

## Soaring flight of monarch butterflies, *Danaus plexippus* (Lepidoptera: Danaidae), during the late summer migration in southern Ontario

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Adult *Danaus plexippus* in southern Ontario frequently engage in soaring flight during their late summer migration. They utilize both ascending air currents (lift) produced by winds blowing up slopes and thermals (bubbles or columns of air that are rising because they are warmer and lighter than the surrounding air). The butterflies appear to be very efficient and exhibit different flying techniques when encountering various types of lift. When the weather is favourable, soaring is the main mode of flight and the butterflies achieve heights above the ground of at least 300 m. Extended soaring flight in thermals was always associated with tail winds.

A sample of 18 specimens gave an average mass of  $566 \pm 81$  mg and an average wing loading of  $0.018 \pm 0.002$  g/cm<sup>2</sup> ( $1.77$  N/m<sup>2</sup>). Gliding performance parameters were measured for two specimens ballasted to 450 mg and the results were extrapolated to 600-mg individuals. The energetic advantages of utilizing soaring flight in terms of extension of maximum range is discussed.

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Dans le sud de l'Ontario, on observe souvent des *Danaus plexippus* adultes en vol plané, durant leur migration de fin d'été. Les papillons utilisent à la fois les courants d'air ascendants, produits par les vents qui soufflent vers le haut des collines, et les courants thermiques (bulles ou colonnes d'air qui montent parce qu'elles sont plus chaudes et plus légères que l'air ambiant). Les papillons sont très habiles et effectuent différentes manœuvres de vol selon la nature des courants. Lorsque la température le permet, le vol plané est le mode le plus utilisé et les papillons peuvent voler à plus de 300 m du sol. Les longs vols planés dans les courants thermiques sont toujours associée à des vents arrière.

Un échantillon de 18 spécimens a permis d'établir la masse moyenne à  $566 \pm 81$  mg et la charge moyenne sur les ailes à  $0.018 \pm 0.002$  g/cm<sup>2</sup> ( $1.77$  N/m<sup>2</sup>). Les paramètres de la performance en vol plané ont été mesurés chez deux spécimens lestés de façon à peser 450 mg et les résultats ont été extrapolés et appliqués à des individus de 600 mg. La discussion porte sur les avantages énergétiques du vol plané qui permet l'extension de l'aire de répartition.

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### Introduction

Each year in late summer and fall in southern Ontario, monarch butterflies, *Danaus plexippus* L., engage in migratory flight to the southern U.S.A. and Mexico. Various aspects of this migration have been investigated by researchers and the general pattern is now well known (Barker and Herman 1976; Beall 1941a, 1941b, 1946, 1948, 1952; Brower *et al.* 1977; Brown and Chippendale 1974; Cenedella 1971; Kanz 1973, 1977; Luger 1890; Urquhart 1960; Urquhart and Urquhart 1976a, 1976b, 1977, 1978; Williams 1930; Williams *et al.* 1942). Briefly, the butterflies in southern Ontario that develop in late summer do not reproduce but instead build up large fat reserves, and begin migrating. Many of these migrating individuals eventually reach overwintering grounds in the Neovolcanic Plateau of Mexico (Brower *et al.* 1977; Urquhart and Urquhart 1976b,

1977, 1978). The migrating population peaks during late August to early September, and then declines over the next several weeks.

If *D. plexippus* adults were to fly directly from southern Ontario to overwintering grounds in Mexico, then the butterflies would travel in excess of 4000 km. The small size of monarch butterflies suggests that energetics of the long-distance migration may be a problem. Butterflies are believed to rely primarily on fat as a fuel during periods of extended flight (Brown and Chippendale 1974; Johnson 1974; Weiss-Fogh 1970) (however, cf. Heinrich and Kammer 1978). Late summer monarchs average approximately 600 mg (Beall 1948; Brown and Chippendale 1974) and have a fat content of approximately 23% (Beall 1948) or 140 mg. Since the weight of fat per unit of energy available is 0.11 mg/cal (1 cal = 4.1868 J) (Weiss-Fogh 1970), if the metabolic rate of *D. plexippus*

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during flight was known, then a rough estimation of the maximum duration of sustained flight of individuals utilizing fat could be calculated. If we assume that the metabolic rate of *D. plexippus* during sustained flapping flight is only  $200 \text{ cal/g} \cdot \text{h}^{-1}$ , the minimal value determined by Zebe (1954) for another butterfly (*Vanessa* sp.), then a *D. plexippus* with an initial weight of 600 mg will utilize approximately  $(0.6)(200) = 120 \text{ cal/h}$  and will consume its fat at the rate of approximately  $(120)(0.11 \text{ mg/cal}) = 13 \text{ mg fat per hour}$ . Consequently, an average *D. plexippus* with 140 mg of fat would have a maximum flying duration between refueling stops of approximately  $140/13 = 11 \text{ h}$ . Wensler (1977) using a lower value of fat content calculated a duration of 10 h.

