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Thermal Influences on Oviposition in the Montane Butterfly *Euphydryas gillettii*

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Summary. *Euphydryas gillettii* in a montane meadow in Wyoming oviposits in clusters on the highest large leaves of its larval host, the shrub *Lonicera involucrata*. Egg masses are found on the underside of leaves which predominantly face the southeast and thereby intercept morning sun. Measurements of leaf temperatures show that, during the cool, clear mornings, these leaves are warmer than leaves of the opposite orientation. Manipulative experiments demonstrate that eggs on these slightly warmer microsites hatch significantly faster than eggs on leaves of other orientations. Because of the rapid onset of winter, an increased developmental rate is likely to correlate directly with increased fitness. The proximal mechanism yielding such a result may be that females choose oviposition sites in the shade.

Introduction

Small scale thermal differences among microhabitats can exert important influences on the ways in which animals interact with their environment. Because they relate directly to fitness, those factors which modify rates of reproduction and development have the most direct influence on an organism's life history. Temperature is known to affect the developmental rates of butterfly eggs and larvae (Ae 1958; Sherman and Watt 1973), as it does the early stages of many organisms. The sites of reproduction can also be influenced by temperature; sand wasps, for example, choose nesting sites based largely on soil surface temperatures (Rubink 1981).

Many characteristics are important in determining where a population or species of butterfly lays its eggs. Leaf shape (Gilbert 1975; Rausher 1978), color of the substrate (Ilse 1937; Saxena and Goyal 1978), and the texture and chemical composition of the foliage (David and Gardiner 1962; Behan and Schoonhoven 1978; Stanton 1979) play important roles in determing the species of plants acceptable for oviposition. Such choices may, of course, change in evolutionary time, based on resource availability (Singer 1971), competitive interactions (Gilbert and Singer 1975), or changing plant chemical defenses (Ehrlich and Raven 1964).

How a given female chooses an individual plant and where on that plant to oviposit remains less well understood. It has been reported, though, that size of leaves and newness of foliage (Ives 1978; Schweitzer 1979; Courtney 1980) and the prior presence of eggs (Rothschild and Schoonhoven 1977; Rausher 1979; Shapiro 1980) may affect her choice. Other factors, such as height above the ground, exposure to sunlight, and the microlimatic zones that are known to occur next to leaves (Waterhouse 1960) may also be important.

In the course of a population study of the nymphalid butterfly *Euphydryas gillettii* Barnes, the eggs of this species were found not only on the uppermost leaves of the larval host, but predominantly on leaves that were oriented in a particular direction. A line drawn perpendicular from the upper leaf surface to the sky yields measurable angles of aspect (azimuth) and elevation; with north as 0°, leaves with eggs mostly faced southeast, giving a mean aspect of 145°. Since oviposition occurs on the underside of the leaves, the eggs actually faced 325° in aspect.

Such leaves intercept morning sun and are warmer at that time of day than leaves otherwise positioned. Eggs on leaves in this orientation could therefore gain a thermal advantage and have a reduced developmental period. Subsequent observations and experiments confirmed that development is accelerated significantly under these conditions, and there are strong indications that the developmental advantage is, in fact, a selective advantage.

Methods

The study was conducted in the Beartooth Mountains of Park Co., northwestern Wyoming, where a population of *Euphydryas gillettii* lives along a small stream at the edge of a montane meadow (2,600 m el). *E. gillettii* oviposits in clusters ranging in size from 23 to 310 eggs, with a mean of 146 eggs ($n = 72$; unpub. data). As first reported by Comstock (1940), the larval host is *Lonicera involucrata* (Rich.) Banks (Caprifoliaceae), an erect shrub 0.5–2 m high which grows in moist areas. The leaves are opposite, 5–14 cm long and 2–8 cm wide, and elliptic-oblong to elliptic-obovate in shape (Hitchcock et al. 1959).

Observations

Late in the flight period of 1979 (Aug. 5, 6) and 1980 (Aug. 6, 7), when the eggs were first beginning to hatch, I systematically surveyed the study area for *L. involucrata* and examined the leaves of each shrub for eggs. For each egg cluster found, I recorded the orientation of that part of the leaf with eggs and the position of the leaf on the stem. Angles of aspect were measured in 5° intervals with a Silva BSA compass. The magnetic declination of the study area is 17° E (USGS 1962), and this correction has been added to the data.

