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MASS FLIGHT RESPONSE OF OVERWINTERING MONARCH BUTTERFLIES (NYMPHALIDAE) TO CLOUD-INDUCED CHANGES IN SOLAR RADIATION INTENSITY IN MEXICO

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ABSTRACT. Seemingly enigmatic behavioral responses to sudden clouding characterize monarch butterflies in their overwintering colonies in Mexico. On sunny days throughout the overwintering season, large numbers of monarchs basking on conifer boughs within their colony repeatedly respond to periodic cloud shadow by taking flight and flying above the colony for approximately 5 minutes before reforming clusters on the boughs. Likewise, monarchs in streaming flights down an arroyo to water reverse direction and head back to their colony when shaded by a cloud. We hypothesize that both of these behaviors are physiologically triggered by rapidly lowering body temperature when solar radiation warming their bodies is obscured by a cloud. The reversal in flight direction is interpreted as an adaptation to the unpredictable duration of cloud cover which, if longer than a few minutes, would result in the butterflies' thoracic temperatures dropping below flight threshold. This could strand butterflies away from their colony for up to several days, subjecting them to freezing at night, and possibly also to greater bird predation. Within their colony, the adaptive significance of the cloud-induced behavior appears to be that it allows individual butterflies to relocate into positions on boughs that are better insulated by the forest canopy against radiant heat loss to the open sky during the night.

Additional key words: cloud-response, microclimate, thermoregulation, thermal ecology, overwintering.

Monarch butterflies, *Danaus plexippus* L., overwintering in the high mountains of the Transvolcanic Range of Mexico cannot fly until their thoracic temperatures reach 12.7–16°C (mean thermal flight threshold = 14.35°C, Masters et al. 1988). Ambient temperatures beneath the shaded forest canopy rarely exceed this flight threshold, and in one overwintering colony it was exceeded on only 2 of 46 days between 20 January and 6 March (Calvert & Brower 1986). Therefore few monarchs should be active during most of the overwintering period. However, on clear days, although the majority of butterflies remain clustered in shaded areas on the trees, hundreds of thousands sun-bask, countless others fly about above the firs in no sustained direction, while still others stream back and forth to water as far as a kilometer from the colony (Brower 1986, Calvert & Brower 1986, Masters et al. 1988). The monarchs are able to fly in the cold ambient environment because they are extremely proficient at raising their thoracic temperatures by solar basking in either direct or diffuse sunlight: in less than a minute an individual monarch can raise its body temperature from below to well above flight threshold (Kammer 1970, Douglas 1979, 1986, Casey 1988, Masters et al. 1988).

A particularly striking behavior of these sun-basking monarchs in the overwintering colonies is that when a cloud casts a shadow, the butterflies invariably fly from their perches in such large numbers that for several minutes the sky is partially darkened (Fig. 1A,B). We first noted this reaction in January 1977 (Brower et al. 1977) and have since observed it on hundreds of occasions over 16 overwintering seasons. If the cloud shadow persists for only a short time, most butterflies land and resume basking. However, if the cloud cover persists for more than about five minutes, the monarchs flutter down and land on less exposed positions of the tree boughs within the protective cover of the forest canopy (Fig. 1B). Both the sky above the colony and the original exposed basking positions become virtually clear of butterflies. Individual butterflies sometimes follow each other in undulating chains as they reform the clusters (arrow in Fig. 1B).

Over the last 16 years, we have observed that the intensity of the cloud-response appears related both to the thickness of the cloud and to the length of sunshine preceding the cloud shadow. The most intense response occurs after a long period of cloudless sunshine and when the cloud is thick. Less intense responses occur when clouds and short periods of sunshine alternate in rapid succession and when the clouds are thin so that they only partly block the radiation falling on the colony. The cloud-response involves both an increased number of butterflies flying and an increase in the tempo of sound caused by the butterflies colliding with each other and with the vegetation. For this study, we chose a situation in which a thick cloud passed over the colony after a long period of cloudless sunshine.

We also have observed repeatedly a second cloud-induced behavior that was first reported by Brower (1986). Binocular viewing from above the colony on clear days documented huge streams of monarchs flowing out of the colony and down an arroyo in search of water. When suddenly shaded by a cloud, these streaming butterflies reverse direction back towards the colony. If the cloud passes before the butterflies reach the colony, they again switch direction towards the water sources.