The above values for maximum duration do not translate directly into a maximum range. Actual maximum ranges are influenced by many factors including weather conditions, altitude of flight, and airspeed. The effect of airspeed is relatively easy to calculate. Zebe's (1954) measurements of metabolic rates were obtained from Lepidoptera engaged in continuous flapping flight. In *D. plexippus* vigorous flight of this type produces an airspeed of approximately 40 km/h (Urquhart 1960). An average *D. plexippus* adult engaging in vigorous flapping flight could travel approximately 480 km on 140 mg of fat. However, during migration *D. plexippus* adults usually adopt a slower cruising flight at an airspeed of 18 km/h (Urquhart 1960), a flying strategy that should result in less fuel being consumed as a result of reduced drag at lower airspeeds. The more rapid flapping-flight mode, which is usually used for escape, involves rapid wing beats with each wing being moved through an arc of  $120^\circ$  (Urquhart 1960). Since profile drag is proportional to the square of the speed, doubling the speed increases the profile drag by four (Irving 1977). Consequently, it seems reasonable to assume that the slower, less energetic cruising flight of *D. plexippus* requires approximately 25% of the energy expenditure of vigorous flight. If this assumption is correct, a maximum endurance of approximately 44 h is possible and *D. plexippus* adults flying at an airspeed of 18 km/h would achieve a maximum range of approximately 790 km. Earlier estimates of maximum range by Hocking (1953) were based on a model now considered inapplicable for insects with slow flapping flight (Pringle 1965).

It is assumed in the above calculations that flight occurs in calm weather. In reality the butterflies have to contend with large variations in weather and terrain. Winds are particularly important.

Head winds, crosswinds, tail winds, and turbulence can all have dramatic effects on animals with low airspeeds. While tail winds increase the maximum range, all of the other conditions reduce the range. Because late summer is often a time of unsettled weather, it is reasonable to assume that the migrating adults frequently encounter difficult flying conditions over much of their route. This assumption is supported by Beall's (1948) finding that some migrants collected in Louisiana have depleted fat reserves. Consequently, even with the most favourable assumptions about the energy requirements of migrating *D. plexippus*, it appears that the butterflies have insufficient fuel reserves for the trip and must frequently stop and feed at flowers. If it is important to minimize the number of days spent in migratory flight, if long stretches of unfavourable terrain such as large bodies of water, mountains, or deserts must be crossed, or if the fat reserves must also serve as an energy source in the spring (Urquhart 1960; Urquhart and Urquhart 1976b), then selection should favour any flying strategies that reduce the energy expenditure during cross-country travel and minimize the effects of unfavourable weather.

An energy-saving flying strategy commonly utilized by migrating insects is to fly near the ground where the wind speed is usually reduced. Although this strategy avoids many of the problems associated with adverse wind conditions, it also eliminates most of the opportunities to make use of favourable tail winds. A more efficient technique is to remain as close to the ground as possible when encountering head winds or crosswinds, and to fly well above the ground when in tail winds. Observations recorded by other investigators (Beall 1941a; Luggler 1890; Urquhart 1960; Williams 1930) indicate that migrating *D. plexippus* use this strategy, particularly in areas where the presence of terrain or buildings present additional obstacles to low flight.

The most efficient flying technique, in terms of cost per unit of distance travelled, is soaring (Pennycuik 1969, 1975). During soaring flight, altitude is gained or maintained by gliding in rising air currents. Since a soaring animal is actually gliding, the wings are held more or less motionless and the high-energy expenditure of powered flight is avoided. However, use of this flying technique has numerous practical problems and requires sophisticated patterns of behaviour.

Rising air or 'lift' can be generated by a variety of mechanisms, and the type of lift encountered usually determines which flying strategies are optimal. Two common types are termed thermal lift and

slope lift. Thermal lift or thermals are frequently used by soaring birds and glider pilots for cross-country travel and are simply air masses that are rising because they are warmer and lighter than the surrounding air. The air masses are heated through contact with warm surfaces which in turn have usually been heated by the sun. Unfortunately, thermals are rather capricious. They are difficult to detect, irregular in cross section, vary greatly in strength and dimensions, drift with the wind, are generated irregularly at any particular source, and are usually weak or absent on overcast days. As a result, thermal lift has usually been assumed to be used by insects only on an accidental or haphazard basis instead of the deliberate manner exhibited by soaring birds (Pennycuik 1972a). However, butterflies have been reported being carried to altitudes of 90 m or more in thermals (Gwynne 1962), and Johnson (1969) suggests that soaring in ascending air currents may play some role during insect migration.

