very worn). Since wings may be torn or tattered at any stage these conditions are not considered in estimating age. For most purposes only three categories are considered: F (VF and F), I (I/F), and W (I/W to VW).

Distribution of these wing condition categories typically follows a regular time course within each individual (as can be seen in the figure). The individual butterflies summarized in the figure were chosen because they were in fresh condition at original capture and were recaptured numerous times. This is a small but representative sample of the H. ethilla wing condition data collected during the study.

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DAYS ELAPSED SINCE MARKING

Butterfly Number	0	10	20	30	40	50	60	70	80	90	100	110	120	130	140	150	160
127	FF			I					I	I			I/W				
131	F												I/W	W		W	W
141	F	FF		F		I		I					I/W				
186	VF							I									
153	FF			I					W								
156	F		F	I			I		I								
163	F		I					I					I/W				
243	F		F	F	I			I		I	I						
190	F											I					
285	F			F				I	I				I			I	W	W
318	F	F						I		I		W			W	W		W
352	F				I			I				W						
432	VF	F					I	I/F		I								
438	F	F			F						I		I/W	I/W				
763	F			I	I					I				W				

Summary

III II II IIIIIIIIIIIIIIII I I I

VFFFF FF F F W WW I/W W I/W WW W W W WW

0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160

FRESH — INTER. — WORN

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for the two sexes together, 50 days.

The minimum life expectancy curves of recaptured males and females do not differ (Fig. 13) even though the probability of recapture differs between the sexes, as has been previously mentioned.

A question not answered by previous studies on long-lived butterflies concerns the reproductive capabilities of older individuals. Blest (1963) has suggested that impalatable, warningly colored insects (such as H. ethilla) might evolve postreproductive longevity which would improve an individual's fitness by educating predators as to the color pattern of its kin. I have gathered field and laboratory data on the reproductive biology of both sexes of ethilla and have found no evidence for postreproductive longevity in this species.

Evidence gathered in the field by offering tethered virgin females to wild males indicates that older males are perfectly capable of normal reproductive function. For instance, in December 1970 one wild male (#438) was attracted to and mated with a tethered female. This male had been marked 120 days before in August 1970. The mating resulted in normal adult offspring.

H. ethilla females are also fully reproductive in later life. For instance, two wild-caught ethilla females in intermediate to worn condition, i.e. about 100 days old (see Fig. 12), averaged 6.75 and 7.3 eggs per day for the first 8 and 7 days respectively. In another experiment, I enclosed 27 wild females of different ages which laid 286 eggs in two days, an average of 5.3 per female per day. The daily egg production of older females also compares favorably to that of five lab-mated females which laid from 5.3 to 9.0 eggs

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Figure 13

Minimum life expectancy curve for recaptured H. ethilla: males (N=210) versus females (N=77). The frequencies of males and females are plotted on log scale against age categories (40 day intervals). The data are condensed from Table 5.

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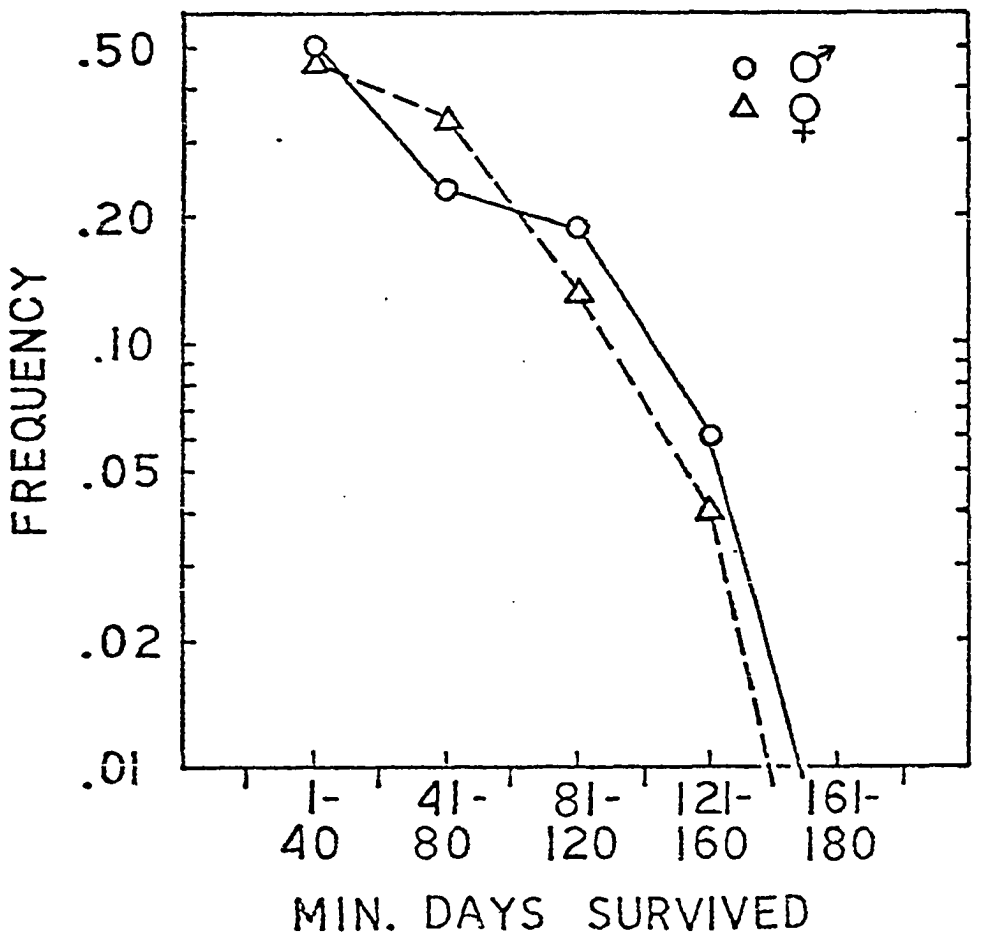