In this paper we present quantitative data on the monarchs' cloud-response behavior when direct sunlight radiating the basking butterflies is obscured by a passing cloud. We then provide a common hypothesis that explains the cloud-induced flight behaviors of the butterflies both within their colonies and while flying to water sources.

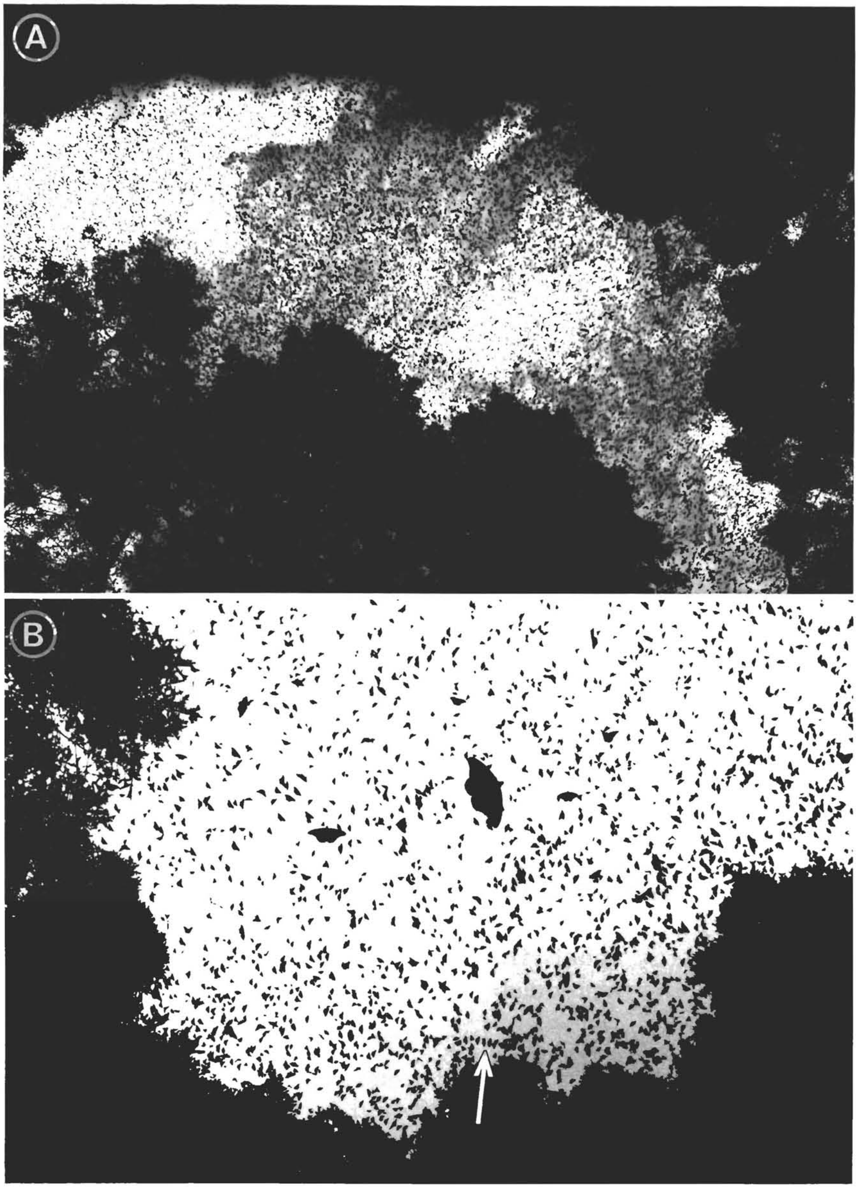

FIG. 1. Cloud-response behavior of monarch butterflies at their Sierra Chincua over-wintering site in Michoacan, Mexico. A) Wide-angle view of the sky, clouds that have just shaded the area, and the *Abies religiosa* roosting trees with several thousand flying monarchs that have been stimulated by the drop in solar radiation to fly above the tree canopy (15 March 1981; original 35 mm kodachrome by L. P. Brower). B) Within about five minutes after the appearance of the cloud, the monarchs begin to reform their clusters. Individual butterflies follow each other in undulating chains (see arrow) as they fly to the tree boughs. Original 35 mm kodachrome by W. H. Calvert.