In contrast to thermal lift, slope lift is more predictable in occurrence and strength. This type of lift is produced by winds moving up obstacles such as slopes, ridges, or buildings. In general, the strength of the lift is directly related to the strength of the wind with the strongest lift being found close to the slope on the upwind side of passes. Soaring birds and glider pilots frequently use this type of lift in hilly or mountainous regions (Conway 1969; Pennycuik 1975). Because the exact pattern of lift on any slope can vary radically from moment to moment as a result of gusts, wind shifts, and complex interactions between the wind and terrain, effective utilization of slope lift requires rapid responses and a flexible flying strategy. Although it may appear that slope soaring can be of use during migration only when some component of the wind direction is also in the direction of the migration (i.e. a tail wind), this impression is incorrect. A head wind or crosswind can also produce favourable slope lift under certain conditions of terrain. Head winds can generate eddies that contain areas of lift on the lee side of obstacles, and crosswinds moving over a ridge that is more or less parallel to the direction of travel can result in long bands of usable lift.

Efficient cross-country soaring requires that one set of optimum aerodynamic properties and flying strategies can be used in areas of lift (to maximize altitude gain) and another set be used for penetrating through areas of subsiding air or 'sink' (to minimize altitude loss). When an animal is gliding through areas of sink, the rate of loss of height depends on an interaction between the downward velocity of the air currents, the intrinsic rate of

descent (sink rate) of the animal, the flying strategy, and the animal's airspeed. In general, an animal gliding in sink will usually achieve minimal loss of altitude by increasing its wing loading and flying directly through a higher airspeed than the speed flown in lift. Within a particular range of airspeeds the resulting increase in the animal's sink rate from flying faster is more than compensated for by the shorter time spent in the area of subsiding air. In gliding animals higher wing loadings are normally obtained by partially folding the wings. However, as the wing area decreases and the wing loading increases, the ability of the animal to utilize lift decreases.

Maximum rates of altitude gain while soaring in lift require a low sinking rate and high maneuverability (to remain within the strongest sections of lift). Both of these traits are normally associated with light wing loading. Consequently, when flying through rising air, an animal must decrease its wing loading, decrease its airspeed, and maneuver to remain within the areas of strongest lift. As a result of the conflicting requirements for efficient flying in lift and sink, all animals (and machines) that rely on soaring as a means of travel are a compromise in design.

Although adults of *D. plexippus* have frequently been observed in gliding flight (Urquhart 1960), indicating that they have the potential to soar, little was known about their aerodynamic properties. However, the behavioural patterns required for effective soaring flight are well understood (Pennycuik 1975). In order to measure the aerodynamic properties of *D. plexippus* adults, to gain a rough idea of their gliding abilities, and to determine if appropriate soaring techniques and other energy-saving flying techniques are exhibited in migrating *D. plexippus*, laboratory and field studies were conducted during the late summer and early fall of 1977.

### Materials and Methods

#### *Laboratory Measurements of Aerodynamic Properties and Gliding Ability*

Aerodynamic properties measured in 18 specimens (7 males and 11 females) of *D. plexippus* were wingspan, aspect ratio, weight, and wing loading. The specimens were collected, brought into the laboratory, and weighed on a top-loading balance. Wing area was measured by placing the specimens on a sheet of graph paper, dorsal surface down, arranging the wings in the gliding configuration that had been observed in the field in butterflies gliding directly overhead, and tracing their outlines. Although in this method the existence of the butterfly's body is ignored, this was assumed to result in minimal error because a gliding *D. plexippus* closely resembles a flying wing. The wing span and aspect ratio (span<sup>2</sup>/area) was also determined by measurements of the pencilled outlines. Wing loading was determined by dividing the wing area of each specimen by its weight.