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per day for their first seven days of oviposition in the insectary (Gilbert, 1971b). Thus, a daily average of 5 to 7 eggs per day per female in natural populations is not unlikely, especially since egg production does not seem to alter appreciably with age. It should be noted that overcast or rainy weather will prevent normal oviposition activity, but this should not affect daily averages since captive ethilla females have been observed to lay up to 18 eggs following two days of bad weather.

Reproductive Effort and Mortality

The important mortality factors acting on a butterfly population fall into two basic groups: 1) those which act on the egg, larval and pupal stages and 2) those which act on the adult. The intensity and predictability of preadult mortality sets a limit on the minimum number of eggs which a female can lay and still have a good chance of leaving at least one female offspring. The nature of adult mortality, on the other hand, determines how the eggs will be distributed in time, and, in the case of ethilla, sets an upper limit on egg production since eggs are produced on a day to day basis (Gilbert, 1971b).

One can ask the following question with respect to the information summarized for H. ethilla thus far: Do individual reproductive strategy parameters (e.g. egg production and longevity) accurately predict measurable population parameters such as preadult mortality? For simplicity let us consider the Andrew's Trace population during a period of size stability such as December 1969 to April 1970. Assuming that the female population equals the male, there would have

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been about 140 females in the population at any given time. Given this situation let us consider two reasonable values for average adult life span, 50 (Case I) and 80 (Case II) days. For each of these life expectancy values consider two possible daily rates of egg production, 5 (a) and 7 (b).

Case I: Population size stable, 140 females, average adult life expectancy is 50 days (see Table 5). It is reasonable to consider this value of average adult life expectancy as a low estimate given the maximum life span of 160 days. Turner (1971) approximates the life expectancy (in days, D) as D=100/(100-S) where S is the daily survival percentage (derived from population estimation procedures). In the present case analyses required to give S directly are not yet complete, but having a value for D provides S indirectly. Thus for D=50, S is .9800. Under the assumption of constant population size and constant daily survivorship, the daily recruitment would therefore be 2% to balance the 2% mortality.

Therefore, one would expect 2.8 new females per day in the population of 140. The proportion of freshly emerged individuals (VF) taken during 8 days in April (5.4%, N=147) is consistent with this low rate of recruitment.

Let us now consider expected preadult mortality on the basis of two different estimates of daily egg production.

Case Ia: Assume 5 eggs per female per day (see previous section). The 140 females laying 5 eggs each produce a total of 700 eggs (350 female) of which 2.8 will become adults. Thus, the preadult mortality rate is $\frac{347.2}{350.0} = .9920$. Returning to the original question, an average female must therefore produce 250 eggs (2 of which will

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mature) for a .75 chance of leaving at least one female offspring. At the rate of 5 eggs per day, this requires 50 days or more.

Case Ib: Assume 7 eggs per female per day. The 140 females will in this case lay a total of 980 (490 female) eggs per day from which again, only 2.8 adult females per day are derived. Thus, the preadult mortality rate is $\frac{487.2}{490.0} = .9943$. This requires the egg production of the average female to increase to 350, which at the rate of 7 eggs per day requires a life expectancy of 50 days or greater.

Case II: Population size stable, 140 females average life expectancy is 80 days. This value (for D) is simply one half of the maximum recorded life span which, although high, is not an unreasonable figure.

For D=80 daily survivorship is .9875. This would obviously be difficult to distinguish from .980 in actual field data as Turner (1971) implies. In this case daily recruitment would be 1.25% as compared to 2.0% for D=50, and the number of new female recruits expected per day is 1.75.

Case IIa: Assume 5 eggs per female per day. Of the 700 (350 female) eggs produced per day per 140 females, only 1.75 will survive to become an adult female. Thus, preadult mortality is $\frac{348.25}{350.00} = .9950$.

In this case, an average female must produce a minimum 400 eggs for the .75 chance to leave at least one female offspring. At 5 eggs per day this requires 80 days.

