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The Role of Adult Feeding in Egg Production and Population Dynamics of the Checkerspot Butterfly *Euphydryas editha*

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Abstract. Carbohydrate intake increases longevity, body weight maintenance and egg production in female *Euphydryas editha*. Amino acid intake leads to heavier eggs, larvae from which are more likely to survive. Females fed nectar produce more eggs in later masses than females which are not fed. During years of normal and below normal precipitation, larvae emerging from these later eggs are unlikely to reach obligatory size for diapause before their food dries up. On Jasper Ridge, where mortality is density-independent, nectar plays an important role increasing production of late egg masses during years of greater than normal rainfall when larvae from these masses are likely to reach diapause. The resulting large population increases, though infrequent, are probably important in maintaining population sizes large enough to reduce the chances of extinction during dry years.

Introduction

A number of recent studies clearly show that butterfly habitat selection and choice of oviposition host are largely determined by larval host plant chemistry and ecology. However, a study by Gilbert and Singer (1973) indicates that adult resource distribution may be a primary determinant of habitat selection by *Euphydryas editha*. More recently Murphy (1982) showed that egg distribution by *Euphydryas chalcedona* is constrained by the proximity of nectar plants.

This report shows that nectar feeding can play a key role in the population dynamics of *Euphydryas editha*. Both carbohydrates and amino acids in nectar are important in reproduction, increasing the number and size of eggs in later egg masses. These masses result in larvae which reach diapause only during particularly wet years. Nonetheless such infrequent population increases may be critical to long term population survival in environments where mortality is largely density-independently controlled.

Though nectar is simple biochemically and has been studied extensively, its role in the energetics, maintenance and oogenesis of butterflies is poorly known. What is known is that nectar is necessary for maximum longevity and fecundity in the few nectar-feeding species studied (Stern and Smith 1960, Labine 1968). While nectar source characteristics (Watt et al. 1974, Levin and Berube 1972) and pollen feeding (Gilbert 1972, Dunlap-Pianka et al. 1977) have been investigated in detail, the connection between adult feeding and butterfly fitness in the field has not.

Since the Lepidoptera exhibit a broadly varied dependence on adult resources, the selection of species for study is important. Many moths do not feed at all. At the other extreme, female *Heliconius* butterflies collect pollen and steep it in a regurgitant to produce an amino acid-rich solution which supports the laying of several eggs per day through the adult life span of several months (Gilbert 1972). Typical of temperate butterflies are *Colias* females which lay up to a thousand eggs singly during a week or so. The onset of normal egg maturation and oviposition in *Colias* is dependent on the availability of adult resources (Stern and Smith 1960). In contrast, *Euphydryas,* which also produce many eggs in a short period, emerge with mature eggs and are able to produce substantial numbers without adult feeding. They are the most "conservative" butterflies in adult resource needs. If nectar resource use is an important factor in the population dynamics of *Euphydryas,* then it should be more so in most other butterflies.

Nectar has long been known to consist of a dilute aqueous solution of sugar. But only relatively recently have "trace" components, amino acids, proteins, and lipids been systematically assayed. Amino acids in particular may be important to butterflies. A series of studies established that 1) amino acids are more abundant in flowers frequented by butterflies than those visited by birds or bees (Baker and Baker 1973, 1975); 2) as mentioned above, butterflies have been found to feed on pollen; and 3) butterflies immediately use radioactive-labelled free amino acids from adult feeding in gamete formation (Rothschild 1974, Boggs and Gilbert 1979). The laboratory feeding experiments described below were designed to determine the roles of the water, sugar and amino acids of nectar in reproduction of *Euphydryas editha* females.

Materials and Methods

Laboratory Procedure

The butterfly of this study is *Euphydryas editha bayensis,* an endemic of serpentine grasslands in the San Francisco Bay Area (Ehrlich et al. 1975, Ehrlich and Murphy 1981). Adults fly from about mid-March through late April. Oviposition begins within a day of female emergence. Females

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deposit masses of up to hundreds of eggs at the base of *Plantago erecta* or *Orthocarpus densiflorus*. Oviposition then continues at a rate of about one mass every two days for the duration of adult female life.