Performance parameters measured were sink rate, airspeed, and gliding angle. Rough approximations for these parameters were obtained by test flights with two preserved specimens. The specimens were the same size and had been pinned and dried with the wings set in a gliding configuration. In specimen A, the wings were set in the same configuration used in the measurements of aerodynamic properties. This specimen was test-flown to determine the glide angle and sink rate. The wings in the second specimen (B) were swept slightly forward, resulting in a 20% increase in wing area. The specimen was test-flown to determine if the change in wing area would produce a significant change in sink rate. After these specimens were dried, the pins were trimmed away and the specimens were ballasted with plasticine to 4.5 g. This weight corresponded to the weights of 4 of the 18 specimens. Unfortunately, higher wing loadings could not be measured because the great fragility of the dried specimens resulted in structural failures upon landing. The lightly ballasted specimens should have lower sink rates and lower airspeeds than an average *D. plexippus* leaving southern Ontario, but may approximate the performance of the same butterfly as it depletes its fat reserve during its migration. Migrants collected in Louisiana by Beall (1948) with depleted fat reserves weighed approximately 450 mg. In any case, the glide angles should be unaffected. Preliminary test flights with each specimen were performed with the centre of gravity at various locations along the body. In both specimens, the only location that produced stable flight was found to be slightly behind the metathorax. The plasticine was then shifted slightly until maximum glides were obtained. All performance measurements were made with the centre of gravity at this position. Since the wings of living butterflies are relatively flexible, may be held at slightly different angles of attack than were used in the tests, and can also be adjusted in flight, all of our measurements must be considered conservative.

Test flights of the specimen took place in a room with no detectable air currents. The specimens were released by hand at flying speed at a height of 1 m. When the butterflies were released with excess speed they would tend to pitch up and climb, and when they were released with insufficient speed they would stall, pitch down, and dive. Only if the specimens were released at the approximate flying speed for their wing configuration and weight, would they glide towards the floor at a relatively constant angle. Only flights, in which no obvious pitching up or stalling occurred after release, were recorded. All flights were timed with a stopwatch and the flight path was measured from the release point to the point of touchdown. The gliding angle, rate of descent, and airspeed were determined for 10 flights for each specimen.

#### *Field Observations of Flying Strategies of Migrating D. plexippus*

At frequent intervals from late August until the end of September, flying adult *D. plexippus* were observed from various observation points. Observations were made during the last 2 weeks of August and the first 2 weeks of September. Because we were primarily interested in the butterflies' possible use of soaring techniques during migration, most observations were made on days when most butterflies were flying at heights of 10 m or more. The adults were observed with field glasses (7 × 35) and the data for each observation period were recorded on tape. This data included weather conditions and flying techniques. The information on flying techniques recorded were direction of flight relative to ground (i.e. track of butterfly), altitude, ground speed, type of flight (i.e. powered, gliding, soaring, or mixed), type of maneuvers (i.e. straight flight, circling flight), and the type of lift being utilized. The category 'powered flight' was further divided into two modes, cruising or vigorous. Gliding flight meant that the butterfly was descending

with its wings extended and immobile. Soaring flight meant that the butterfly was gliding but was either maintaining or gaining altitude.

The wind speed, ground speed, and the altitudes of the butterflies were estimated. The wind speed was estimated by observing the effect of the wind on smoke, trees, or leaves thrown into the air. Although this method is crude, both authors are glider pilots and have been trained to estimate wind speeds from these cues. Wind speeds were categorized as being very light, light, moderate, strong, and very strong. These categories correspond to wind speeds of approximately 5, 10, 20, 30, and 40 km/h respectively. It should be noted that butterflies flying in the cruise mode cannot make progress against a 'moderate' wind and butterflies flying at maximum effort cannot make progress against a 'very strong' wind. Ground speed of the flights (airspeed corrected for head or tail winds) was estimated by observing the rate at which the butterflies moved past our area of observation. Altitude of flight was either estimated by reference to adjacent landmarks or buildings of known height or by the apparent size of the butterflies when viewed through the field glasses. It was determined by measurements that we could no longer accurately distinguish butterflies with the field glasses at altitudes above the ground of approximately 300 m.

Observations were made primarily at three sites: the Erindale College campus of the University of Toronto, Turkey Point Provincial Park, and Long Point Provincial Park. Erindale College was particularly suitable because slope lift and thermal lift are produced at various locations and regular observations could be made whenever conditions were favourable. The south building is a large complex with several wings that form a series of artificial cliffs. Slope soaring was possible along at least one wing of the building on many days. A nearby abandoned gravel pit also had local areas of slope lift and on most days was a good source of thermals. Thermals were also generated over various fields and parking lots on campus whenever conditions were favourable. Finally, there were large stands of goldenrod (*Solidago* sp.) and asters (*Chrysanthemum* sp.) on campus on which the butterflies could forage. Observations at Erindale College were made for periods ranging from 15 to 90 min during the morning, midday, and afternoon on most days that the butterflies were flying.

Both Turkey Point and Long Point Provincial Park are situated on the north shore of Lake Erie. Observations were made at, and in the vicinity of, these sites on the 10th and 11th of September. These sites had complicated topography and, like Erindale College, produced slope lift and thermals.