Case IIb: Assume 7 eggs per female per day. Of 980 (490 female) eggs produced per day per 140 females only 1.75 will

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survive, a preadult mortality rate of $\frac{488.25}{490.00}$ = .9964. This requires 560 eggs from an average female which, at 7 eggs per day, takes at least 80 days.

Even with the unrealistic estimate of 1 egg per day per female the preadult mortality is .950 (D=20), .980 (D=50), and .988 (D=80). Thus, on the basis of empirical estimates of average life expectancy and average daily egg production, egg to adult mortality is projected to be as high as that estimated for E. editha (Singer, 1971b), a species typically thought to illustrate a very different reproductive strategy from that of Heliconius (Labine, 1968).

It is therefore appropriate to point out that under ideal circumstances the reproductive output of an H. ethilla female, e.g. 700 eggs (7 per day for 100 days), would exceed that of E. editha due to the larger egg of H. ethilla (approximately twice the weight of an E. editha egg).

Field observation also tends to support the hypothesis of high early stage mortality. The food plant, Passiflora cyanea, is very abundant and is practically undamaged by heliconiines. The early stages of ethilla are always difficult to find relative to those of H. aliphera which feeds on the same plant. Of eight ethilla eggs collected at widely separated points in space and time, seven (88%) were parasitized by a chalcid wasp. No extensive data has been gathered on parasites of later stages though they undoubtedly exist. Ants coming to the extra floral nectaries of Passiflora are known to be important predators of heliconiine larvae in Costa Rica (Benson, 1967) and may well be important predators of H. ethilla. Ants have occasionally been observed on the P. cyanea vines but

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their effects on the ethilla larval population are not known. More information on the parasites and predators of H. ethilla is clearly needed. It seems certain, however, that egg parasitism is a major factor in preadult mortality and any interpretation of reproductive strategy in this species must take the chalcids into account.

Egg Production, and Pollen as an Adult Resource

During the April 1970 sampling period, I observed that H. ethilla adults were occasionally carrying large masses of pollen on their proboscides. Close observation of adult feeding behavior revealed what appeared to be definite pollen gathering behavior. The plants visited for pollen, Palicourea crocea, Gurania spinulosa, and Anguria triphylla, also provided nectar. It seemed significant that while Palicourea was the sole nectar source for two species of Parides (Papilionidae) which live along Andrew's Trace, these butterflies were never observed to pick up pollen on the same inflorescences from which H. ethilla gathered large masses.

The possibility that pollen provided a protein source for ethilla adults stimulated experiments, reported elsewhere (Gilbert, 1971), on three Heliconius species: H. ethilla, H. erato, and H. melpomene. Briefly, the evidence for pollen as a protein, or nitrogen source, is as follows:

1.) There is a specific pollen collecting behavior pattern. Heliconius erato collecting pollen in the greenhouse have been observed to remain at a single Lantana flower (floret) for up to 10 minutes as opposed to nectar visits which last a few seconds

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at most. During pollen visits extensive scraping of the anthers with the proboscis tip occurs and no attempt is made to probe for nectar.

2.) There is an elaborate pollen processing procedure which involves the formation of a mass of pollen on the ventral side of the proboscis near the head. Then, after the mass is formed it is mixed with a clear liquid exuded from the proboscis tip. Large mechano-receptors which presumably allow the butterfly to "feel" the pollen load are located in the region where the pollen mass is formed. These structures do not appear to be well developed outside the genus Heliconius.

3.) Experiments with artificial flowers show that Heliconius erato and melpomene will collect pollen-sized glass beads in preference to nectar indicating that the shape and size is more important than possible chemical attractants on the pollen. This observation is difficult to explain unless pollen is being collected for its own sake.

4.) Pollen loads were removed from greenhouse Heliconius, washed gently in .4 m sucrose and the supernatent run on gel electrophoresis; pollen was also collected directly from suitable plants, incubated in .4 m sucrose, and the supernatent solution was electrophoresed. Both samples were analyzed for protein, and in both all proteins present were those of the pollen rather than those of the butterfly gut juices.

5.) Experiments by Linskens and co-workers show that Petunia pollen incubated in weak sucrose solution releases most of its protein into solution within 3 hours (Stanley and Linskens, 1965).

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Of greater interest are the more recent experiments which show that 50% of the free amino acids of incubated pollen leaves within one minute. Proline, an important compound in insect metabolism (Bursell, 1963), comprises one half of all free amino acids released by germinating pollen (Linskens and Schauwen, 1969).

Protein or amino acid nutrition goes a long way toward explaining both the extreme adult longevity and the patterns of egg production in Heliconius. For instance, females of all the three species mentioned above eclose with no mature eggs visible in the ovarioles. This is in contrast to E. editha which ecloses with as many as 200 eggs mature (Labine, 1968). Furthermore, I have found that the number of visible immature oocytes per ovariole is constant through the life span for H. erato and melpomene. Meanwhile, eggs are produced at a continuous rate (Gilbert, 1971b). Experiments with ethilla indicate that pollen feeding soon after mating greatly improves egg production (Gilbert, 1971b). Such results are well known for other insects such as syrphid flies (Stürken, 1964).

