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THE EFFECTS OF UNDERSTORY VEGETATION ON THE SURVIVAL OF OVERWINTERING MONARCH BUTTERFLIES, (*DANAUS PLEXIPPUS* L.) IN MEXICO

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RESUMEN

Para determinar el efecto de la vegetación del sotobosque sobre la supervivencia de las mariposas monarca en el Eje Volcánico Transversal en México, se expusieron mariposas a pernoctar bajo condiciones ambientales con y sin la protección del sotobosque. Las mariposas privadas del sotobosque sufrieron significativamente más daño que la mariposas expuestas en parcelas con sotobosque. Las mariposas expuestas en parcelas desnudas también soportaron temperaturas mínimas más frías y acumularon más escarcha y rocío que las que estaban protegidas por el sotobosque. El análisis estadístico sugiere que la temperatura es el factor primario en la protección que brinda el sotobosque. La reducción en la acumulación de escarcha y rocío también puede haber contribuido a la supervivencia de las monarcas, pero esto requiere mayor investigación. Bajo las condiciones naturales del Eje Volcánico Transversal, se espera que la influencia del sotobosque sea especialmente importante después de períodos de tormenta y vientos fuertes cuando muchas mariposas son separadas de sus agrupaciones y se deslizan hacia el suelo en áreas clareadas o en pequeños claros. Además de proveer condiciones más cálidas y suelo más seco que en áreas desprovistas de vegetación, el sotobosque proporciona estructuras sobre las cuales las mariposas pueden trepar a posicio-

nes que ofrecen mayor seguridad contra la depredación por ratones y que son más secas que el suelo. Ya sea que las mariposas trepen a la vegetación o permanezcan en el suelo, la presencia del sotobosque aumenta la probabilidad de que las mariposas que sean separadas de sus agrupaciones sobrevivan hasta que el clima sea más cálido y puedan regresar a sus agrupaciones en lo alto de los árboles.

ABSTRACT

To determine the effect of understory vegetation on the survival of Monarch butterflies in Mexico's Transvolcanic Belt, Monarchs were exposed overnight to ambient conditions with and without understory protection. Butterflies deprived of understory suffered significantly more injury than butterflies exposed in plots with understory. Butterflies exposed in bare plots also experienced significantly colder minimum temperatures and accumulated more frost and dew than those protected by the understory. Statistical analysis suggests that temperature was the primary factor in the protection afforded by the understory. The reduction of frost and dew accumulation also may have contributed to Monarch survival, but this requires further investigation. Under natural conditions occurring in Mexico's Transvolcanic Belt the influence of the understory is expected to be especially important after periods of stormy weather and high winds when many butterflies are dislodged from their clusters and glide down and land in thinned areas or small clearings. In addition to providing warmer and drier ground conditions than in areas devoid of vegetation, the understory provides structures upon which the butterflies may crawl to positions which are safer from mouse predation and are warmer and drier than those on the ground. Whether they crawl up onto vegetation or remain directly on the ground, the presence of understory increases the likelihood that dislodged butterflies will survive until warm weather returns when they can fly back to their clusters high in the trees.

INTRODUCTION

Each autumn Monarch butterflies (*Danaus plexippus* L.) migrate from their breeding grounds in the eastern United States and Canada to a few locations in the Transvolcanic Belt of Mexico (Urquhart and Urquhart, 1976). On branches and trunks of trees of the mountainous forests of this zone they form densely packed colonies covering areas ranging from a few tenths of a hectare to over 5 hectares (Calvert and Brower, in press and Calvert, unpubl. obs.). Solar influx and nighttime radiational eflux are extreme during the butterflies' overwintering tenure due to the high elevation, low latitude, and seasonally low levels of airborne moisture (Calvert *et al.*, 1982). Within clearings in the forest, nighttime temperatures characteristically drop to freezing, and on clear or partly cloudy days temperatures may rise to 20-25 C (Calvert and Brower, in press). When temperatures fall 5 C below zero within the forests, as ocassionally happens when cold air masses impact the area, many millions of Monarch butterflies perish (Calvert *et al.*, 1983). Many others may be killed because warm daytime temperatures cause them to metabolize limited lipid reserves before the spring when they can be replenished at local nectar sources (Calvert and Brower, in press). Local forests are extremely important to the survival of the butterflies because they impede the escape of heat at night and reflect some of the incident solar energy during the day, thereby diminishing temperature and humidity extremes within and under their canopies (Calvert and Brower, 1981; Calvert, *et al.*, 1982). When thinned by lumbering, forests lose some of their ability to hold heat at night and reflect it during the day. Their capacity to protect the butterflies is, therefore, diminished (Calvert *et al.*, 1982).