## Results

### *Aerodynamic Properties*

In Table 1 *D. plexippus* is compared to the white-backed vulture, the standard Rogallo hang glider (a low-performance glider somewhat similar in shape to a butterfly), and the Nimbus II, a high-performance glider. The monarch butterfly, with an average weight of 0.566 g and a wing area of 32 cm<sup>2</sup> has an average wing loading of only 0.018 ± 0.02 g/cm<sup>2</sup> (1.77 N/m<sup>2</sup>), a low value compared to 0.780 g/cm<sup>2</sup> for the white-backed vulture (Pennycuik 1972b) or 0.391 g/cm<sup>2</sup> for the Rogallo hang glider (Rodgers 1974), but typical for butterflies (Weiss-Fogh 1976). The monarch butterfly has a low aspect ratio, suggesting that the wings are a compromise between flight performance and other

TABLE 1. Comparison of the aerodynamic properties of the monarch butterflies (*D. plexippus*), the white-backed vulture, and two gliders

	Monarch	White-backed vulture*	Standard Rogallo hang glider†	Nimbus II‡
Mass (g)	0.566 ± 0.081	5.38 × 10 <sup>3</sup>	6.8 × 10 <sup>3</sup>	4.7 × 10 <sup>4</sup>
Span (cm)	11.07 ± 0.41	2.18 × 10 <sup>4</sup>	6.71 × 10 <sup>4</sup>	2.03 × 10 <sup>5</sup>
Aspect ratio	3.94 ± 0.08	6.9	2.6	28.6
Wing area (cm <sup>2</sup> )	31.18 ± 2.01	6.9 × 10 <sup>3</sup>	1.74 × 10 <sup>6</sup>	1.44 × 10 <sup>6</sup>
Wing loading (g/cm <sup>2</sup> )	0.018 ± 0.002	7.80	0.391	3.27
(N/m <sup>2</sup> )	1.77 ± 0.197	76.55	38.7	320.76

\*Adapted from Pennycuik (1972b).

†Adapted from Rodgers (1974).

TABLE 2. Performance measurements of two preserved monarch butterflies\* (*D. plexippus*) compared to the white-backed vulture and two gliders

	A	B	White-backed vulture†	Standard Rogallo hang glider‡	Nimbus II‡
Glide ratio (L/D)	1:3.6 ± 0.5	1:2.8 ± 0.3	1:15	1:4	1:45
at speed (m/s)	2.60 ± 0.46	1.60 ± 0.22	13–14	10	25
Min sinking rate	0.68 ± 0.11	0.58 ± 0.06	0.76	2.30	0.50
at speed (m/s)	2.60 ± 0.46	1.60 ± 0.22	10	9	21

NOTE: Monarch A has wings set in a maximum glide ratio configuration, specimen B has wings set in a low sink rate configuration.

\*Ballasted to 450 g.

†Adapted from Pennycuik (1972b).

‡Adapted from Rodgers (1974).

requirements. Long narrow wings are more efficient for flight but may be unwieldy.

The values for gliding angle, minimum sink, and average airspeed for specimens A and B are shown in Table 2. The observed differences between specimens A and B in gliding angle, sinking rate, and airspeed were all subjected to Kruskal-Wallis tests (Sokal and Rohlf 1969), and found to be significant with  $N = 20$ ,  $df = 1$ ,  $H = 5.663$ ,  $p < 0.025$  for glide angle;  $N = 20$ ,  $df = 1$ ,  $H = 4.234$ ,  $p < 0.05$  for sinking speed; and  $N = 20$ ,  $df = 1$ ,  $H = 7.879$ ,  $p < 0.005$  for airspeed.

Specimen A, ballasted to 0.450 mg, had a glide ratio of approximately 1:3.6, similar to the glide ratio of the Rogallo hang glider. However, the airspeed of the monarch butterfly was only 2.6 m/s (9.4 km/h) or approximately half the speed the butterfly utilizes for cruising flight. The low airspeed was accompanied by a sinking rate of 0.68 m/s. Had specimen A been ballasted to 600 mg, its airspeed and sink rate would have increased while its glide ratio should have remained unchanged. If a heavily ballasted individual could achieve gliding airspeeds in excess of 3.6 m/s (13.0 km/h) or approximately 75% of the cruising speed, its sink rate should be approximately 1 m/s. Both the measured and the extrapolated values for sinking rate in gliding monarch butterflies compare favourably with the values recorded for the

white-backed vulture and are achieved at much lower airspeeds.

The performance measurements of specimen B (Table 2) indicate that the butterflies may be able to reduce their rate of sink even further by changing their wing configuration, although at a significant cost in glide ratio and airspeed. However, if the butterflies assume the wing configuration of specimen B when they are circling in lift, then the rate of climb of a 600-mg individual would probably approximate the value that can be achieved by the white-backed vulture and a 450-g specimen could approach the climb performance of the Nimbus II.