Postdiapause larvae were collected for this study at Woodside and Edgewood (see White and Singer 1974, Murphy and Ehrlich 1980) and were fed mixed flats of *Plantago* and *Orthocarpus* until pupation in the lab. They were then transferred to plastic boxes and placed in controlled environment chambers with 25° C days and 14° C nights, and a photoperiod of 16 L:8 D.

Newly emerged adult males were fed a mixture of 20% sucrose and 0.004 M amino acids (described below). Females were stored unfed in a cold room at 9° C for twelve to twenty-four hours and then placed with fed males in spherical net cages under greenhouse conditions. After mating, females were transferred to 13 × 8 × 7 centimeter plastic boxes containing bouquets of *Plantago* and *Orthocarpus* as an oviposition substrates and returned to the growth chambers.

Females were segregated in six groups and fed different diets to satiation once a day. The butterflies were placed at feeding stations and when necessary their proboscides extended with the aid of an insect pin. Light and heat from incandescent lamps stimulated feeding.

A female was defined as satiated when she coiled her proboscis, retreated from her feeding trough and walked or attempted to fly away for a third time during her single daily feeding bout. On the first and second retreats the butterfly was repositioned near food, the proboscis uncoiled and reintroduced into the mixture.

Egg masses were removed daily from the boxes, then weighed and individual eggs counted. Females were weighed after mating, after each egg mass was laid, and at death. In order to provide samples for fat body analysis five females from each diet group were frozen after laying one, two, or three masses. A final group of five was allowed to lay all their eggs and was frozen after natural death. Thus reported results are for an $N=20$ for "one mass" data including female weights, egg mass weight and egg number, $N=15$ for "two mass" data, $N=10$ for "three mass" data and $N=5$ for totals.

Body condition was measured in two ways: first, by measuring losses of body weight after each oviposition and, second, by measuring the proportion of body weight remaining as fat body. Fat body size has been used as an indicator of metabolic reserve status in studies of butterflies (i.e. Tuskes and Brower 1978, Brown and Chippendale 1974) and this analysis closely followed those procedures.

The Diets

Females were fed six diets to determine the independent effects of water, sugar and amino acids on reproduction and body weight maintenance:

1) Nothing.

2) Water. The water in nectar is normally the only moisture available to *Euphydyras editha* on Jasper Ridge. The laboratory butterflies would not feed on pure water. Artificial sweeteners were not used since the effects of the "nonsugar" carbohydrates are unknown. We were able to elicit a feeding response with as little as 0.25% sugar in water (determined by pocket refractometer). The "water" diet therefore included this small fraction of carbohydrate.

3) Water containing 20% sugar. This concentration is about the mean value for the nectar of temperate zone flowers frequented by butterflies. Both mono- and disaccharide sugars were mixed in a ratio of 2:2:1 (glucose:fructose:sucrose) by weight, also about average for butterfly-visited flowers (Wykes 1952).

4) Water and amino acids. A mix of five amino acids was prepared, each at a concentration of 0.004 M. This approximates the mean both for most common amino acids and the sum of total amino acids in floral nectars used by butterflies (Watt et al. 1974). The amino acids selected – proline, serine, alanine, arginine and lysine – were among those commonly found by Watt et al. (1974) and Irene Baker (pers. comm.) in nectars from "butterfly" flowers. This diet also required inclusion of 0.25% sugar to promote feeding.

5) The laboratory equivalent of natural nectar. It contained the components of the sugar-only and the amino acids only diets (0.004 M).

6) Laboratory nectar with more amino acids. This diet is the same as diet 5, but with five times the concentration of amino acids.

Correction for Size

A positive correlation between fecundity and female size at emergence has been found in Lepidoptera that do not feed as adults (see Benson 1973 for review). Although a relationship between larval nutrition, pupal weight, and adult size has been observed for Lepidoptera that feed as adults, few data exist linking these factors with egg production (Stern and Smith 1960). However, larger *Euphydryas* females will nearly always lay more eggs than smaller females on the same diet.

Wing length is a standard indicator of adult size in Lepidoptera, but for *Euphydryas editha* females there is no correlation between wing length and female weight or between wing length and egg production. However, a correlation between female weight at emergence and egg production was found; that for first egg masses from unfed females is shown in Fig. 1 ($N=20$, $r=0.683$, $P<0.01$). We therefore have used female weight at emergence as our indicator of female size, and have corrected the number of eggs per mass for female weight at emergence.