The Nature of Adult Resources and Home Range Behavior

A female E. editha emerging into an environment void of nectar is capable none the less of ovipositing as many as 200 eggs without adult nutrition. In contrast, H. ethilla is much more dependent upon daily adult feeding from the time it emerges since eggs are manufactured on a day to day basis. To deposit the same 200 eggs, an H. ethilla female must find adequate pollen supplies daily for about 40 days. It is therefore important to know how the availability of pollen is distributed in space and time at Andrew's Trace.

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At least some individuals of all three plants, Palicourea, Gurania, and Anguria can be found in bloom at any season of the year. The requirement for continuous pollen sources are therefore met. Palicourea bushes which are common along the top of the trace tend to bloom continuously through the year. On the other hand, Gurania and Anguria, which are more scattered through the area, typically occur as sterile individuals, with only a small fraction in bloom at any point in time. Thus, the location of Anguria and Gurania pollen and nectar tends to change through time depending on which individuals are in bloom. It is very important to note that both of these plants put very little into reproductive versus vegetative activity. That is to say, a large Gurania vine covering 100 m^2 will produce no more than 10 or 15 inflorescences, each of which produces only one flower per day. Anguria is similar in this regard, as each of the several plants regularily visited by H. ethilla had only one inflorescence, each inflorescence averaging less than one flower per day. Once in bloom, however, this single inflorescence can be a predictable source of pollen and nectar for several months (though not day to day), as calculated by dividing the number of flowers previously shed by the average daily production observed over several weeks. I have followed the fate of numerous inflorescences of Gurania and Anguria (Gilbert, 1971c) and have estimated that the "life span" of a single inflorescence can be up to 80 days in the case of Gurania and 170 days for Anguria. For each inflorescence, therefore, it is possible to extrapolate back in time to estimate the length of time that it has been available to the butterflies.

Census of the relative numbers of flowers available from each of

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Figure 14

Alteration of spatial pattern of H. ethilla adult movements with changing resource patterns. The fine lines connect successive captures of same animal, dark lines represent transfer between subareas, dashed lines represent paths over which individuals have been observed to fly. Dots represent areas of the larval food plant Passiflora cyanea; P = Palicourea crocea, A = Anguria triphylla; G = Gurania spinulosa. Plants not in flower during period are not represented.

(A) Movement pattern of individuals numbered 356-679 which were marked over the period 18-VI-70 to 8-X-70 and recaptured from 25-VI-70 to 16-I-71. The Gurania at station 49 is estimated to have bloomed from 20-VII to 15-X-70 at which point it was cut down by a road crew. The Anguria (single inflorescence) at station 44 is estimated to have bloomed from 10-V to 24-IX-70.

(B) Movement patterns of individuals numbered 680-1018, which were marked from 9-X-70 to 18-XII-70 and recaptured 15-X-70 to 4-III-71, after removal of the Gurania at station 49. Most of the recapture period is subsequent to the end of blooming of the Anguria at station 44.

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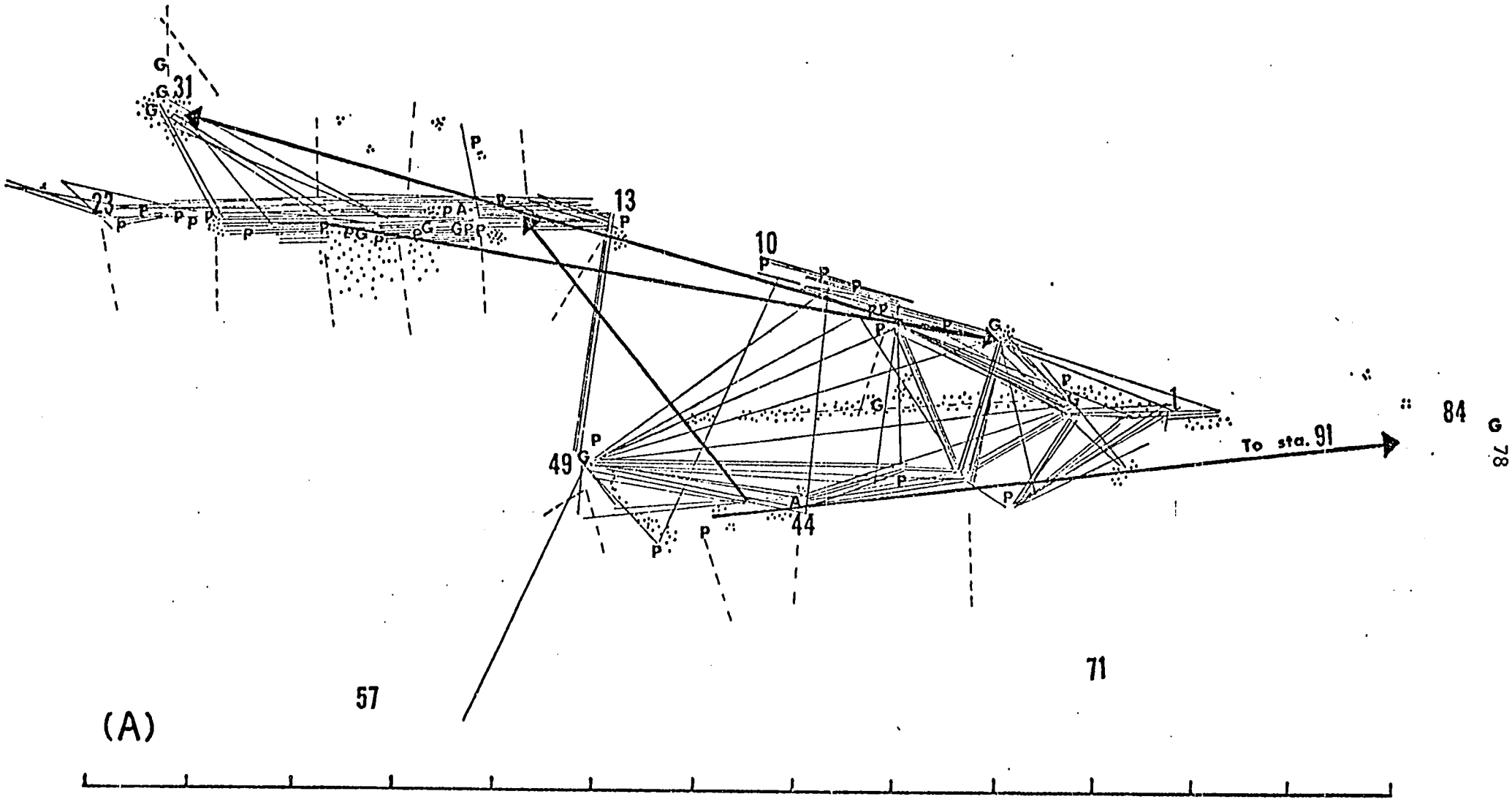