#### Flying Strategies

Detailed observations were made of the flying techniques of 358 *D. plexippus* for a total of 167 min of observations. The butterflies were flying at temperatures ranging from 12 to 25°C under a wide range of weather conditions. It was found that migrating *D. plexippus* make extensive use of a variety of energy-saving flying techniques.

Apparent avoidance of strong head winds and utilization of tail winds were frequently observed. When the wind was from the south, southwest, or west, the butterflies remained within 1 m of the ground, and used powered flight, or did not migrate at all. An example of migration, apparently being prevented by unfavourable winds, was observed on

September 9 at 8:00 a.m. (standard time). The wind was from the south at an estimated 30 km/h and air temperature was 20°C. Several hundred butterflies were resting in a large field and only one attempted an extended flight during a 15-min observation period. Kanz (1977), Lugger (1890), and Urquhart (1960) report similar observations.

In contrast, when the wind direction was north-western to eastern, flying techniques changed. The butterflies tended to fly at heights ranging from 2 to 15 m, obtained the benefit of the tail wind, and achieved much higher ground speeds than would be possible by powered flight alone. On some days, the butterflies were achieving estimated ground speeds of more than 50 km/hr.

The butterflies' flying technique for crossing obstacles such as buildings or ridges in a head wind was very efficient (Fig. 1A). The butterflies generally remained within 1 m of the ground until they reached the lee area of a building or ridge. They then began a steep climb. Upon reaching the top where the full force of the head wind was encountered, the butterflies would flap vigorously while remaining close to the surface. Once over the top they would continue to flap their wings vigorously and descend rapidly to within 1 m of the ground. Butterflies, upon clearing an obstacle, were occasionally observed to fold their wings partially and dive towards the ground. This behaviour occurred when the wind speed on the upwind slope appeared to be particularly strong. Each step of this technique tends to conserve energy. Initiating the climb in the lee area of the obstacle allowed the butterflies to ascend through an area of relative calm. Remaining close to the surface at the top of the obstacle allowed the butterflies to take advantage of any reduction in wind speed in that region. Descending rapidly under power, or even diving through the strong lift and turbulence on the upwind side, allowed them to penetrate this area as quickly as possible and resist being blown backwards. This behaviour was particularly obvious when the butterflies were crossing the artificial ridges formed by large buildings.

When conditions were favourable for soaring, powered flight decreased in frequency and duration while soaring flight increased. Of the 358 adults observed, 121 were proceeding with a mixture of powered and soaring flight, 120 were proceeding solely by soaring, and 117 were proceeding by power. Both forms of lift, thermal, and slope were used for soaring flight and the butterflies exhibited a variety of flying strategies in response to the demands of local conditions. The proportion of the soaring flight varied greatly, apparently depending

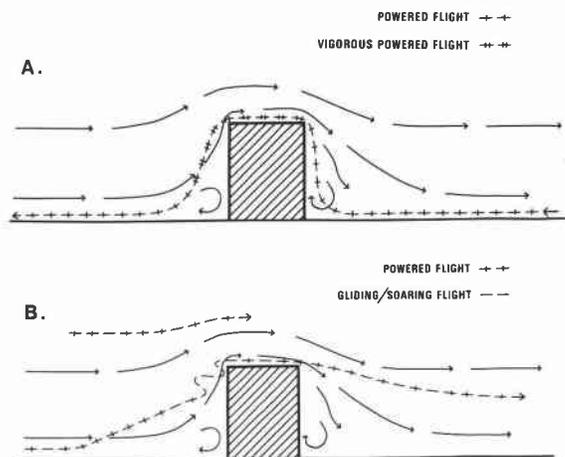


FIG. 1. Pattern of air currents produced by wind passing over an obstacle and corresponding flying techniques of *D. plexippus*. Rising air currents (lift) are produced on upwind side, descending air currents (sink) are produced on the downwind side. Turbulence can occur near the base of the obstacle on either side but is generally stronger on the downwind side. Wind velocity achieves maximum values near the top of the obstacle. (A) Flying techniques of *D. plexippus* when proceeding against the wind. Further explanation in text. (B) Flying strategies of *D. plexippus* when flying with the wind. Further explanation in text.