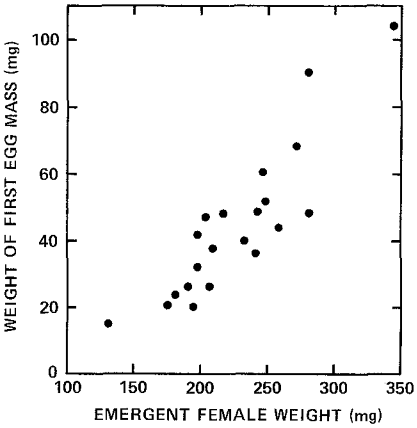

Fig. 1. Relationship of female weight at emergence and weight of first egg mass produced by unfed females

For comparisons of egg production among diet groups for egg masses 1, 2 and 4, an Ancova program with one covariate (female body weight at emergence) was used. This adjusts the mean of the dependent variable (number of eggs) through linear regression procedures which standardized for the covariate, the independent variable. For the three egg mass and lifetime groups the mean initial weights of the treatment were not significantly different from each other. No correction factor was therefore required, and the treatment means for these groups were compared by a t-test.

For comparisons of individual egg weights, total egg weight in given egg masses laid by all individuals in a diet group was divided by the total number of eggs laid. Groups were compared by the Mann-Whitney U-test. Comparisons of longevity were done by t-test.

Model 1 Anova and the Student Neuman-Kuels test (Sokal and Rohlf 1981) were used for comparisons of the effect of diets on body weight maintenance.

Results

Longevity

In the laboratory, females fed live significantly longer than those fed nothing at all (no feed, $\bar{x}=9.9$ days, significantly less than both water fed, $\bar{x}=11.8$, and amino acid-only fed butterflies, $\bar{x}=12.0$, $P<0.05$; no feed is significantly less than sugar diets, $P<0.01$). Females fed diets containing sugar (sugar only, $\bar{x}=16.0$ days; sugar and 0.02 mAA, $\bar{x}=15.1$; sugar and 0.004 mAA, $\bar{x}=16.4$) have significantly greater longevity ($P<0.05$) than the groups fed water or water and amino acids. Complete diets, containing both sugar and amino acids, do not result in significantly greater longevity than the sugar-only diet.

Egg Production

Total lifetime egg production by butterflies fed diets containing sugar is significantly greater than by butterflies fed other diets ($P<0.05$, Table 1). Regardless of diet, first egg masses (those largely formed before feeding is initiated in the field) have a maximum size of about 130–180 eggs. Diets combining sugar and amino acids do not increase first egg mass size. Additionally, there are no significant differences for second egg masses or for the sum of first and second egg masses.

By the third egg mass the diets containing sugar result in significantly more eggs than the non-sugar diets (Mann-Whitney U-test, $P<0.05$). For the fourth and subsequent masses this trend is obscured by small sample sizes, hence no significant differences in mass sizes are observed. The presence of sugar in the diet, however, allows a relatively high rate of egg production to continue through at least five egg masses. Butterflies fed diets that lack sugar produce a very large percentage of their total egg output in the first two masses (Fig. 2).

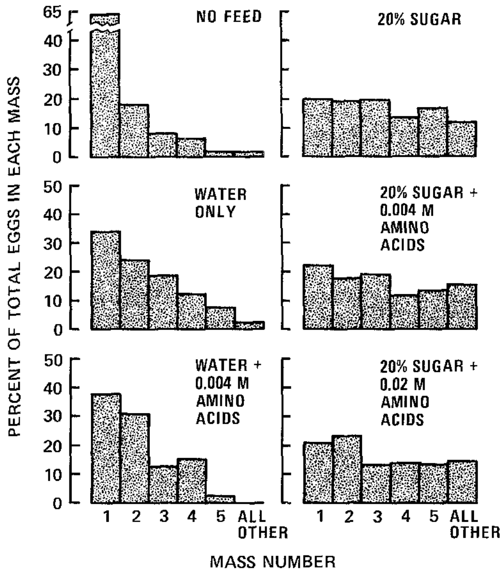

Fig. 2. Percent of total eggs produced in each egg mass

Egg Weight

As expected, mean weights of first mass eggs are similar regardless of diet (Table 2), and no significant differences are found for second and third egg masses. But butterflies fed diets containing amino acids lay fourth masses with mean individual egg weights greater than the eggs of females fed diets lacking amino acids ($P<0.05$).