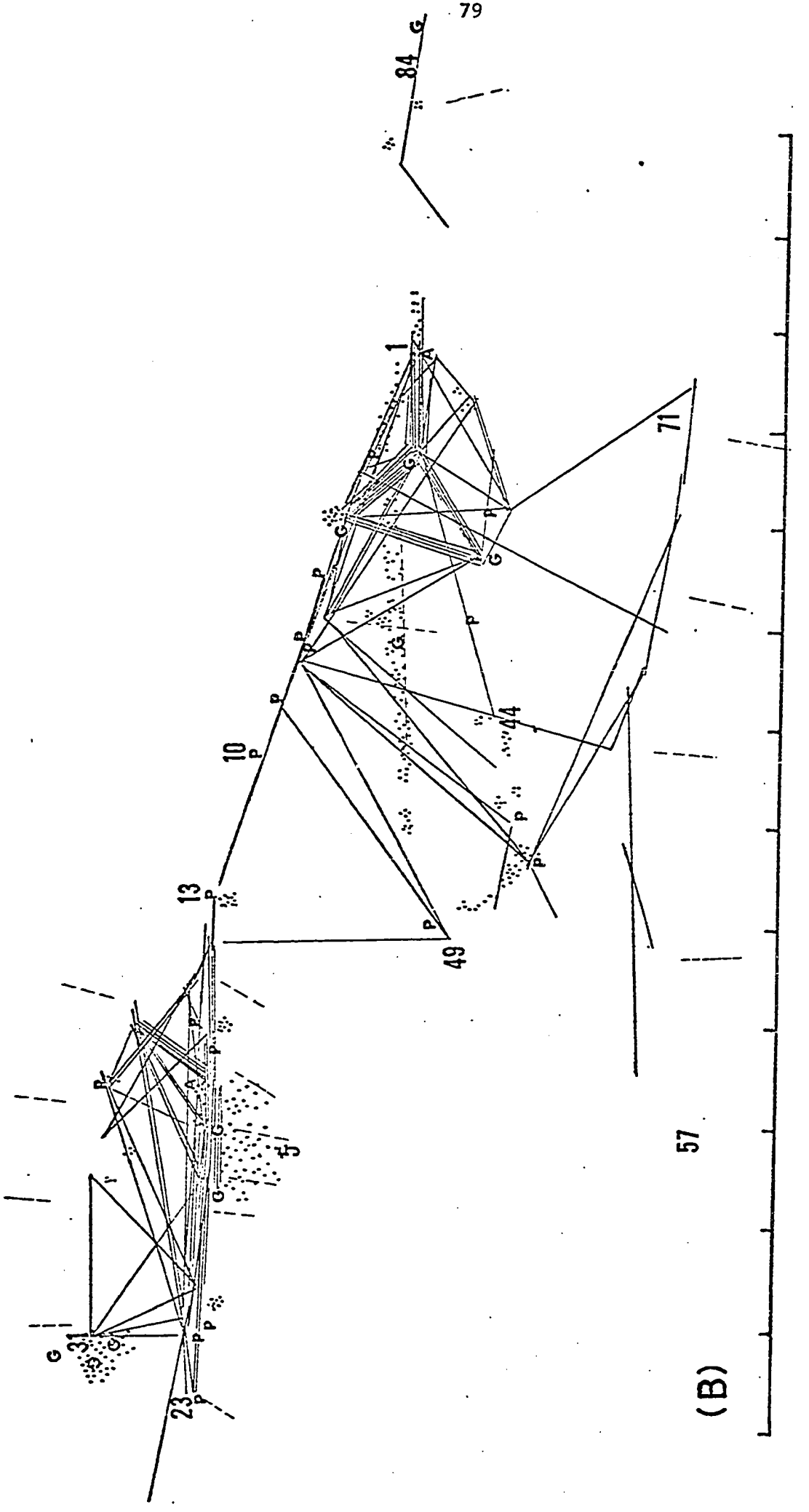

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the three plants is difficult due to the inaccessibility of many areas where Gurania and Anguria occur. In addition, Anguria inflorescences are very small (mature flowers are 1 cm. high) and inconspicuous and are usually located by first seeing one or more ethilla fluttering about the plant.

The fact that such an inconspicuous plant with only one small flower is apparently known to so many butterflies (see below) is good evidence that Anguria is preferred over Palicourea as a pollen source. Moreover, microscopic examination of numerous pollen loads removed from wild caught ethilla has shown (Gilbert, 1971b) that the large dark staining tetrads of Anguria and Gurania predominate over the round non-staining Palicourea pollen. In fact, large pollen loads from butterflies caught while visiting Palicourea have on occasion proved to be as much as 98%-100% tetrads. Yet the total number of inflorescences of Gurania and Anguria known to exist at any one time in the sampling area does not exceed 100, which would yield less than fifty widely scattered flowers (up to 400 yards between adjacent Anguria plants, for instance) per day to the butterflies.

Consider once more the problem faced by a newly emerging female ethilla. Its Darwinian fitness depends upon how rapidly it can initiate daily egg production, the magnitude and consistency of this rate and the length of time that it can continue producing eggs. It must therefore quickly locate sufficient inflorescences of the major pollen sources so that the daily unpredictability in flower production by single inflorescences is no longer important. (From the plant's point of view this unpredictability forces pollinating

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organisms to seek other plants and thereby promotes outcrossing.)