upon the type of lift available (slope or thermal), the strength of the lift, and the wind conditions. Slope soaring (Fig. 1B) appeared to occur whenever slope lift was encountered, but was usually associated with a tail wind. When low-flying butterflies encountered a ridge or building they would usually begin a powered climb, well in advance of the obstacle. The area of slope lift was normally entered approximately half way up the side of the obstacle. At this point the butterflies would abruptly turn away from the ridge, stop flapping, and begin to soar. The butterflies usually circled within the lift or beat back and forth as they ascended. The exact soaring technique varied, with some individuals using the traditional figure 8 pattern recommended for glider pilots (Conway 1969; Wolters 1971) in which all turns are made away from the ridge, while other butterflies soared in a more or less oval pattern. The size of patterns ranged approximately 1 m to more than 10 m. When slope lift was being produced along one section of the main building at Erindale College, some butterflies were observed to soar more than 50 m in a straight line. Upon reaching the top, most butterflies resumed cruising flight, although some individuals sailed across by gliding. When they reached the upwind side, the butterflies usually continued in powered flight and maintained most of the altitude that had been gained. This flying technique is similar to those

described for soaring birds (Pennycuik 1975) and is very efficient. The timing of the butterflies' powered climb tended to avoid any turbulence at the base of the obstacle. When they encountered the region of slope lift, which is usually strongest close to the top of the ridge, the butterflies gained maximum benefit by soaring and circling to remain within this area. The use of power by the butterflies on the opposite side of the ridge allowed them to penetrate through the downwind region of sink and turbulence with minimal altitude loss.

The time required to ascend a slope by soaring depended upon the wind conditions. One day at Erindale when there was a light wind from the NE, five butterflies slope-soaring along the south building required an average of 17 s each to gain approximately 10 m of altitude. On other days with stronger winds, much less time was required. Soaring birds are often seen using slope lift to climb high above the ridges, consequently gaining more benefit than does *D. plexippus*. However, this type of soaring requires heading into the wind to remain within the area of lift, a feat the low airspeed of gliding *D. plexippus* makes impossible under most wind conditions.

Thermal soaring (Fig. 2a, b, c) was very common. The butterflies were observed to use this type of lift, when available, with light northwesterly winds and with moderate to strong northern and eastern winds. The butterflies would frequently use thermals to achieve altitudes of 300 m, the limits of our observation. When last seen butterflies at these altitudes would usually still be climbing. A description of the thermal soaring activity observed on September 7, a particularly favourable day, provides a clear picture of the relative importance of this type of flight. On this day we recorded the greatest proportion of soaring flights for any single day of observation. Observation times were 8:00–9:00 a.m. and 12:00–1:00 p.m. During the morning observation period there was a strong east wind, the temperature was 15°C, and the sky was overcast with low clouds (cloud base estimated to be 150 m). By the midday observation period, the wind had dropped to approximately 10 km/h, the temperature was 18°C, the cloud base was broken, and cloud bases were estimated as 250 m. During the observation periods approximately 300 butterflies were observed, of which approximately 90% were using soaring as their main method of flight. The flying techniques of 87 migrants were recorded in detail. Thirty-five (40.2%) of 87 individuals were proceeding strictly by soaring, 44 (50.6%) alternated between soaring and brief bursts of powered flight, and 8 (9.2%) were proceeding

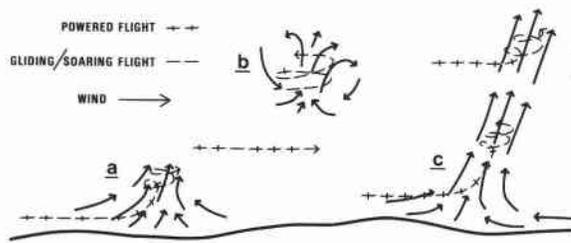


FIG. 2. Flying techniques used by *D. plexippus* when soaring in warm masses of rising air (thermals). (a) Climbing entry into thermal forming near ground, (b) circling and centering to remain within a thermal bubble, (c) butterfly near ground exhibits climbing entry, butterfly at higher altitude exhibits circling and centering entry.

strictly by power. The dominance of soaring flight over power on September 7 is also indicated by the proportion of their flight time that individual butterflies devoted to soaring. The 87 individuals were observed for a total of 2351 s. Soaring accounted for 1964 s or 83.5% of this time, and powered flight for 359 s or 15.3%. Eight individuals (9.2%), which did not soar at all during the observation period, accounted for 148 s or 41.2% of the powered flight time. The butterflies used a variety of flying techniques. Individuals already in lift were observed to soar in circles, often changing direction as they gained altitude. Pairs or small groups of butterflies were observed circling each other, soaring in close formation (within 1 m of each other), and ascending as a group. During the morning observation period larger groups of 10–30 individuals were observed soaring in loose flocks. Some individuals within a flock appeared to ignore the others and circled individually in various directions, while others within the group circled each other. Occasionally some individuals would use brief bursts of power, usually while pursuing another individual. The entire group gave the same impression of disorganization that is seen in flocks of vultures. During the morning some of the groups ascended to cloud base (150 m) and were observed flying through streamers of mist that projected below the clouds. Migrating *D. plexippus* that were not soaring were found predominantly within 30 m of the ground. By midday, the butterflies were more dispersed and large groups were no longer seen. A brief check at 5:30 p.m. indicated that almost all butterflies were foraging on the goldenrod and migrating flight had essentially stopped.

