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BEHAVIORAL RESPONSE OF MONARCH BUTTERFLIES (NYMPHALIDAE) TO DISTURBANCES IN THEIR HABITAT—A GROUP STARTLE RESPONSE?

WILLIAM H. CALVERT

Department of Zoology, University of Florida, Gainesville, Florida 32611 USA

ABSTRACT. Monarch butterflies (*Danaus plexippus* L., Nymphalidae) overwintering in fir forests of Mexico's Transvolcanic Belt fall from their perches at once *en masse* in response to "disturbance" by people or other animals that traverse their colonies. Roosting butterflies were stimulated by movement, noise, wind and breath. Their response, as measured by the number falling from perches, indicates that only breath is overwhelmingly effective in initiating the massive roost disintegrations observed. The response is temperature dependent; it begins about 7°C and increases as temperature rises. This group behavior is likely an adaptation to confuse and disorient bird and possibly mouse predators, increase their reaction time thus allowing the escape of the prey. Advantage may accrue to an individual belonging to a group whose size enhances the startle-effect of roost disintegration.

Additional key words: *Danaus plexippus*, Mexico, overwintering biology, predation, protean behavior.

Monarch butterflies (*Danaus plexippus* L., Nymphalidae) overwinter in huge aggregations numbering in the millions in the high altitude fir forests of Mexico's Transvolcanic Belt (Calvert & Brower 1986). When people or other animals pass through the colonies, butterflies may drop from their clusters *en masse* sometimes in great numbers. Their collective falling was named "cascading" by K. Brugger, one of the Mexican monarch colony discoverers (Urquhart 1976). The behavior is not a passive event (Brower & Calvert 1985). The butterflies actively use their wings to cast themselves off their perches in a process that during warm weather sometimes appears explosive. The process may involve a few butterflies to hundreds of thousands of butterflies. When the wings are opened in the process of pushing off, the bright orange dorsal surface is suddenly exposed to view. The effect of tens or even hundreds of thousands of butterflies exposing these surfaces at once and falling from their perches is startling and beautiful.

Guards and posted signs at two overwintering colonies open to tourists located within the ejidos (collective farms)—Rosario, near Ocampo, Michoacan, and Macheros, near Donato Guerra in the state of Mexico—admonish the public not to make loud noises while in the colonies. This request is in part an attempt to preserve the spirit of sanctuary within the butterfly colonies. But its main purpose is derived from a commonly held belief among local people that the cascading behavior of the monarch butterfly is a response to noise, such as speech, made by the visitors as they pass through the colony.

Although there is a strong association between the presence of people and cascading of butterfly clusters, the precise cause(s) of roost disintegration have not been investigated. In this paper I explore several likely causes.