If in its first few days of exploration the new female locates enough sources of pollen and nectar for maximum egg production, further exploration would be deleterious to reproductive success. The time spent searching would detract from time spent exploiting known resources, particularily in view of strong competition for these resources from other females. In addition, homing behavior (or more precisely, piloting) would minimize the time required to relocate previously visited flowers. Thus, after an initial exploratory phase, the optimum strategy for an individual given the nature of the resource dispersion, would be the adoption of a regular beat, home range or "trapline" (Janzen, 1971b).

That H. ethilla adults have somewhat restricted home range behavior is evidenced by extensive recapture information. For instance, during the study 26 butterflies have been recaptured on seven or more occasions. With respect to the ridge top stations, none of these individuals has been recaptured more than 5 stations (250 yards) away from point of original marking, while 31% (N=8) had moved no more than 2 stations (100 yards). The locality records of multiply recaptured individuals also support the idea of home range (Table 6), as does the low percentage of transfers observed between Areas A and B.

While home range and familiarity with local landmarks will help the new female solve the problem of exploiting spatially and temporally dispersed pollen sources, there is nothing to prevent other females from finding and exploiting the same sources. Judging from the estimated numbers of butterflies and the apparent low numbers of

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TABLE 6

SOME REPRESENTATIVE DATA SHOWING INDIVIDUAL RECAPTURE PATTERNS ALONG THE ANDREW'S TRACE (STATIONS 1-26).

Butterfly Number	Sex	Recapture Stations	Days First to Last Recapture
3	M	5, 7, 3, 5, 8, 5, 7, 6	138
22	M	9, 9, 9, 7	76
119	M	2, 2, 22, 22	35
127	M	4, 7, 5, 5, 3, 6, 9	123
153	M	16, 16, 16, 16, 16	83
168	F	22, 21	152
170	M	21, 20, 20, 20, 21, 21, 20	82
181	F	16, 17, 17, 20, 20	73
255	F	16, 17, 18, 19	117

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Gurania and Anguria flowers, intraspecific competition may be intense (also perhaps interspecific competition from hummingbirds). The low incidence of large pollen loads on butterflies in the field compared to those in an insectary with flowers superabundant (Gilbert, 1971b) is a possible indication that pollen is in limited supply at Andrew's Trace.