Temperatures were measured with a Markson model 5650 digital thermometer, with a YSI model 729 small surface probe for leaf temperatures and a YSI model 705 air probe for ambient values. Leaf temperatures were recorded between 0700 and 1100 MST from the lower surfaces of leaves perpendicular and parallel to the sunlight. A Cole-Parmer hygrothermograph recorded daily temperatures contin-

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uously throughout the flight period. Late in the flight period the position of the sun was recorded each half hour by measuring the angle of the shadow cast by a ruler on a flat surface.

Experiments

I measured the developmental period of 57 egg clusters oviposited during the first half of the flight period in 1980 (July 8-21); the data are insufficient to derive statistically significant results from later ovipositions. When each female left the newly oviposited cluster, I marked the leaf with the eggs and recorded the time and date of oviposition. Later the same day I reoriented that branch of the shrub so that the eggs were either parallel or perpendicular to morning sun. A wooden stake was driven into the ground next to the shrub, and the stem was twisted and attached to the stake with tape to change the orientation. Care was taken to avoid damaging the shrub, and later observations revealed no apparent harm to the plants. The attachment was made so that the stakes did not interfere with sunlight striking the leaves.

The leaves of *L. involucrata* are opposite and point upwards at an angle of roughly 45° from a level surface. Consequently, when viewed from the side, the geometric plane in which the surface of a leaf falls may be seen to intersect the plane formed by the surface of the opposite leaf at approximately a 90° angle. Thus, if one leaf of a pair is perpendicular to incoming sunlight, the opposite leaf is parallel. When viewed from directly above, however, the two leaves of a pair point in opposite directions from the stem of the shrub and therefore differ in aspect by 180°. It follows that a leaf with an aspect of 325° is, in fact, perpendicular to morning sun, while a leaf with an aspect of 145° is parallel to sunlight. The leaves on which eggs occurred in 1980 had a mean angular elevation of 55° ($n=230$), so the parallel and perpendicular relationships are approximate. I chose 325° and 145° as the two orientations for the experiment because the mean angle for egg orientation in 1979 was 325°.

An alternating sequence of the two orientations was chosen for the experiment; thus, each new cluster was numbered sequentially, and odd numbered clusters were oriented to 325° and even numbered ones to 145°. This pattern was not invariate because sometimes a butterfly would oviposit on a leaf of a stem which had already been staked down, and occasionally it was impossible to orient a leaf in a particular direction without twisting the stem so much as to damage the shrub. In the latter case the one possible orientation was chosen. Whenever the alternating sequence could not be followed for these reasons, the next newly oviposited cluster was used to fill in the incomplete sequence.

The clusters were then observed daily or as close to daily as possible to determine the date of hatch. Since the eggs within a single cluster hatch at different times, generally proceeding from the middle of the egg mass outwards, the date at which 50% of the eggs had hatched was chosen as the standard for comparison. Measurements of all hatching times revealed a time lag of 1.1 days from 10% to 50% hatching and 1.2 days from 50% to 90% hatching ($n=37$), so the time window in which 50% were recorded as hatching was small in comparison to the total development times of approximately 29 days. Of the 57 clusters so manipulated, 44 were used for the subsequent analysis. Those eliminated included 6 egg masses that were consumed by browsers and 7 on leaves that, after manipulation, changed direction extensively due to slippage or further shrub growth and thus did not fall continuously within one of the two chosen developmental regimes.

Results

Observations

In both 1979 and 1980 eggs were found more frequently on leaves which intercept morning sun than on those which are parallel to it (Fig. 1). The distributions from each year are significantly non-random as verified by Rayleigh's Test (Zar 1974) (1980: $z=21.50$, $n=235$, $p<0.001$; 1979: $z=20.09$, $n=212$, $p<0.001$), and there is no significant difference between the mean angles for the two years as given in Table 1 (Watson-Williams Test, $F=0.523$, $df=1{,}445$, $p>0.50$). The leaves themselves display no preferential compass orientation. *L. involucrata* has opposite leaves on mostly vertical stems, so for each leaf intercepting the sun, the opposite leaf of that pair is more or less parallel to the sun's rays. Because the leaf arrangement is decussate, apical and subapical leaves provide the butterflies with a wide choice of leaf orientations from which to choose. One may therefore conclude that *E. gillettii* chooses oviposition sites such that the eggs face roughly 325° from true north, that is, on leaves that intercept morning sun.