METHODS

The overwintering colony of several hundred thousand monarchs occupied 0.54 hectares of the *Abies religiosa* (Pinaceae) fir forest in the Sierra Chincua of Mexico's Transvolcanic Belt (19°41'N, 100°18'W, altitude 3000 m). The colony was on the high slopes of the Arroyo La Plancha drainage immediately below an area locally know as Peña Cargada, near the town of Angangueo, Michoacan (Calvert & Brower 1986). We estimated butterfly flight response to a cloud that rapidly obscured solar radiation on 22 January 1986, a clear to partly cloudy day. Using a Nikon 50 mm lens set at a focal distance of approximately 25 m, we took a series of 35 mm color slides of an area of sky from the same point within the colony before, during, and after the passage of a large, thick cumulus cloud. We projected 18 of these slides taken at one minute intervals from 1438–1455 h and counted the flying butterflies in each image. The field of view on the projection screen consisted of a column of air with a focal midpoint cross sectional area of approximately 20 × 30 m. While taking the photographs, we also recorded the time of appearance and duration of the shadow produced by the cloud that passed over the colony. Variation in the solar radiation was recorded simultaneously in a nearby forest clearing located ca. 0.5 km south of the butterfly photographing position. We used a pyranometer (Model No. LI-200SB) attached to a printing integrator (LI-550B; Li-Cor Inc., Box 4425, Lincoln, Nebraska 68504) to measure the incident radiation (watts per m^2 across the spectrum from 400 to 1200 nm) at one minute intervals from 1420–1459 h. By synchronization of the pyranometer clock and the photographer's watch, and by noting the time of onset of shading above the butterflies and above the pryanometer, we determined that it took 5 minutes for the cloud to travel from the pyranometer site to the butterfly colony. Thus Table 1 and Fig. 2 show 18 butterfly counts from 1433–1450 h with times adjusted to correspond to the pyranometer readings.

RESULTS

A few cumulus clouds appeared around the mountain massif shortly after noon on the day of our study, and high, thin cirrus clouds also were present intermittently. The radiation data and butterfly counts are in Table 1. During a cloudless period from 1420–1436 h, the average irradiance in one minute samples varied between 620–812 w/m^2 (mean = 745 w/m^2). At 1437 h the cloud drifted between the sun and the monarch colony. During the 10 minutes that the shadow persisted (1437–1446 h), the mean radiation was 143 w/m^2 with a low of 102 w/m^2. From 1447–1459 h after the cloud passed, it varied between 501–762 w/m^2 (mean = 725 w/m^2).

TABLE 1. Solar radiation as watts per m^2 measured at one minute intervals from 1420–1459 h and samples of the numbers of monarch butterflies flying in the sky above the canopy in the Sierra Chincua overwintering colony, 22 January 1986. Butterfly counts were made from photographs taken at one minute intervals over an 18 minute period when a cumulus cloud drifted across the forest and shaded the roosting monarchs for approximately 10 minutes.

Minutes after 14 h	Solar radiation (watts/m^2)	No. of flying butterflies/600 m^2
20	810	—
21	812	—
22	796	—
23	798	—
24	804	—
25	801	—
26	798	—
27	798	—
28	776	—
29	745	—
30	750	—
31	716	—
32	679	—
33	637	20
34	620	16
35	662	8
36	665	9
37	249	54
38	119	193
39	113	308
40	110	232
41	105	232
42	102	263
43	102	881
44	113	766
45	142	420
46	277	419
47	501	282
48	671	194
49	668	13
50	651	56
51	702	—
52	742	—
53	728	—
54	745	—
55	753	—
56	716	—
57	736	—
58	762	—
59	626	—

Fig. 2 is a plot of the radiation data measured over one minute intervals from 1420–1459 h, and the numbers of butterflies flying at 18 one minute intervals extending from 4 minutes before to 4 minutes after the cloud passed. Flying butterflies counted in the space above