Currently steps are being taken to protect the overwintering populations of Monarch butterflies in Mexico by the establishment of parks or forest reserves in their overwintering areas. One proposal envisions a managed forest where some lumbering would be permitted. In addition to the removal of trees which disrupts the forest's relatively stable, moist warm habitat (Calvert, *et al.*, 1982), logging can have a pronounced effect on understory. Even selective logging can temporarily destroy large areas of understory where trees are felled and logs are transported to trucks. In the long term, logging may dramatically increase understory biomass by opening the canopy thus permitting more light to reach the ground. Increased tourism within butterfly colonies may also result in understory destruction by trampling of vegetation. In view of our present ignorance about the importance of understory to overwintering Monarch butterflies, we initiated this study to determine how forest understory alone affects Monarch survival.

Forest and understory

At 3000 m elevation the forests of Mexico's Transvolcanic Belt are mixed coniferous species dominated by the "oyamel" fir, *Abies religiosa* H.B.K. (Urquhart and Urquhart, 1976; Brower *et*

al., 1977). The community also includes other species such as *Pinus pseudostrobus* Lindl., *Quercus* spp. and *Cupressus lindleyi* Krotsch. Wet canyon bottoms within the *Abies* forests contain species in the genera *Buddleia, Prunus,* and *Alnus.* Occasional specimens of *Salix* are found scattered through the forest (Calvert and Brower, in press; Rzedowski, 1978).

A well developed understory is usually present, especially in areas where the canopy has been thinned by recent logging or diminished by fires. The most conspicuous components are tall (up to 4 m) woody species including the composites, *Senecio angulifolius* D.C., *S. barba-Johannis* D.C., *Eupatorium mairetianum* D.C. and *E. patzcuarense* H.B.K. Non-composites present are *Cestrum anagyris* Dun., *Salvia elegans* Vahl. and *S. cardinalis* H.B.K. Ground cover includes *Acaena elongata* L., *Alchemilla procumbens* Rose. and a lush carpet of mosses including species in the genera *Thuidium* and *Mnium* (Calvert and Brower, in press). In recently burned areas *Lupinus* spp. are especially abundant.

METHODS

While winter temperatures in the forests of the Transvolcanic Belt seldom fall into the lethal range for the Monarch butterfly (<–2 C), in nearby clearings nighttime minima often fall below –2 C. (Calvert *et al.*, 1982). To obtain meteorological conditions in the lethal range, we exposed Monarch butterflies overnight in several large clearings located at approximately 3000 m in the Sierra Chincua overwintering area (originally designated Site Alpha, Calvert and Brower, in press) above Angangueo, Michoacán, during two periods at the end of January and February, 1984. Groups of 20 or 30 butterflies containing equal numbers of both sexes were placed in two 2.5 m x 2.5 m plots, one covered by understory vegetation and the other bare. Understory plots were constructed of fresh stems and leaves of *Senecio angulifolius* or *S. barba-Johannis* cut to 1-2 m lengths from nearby forests and placed 6 plants per row in 6 rows so that each plant was ca. 50 cm from its neighbor (Fig. 1). These plots approximated the composition and density of large understory species in many areas of forest where monarchs have formed overwintering colonies. The bare plots, located one meter from the understory plots, consisted of short (grazed) grass only. All experiments