METHODS

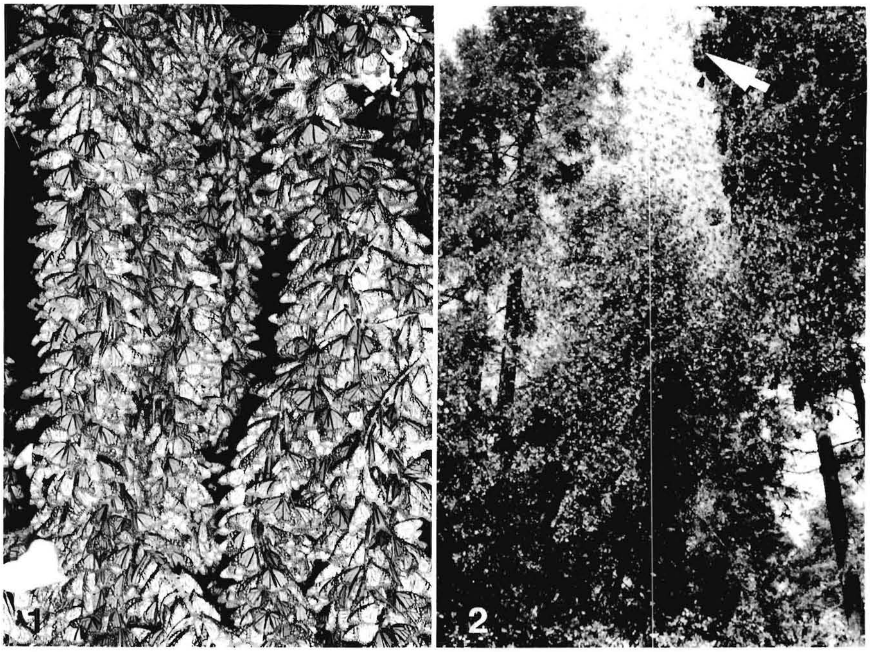
Ten trunk and ten bough clusters ranging in height from 1–2 m and containing several hundred butterflies were artificially "disturbed" by movement, noise, air currents, and human breath. The degree of disturbance was assayed by estimating the number of butterflies cascading out of the roost. The response of roosting butterflies to movement was measured by moving the 2.5 cm diameter × 20 cm long grey plastic casing of an Omega RH-21C temperature/humidity probe slowly past the clusters approximately 2 cm from the butterflies. The response to loud noise was measured by clapping the hands twice 5–10 cm from the cluster. The hands were clapped together so that air was directed towards the researcher, not towards the butterflies. To test for air movement, the research notebook was waved once back and forth past the cluster rapidly enough so that the wind generated caused a passive movement of the wings. These tests put the researcher and his assistant in close proximity to the butterfly clusters. To avoid the possibility of confounding the tests above with breath, we held our breath and periodically exhaled away from the butterfly cluster. Disturbance from breath was created by the researcher breathing directly on a cluster from a distance of 20 cm. The four types of disturbance were always tested in the order described on each of the ten bough and trunk clusters. The experimentally induced cascading of butterflies had no effect on adjacent clusters as is sometimes observed during warm weather.

The experiment was performed on 29 and 30 January 1988 at the Palomas overwintering colony located on the west face of the Cerro de las Palomas approximately 35 km southwest of Toluca in the state of Mexico (Calvert & Brower 1986). Temperature and humidity of ambient air were recorded by an Omega Engineering, Inc. RH-21C temperature/humidity probe.

RESULTS

Disintegration of Roosts or Cascading Behavior

In response to a stimulus, clustered butterflies (Fig. 1) cast themselves off their perches in near synchrony (Fig. 2). This behavior involves more than the opening of the tarsal claws that grip the substrate. Using their wings, they actively push against each other, tree trunks or surrounding foliage. After casting off, they fall *en masse* tumbling over one another, and over foliage and branches until they either gain control



FIGS. 1, 2. **1,** Monarch butterflies clustered on a bough of the oyamel fir (*Abies religiosa*). The tightly packed butterflies are oriented in an orderly manner with their wings upright. Original Kodachrome slide by W. H. Calvert. **2,** A monarch roost in the process of disintegration. The butterflies are falling in random disarray from a position marked by the white arrow. Original Kodachrome slide by Carlos Gottfried.

and fly or until they strike the ground. The phenomenon gives the impression of a stream of large colored particles pouring downward over branches and foliage (Fig. 2). Cascading in one area of the colony may trigger similar disintegration of roosts in other areas resulting in tens or hundreds of thousands of butterflies leaving their clusters in a half hour period.

An extreme example of cascading behavior occurred on a warm, sunny day in February of 1989 at the Palomas Colony (Calvert & Brower 1986). Cascading began in one cluster at ca. 1400 h. Sequential cascading of clusters throughout the colony continued sporadically for the next hour. By 1500 h a section of forest approximately 20 × 30 m was covered in a living carpet of monarch butterflies ca. 8 cm deep. Excited butterflies were unable to fly but opened and closed their wings, thus pushing and moving against one another giving the appearance of a writhing mat of color. On grades this behavior caused them to flow *en masse* down slope where they piled up against trees or other obstacles such as fallen logs, brush piles or rocks. After several minutes of pushing themselves about with their wings, unless stimulated by more cascading butterflies falling upon them, they ceased moving their wings and began to crawl. When they encountered vegetation, they crawled upward (Alonso-Mejia et al. 1992).

