The Effect of Rain, Snow and Freezing Temperatures on Overwintering Monarch Butterflies in Mexico

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ABSTRACT

Approximately 2.5 million monarch butterflies in an overwintering colony in Mexico were killed by a severe winter storm in January 1981. Flight testing of butterflies sampled from four locations within the colony during and after the storm gave an overview of the general flux of butterflies from clusters to the ground and back due to the storm's effects. Normally adapative behavior to avoid freezing ground temperatures, including high roosting and crawling up onto low vegetation, were only partially effective against the severe cold. Selective wetting and subsequent freezing appears to account for the mortality patterns observed in the roosting clusters.

EACH FALL TENS OF MILLIONS of monarch butterflies (*Danaus plexippus* L.) from eastern North America migrate to Mexico's transvolcanic belt (Urquhart and Urquhart 1976, Brower *et al.* 1977). Arriving in early November and leaving at the end of March, they pass the late fall and winter in this area. Within the protective canopy of high altitude forests, they aggregate in enormous numbers on trunks and branches principally of the oyamel fir, *Abies religiosa* H.B.K.

One major cause of mortality of butterflies at the overwintering sites is bird predation (Calvert *et al.* 1979, Fink and Brower 1981), as evidenced by damaged body parts or missing wings. In two of the past five overwintering seasons we observed beneath trees with dense clusters accumulations from 2 to 15 cm deep of undamaged, dead butterflies which we assumed were killed by winter storms. In January 1981, a severe winter storm impacted a major overwintering colony in the area previously designated Site Alpha (Brower *et al.* 1977). We report here the effects of this storm.

METHODS

ESTIMATES OF CUMULATIVE MORTALITY.—Cumulative butterfly mortality was estimated for December through February of the 1980–81 overwintering season. A transect with stations marked at 10-meter intervals was established through the colony center for each sample date. Cardinal azimuths were used to divide the area around each station into four quadrats. Pairs of numbers from 0 to 4 taken from a random number table were used to designate a sample plot within each quadrat for a total of four plots per station. In December and January when mortality was low plots 1 meter square were sampled; quarter-meter square plots were used in February after the storm. Apparently undamaged, dead butterflies were counted on the ground in 32 to 40 plots per transect, and averages per quarter-meter square were corrected to numbers per square meter, and then multiplied times the respective colony areas to give the total number of dead butterflies as of that date (Calvert *et al.* 1979).

MORTALITY AND IMPAIRMENT OF FLIGHT CAPACITY IN RELATION TO TEMPERATURE.—The effects of intensely cold weather on mortality and flight capacity of butterflies located in different parts of the colony were monitored for a five-week period during and after the storm. At least 50 butterflies were sampled from each of the following locations within the colony: branch clusters situated three to four meters above the ground, trunk clusters at three meters height, low vegetation 20 to 100 cm above the ground, and on the ground. Each sample was placed in a nylon-mesh cage and allowed two hours to warm in sunlight. The butterflies were then released individually and categorized as follows: dead, moribund (*i.e.*, unable to fly but showed some sign of life), flew but landed within 15 m, and flew off normally.

Taylor or PSG max-min thermometers were placed along colony transects and at various other locations within the colony to record minimum nightly temperatures at ground level.

RESULTS

On January 13, 1981, a ten-day period of unusually severe inclement weather occurred throughout a large area of the central highlands of the States of Michoacan and Mexico. The storm began with moderately cold temperatures and daily rain and hail that soaked the butterfly clusters (Table 1). Three days with snowfall commenced on the afternoon of January 17 and loaded the already rain-soaked, butterfly-laden branches with wet snow. Many butterflies were dislodged or injured when branches broke off (Fig. 1), others were buried by the snowfall,

TABLE 1. *Storm chronology and its associated effect on an overwintering colony of monarch butterflies. Total rainfall (includes melted snow) for the ten-day period beginning January 13 = 71.79 mm.*