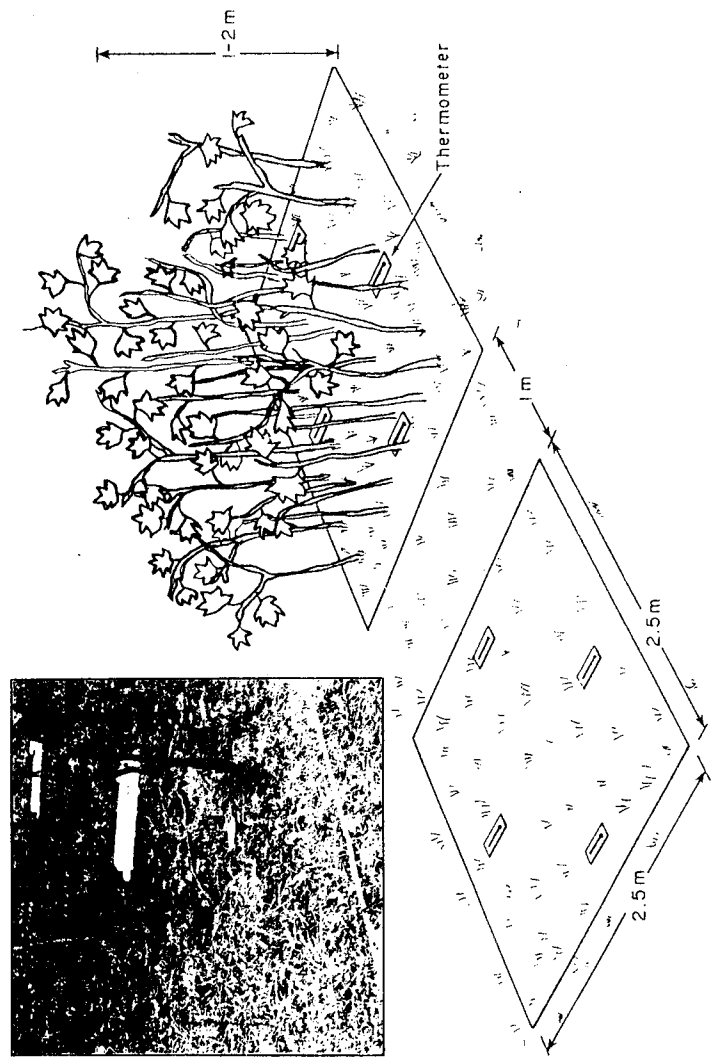

Figure 1.

The experimental plots. The understory plot is constructed of fresh-cut stems of *Senecio angulifolius* or *S. barba-Johannis* placed in holes in the ground. The control plot is bare grass. Three to four thermometers are scattered in each plot.

were carried out in the centers of clearings to minimize the influence of the forest (see Geiger, 1965).

Each group of butterflies was divided into subgroups by sex, and each subgroup was weighed. The subgroups were recombined, and the individual butterflies were placed randomly on the ground in the plots between 8 and 10 PM when temperatures were too cold for them to fly. Early the following morning, while the plots were still in the shade, the butterflies from each plot were collected by sex, the subgroups were reweighed, and the length of the left forewing of each individual was measured. Butterflies were not included in the morning tally if they had been preyed upon or had crawled up off the ground into the understory. Later in the morning, after allowing a minimum of 30 minutes in sunlight to warm, the Monarchs were released one at a time to assess each individual's ability to fly. Butterflies were classified as "normal" if they flew off exhibiting the usual escape behavior, "flight impaired" if they flew but landed within 10 m, "moribund" if they dropped to the ground without any attempt to fly, and "dead" if they failed to move after we gently blew on them. For the purpose of analysis and discussion, some of these categories were combined. All butterflies that failed to fly off normally were considered to be "injured". The category "injured" includes those classified as "dead".

A Pesola 50 g scale accurate to 0.1 g was used to weigh the butterfly groups. Three or four max-min thermometers were positioned on the ground in each plot to record nightly minimum temperatures. The experiment was repeated 7 nights, 3 in January and 4 in February. The butterflies were not weighed on the first of the seven nights.

The statistical tests employed are described in detail in Siegel (1956; Fisher's exact test) and in Sokal and Rohlf (1969; correlation regression and Wilcoxon's signed rank test). Finney (1952) described the use of probit transformations.

RESULTS

Butterflies exposed overnight in plots with understory suffered much less injury than butterflies in bare control plots (Table 1). For all nights, an average of 9.6% of the butterflies from plots with understory were dead or moribund the following morning compared

Table 1
Mortality and injury to monarch butterflies after overnight exposure with and without understory.