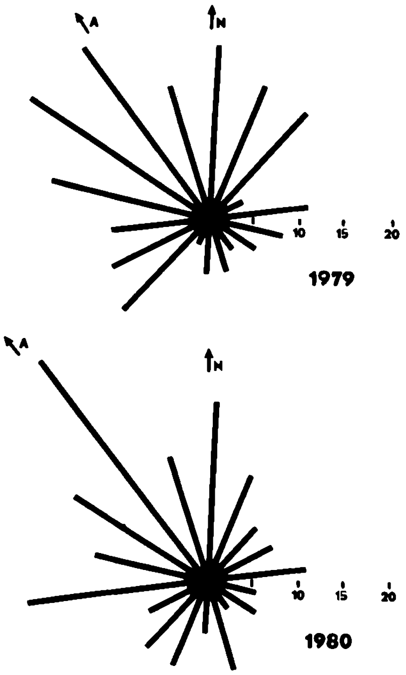

Fig. 1. Orientation of egg clusters. The number of clusters facing each compass direction is shown, as grouped into 20° sectors. Sample sizes were 212 in 1979 and 235 in 1980. North is designated by N and the mean angle for each year by A

Table 1. Mean angles of egg clusters. "Multiple" clusters are those from leaves with more than one cluster per leaf

Egg clusters	Mean angle (°)	Angular deviation (°)	*n*
1980 all[a]	319.4[c]	88.6	235
multiple[b]	309.0	86.2	96
single[b]	327.4	89.5	139
1979 all[a]	326.0[c]	88.0	212
multiple[b]	334.5	82.5	96
single[b]	317.3	92.0	116
Experimental			
lvs perpendicular[d]	329.3	28.5	22
lvs parallel[d]	141.8	55.1	22

[a] No difference between years, $p>0.50$, Watson-Williams Test

[b] No difference between single and multiple clusters, both years, $p>0.10$, Watson-Williams Test

[c] 95% confidence interval is ±17° (Batschelet 1972)

[d] Aspect of surface projection

Many of the leaves have more than one egg cluster, with a mean of 1.37 clusters per leaf. The congeneric *E. phaeton* also groups egg masses together on a single leaf (Stamp 1981). As a test of whether the distribution of clusters on leaves is random or not, I compared the number of leaves with different numbers of clusters to a Poisson distribution (Table 2). The results show that egg masses occurred together more often than random; instead of avoiding leaves that already have eggs, a female is more likely to oviposit where another cluster can be found. Although positive egg load assessment remains a possibility, the mechanism for such grouping of clusters is likely to be that certain leaves are preferred for oviposition much more than others. A truncated Poisson is used as the standard in this comparison because the number of available leaves without an egg mass is unknown due to the impossibility of judging whether or not a certain leaf would be "acceptable" to a butterfly.

If one then assumes that leaves with multiple egg masses are better oviposition sites than those with only one, a comparison of leaves with single and multiple clusters can further confirm the choices a female makes when choosing where to oviposit. First of all, as one would expect (Table 1), the mean angle of leaves with one egg mass is not significantly different from that of leaves with more than one (Watson-Williams Test. 1979: $F = 1.68$, $df = 1{,}210$, $p > 0.10$; 1980: $F = 2.06$, $df = 1{,}233$, $p > 0.10$). The angular deviations are lower for leaves with multiple clusters, however, implying that the better oviposition sites deviate less from an aspect of 325°.

The data reveal additional aspects of female preferences as well. Approximately 51% of the egg clusters from both years combined were found on apical leaves, with progressively lower percentages for leaf pairs farther down the stem (Table 3). The eggs are therefore on leaves in the least shady locations. Making a similar comparison between leaves with one or more than one egg mass, the better oviposition sites again appear to be the highest leaves (Table 3).

Measurements of leaf temperatures demonstrate that eggs on the leaves most commonly chosen by the butterflies are in warmer locations than if they were oviposited on leaves of other orientations. Although leaves parallel to sunlight are warmer than ambient temperatures by several degrees, leaves perpendicular to sunlight average 1.5° C ($n = 79$) warmer than those parallel to the sun's rays.

Experiments

The experimental manipulations demonstrate that orientation of the egg mass is an important factor in the developmental rate of the eggs. Eggs on leaves which intercept morning sun hatched significantly faster than those on leaves parallel to sunlight (normal approximation, Mann-Whitney Test, $t = 3.37$, $df = \infty$, $p < 0.001$), with a difference of 6.1 days (Table 4). Because those eggs oviposited late in the flight period are apt to experience colder weather as the growing season passes and thus take longer to hatch, comparisons of developmental times from eggs laid on different dates could increase the variance enough to obscure any significant thermal effect. A linear regression of developmental time against oviposition date gave a non-significant relationship, however, for eggs oviposited in the first half of the flight period ($F = 2.79$, $df = 1{,}49$, $p > 0.10$). It was therefore judged acceptable to ignore any effect of date on hatching times of the experimental clusters, all of which were oviposited in that initial time span. The thermal advantage described here is apt to be even more important to eggs oviposited later on.