Date	Weather	Colony minimum temperature	N of thermometers	Effect of the storm
Jan 12	Beginning of major cloud cover	—	—	
Jan 13	Cloudy, rain, hail in morning	—	—	Butterflies begin to fall from wetted clusters
Jan 14	Rain, hail	1.50	1	Butterflies continue to fall from clusters
Jan 15	Partly cloudy, no rain	1.50	1	Butterflies continue to fall, but less than previously
Jan 16	Cloudy, high winds, light rain	2.00	1	Butterflies continue to fall, but less than previously
Jan 17	Snow (3″ in clearing)	−1.00	1	Butterflies continue to fall, but less than previously
Jan 18	Rain during day, snow at night (6″ in clearing)	Thermometers buried	—	Pine and fir branches break, tens of thousands of butterflies come down with branches
Jan 19	Snow continues to early morning	Thermometers buried	—	Many butterflies buried in snow
Jan 20	Clear morning, cold	−1.40	7	Butterflies trapped in snow by frozen surface
Jan 21	Cold, heavy frost in clearing	−1.34	20	Butterflies trapped in snow by frozen surface
Jan 22	High winds, rain, hail, more snow (8″ in clearing)	−0.93	25	More branches break, more tens of thousands of butterflies come down
Jan 23	Cloudy, cold, ice storm at unsheltered locations	−0.80	25	Butterflies unable to regain clusters
Jan 24	Clears completely, extremely cold	−4.08	25	Thousands of butterflies freeze to death
Jan 25	Clear cold morning	−0.99	25	Butterflies begin to drop out of clusters
Jan 26	Clear morning, somewhat warmer	1.84	25	Many thousands drop straight from clusters

and others crawled onto nearby vegetation or higher up onto the fallen branches. A two-day period of partial clearing and sub-freezing temperatures followed. Butterflies buried or partly buried in the snow were trapped by the freezing of the snow's surface. On January 22, a second major snowstorm added more wet snow to the already soaked branches and butterfly clusters. Many more branches containing butterflies fell, several small butterfly-laden tree tops broke off, and one tree was uprooted. In the early morning of January 24, the sky cleared completely and temperatures plummeted to an average of −4.1°C in the colony with readings as low as −5.0°C at several locations (Fig. 2). A thermometer mounted on a tree 3 m above the ground registered −3.3°C.

The storm had an especially strong effect on vegetation. In addition to scores of broken branches and tree tops, many herbaceous and woody understory plant species (which later become important nectar sources) had stems and flower heads broken off, and developing flowers and setting fruits were damaged. In particular, two composites, *Stevia monardifolia* H.B.K. and *Senecio angulifolius* D.C., which were just beginning to flower before the storm, suffered frozen leaves, damaged flower buds which failed to mature, and abortive seeds. Another important nectar source, *Senecio prenanthoides* A., suffered less bud damage. In contrast, two herbaceous species, *Senecio tolucanus* D.C. and *Senecio sanguisorbae* D.C., weathered the storm as basal rosettes and flowered normally in March.

Butterflies fell or were dislodged from their clusters during the entire stormy period, and individuals continued falling out of the clusters for several weeks afterwards. Marked differences were apparent in the trajectory of fall before and after the extremely cold morning of January 24. Prior to this date and after February 8, their falling was typical of that observed in previous years: upon dislodgement, they half glided and half fell to the ground in a manner resembling uncontrolled flight. After January 24, most plummeted to the ground like inanimate objects. Except when they came down with branches, entire roosting clusters were never observed to fall. The general shape of the clusters remained unchanged, except that they looked thinned. A tarpaulin placed near trees with clusters showed many more butterflies fell during the day than night. The number falling per unit time was also markedly greater after January 24. During a 45 minute interval late in the morning of January 26 a phenomenal 88.4 butterflies/m^2/hour fell, whereas during an equivalent interval in the earlier part of the storm period the rate was only 1.1 butterflies/m^2/hour. The former group was tested for their flying ability. In a sample of 137 insects, 53 percent were dead, 34 percent moribund and