The majority of cascading events are much less spectacular. Bird predators such as blackheaded grosbeaks (*Pheucticus melanocephalus*) and blackbacked orioles (*Icterus galbula abeillei*) induce butterflies to cascade from positions where they are feeding. Tens to hundreds of butterflies have been observed to fall. More fell during warm ambient temperatures than cold.

Cascading behavior occurs most often when air temperatures are near flight threshold, between 13–15°C (Masters et al. 1988, Kammer 1970) or higher. At high air temperatures (20–25°C), clusters sometimes appear to break up spontaneously and the disintegration of one cluster nearly always triggers the disintegration of others. At air temperatures below flight threshold, multiple disintegrations are rare. Butterflies from a cascading cluster spill onto the ground and flap their wings helplessly. If it is not too late in the day, most of them will crawl up onto foliage (Brower et al. 1977). If air temperatures are above flight threshold or if the butterflies have had an opportunity to bask and have raised their thoracic temperatures to flight threshold (Masters et al. 1988), the falling butterflies will fly before they reach the ground. Sometimes they fly off in the same direction making a striking formation in the air.

Butterfly Response to Movement, Noise and Wind

The response of clustered butterflies to "disturbances" by movement, noise and wind were measured by counting the number cascading from the roost. There was very little response to the movement of the probe near the clustered butterflies (Table 1). Only on one occasion did a few butterflies fall from a cluster in response to probe movement. This occurred at the relatively high temperature of 9.3°C. There was even less response to a sharp clapping noise. Only one butterfly fell from a cluster (temperature = 4.9°C). More response was evident to the winds generated by the research notebook. Some wing opening occurred at low temperatures of 0.9°C. Movement involving wing opening and small shifts in position occurred at 8.4°C. A few butterflies fell from the roosts at 13°C and higher.

Butterfly Response to Breath

The major cause of clustered butterflies falling from their perches was breath (Table 1). Butterflies directly in the path of the breath stream cascaded from their perches. A regression of temperature against

TABLE 1. Reaction of clustered overwintering monarch butterflies to movement, noise, air currents and breath.

Time	Exposure	Cluster type	Temp. (°C)	Hum. (%)	Type of disturbance			
					Motion	Sound	Wind	Breath
08:02	Shade	Bough	−0.8	61.1	nc	nc	nc	7+
08:06	Shade	Bough	0.1	63.2	nc	nc	nc	5+
08:09	Shade	Bough	0.1	62.3	nc	nc	nc	4+
08:18	Shade	Trunk	0.9	56.4	nc	nc	1+	2+
08:22	Shade	Trunk	0.9	50.1	nc	nc	1+	3+
10:27	Shade	Trunk	4.9	41.1	nc	1	nc	10
10:31	Shade	Trunk	4.9	43.4	nc	nc	nc	2
10:34	Shade	Bough	5.6	42.0	nc	nc	nc	2
10:38	Sun	Trunk	7.5	37.1	nc	nc	nc	30–40
10:44	Sun	Bough	11.8	34.2	nc	nc	nc	10
13:39	Shade	Trunk	8.9	43.1	nc	nc	nc	40–50
13:43	Shade	Trunk	9.0	42.6	nc	nc	nc	40–50
13:48	Dappled	Trunk	9.3	41.5	3	nc	nc	25–30
13:54	Shade	Trunk	8.3	45.8	nc	nc	nc	15–20
13:58	Shade	Trunk	8.4	43.8	nc	nc	mov't	15–20
14:02	Shade	Bough	8.4	43.2	nc	nc	mov't	40–50
14:06	Shade	Bough	9.0	43.2	nc	nc	nc	~100
14:14	Sun	Bough	13.0	30.4	nc	nc	4	~100
14:18	Sun	Bough	15.0	32.2	nc	nc	3	200–300
14:22	Sun	Bough	15.0	30.3	nc	nc	nc	200–300

nc = no change; mov't = movement without opening wings; + = opened wings but did not drop.