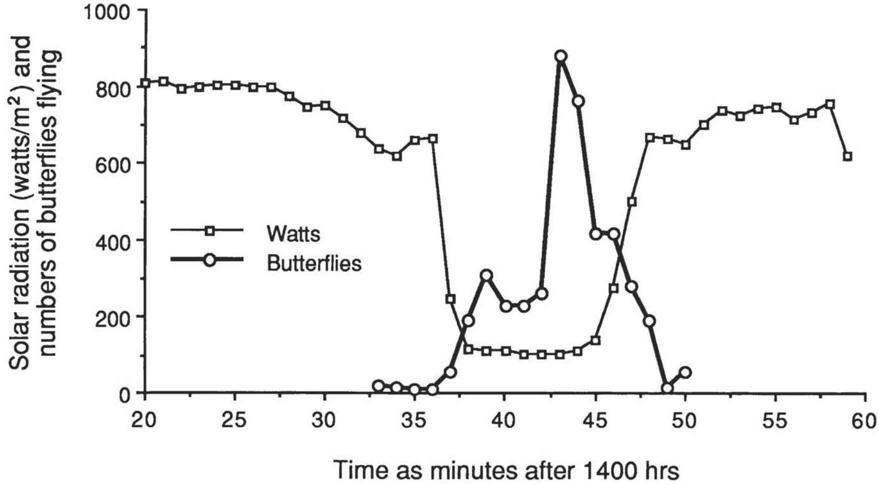

FIG. 2. Cloud-response behavior of sun basking monarch butterflies to the sudden attenuation of radiation by a cloud. Sierra Chincua, Mexico, overwintering colony, 22 January 1986. Data are from Table 1.

the camera during the last 4 minutes of the initial cloudless period (1433–1436 h) ranged from 8 to 20 individuals (mean = 13 butterflies). During the cloudy period the numbers of butterflies flying rose to 881 individuals, a 40 to 100 fold increase over the numbers flying before the cloud shadow. The cloud began passing the sun at 1444 h and the number of butterflies dwindled back to less than a hundred over the next 5 minutes.

DISCUSSION

Masters et al. (1988) experimentally determined that when sun basking monarchs were moved into the shade at an ambient temperature of 11.3°C, their thoracic temperatures dropped from 29°C to below the lower flight threshold (12.7°C) in less than 7 minutes. In the current study, we documented that the butterfly flight response within the colony is correlated with the rapidly diminishing amount of radiation caused by the passage of a cumulus cloud. Our data also indicate a 6–7 minute delay between the onset and peaking of the cloud-response (Table 1). This delay is consistent with the heat loss curve identified by Masters et al. (1988) and strongly suggests that the cloud-response is triggered by the butterflies' rapidly decreasing body temperature rather than by the decreased light intensity *per se*.

Periodic clouding occurs frequently at the Mexican overwintering sites from December through February, the coldest part of the overwintering season (Mosino-Aleman & Garcia 1974, Anonymous 1976, Calvert et al. 1989). Early mornings are typically clear but cumulus clouds begin to form over the mountain massifs towards noon and continue to build through the afternoon leading to partly cloudy and then often overcast late afternoons. The duration of cloud shadow is unpredictable. Thus when the first cloud appears it may cast a shadow for only a few seconds, or it may be the harbinger of complete sky closure for several days (Calvert et al. 1983).

We therefore hypothesize that taking flight and reforming clusters under the thermally insulating canopy of the forest allows individual butterflies to avoid being trapped in positions that are directly exposed to the sky. Such trapping is extremely dangerous because intense clearing at night frequently results in temperatures plummeting to as low as −5°C (Calvert & Cohen 1983, Calvert et al. 1982, 1983, 1984, 1986). This, in combination with heavy dew that forms on surfaces exposed to the open sky, greatly increases the danger of the butterflies freezing through inoculative ice crystal formation (Salt 1936, Calvert & Brower 1981, Brower 1985, Anderson & Brower 1992).

We also deduce from our research in another Sierra Chincua overwintering colony (Brower & Calvert 1985) that an additional advantage of the cloud-response behavior may be a reduction of bird predation. During the winter of 1978–79 birds consumed an average of 15,000 monarchs per day. However, the risk of predation for individual butterflies in exposed positions within the colony was greater than for individuals in clusters (see also Calvert et al. 1979, Hamilton 1971). Thus, if butterflies were to be trapped thermally while more dispersed, the probability of bird predation on individuals would be increased.

CONCLUSIONS

Two heretofore enigmatic and very different behaviors of tens of thousands of butterflies responding dramatically to cloud shadow appear to have a common proximate cause. We hypothesize that both behaviors are an innate behavioral response to the butterflies' rapid cooling that results from reduced solar radiation caused by the cloud shadow.

The ultimate evolutionary advantage of the cloud-response behavior is that it reorganizes the individual butterflies into tightly clustered positions on the boughs that are better insulated by the forest canopy against radiant heat loss to the open sky during the night. Away from the colony, the butterflies' reversal in flight direction back towards their colony prevents individuals from becoming stranded and subjected to a higher probability of freezing or being eaten while engaged in normal behaviors critical to winter survival.

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