		With Understory			Without Understory			
Date	Number & Sex*	Ave. min. temp.	Dead or moribund/ Flight impaired	Normal	Ave. min. temp.	Dead or moribund/ Flight impaired	Normal	Prob.
Jan 28/29		−1.8			−4.2			
	10 F		0/0	10		7/1	1	
	10 M		0/0	9		8/1	1	
Total			0	19		17	2	<.001
Jan 29/30		+0.5			+0.8			
	15 F		0/0	10		0/0	15	
	15 M		0/0	13		0/0	15	
Total			0	23		0	30	N.S.
Jan 30/31		−1.0			−2.5			
	15 F		0/0	12		3/4	7	
	15 M		0/1	9		5/5	5	
Total			1	21		17	12	<.001
Feb 23/24		−0.6			−2.1			
	15 F		0/0	15		0/2	13	
	15 M		0/1	14		0/5	10	
Total			1	29		7	23	<.025
Jan 24/25		−3.5			−5.2			
	15 F		9/3	3		15/0	0	
	15 M		8/0	7		12/2	0	
Total			20	10		29	0	<.001
Feb 25/26		+1.3			+0.2			
	15 F		0/0	13		0/0	14	
	15 M		0/0	10		0/1	14	
Total			0	23		1	28	N.S.
Feb 26/27		−1.6			−3.7			
	15 F		0/0	15		6/1	8	
	15 M		0/1	14		4/0	11	
Total			1	29		11	19	<.005
All dates		−0.96			−2.39			
	Females		9/3	78		31/8	58	
	Males		8/3	76		29/14	56	
Total			23	154		82	114	

* Not all butterflies were found the following morning (see text).
\+ Fisher's Exact Test.

to 30.6% of those from bare plots. An average of 87.0% of butterflies from the understory plots flew off normally the following morning while only 58.2% of those from the bare plots did so. Males and females did not differ significantly with regard to injury within any plot, during any night, for either treatment or for all nights combined (injured/normal: all males 54/132, all females 51/136; $p > 0.05$, Fisher's exact test, Table 1), so data for both sexes were combined for the analysis below. The most dramatic difference occurred on the night of Jan. 28/29 when all 19 of the butterflies in the understory plot flew off normally, compared to only 2 of 19 butterflies in the bare plot (injured/normal: understory 0/19, no understory 17/2; $p < 0.001$, Fisher's exact test, Table 1). On the two nights, when temperatures did not drop below freezing, no mortality occurred and only one butterfly (from the bare plot on Feb. 25/26) failed to fly off normally in the morning.

On all mornings following exposure, some butterflies which had been placed in the plots the night before could not be found. For all nights combined, only 4 butterflies were missing from bare plots, but 23 were missing from the understory plots (see Table 1). The greater loss of butterflies from undestory plots was most likely due to butterflies crawling up onto understory as only a few butterfly remains due to predation were found near the plots and the greatest losses occurred on the warmest nights when butterflies were best able to crawl.

Butterflies exposed overnight in plots with understory experienced minimum temperatures that averaged 1.43 C warmer then the minimum temperatures experienced by butterflies exposed in plots without understory ($n = 7$ nights, $p<0.01$, Wilcoxon's signed rank test; Table 1). The largest differences between plots occurred on the coldest nights. On the three coldest nights, the minimum temperatures in the plot with understory averaged 2.07 C warmer than the plot without understory. For all nights, the temperature difference between the plots (ave. min. temperature with understory–ave. min. temperature without understory) was negatively correlated with the (ave. min.) temperature of the bare, control plot ($n = 7$ nights, $r = -0.83$, $p<0.05$; Fig. 2).

During most nights copious frost occurred in all areas exposed to the night sky. Frost always ceased at the edge of the forest and usually ceased at the edge of the understory plot (Fig. 1, inset). Butterflies exposed in both plots tended to gain weight overnight due to accumulation of frost or dew (Table 2). Weights were recorded for six of seven nights and are reported below as weight gained per butterfly. Dif-