the number of butterflies cascading showed the response to be temperature dependent ($F = 38.8$; $P = 0.0001$; $r^2 = 0.82$). At all but the lowest temperatures, tens to hundreds of butterflies cascaded from their clusters in response to breath. Extremely cold butterflies (air temperature is 1°C or lower) responded to breath by opening their wings without falling from their perch. A few fell from their perches between 4.9°C and 5.6°C. At temperatures between 7.5°C and 9°C, 15 to 100 butterflies fell from their perches. At temperatures greater than 9°C, numbers near a hundred or above fell.

No differences were apparent between cluster types. Bough clustered butterflies were as likely to cascade from their perches as were trunk clustered butterflies. No butterflies left their perches when relative humidity was above 50%, but this is likely an artifact of the inverse relation between temperature and relative humidity ($r = -0.92$) with temperature being the primary determinant of the butterfly response.

DISCUSSION

These data indicate that neither noise nor movement in the vicinity of clusters caused the cluster disintegration or cascading of butterflies observed during visits to the monarch butterfly colonies. Air currents directed onto clustered butterflies also did not evoke much response.

Some component of breath other than air current appears to be the cause of the massive cascading response. The failure of the butterflies to respond to the close presence of the researcher near the cluster until breathed upon suggests that heat *per se* is not the cause of roost disintegration.

Erratic Escape Behavior

Cascading behavior of monarchs is clearly more than a simple escape behavior. It involves a rapid, at times explosive, expulsion of numerous animals from a roost nearly simultaneously. The cryptic coloration of the roost suddenly erupts into the vivid orange colors of collective dorsal butterfly surfaces.

Cascading behavior is analogous to behaviors in other animals. Prey animals in many different taxonomic groups behave erratically when attacked by predators (Tinbergen 1951, Roeder 1962, Cott 1940, Marshall & Orr 1955). Such erratic escape behavior, called protean behavior (Chance & Russell 1959), functions as an antipredator device by confusing and disorienting the predator, increasing its reaction time and enhancing the survival of the prey (Humphries & Driver 1967). The erratic and unpredictable nature of the response makes learned countermeasures by the predator less likely (Humphries & Driver 1970).

Cascading behavior is perhaps most analogous to behavior exhibited by certain marine organisms. Antarctic krill maintain synchronized swimming patterns in apparent response to rheotactic cues supplied by the wake of preceding animals (Hamner et al. 1983). When frightened, their synchronized swimming pattern breaks apart, and they disperse in random directions. Monarchs roost in a very orderly manner with their folded wings oriented vertically on boughs or tree trunks (Fig. 1). When disturbed, this oriented assemblage breaks apart; initially the once clustered group tumbles towards the ground (Fig. 2), and if warm enough, flies off in random disarray. If they are able to fly, some sort of orderly flight pattern, likely towards a bright sky, is rapidly obtained.

The elicitation of antipredator responses by mammalian breath may be of general occurrence in some groups of arthropods (Conner et al. 1985). Certain millipeds react to breath by coiling, and they react to a warm surface by emitting defensive secretions. The tenebrionid beetle, *Bolitotherus cornutus*, everts quinone-producing glands when breathed upon. Some component of breath other than CO_2 seems to have elicited the response in the beetle. Possible components eliciting the response in monarchs include heat in the breath or one of the gaseous components of breath such as CO_2 or water vapor. Additional research is needed to determine which breath component evokes this startlingly beautiful defensive behavior in monarchs.