Lifetime mean egg weights are not good figures for comparing the effects of amino acids in diets. The group fed water plus amino acids and the group fed water only do not survive long enough to produce the lighter eggs typical of older females. The group fed sugar-water without amino acids lays comparatively large individual eggs early, then significantly lighter eggs in subsequent masses, resulting in a much lower lifetime mean.

Table 1. Egg production on various diets. Results are corrected for female weight at emergence

	No Feed		Water		Sugar water		Sugar water +0.004 MAA		Sugar water +0.02 MAA		Water and amino acids	
	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
Mass 1	180.47	*18.32*	149.64	*14.91*	139.95	*18.56*	126.55	*17.66*	143.96	*17.14*	162.54	*19.62*
Mass 2	85.25	*10.84*	99.45	*11.45*	131.15	*17.37*	116.58	*14.54*	120.08	*17.07*	120.97	*15.62*
Mass 3	43.33	*12.24*	74.29	*7.98*	110.71	*18.17*	117.83	*11.95*	97.00	*16.42*	43.86	*11.15*
Mass 4	70.33	*37.01*	115.07	*16.02*	87.16	*37.93*	40.18	*26.15*	101.83	*8.79*	88.84	*12.13*
Lifetime Egg Production	426.60	*38.24*	401.20	*38.85*	774.60	*88.99*	805.00	*137.24*	649.00	*86.18*	424.25	*32.59*

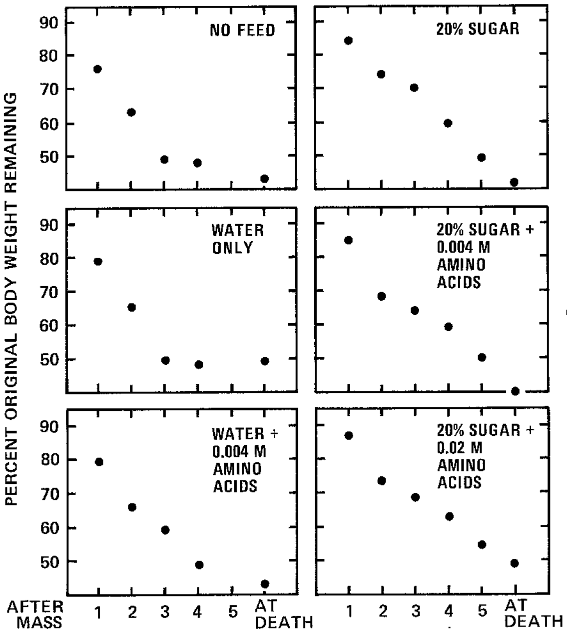

Fig. 3. Percent of female weight at emergence remaining after each egg mass and at death

Female Body Weight Maintenance

Female body weight declines rapidly in butterflies given no food (Fig. 3). After laying three egg masses these females are at about 50% of their emergence weight, about the normal weight at death. This weight is not reached until after four masses in the group fed amino acids only and not until five or more egg masses for females fed diets containing sugar.

Changes in body weight between ovipositions are shown in Table 3. Lifetime totals are weight changes from emergence to death minus total egg weight; thus females fed nothing lose more than 16% body weight independent of eggs laid. Butterflies fed water only and those fed water plus amino acids lose significantly less weight than unfed butterflies ($P < 0.05$). Females fed diets containing sugar actually lose less body weight than weight in eggs laid, a body weight gain during their lifetimes by this measure. Body weight changes of sugar fed females significantly differ from unfed females ($P < 0.01$) and those fed water or water and amino acids ($P < 0.05$).