Because of the warm night temperatures in tropical regions, insect flight activity is possible on a 24 hour basis with a minimum of energy loss due to thermoregulatory activity. Competition for some limiting resource can in the tropics lead to early morning flight of diurnal insects. For instance, bees which forage before daylight are known from Central America (Janzen, 1971a), and I have observed early morning (5:15 a.m.) flower visiting in the ithomiine butterfly Mechanitis isthmia in Costa Rica (Gilbert, 1966). Striking evidence of the degree to which earlier foraging can lead to competitive advantage in bees is provided by the work of Woyke (1969) on the African honeybee in Brazil. The African bees, Apis mellifera adansonii, begin foraging 1/4 to 3/4 hours earlier than the Italian A. mellifera in the same apiary, with the result that the average honey production by the African colonies is twice that of the Italian.

The fact that Gurania flowers were largely devoid of pollen by 0830 or 0900 hours each morning suggested early morning visitation by the ethilla. I was unable to investigate this question in April 1970, because of a country-wide curfew which prevented early morning human activity. In August 1970, however, early morning trips to Andrew's Trace revealed that the ethilla visited the Gurania flowers at station 49 as early as 0545, just at the break of dawn.

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Several observations made at station 49 in a 5 day (18-22 August 1970) intensive study of early morning activity are of particular relevance to the discussion of competition for pollen and home range. First, almost all early morning visits were by females (8/9 visiting before 0630 were female). After 0830, on the other hand, only 2/14 of the ethillas visiting were female. Brown (1970) has also observed early morning (0730) foraging by females of Heliconius mattereri in Brazil. This sexual difference is correlated with the fact that females have a higher daily requirement for pollen since they lay eggs daily. On the other hand, with the daily recruitment of virgin females in the population as low as it is (see above), males do not need to manufacture spermatophores on a daily basis, and therefore do not require the extra protein that extreme early morning flight provides.

Also of interest is the fact that all of the early individuals arrived within a period of about 10 minutes, coming singly and in groups of two or three. From what I could see in the early morning darkness, all females arrived from the ENE (toward Sta. 63, Fig. 10). Four females, Nos. 466, 483, 510, 511 were regular visitors (each seen 4 days) and several others were recorded twice.

Of this group of early morning females, #466 is of special significance. The recapture record of this individual provides evidence for temporal regularity in daily movement patterns similar to that described for certain tropical bees (Janzen, 1971a). On 20 August, this female was recaptured 3 times: 1) Station 49, Gurania, 0550 hrs.; 2) Station 8, Palicourea, 1150 hrs.; 3) Station 44, Anguria, 1345 hrs. On the following day (21 August) #466 was once

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again seen early at station 49, and was seen or taken there on two other early morning visits. It was also taken at 49 at 1025 and 1125 hours. The Anguria at station 44 was always visited late by #466: 1410 hours, 1450 hours, and 1345 hours.

Males of H. ethilla may also be somewhat punctual in their arrival at various points along daily routes. During the experiments, previously mentioned, in which tethered virgin females were presented to wild males, it was found that at least one of the males observed returned at approximately the same time each day to the clearing where the experiments were carried out (near Sta. 17, Fig. 10). On 6 December, male #438 entered the clearing at 1330 hours, was attracted to the tethered female but mating was not achieved. On 7 December the same male arrived at 1340 hours and this time mating was accomplished. Male #438 was captured at the same spot on 10 December, 1340 hours, on 12 December at 1225 hours, and on 13 December at 1440 hours.

On 15 December, 1210 hours, between stations 27 and 28, a worn, brown ethilla was seen flying rapidly up the slope toward the top of the ridge. I correctly guessed that this was #438 apparently on its way to the clearing at station 17. It should be pointed out that other males were observed to enter and leave the clearing all through the late mornings and afternoons, Thus, different males could be following parts of the same daily route but on different time schedules.

Distribution and Abundance of Resources X Population Structure

With an understanding of what the important resources are,

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how they are dispersed, and how individual butterflies must behave in order to survive and reproduce, it is possible to achieve some understanding of patterns observed at the population level.

At Andrew's Trace, two major features of H. ethilla population structure to be explained are as follows: 1) The subdivision of the colony into two rather isolated populations, A and B, and 2) The size of the population and its relative stability through time.

First, in considering the two subareas, A and B, which were defined by recapture information on individuals, it is interesting that area A, stations 9 and 49, are much closer to area B stations in the center of adult density, stations 16-19, than they are to other area A stations, such as 3 and 71. In other words, individuals initially marked at station 9 are much more likely to be recaptured at 3 or 71 than at 18 or 19.

Clearly, there are more important factors acting to limit interarea adult movement than distance alone. If we consider each population as the summation of individual feeding routes, the basis for the subdivision of the colony into local population units becomes clear. Figure 14 (A) shows the distribution of larval and adult resources at Andrew's Trace superimposed upon a representation of adult dispersal patterns during one period of the study. If one assumes that an ethilla individual seeking to add an additional pollen/nectar plant to its feeding route will be more likely to add the nearest neighbor plant, it is possible to see how stations 9 and 49 can be effectively closer to 3 and 71 than to 18 and 19, since between stations 10 and 13 is dense forest with heavily shaded

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understory lacking larval or adult resources. This heavy shading and lack of small openings or clearings continues SE from the ridge to the area between stations 13 and 49. H. ethilla flys in the canopy, so that unbroken forest is not an extrinsic barrier to it any more than is a strip of nonserpentine grassland for E. editha in California (Ehrlich, 1961; Chapter I). However, the lack of suitable adult food resources in this zone tends to prevent movement across it much as the Jasper Ridge populations of E. editha are separated on the basis of discontinuous nectar distribution (see Chapter I).