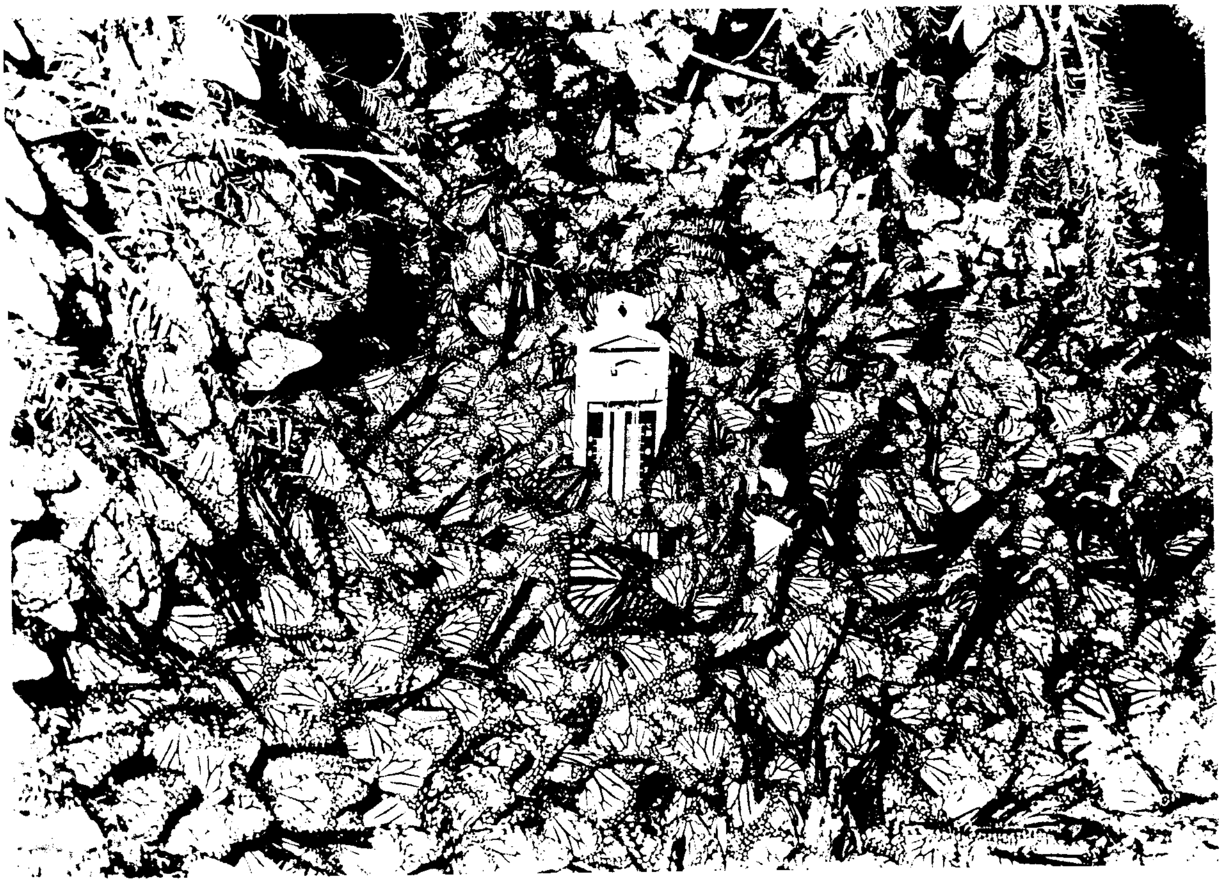

FIGURE 1. Butterflies dislodged by storm action. The accumulation of dead, moribund, flight-impaired, and normal butterflies was 13 cm deep at this location beneath a tree with thick roosting clusters. The maximum-minimum thermometer, partly obscured by the pile of butterflies, is 26.5 cm high.

4 percent flew less than 15 m; only 9 percent of the butterflies flew normally.

The effects of extreme cold weather on survivability were investigated further by monitoring flight capacity of butterflies taken from various locations within the colony for 5 weeks during and after the storm (raw data in Table 2; Figs. 3a–h). Several trends were evident. The proportion of dead butterflies in ground samples increased steadily, and conversely, the proportion of normal butterflies decreased steadily (Figs. 3h, g). Many of the changes appeared related to January 24, the day of extreme cold. For example, the percentage of dead and moribund butterflies in bough clusters rose from 0 percent, peaked at 26 percent on the cold day, January 24, then fell back to 0 percent (Fig. 3f). A similar progression was seen for the trunk clusters except that the dead and moribund butterflies peaked on January 26 and percentages of the injured were smaller (Fig. 3e). The percentage of all impaired insects (including dead and moribund) in bough clusters rose from 24 percent, peaked at 44 percent on the cold day, then fell to 1 percent by February 27 (Fig. 3d). The percentage of all impaired butterflies on the ground rose rapidly from an initial 13 to 93 percent on January 26, then more slowly to 99 percent on February 27 (Fig. 3c).