Analysis of fat body lipid yielded no significant differences, probably because of small sample sizes (120 individuals assayed, $N = 5$ for each group). There was high intragroup variation (Table 4). Two trends warrant further in-

Table 2. Mean weights of individual eggs in each egg mass

Egg mass	Diets					
	No Feed	Water	0.004 MAA only	Sugar and 0.004 MAA	Sugar and 0.02 MAA	Sugar only
1	0.256	0.262	0.255	0.247	0.249	0.249
2	0.229	0.238	0.253	0.262	0.220	0.255
3	0.232	0.240	0.244	0.241	0.233	0.215
4	0.202	0.203	0.234	0.230	0.223	0.214
5	–	–	–	0.227	0.223	–
Total	0.248	0.250	0.247	0.258	0.236	0.220

Table 3. Percent of female body weight change after each egg mass was laid with weight of eggs substracted

After egg mass	Diets					
	No Feed	Water	0.004 MAA only	Sugar and 0.004 MAA	Sugar and 0.02 MAA	Sugar only
1	– 4.03	– 5.63	–3.49	– 0.91	+2.12	– 1.29
2	– 2.26	– 4.91	–2.86	– 3.36	+3.21	+ 7.72
3	–17.65	–16.02	–2.66	+21.96	+7.48	+ 0.09
4	–	–11.21	–5.93	+ 7.19	+5.85	–12.06
5	–	–	–	– 0.11	–0.75	–11.24
Lifetime	–16.42	– 7.88	–6.84	+ 5.49	+8.70	+ 4.98
s_Y	3.62	4.26	1.48	7.34	3.68	6.95

Table 4. Percent of abdominal fat body remaining after each mass (wet weight)

After egg mass	Diets					
	No Feed	Water	0.004 MAA only	Sugar and 0.004 MAA	Sugar and 0.02 MAA	Sugar only
1	20.04	26.88	28.56	27.37	27.37	19.77
2	27.20	21.99	16.67	25.52	27.48	17.05
3	13.25	12.54	14.23	21.77	19.49	12.92
At Death	10.86	11.02	8.91	8.91	9.94	11.29

vestigation: 1) the differences in fat body lipid after three egg masses between groups fed sugar-amino acid diets and those fed other diets, and 2) the slightly smaller fraction of lipid remaining at death in females fed amino acids than in those fed other diets. The former show that the availability of amino acids in adult food may delay the drain on stored larval reserves. The latter indicates that amino acids acquired by adults might be a limiting factor necessary for conversion of those reserves to more complete egg precursors, probably those that enhance egg weight.

Discussion

The Role of Dietary Components

Water. The results of this experiment show that water alone plays no direct role enhancing fitness in female *Euphydryas editha.* Since a major fraction (~85%) of the weight of eggs is water and water is necessary in a wide variety of metabolic reactions we presumed that it could be a limiting factor in reproduction. Although laboratory females fed only water live longer than unfed females, they do not significantly differ in egg production, mean individual egg weights or body weight maintenance.

Water availability has been shown to increase egg output in some Lepidoptera (Benson 1973, Engelmann 1970, Jacobson 1965, Kozhantsikov 1938), although in moths, of two species of *Ephestia,* one exhibited a water induced increase in egg production, while the other did not (Norris 1934). *Colias* butterflies fed water produce more eggs than those fed nothing, but less than those fed water and sugar (Stern and Smith 1960). But a key means by which water probably indirectly effects reproduction in *Euphydryas editha* could not be tested. These laboratory *Euphydryas* did not fly, an activity greatly affecting water balance. Thus one might expect the differences between the performances of butterflies in the unfed and water-only fed groups to be even less than differences that would occur in the field.

Sugar. Unfed butterflies exhibit reduced longevity and increased rate of weight loss, associated with not only a decreased period of oviposition but a rapid reduction in the size of each egg mass. The results from females fed sugar indicate that carbohydrate availability increases *Euphydryas* longevity, concomitantly aiding adult weight maintenance and reproduction. Most important, however, nectar carbohydrate increases total egg production (Table 2). Females fed sugar continue to lay large egg masses after the first two egg masses and, therefore, differences between females fed sugar and females not fed sugar dramatically increase in these later masses. Extending the period of egg production and maintaining the large size of later egg masses are the primary factors which enhance fitness.