Station 13 is the only spot known which is occasionally incorporated into the daily feeding routes of butterflies from both populations. Hypothetically, the creation of several feeding stations between stations 10 and 13 and 49 and 13 would promote much more extensive intermingling of the two populations.

It should also be pointed out that the bulk of adult resources for each of the two populations, A and B, lies on the opposite slopes of the ridge, which must be an additional factor keeping the areas separate.

It was mentioned previously that the dispersion of reproductive Gurania and Anguria plants changes with time. According to everything said thus far, a change in the spatial pattern of these resources should drastically alter the patterns of adult movement and thus population structure. The appropriate experiment was carried out by a road crew of the Trinidad and Tobago Highway Department. On October 15, the Gurania at station 49 was cut down after it had provided a steady pollen source for approximately three months.

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Also disappearing about this time was a heavily visited inflorescence of Anguria (station 44). Figure 14 (A) and (B) compare observed adult movement patterns before and after the removal of these adult food sources. Since the spatial patterns of the other adult plant, Palicourea, and the larval food plant P. cyanea did not appear to alter, it must be concluded that the observed change in adult dispersal patterns was due to the altered pattern of Gurania and Anguria. It is tempting to speculate that the flowering of a single large Gurania or Anguria vine near some outlying point of the subareas (e.g. 10, 13, or 49) would substantially increase the probability of interarea transfer. Indeed, during the period that the Gurania was blooming at 49, at least 3 transfers between A and B took place, plus an additional individual which went from B to A and back to B via station 49. Subsequent to the removal of this plant as shown in Figure 14 (B), no interarea transfers were recorded.

The patterns of adult movement shown in Figure 14 are reminiscent of adult movements by E. editha at Del Puerto Canyon, (Figs. 6 A, B, Chapter I). Indeed, the ability of local homing by land mark and regular feeding station cannot be excluded for the Del Puerto E. editha. Unfortunately, large adult numbers and short life span make it less likely that the conclusive data can be gathered for individual E. editha.

Now consider the second major feature of ethilla population structure at Andrew's Trace, that of the size and stability of the adult population. Benson (1970) suggests that for some H. erato populations in Costa Rica, larval food plant may be an important factor limiting population size. At Andrew's Trace, however, the food plant

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Passiflora cyanea is very abundant, and seems to be in no way limiting. Thus, numbers are probably kept below the carrying capacity of the larval food plant by the intense early stage mortality which is apparently occurring at Andrew's Trace.

One might then ask why these populations appear to be so stable through time. One part of the answer will quite likely concern the complexity of the mortality factors which operate on the early stages. If, for instance, predators such as ants and vespid wasps are present in addition to egg and larval parasites, these predators would tend to damp any host parasite cycling since they undoubtedly take parasitized as well as nonparasitized prey. I have suggested elsewhere that this may be an important factor for ithomiine butterflies in Costa Rica (Gilbert, 1969) and for tropical butterflies in general. The long life expectancy of adult females may also be an important factor in stability of numbers as Wynne-Edwards (1962, p. 601) has suggested. However, in Wynne-Edward's view population "regulation" is the ultimate goal which is achieved in some cases by the evolution of longer individual life expectancy. A different, more plausible interpretation of the evolution of longevity in H. ethilla would be that in the face of high preadult mortality due to predators and parasites, those individuals which disperse their eggs in time (by increasing reproductive longevity) will on the average leave more offspring than those clumping their eggs in time. Because of the lack of climatic restraints on when eggs must be laid, and because adult resources are predictable through the year, tropical insects like H. ethilla can respond fully to the selective pressures operating to increase reproductive life. The distasteful qualities of this insect

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would also enhance this response.

Regardless of the ultimate factors involved, however, increased adult longevity (of reproductives) would be expected to reduce the probability of local extinction, and in that sense is involved in the stability of the population. Since adult longevity depends upon the availability of adult resources, it is obvious that the abundance of these resources would determine the extent to which potential longevity is realized by the average individual.

The amount of adult resource would play another, probably more important role in stabilizing numbers, in setting an upper limit to total egg production by the population. For instance, in the case of H. ethilla at Andrew's Trace, even if the intensity of early stage mortality is relaxed temporarily leading to an increase in adult recruitment (and there is some evidence for this from age structure differences from wet to dry season at Andrew's Trace), the total number of eggs cannot increase if pollen availability remains as constant and as limited as it seems to be. In butterflies like E. editha, in which the larval stage collects all of the necessary protein for egg production and which eclose with large numbers of mature eggs, population response to reduced preadult mortality would be rapid and drastic, thus setting the stage for an equally drastic response by a parasite and subsequent parasite-host cycling.

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