Perhaps the most informative butterfly group with respect to explaining the effect of abnormally cold weather on the colony was that resting on low vegetation. The percentage of dead insects in this group is usually 0 (Fig. 3b), because they have to be functioning normally to reach the low vegetation in the first place. But on January 24, it was so cold that even this usually effective escape behavior failed to protect them. Forty percent of these butterflies froze to death (Fig. 3b).

Interchange between the various butterfly groups was evident in these data. Both normal and storm-injured butterflies fell out of the clusters or came down with broken branches. The largest percentage of injured but-

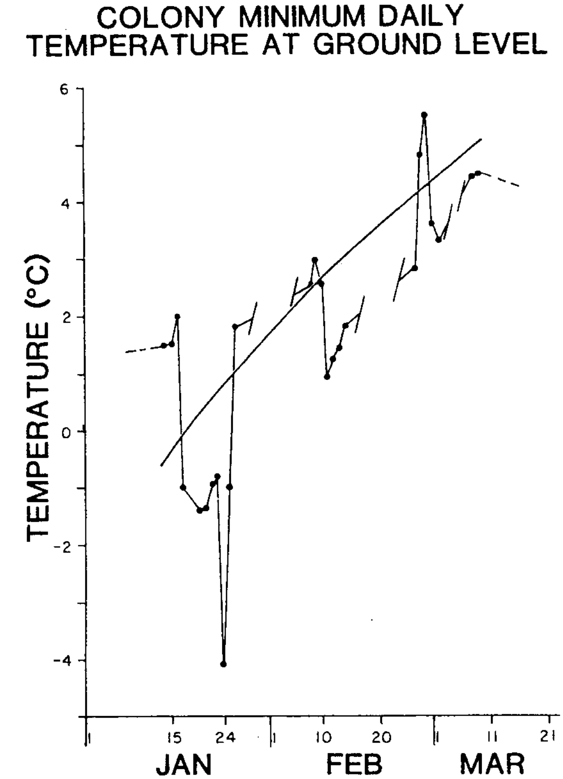

FIGURE 2. Minimum daily temperatures at ground level for an eight-week period 14 January to 11 March. After January 19 readings are an average of 7 to 25 thermometers. Before this date only one thermometer was read.

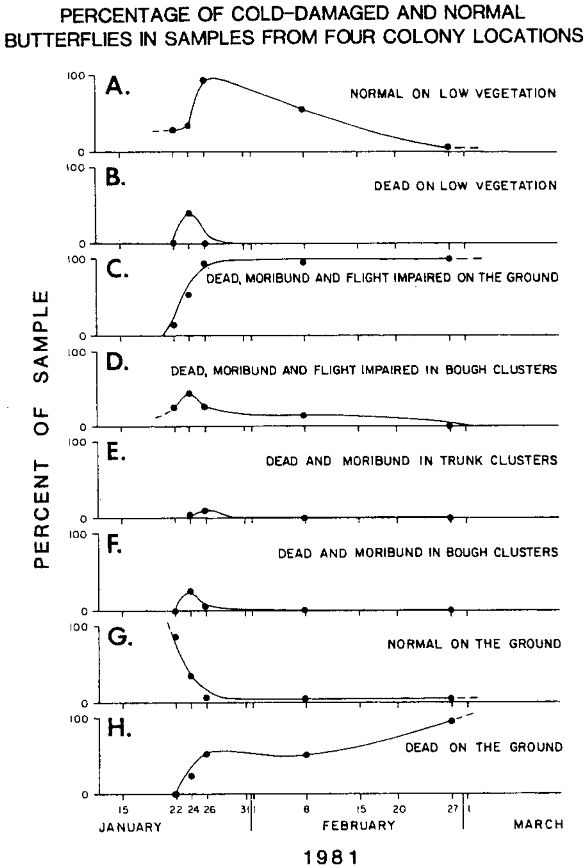

FIGURE 3. Percentage of cold-damaged and normal butterflies in samples from four colony locations; based on data in Table 2.