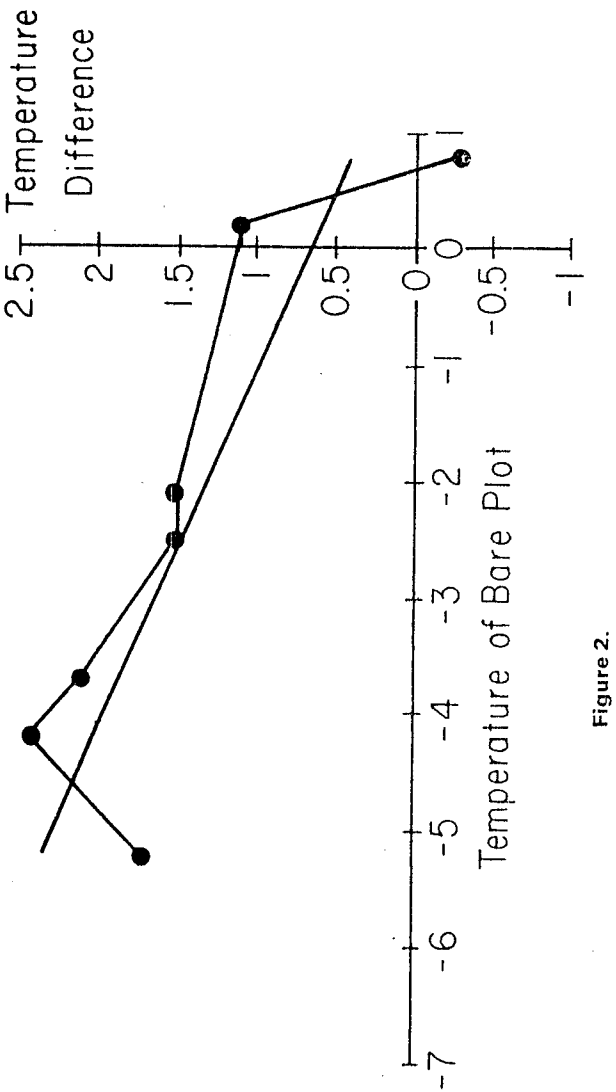

Figure 2.

Temperature difference between the understory and control plots vs. temperature of bare control plot. The differences between plots are greatest at the coldest temperatures.

Table 2

Differences in overnight weight gain (g) of monarch butterflies exposed with and without understory vegetation. Weight gains are due to accumulations of water of dew or frost.

			With Understory				Without Understory			
Date	Sex	Weather	Evening wt.	Morning wt.	Wt. gain	% gain	Evening wt.	Morning wt.	Wt. gain	% gain
					1984					
Jan 29/30	F	Cloudy	0.54	0.80	0.26	48	0.54	0.79	0.25	46
	M		0.56	0.75	0.19	34	0.53	0.71	0.18	34
Jan 30/31	F	Clear	0.55	0.67	0.12	22	0.52	0.77	0.25	48
	M		0.56	0.72	0.16	29	0.57	0.76	0.19	33
Feb 23/24	F	Clear &	0.46	0.48	0.02	4	0.48	0.55	0.07	15
	M	windy	0.49	0.52	0.03	6	0.50	0.61	0.11	22
Feb 24/25	F	Clear &	0.48	0.51	0.03	6	0.49	0.63	0.14	29
	M	windy	0.52	0.55	0.03	6	0.47	0.63	0.16	34
Feb 25/26	F	Clear &	0.50	0.49	−0.01	−2	0.46	0.50	0.04	7
	M	very windy	0.50	0.54	0.04	8	0.52	0.52	0.00	0
Feb 26/27	F	Clear &	0.49	0.49	0.00	0	0.51	0.51	0.00	0
	M	calm	0.51	0.50	−0.01	−2	0.54	0.53	−0.01	−2
Average	F		0.503	0.573	0.070	13.9	0.520	0.625	0.125	25.0
	M		0.523	0.597	0.074	14.1	0.522	0.627	0.105	20.1

ferences or lack of differences in weight gained between groups cannot be attributed to size differences since no differences in forewing lenghts were found between any groups of butterflies (Wilcoxon's signed rank tests). No significant difference in weight-gain between sexes was observed ($n = 12$ plots or $n = 6$ nights, Wilcoxon's signed rank test), so the data for males and females for each night's plots were combined for analysis. Butterflies in the plots without understory gained 58% more weight overnight than the butterflies from the plots with understory (with understory $\bar{x} = 115$ mg, without understory $\bar{x} = 72$ mg) and this difference was significant ($n = 6$ nights, Wilcoxon's signed rank test, $p<0.05$). Average weight gain was not correlated significantly with average minimum temperature ($n = 12$ plots, $r = 0.09$), but differences in weight gain between plots with and without understory were negatively correlated with average minimum temperature in the bare plot ($n = 6$ nights, $r = -0.73$, $p<0.05$).