Table 2. The number of leaves with different numbers of egg clusters. The data were compared to a truncated Poisson distribution, with $\bar{x} = 1.373$

# clusters on leaf	# leaves observed	# leaves expected[a]	% clusters
1	255	233.06	55.9
2	49	78.35	21.5
3	18	17.60	11.8
4	5	2.99	4.4
5	1 }10	0.33 }3.35	1.1
6	4	0.03	5.3
# leaves	332		100.0
# clusters	456		

[a] chi-square $= 26.27$, $df = 3$, $p < 0.001$

Table 3. Distribution of egg clusters on different pairs of leaves. The pairs were numbered from the apex of each growing stem; the newest apical leaves less than one half the length of mature leaves, none of which had eggs attached, were excluded. As in Table 1, "multiple" refers to those leaves with more than one cluster

Leaf pair	all clusters		multiple		single	
	#	%	#	%	#	%
first	231	51.0	111	58.4	120	45.6
second	164	36.2	56	29.5	108	41.1
third	56	12.4	23	12.1	33	12.5
fourth	2	0.4	0	0.0	2	0.8
	453		190		263	

Table 4. Experimental hatching times

Experimental group	$\bar{x}$ (days)	s.d.	n
leaves perpendicular	26.7[a]	3.6	22
leaves parallel	32.8[a]	6.4	22

[a] $p < 0.001$, Mann-Whitney Test

Though the hatching times are suggestive of this relationship, not enough egg masses hatched before the field season ended to make the comparison statistically. The significance of delayed hatching will be considered later.

Though all the egg clusters were manipulated initially to face 325° or 145°, subsequent slippage or growth of the shrubs somewhat altered the orientation of the leaves. When measured just before hatching, however, the mean angles were very close to the intended angles (Table 1) for the experimental clusters. It should be noted, however, that the angular deviation was nearly twice as large in the parallel group (Table 1) because the butterflies tend to choose leaves perpendicular to the sun; thus, greater twisting of the shrubs was necessary to change an egg mass to a parallel orientation than to a perpendicular one. The stems may have then slipped more from the parallel orientations or responded to greater twisting with greater growth.

The path of the sun across the sky was measured toward the end of the flight period to determine the time of day when sunlight was directly perpendicular to the leaves preferentially chosen for oviposition, that is, when the sun's azimuth was 145°. Remarkably enough, that time was approximately 1145 MST, the time that most oviposition occurred (Fig. 2). Be-

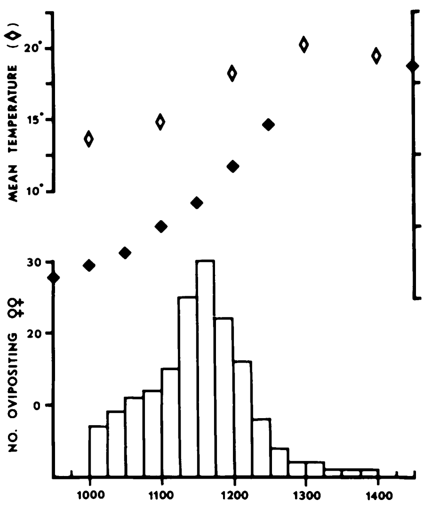

Fig. 2. Daily patterns in the frequency of oviposition and in factors which affect oviposition. The number of ovipositing females is summed for each 15 minute span across the entire flight period, and the hourly temperatures shown are the mean values for the same period. The sun's orientation was measured at the end of July. Local noon occurs at 1218 MST

cause the study site is several degrees west of the center of the time zone, 1145 MST is 1125 local time, which is measured so that local noon occurs when the sun is at its local zenith.

Discussion

It is clear from the observational data that *E. gillettii* oviposits primarily on the lower surface of those leaves that face the southeast, and that leaves which intercept morning sun are warmer than those parallel to sunlight. It is equally clear from the experimental results that oviposition on leaves with the preferred orientation results in a significant developmental advantage to the larvae that hatch from those eggs. A similar effect has been observed in the fall cankerworm *Alsophila pometaria* (Schneider 1978; Mitter et al. 1979), which lays its eggs on tree trunks; those eggs facing south break diapause and hatch before those facing more northerly directions. Again, the thermal regime of the oviposition site is an important factor in development. The effect is not limited to insects since Mosher and White (1976) have shown that golden eagle nests in northern latitudes are oriented so as to intercept and be warmed by sunlight.