The largest number of eggs in a mass were recorded for first masses of butterflies that received no food at all. These unfed butterflies in the lab may be analogous to butterflies in drought environments, faced with few or no nectar resources. Such butterflies have limited survival potential and are unable to contribute adult resources to offspring. Furthermore, they produce offspring that are faced with host plants that senesce more rapidly than usual. For both reasons quick evacuation of eggs is advantageous so that they are not reabsorbed nor larval nutrients redirected by the starving adult female, and so that larvae might reach diapause size as early as possible. Figure 2 indicates that some mechanism exists allowing females under the worst of circumstances to unload as many eggs as quickly as possible.

Amino acids. Euphydryas editha females tend to lay smaller individual eggs later in the season. The presence of dietary amino acids results in production of significantly larger individual eggs in these later masses. This could directly enhance the survival of offspring in the field by three means. First, *Euphydryas editha* eggs weighing less than 0.20 milligrams have greatly decreased hatchability, while nearly 100% of those weighing more than 0.22 milligrams hatch in the lab (Murphy, unpubl.). Second, larger first instar larvae emerging from larger eggs probably possess larger mandibles, advantageous for feeding on a wider range of plant materials. This could be critical for rapid prediapause maturation. Third, larger hatchling larvae require a shorter growing period to reach diapause size, and can travel farther, increasing the likelihood of contacting necessary additional host plants.

Euphydryas, when fed diets containing sugar with amino acids in concentrations well above that in nectars they would normally encounter, do not show increased vigor or reproductive output compared to those fed sugar with naturally occurring amino acid concentrations. Where sugar was the important nutrient, in longevity and egg production, the diet of sugar with high amino acid concentrations provided the poorest results. Where amino acids were key, increasing individual egg weights in late masses, the diet with high amino acids concentration was again the poorest of the superior diets.

These results considered in concert indicate that the small free amino acid concentrations available in nectars might be quite close to optimum for *Euphydryas.* Amino acids at five times that level may be a wasted luxury since active transport by the insect rectum and subsequent excretion of superfluous amino acids requires a series of ATP-requiring reactions and this exacts a cost.

Feeding and Population Dynamics: A Hypothesis

We have shown that adult feeding increases fecundity in *Euphydryas editha.* Unfed butterflies lay only about 60% of the total eggs laid by butterflies fed either sugar-water or nectar equivalents. But, the total size of the first two egg masses of unfed and fed females is the same. Adult feeding extends the period of oviposition and allows the butterfly to lay later egg masses of larger sizes. This finding provides the clue for the role of nectar in population dynamics. Large, nectar-induced increases in reproductive output cannot result in equally large increases of survivors, unless there is an identical likelihood of larvae from early and late egg masses surviving. In fact, this does not occur in *E. editha bayensis.*

Dramatic population fluctuations have been recorded in several demographic units of *Euphydryas editha bayensis* on Stanford University's Jasper Ridge Biological Preserve (Ehrlich 1965, Ehrlich et al. 1975). These fluctuations are due to year to year changes in the survival of prediapause larvae each spring. Almost all prediapause larvae die in most years because they are unable to reach obligatory size for diapause before their host plants, the annuals *Plantago erecta* and *Orthocarpus densiflorus,* senesce (Singer 1972).

Population size changes are indirectly attributable to local weather conditions (Singer and Ehrlich 1979); greater prediapause mortality in drier years results in reduced adult population size the following year. In this sense, *Euphydryas editha bayensis* appears to be near the ecological tolerance limit for survival of its prediapause larvae. Recent population extinctions during back-to-back drought years indicate just how precarious existence is in this habitat (Ehrlich et al. 1980).

As each spring progresses, the chances of prediapause larval survival diminish rapidly while the egg production of each female becomes increasingly dependent on adult resource availability. In seasons of normal precipitation the earliest emerging females produce several egg masses that may result in some larvae surviving to diapause. Females emerging later, during the period of peak oviposition, may produce only one or two egg masses that result in larvae surviving to diapause. The very latest emerging females are unlikely to produce any egg masses resulting in larvae that survive.

Therefore, the first egg masses produced by females tend to contribute much more to fitness. Early egg masses, however, were shown to be near maximum size in the absence of adult feeding. It is later egg masses that are particularly dependent on nutrients aquired by adults. Hence increases in egg production resulting from adult feeding are unlikely to result in comparable increases in surviving offspring under average conditions, except from very early eclosing females.