TABLE 2. *Numbers of butterflies killed, flight-impaired, and surviving a winter storm at Site Alpha, January–February, 1981, in 19 samples taken at four locations in the colony. Total number of butterflies flight tested = 3018.*

Location of sample	Butterfly status	Collection date				
		January 22	January 24	January 26	February 8	February 27
Bough cluster	Dead	0	3	0	0	0
	Moribund	0	26	5	0	1
	Flight impaired	24	19	15	33	2
	Normal	77	61	96	183	200
Trunk cluster	Dead	—	1	2	0	0
	Moribund	—	3	2	1	0
	Flight impaired	—	22	3	6	0
	Normal	—	91	35	146	145
Low vegetation	Dead	0	68	0	0	2
	Moribund	15	30	1	11	54
	Flight impaired	56	11	6	50	104
	Normal	29	59	90	78	14
Ground	Dead	0	81	108	162	287
	Moribund	2	13	72	107	6
	Flight impaired	19	1	10	42	9
	Normal	136	48	15	16	4

terflies appeared in the clusters after the coldest morning, January 24 (Figs. 3d–f). After this date the percentage declined as the clusters were purged of injured butterflies which fell to the ground. Correspondingly, the proportion of dead butterflies on the ground rose dramatically to 99 percent in late February as more injured insects dropped from the clusters and normal butterflies removed themselves from the ground (Figs. 3e–g). The speed at which they removed themselves from the ground was evident in the rapid decrease in the proportion of normal butterflies on the ground (Fig. 3g) and the corresponding peaking of this group on low foliage at 95 percent on January 26 (Fig. 3a). Within a few days, normal and flight-impaired (and perhaps moribund) butterflies were able to remove themselves from the dangerously cold temperatures near the ground by crawling up onto low vegetation. Because colony temperatures remained below flight threshold, these butterflies were kept from rejoining the clusters until warmer weather returned to the area, whereas moribunds and flight-impaired butterflies that had crawled up eventually died and fell back to the ground.

The total cumulative number of dead, nondamaged butterflies was monitored for three of the overwintering months (Fig. 4). The number of non-predated dead butterflies/m^2 began at a low level in December and continued at that low level into early January. It then climbed to 418 butterflies/m^2 after the storm. Estimation of the total number of butterflies killed was made by multiplying the number dead/m^2 times the colony area appropriate for that date and subtracting those that died before from those that died after the storm (Fig. 4). Approximately 2.5 million butterflies were added to those already on the ground before the storm. This storm wreaked more destruction on this colony than any whose effects we have observed in our previous 5 years' experience at these overwintering sites.

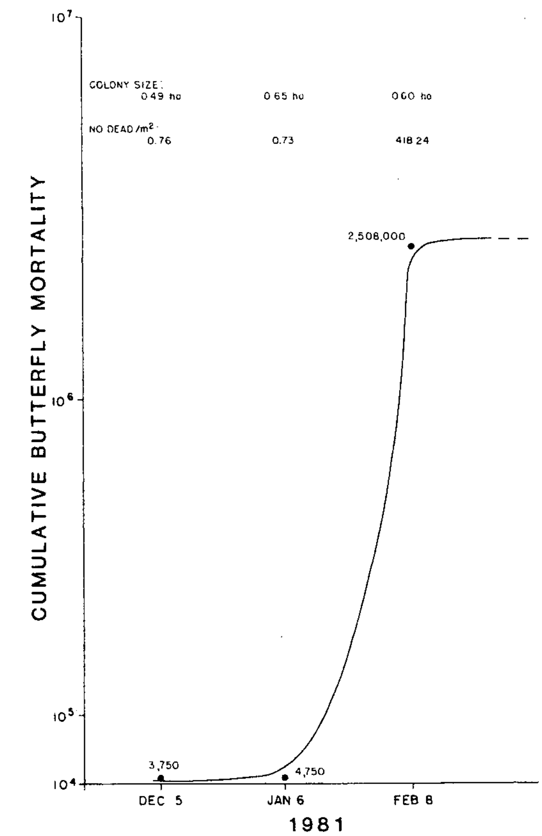

FIGURE 4. Cumulative mortality of butterflies for three months in the 1980–81 overwintering season. The number of dead/m^2 is an average of the number dead in 32–40 plots per date. The total number dead is obtained by multiplying the number dead/m^2 by the appropriate colony size.