Microclimate and Bird Predation

Because of their unique position in high altitude tropical forests and presence during the middle of the dry season, the microclimatic regimes of the overwintering colonies are precisely determined by the amount of radiation falling on the area. From the moment solar radiation strikes the area in the morning, parts of the forest begin to heat up and butterflies in the solar path or in the path of diffuse radiation are warmed to flight threshold and empowered to fly. Once solar input ceases in late afternoon, heat accumulated during the day rapidly radiates into the clear, dry sky. Temperatures drop precipitously and the butterflies rapidly lose the ability to respond to stimuli and to escape predators. If temperatures are cold so that the butterflies cannot fly and are forced to remain on the ground or on low foliage until the following day, they are subject to a possibly lethal combination of colder temperatures and higher humidities near the ground (Calvert & Brower 1981, Calvert & Cohen 1983) and to nocturnal mouse predation (Glendinning et al. 1988). If temperatures are warm, or if it is early in the day so that a sun-fleck is likely to strike them, most butterflies will return to their elevated roosts before harm comes to them. However, even when no direct harm comes to them, they must use scarce lipid reserves to crawl up onto foliage or to fly back to their roosts (Masters et al. 1988). Because nectar sources are limited during the overwintering season (Brower & Malcolm 1991), this use of energy reserves could result in premature starvation.

In Mexico's overwintering sites bird, mainly blackheaded grosbeaks (*Pheucticus melanocephalus*) and blackbacked orioles (*Icterus galbula abeillei*), and mouse, mainly *Peromyscus melanotis*, predators killed an estimated 926,000 butterflies/ha in a 135 day season (Brower & Calvert 1985, Glendinning et al. 1988) which may have amounted to as much as 10% of the colony population (Calvert et al. 1988). Birds feed during the coldest times of the day usually from dawn to 0900 or 1000 h and from ca. 1630 h till dark (Brower & Calvert 1985). Feeding early and late, birds are likely to encounter cold butterflies unable to move quickly to escape. Birds feeding when solar radiation is striking the colony may encounter butterflies with thoracic temperatures above ambient that are capable of vigorous movement and flight. Attacking while the butterflies are inactivated by the cold would be likely to insure minimum handling cost per effort (Krebs 1978, Brower & Calvert 1985). If the majority of predators are birds which exhale upon clustered monarchs in the process of capturing them, a group startle response such as the cascading behavior designed to confuse and disorient the predator to increase its reaction time would be a beneficial adaptive response to the butterflies.

These data suggest that the butterflies benefiting the most from the cascading response are those whose thoracic temperatures are between ca. 7°C and flight threshold (Table 1). At temperatures lower than this, it is more difficult for them to cast off their perches. At higher temperatures they can fly away to escape predation. Except for the coldest hours of early morning or late evening, most clustered butterflies are likely to experience temperatures in this range. (Exceptions include parts of November and March when ambient temperatures in the forest climb above flight threshold and cold overcast days of winter when ambient temperature never reaches 7°C.) Cascading behavior is unlikely to benefit butterflies being preyed upon by mice since nighttime temperatures when mice feed are nearly always colder than 7°C. The cascading response is most likely to benefit butterflies that are able to cast off of their perches *en masse*, but are unable to fly due to cold air temperatures.

There remains the possibility that two different kinds of cascading phenomena occur in the monarch overwintering colonies. The dramatic disintegration of monarch roosting clusters involving tens of thousands of individuals may be an artifact of gregarious roosting and a different phenomenon from the smaller scale cascading response elicited by avian predators. These multiple cluster disintegrations are especially apparent during warm periods late in the season (February or March) and may be part of the colony breakup in preparation for the return migration to the north. Drawn to nectar and water sources at lower elevations, the colonies rapidly move down slope, often dividing into two or more segments (Calvert & Brower 1986). Mating activity is intensified and each day a portion of the colony leaves to begin its remigration northward (Van Hook 1993).

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