Additionally, the phase relationship between peak oviposition and plant senescence varies from year to year depending on winter rainfall. Comparatively dry winters reduce the period available for prediapause feeding while wet winters increase it. Singer (1971) monitored this phase relationship during four years on Jasper Ridge which included the driest (1968) and wettest (1969) winters of the 1960's. The interval between the estimated date of maximum oviposition (derived from mark-release-recapture data and data on reproductive biology of *Euphydryas editha* from Labine 1968) and the date at which 50% of *Plantago erecta* became senescent ranged from 23 days in dry 1968 to 29 days in wet 1969. Therefore, the effective increase in the length of growing season encountered by larvae hatching in 1969 compared to 1968 was 6 days. Six days is sufficient time for an ovipositing female to produce three egg masses. Hence, if a female emerging at the period of peak oviposition during a year of normal rainfall realizes survivors from its first two egg masses, oviposition after emergence on the same date in a drier year might result in only first egg mass larvae surviving, or perhaps no larvae surviving at all. Reproduction at peak oviposition during a particularly wet year, on the other hand, could result in survivors from three, four or perhaps more egg masses.

The significance of the role of adult feeding in reproduction seems straightforward. In wet years, in contrast with dry or normal ones, adult feeding which increases the number and size of later egg masses results in increases in the number of larvae successfully entering diapause. Thus in areas like Jasper Ridge where mortality is entirely density-independent, nectar sources aid long term population survivial primarily by increasing population size in wet years. Larger population size should serve as a buffer against random extinctions, assuming that the size of oscillations does not increase commensurately (a phenomenon of which there is no sign in Jasper Ridge population data – Ehrlich et al. 1975 and unpubl.).

Support for the Hypothesis

The recent history of one demographic unit on Jasper Ridge may be explained by this hypothesis. The population in area G went extinct in 1964–1965, was reestablished in 1966–1967, and went extinct again in 1974–1975. There, primary and secondary larval host plant density is approximately the same as that found in areas C and H which have not suffered extinctions. In area G, however, nectar source density is significantly lower. Furthermore, whereas areas C and H have three available nectar source species present, the annuals *Lasthenia californica, Layia platyglossa,* and *Linanthus androsaceous,* area G has only one, which also occurs in the other areas, the very early senescing perennial, *Lomatium macrocarpum.* It appears that several additional adult resource inadequacies have made the demographic unit in area G particularly vulnerable to extinction:

1) The northeast exposure of this area resulted in a late emergence of adults and extremely poor synchrony with *Lomatium.*

2) This asynchrony was not reduced in wetter, more favorable years, and later-blooming nectar sources such as *Lasthenia* and *Layia* are not present to enhance late season egg production. In these favorable wet years, populations in areas C and H greatly increase in size which then improves the chance of colony survival during inevitable dry years when the probability of larval survival is greatly reduced.

3) Dry year shortages of *Lomatium* are particularly critical since they are not ameliorated by the presence of these other sources.

4) Butterflies appear visually to identify and orient to nectar sources from distances of several meters or more, yet must assess oviposition host suitability by physical contact (Singer 1982). Therefore it is likely that nectar sources are key indicators of habitat suitability. A paucity of mid-season nectar may well be cause for emigration (Ehrlich, Murphy and Launer, unpublished).

The drought of 1961–1962 produced an irreversible downward trend in the area G butterfly population which then numbered less than 30 adults, apparently below the threshold necessary for persistance under such severe environmental conditions. The population did not recover to previous numbers and went extinct three years later. After reestablishment, numbers rose to more than 200, and a drought of the same magnitude in 1968 had little effect on population size. The 1974–1975 extinction showed again that the colony was unable to rebound from a major population decrease, this time due to the dry winter of 1973–1974 that was weathered by more dense colonies in areas C and H. The lack of nectar sources in area G appears to have limited resident populations to low levels even during favorable seasons. They were therefore at particularly high risk of extinction during less favorable years.

Conclusion

It appears then that nectar resources serve to increase reproductive success only occasionally – but those occasions may be of crucial importance in the dynamics of the population.

Whether nectar plays a similar role in other time-constrained holometabolous insect populations remains to be seen.

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