DISCUSSION

Normally there is a constant flux of butterflies in and out of the clusters. During warm days some roosting butterflies leave and return at various times, usually in mid to late afternoon. Some of these fail to regain the clusters and land on low vegetation or the ground. At Site Alpha during the 1978–79 overwintering season, a period devoid of major storms, an average of 9.3 butterflies landed in each square meter/day and remained there overnight (Calvert, unpubl. obs.). Normally a majority of the butterflies fly off the following day when sunlight reaches them and allows them to warm to flight threshold or, as occasionally happens early and late in the season, the ambient temperature in the forest reaches flight threshold. The ten-day storm period altered this normal pattern.

The cold weather created conditions where butterflies could exit the branch and trunk clusters, but could not return. At least 2.5 million dead had accumulated on the ground by February 8. At the beginning of the 5-week period the majority of those that were down were alive; at the end of the period, 99 percent were dead (Fig. 3g, h). Some of the grounded butterflies crawled up onto low vegetation, but even this normally effective behavior (Calvert and Brower 1981) failed to protect them from the coldest weather (Fig. 3b). The eventual return of warmer weather allowed the healthy, stranded butterflies to return to the clusters, but only after a period of enhanced risk due to colder temperatures prevailing near the ground (Geiger 1965, Calvert and Brower 1981). Perhaps the greatest risk occurs after a storm breaks. Extremely cold temperatures are likely to prevail during the first clear night because cold temperatures brought in with the storm are enhanced by radiational cooling (Fig. 2, Geiger 1965). Impaired butterflies cannot return to the clusters and eventually join the dead on the colony floor. If any wind is present at all, convectional cooling would further enhance the freezing of exposed butterflies.

Our flight monitoring experiments were conducted at an optimum time to demonstrate the effects of killing-cold temperatures penetrating into the canopy and affecting clustered butterflies directly. Previously observed accumulations of apparently undamaged, dead butterflies under tree canopies (Calvert *et al.*, l.c. and unpubl. obs.) can now be attributed to freezing temperatures associated with storms.

Although 2.5 million butterflies died, the majority in the colony survived. Tens of thousands fell from the clusters, yet they fell as individuals or small groups and not in whole clusters. An intriguing question concerns the factors that determine which ones survive and which ones succumb. The differential mortality between those in branch and trunk clusters may provide a clue. Insects that have moisture frozen on their exoskeletons are much more susceptible to injury than those with dry surfaces. The greater risk is thought to occur because ice crystals penetrate the cuticle and act as nuclei for the internal freezing process to begin, whereas freezing in the absence of such nuclei cannot occur until much lower temperatures (Salt 1936, 1963; Bevan and Carter 1980). In general, butterflies in branch clusters are less shielded from wind and soaking actions of precipitation than those in trunk clusters and are therefore more likely to be wetted by precipitation. Indeed some branches that came down contained butterflies that were soaked with water. Specific location within a cluster or nearness to a protective branch may also determine the degree of wetting of a individual butterfly, and hence, the degree of injury. Since frost damage to the butterflies depends both on the degree of wetting and the lower extreme temperature experienced, the percentage of the colony that succumbs to storm conditions will be a probabilistic function of these factors, and the amount of time that they are exposed (Salt 1963). Another factor which may be involved is the extreme variability of lipid content in overwintering butterflies, which ranges from 3 to 241 mg (personal observation).

Although it is clear from this study that forest cover is not sufficient to protect all butterflies within a colony from occasional winter storms (Fig. 4), several factors probably increase their chance of surviving such a storm. The more closed the canopy, the less radiation is expected to escape to the night sky and cosmic cold, and the higher the minimum temperature is expected to be (Hansen 1937). The effect of forest cover on microclimate in these overwintering areas is under study. The density of the butterflies in the clusters *per se* may also provide some of the butterflies protection from wetting, and therefore subsequent freezing. We are in the process of evaluating relationships between cluster structure, position with respect to protective cover, degree of wetting, and butterfly survival.

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