There are other clues to how important the oviposition site may be. Females often spend 30 to 60 minutes searching leaves of the same shrub before finally settling and ovipositing. Figure 3a shows the general appearance of egg clusters in the field: several clusters grouped together on a single leaf, that leaf being the highest on the stem and the one which faces southeast. Those clusters which were found in mostly shady areas took much longer to hatch than average, often 40 to 45 days, again indicating the significance of the sun.

Warmth in the morning is important because of the diel thermal cycle. Mornings are cold in the study area, with the daily minimum temperature averaging 4° C in July and 1° C in August. The sky is usually clear in the mornings, but as is common in mountainous areas, the afternoons become partly or entirely cloudy. Afternoon temperatures remain high, dipping only slightly in cloudy periods. Thus, it is during the cool, clear mornings when a thermal advantage may be derived from sunlight.

The significance of accelerated development lies in its influence on fitness, and clues to such effects may be seen by examining the relationship of the butterfly's life history to the seasonal climatic cycle. The population of *E. gillettii* studied here flies in July, and the eggs hatch from early August on into September; early instar larvae feed until diapausing in the second instar. Since the first ephemeral snow falls around the first of September and heavy snows begin later that month, the eggs and larvae are quickly subjected to the beginning of winter. The first fall freeze usually occurs in the middle of July, and $-5°$ C is reached around the middle of August (U.S. NOAA 1979), which again indicates the shortness of the growing season.

There are three lines of evidence which suggest a selective advantage for reduced time in development. Eggs oviposited late in the flight period may require more than 40 days to hatch because of lower temperatures, and many do not hatch until well into September, when the snow begins to fall. Some may never hatch. Secondly, *L. involucrata* sheds its leaves in September, resulting in disappearing larval food before all eggs have hatched or all larvae have reached diapause. Finally, unusually small individuals are to be found in communal webs of diapausing larvae. Though most of its congeners diapause in the fourth instar, *E. gillettii* diapauses in the second instar.

The evidence, then, is strong that accelerated development increases fitness by giving the larvae enough time to feed and reach diapause before winter. It is unknown whether mortality due to the onset of winter varies from year to year. The measurement of survivorship from egg clusters in the two experimental orientations has proven difficult for two reasons: the larvae from different clusters mix in the communal webs, and some of the larvae may diapause away from the webs. Unlike its congener *E. phaeton* (Bowers 1978), most, if not all, larvae remain in the webs, however.

The choice of certain leaves as oviposition sites may benefit the females as well as the resultant larvae. When oviposition occurs on the back of sunlit leaves, a female remains in shadow (Fig. 3b) and thus better concealed from predators, parasitoids, and courting males. *E. gillettii* is a conspicous butterfly in appearance; it feeds and oviposits with the wings open, but the bright red-orange markings are much less apparent on a female in shade. Although dangers to an ovipositing female may still exist, my observations revealed no apparent dangers that could be avoided by choosing leaves with specific orientations. Even though females may gain some benefit from choosing southeast facing leaves, such an advantage would be completely independent from the thermal benefit derived by larvae, and the two selective forces could work in conjuction. A mechanism that would yield both the confirmed advantage for larvae and a postulated advantage for adults is for the females to choose oviposition sites on the shady side of sunlit leaves; the best indication that they may do this is the relationship between times of maximal oviposition and the sun's azimuth (Fig. 2).

Whatever the proximal mechanism, movement of the sun across the sky should alter the leaf orientation preferred for oviposition as the time of day advances. Change in the sun's azimuth should produce variance in the observed mean angles, and though the mean angles are constant from year to year, there is high angular deviation in the data for each year. Oviposition begins in earnest after 1000 MST, peaks between 1100 and 1200, and falls rapidly in the early afternoon; the sector subtended by the sun during most oviposition therefore ranges from approximately 100° to 190° (Fig. 2). About half of all egg masses were observed to be opposite that quadrant, and the sun's azimuth at the height of oviposition was 145°, directly opposite

Fig. 3. **a** Apical pair of leaves, with four egg clusters on the leaf perpendicular to sunlight and no eggs on the opposite leaf.
b Female in shadow while ovipositing on a leaf perpendicular to sunlight

the mean angle for all egg masses. Later in the flight season, oviposition should be concentrated in time between 1100 and 1200 because of reduced insolation and lower daily temperatures, thereby reducing the variance in orientation of leaves chosen as oviposition sites.

The results of this study demonstrate some aspects of how female *E. gillettii* choose oviposition sites. It is clear that the developmental rate of the eggs is reduced by the choices the females make, and likely that individual fitness is thereby increased. Similar patterns may obtain for other organisms in cool climates.

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