Figure 3 shows the percentage of injured butterflies plotted as a function of average minimum temperature. Since the usual regression techniques cannot be applied to percentages, we applied a Spearman rank correlation test and found that butterfly injury was significantly negatively correlated with average minimum temperature ($n = 14$ plots, $r_s = -0.93$, $p<0.001$). In order to analyse this relationship further, the percentages of injured butterflies were transformed into probits. The fitted line resulting from the probit analysis shown as the curve in Fig. 3. The temperature at which 50% of the butterflies are expected to be injured (effective dose 50 = ED 50) is −3.1 C. Including average weight gain as a variable in the analysis had a negligible effect and average weight gain alone was not correlated with the percentage of injury ($n = 12$ plots, $r_s = 0.04$, $p<0.05$).

DISCUSSION

In a fully mature forest stand, the lowest temperatures and, hence, the maximum deposition of dew occur in the zone of greatest nighttime radiation exchange, ie., at the level of the canopy (Geiger, 1965). Temperatures are warmer and the amount of dew deposited falls sharply at heights below the canopy compared to those at its surface or above. At night in clearings, the lowest temperature and greatest dewfall are expected to be on or near ground level for the same

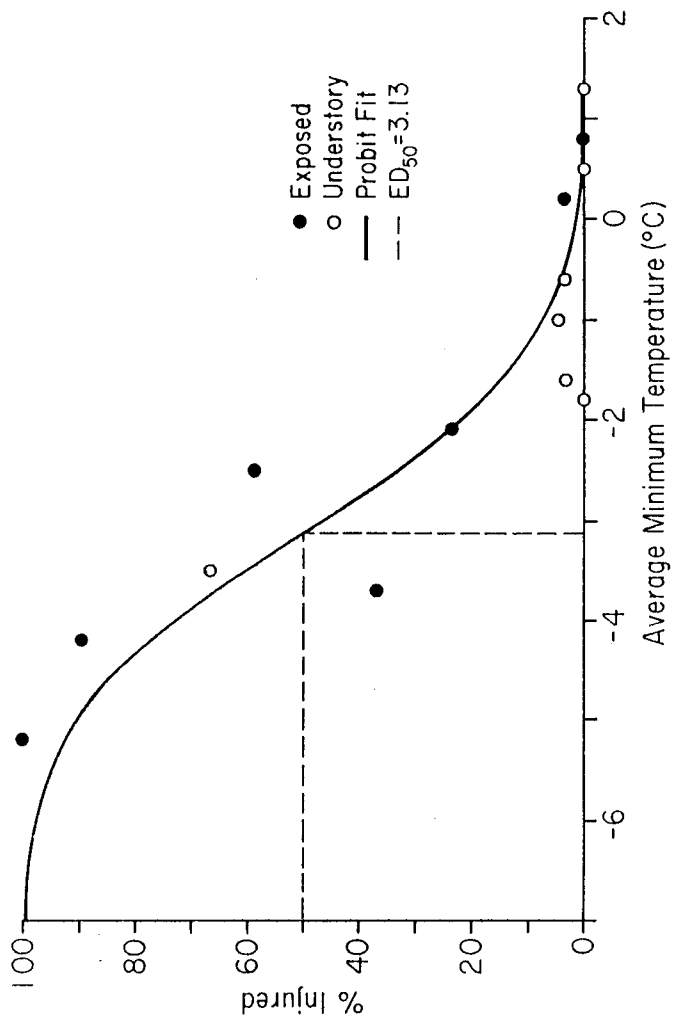

Figure 3.

The percentage of butterflies injured as a function of average minimum temperature in both understory and control plots. The temperature at which 50% of the butterflies are expected to be injured (includes those killed) is –3.1 C.

reason. The greatest dewfall and lowest temperatures in a stand of low shrubs exposed to open sky are expected to be at the level of its canopy where the greatest nighttime radiation exchange takes place. This pattern is modified when the low shrubs are understory inside a forest because temperature and humidity regimes within the understory are influenced by the forest canopy. Below the understory temperatures are warmer than in corresponding locations above open ground in nearby clearings because of the shielding effect of both the understory and the overstory canopy. Within the forest the effect of the understory on temperature and humidity is most profound in thinned areas where the effect of the overstory canopy is diminished and meteorological conditions approach those over open ground. In all cases the influence of forest and understory are superimposed on the temperature and humidity of air masses dominant in the area at the time.

Normally, overwintering monarchs are found clustered high in trees in moderate dense forests of 300-500 trees/ha (Calvert, unpubl. obs.). Butterflies are dislodged from these clusters by the physical actions of winds, the breaking of snow –and butterfly– laden branches, and the wetting effect of precipitation. Dislodged butterflies fall or glide down, catch and cling to understory vegetation, or land on the ground (Calvert and Brower, 1981). When temperatures are too cold for them to fly (below 12.7-16 C; Masters, 1965), they are trapped on the ground or on understory vegetation until they can warm themselves in the sun. When temperatures are below flight threshold but are above ca. 4 C, they may improve their situation somewhat by crawling up on understory vegetation into warmer air (Calvert and Cohen, 1983) or by shivering until their flight muscles are warm enough to fly back to their roosts (Kammer, 1970). Meanwhile they are exposed to colder and wetter conditions on or near the ground (Calvert and Brower, 1981; Calvert and Cohen, 1983).

Our experiments provide strong evidence that natural understory in the Mexico's Transvolcanic Belt aids the survival of overwintering monarchs temporarily grounded by storms and cold weather. As with the overstory, the understory protects grounded monarchs by shielding them from radiation loss to the open sky thus providing a warmer environment than that above more exposed ground. The greatest differences in temperature between plots occurred on the coldest nights suggesting that the understory protects the butterflies best when they need it the most, i.e. when it is the coldest (Fig. 2).

In natural circumstances where understory plants are generally available monarchs do not remain on the ground. Crawling up onto understory foliage affords them even more protection than that noted in these experiments where they were forced to remain on the ground. A position off the ground under an umbrella of foliage is warmer and safer than the one they left for the following reasons. At night a butterfly positioned on an understory plant will lose radiation in proportion to its temperature, but, unlike butterflies with open space above, it will recover a large portion of lost heat energy because it is in near radiation equilibrium with understory plant parts (or other butterflies) nearby which also are radiating to it. In a closed dense understory a butterfly will lose much less heat than it would if it were positioned in a more open area where there are fewer plant parts around it and more open sky above (Geiger, 1965; Calvert and Brower, 1981; Calvert and Cohen, 1983). Therefore, the understory protects the butterflies the most when they glide into thinned areas or clearings in the forest. A position on understory foliage is also likely to be safer from several species of mice which prey upon large numbers of monarchs in the overwintering colonies (J. Glendinning, unpubl. obs.).

In addition to helping retain heat at night, the understory acts to conserve moisture during the day –a factor of critical importance to the maintenance of Monarch water balance (Calvert and Brower, in press). Although not as effective as the overstory canopy, the understory acts in the same manner by reflecting incident radiation away from the forest floor thereby allaying soil dessication.

Because insects with frozen moisture on their exoskeletons are more susceptible to internal freezing than those without moisture (Salt, 1969; Bevan and Carter, 1980), and because the amount of dew (and frost) formed depends in part on the temperature at the particular site (Geiger, 1965) factors which affect temperature will be crucial to Monarch survival. The additional shielding of the understory foliage is expected to reduce the dangers of dew and frost forming on butterflies especially in thinned areas where the shielding of the overstory is less. Although butterflies exposed in open areas were significantly heavier than those under the understory (Table 2), temperature was more closely related to injury than was surface moisture under the conditions of these experiments. The formation of dew is a complicated phenomenon and includes factors other than temperature, eg. wind speeds within a critical

range (Oke, 1978). More work is planned to elucidate the relationship between water accumulation and butterfly injury (Calvert and Hyatt, in prep.).

Although butterflies positioned beneath understory foliage are generally safer from cold temperatures than those in more exposed positions, protection is not as great as in roosting clusters higher in the canopy. Nighttime cold air drainage through the forest generally results in colder temperatures near the ground (Geiger, 1965; Calvert and Lawton, unpubl. obs.). The air in the forest canopy where butterflies normally roost is expected to be warmer than air in the understory or on the ground.

To minimize large scale mortality when cold advective air masses move into the overwintering area, Monarch butterflies need dense forest and understory to protect them from temperature extremes. The forests where they overwinter should be managed to provide as closed an overstory as is possible and a fully developed natural understory. Means to accomplish this would include prohibiting lumbering activites within areas set aside as parks or reserves and channeling tourists into established access paths so that the understory is not trampled.

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