Transitions from slope soaring to thermal soaring was frequent when conditions were favourable. After soaring to the top of a slope, some butterflies were observed to continue soaring and circling while drifting beyond the slope. The soaring butterfly would shift its technique from the ovals or figure 8's typical of slope soaring to the circles

typical of thermal soaring. Usually these butterflies were observed to continue soaring and gaining altitude until they drifted out of sight.

Team flying was common among butterflies soaring in thermals and appearing to increase the efficiency of the group in locating the stronger sections of the thermal. Since the lower butterflies within a group tended to fly upwards to join individuals soaring above them, this behaviour should continuously shift the centre of the group to the areas of strongest lift. On favourable days we were able to observe the formation of groups of two or three individuals. One butterfly would begin to circle and climb in lift and adjacent butterflies would quickly alter their course, using power when necessary, to join the higher individual. The group would then more or less circle in formation and climb until they were lost to view. If a pair was involved in this activity the circles would often be very symmetrical and have a diameter of about 0.5 to 1 m. With increased numbers, as already stated, formation flying was less organized. Occasionally individuals were observed briefly soaring adjacent to gulls or hawks.

Some butterflies appeared to exhibit specialized behaviour for entering thermals. Butterflies which were flying in a straight course approximately 1–2 m above the ground were observed to initiate suddenly a powered climb. The butterflies climbed more or less vertically, drifted with the wind, and often flew an ascending spiral pattern. Upon reaching an altitude of 15 to 20 m they would stop flapping and begin to soar in circles (Fig. 2a, c). In almost all cases the butterflies would gain altitude, and would usually still be ascending when lost from sight. In a few cases the butterflies did not gain altitude, and after a few circles in various directions, would again resume the original course. Butterflies that were proceeding in cruising flight at higher altitudes did not appear to climb under power when encountering a thermal. Instead they would turn abruptly and begin soaring (Fig. 2c). These butterflies could then be seen to be gaining altitude, often quite rapidly. At altitudes above 100 m soaring butterflies frequently abandoned circling and proceeded to soar on a straight course.

### Discussion

The aerodynamic properties of *D. plexippus* are those of an ultra-light-powered glider. Their low wing loading, low airspeed, relatively low sink rate, and high maneuverability allow them to meet one of the first requirements of cross-country soaring: the ability to remain within and gain altitude from a variety of conditions of lift. However, these same

qualities, combined with a low glide ratio, make it difficult for the butterflies to fulfill two other requirements for cross-country soaring: the ability to make long glides with a minimum loss of altitude, and the ability to make progress against a head wind. Despite these handicaps, adults of *D. plexippus* in southern Ontario make extensive use of soaring flight during their annual migration to Mexico.

Monarch butterflies appear to be highly tuned to exploiting lift. They apparently use slope lift and thermal lift whenever possible and appear to adjust their flight continuously to the needs of the moment. The butterflies apparently have the ability to detect and centre in thermals, even when flying near the ground. In addition, they restrict the use of soaring flight in thermals to days when there is a tail wind component. As a result of these attributes and flying techniques, *D. plexippus* adults regularly soar to altitudes of at least 300 m above the ground (the limits of our observation techniques) and, by making use of tail winds, frequently obtain ground speeds that are much higher than the butterflies' cruising airspeed.

The maximum altitude that the butterflies can attain was not determined but may be temperature-limited. On a day with good thermal activity, an air temperature of 20°C at ground level, and a standard lapse rate of 6°C/km, the butterflies could soar to an altitude of approximately 1300 m before the temperature dropped below 12°C, the minimum temperature for flight (Urquhart 1960). On a 15°C day the upper limit drops to approximately 800 m. Of course, at any particular time the lapse rate is influenced by a variety of factors that would raise or lower the butterflies' temperature ceiling.

Substantial energy savings could be achieved by migrating *D. plexippus* if soaring flight is utilized. Flying Lepidoptera have a metabolic rate that is as much as 100 times above the basal rate (Zebe 1954). Consequently, if soaring requires approximately the basal level of metabolic expenditure, an average *D. plexippus* with an initial fat supply of 140 mg, which could fly under power for only 11 h, may be able to soar for 1060 h. For gliding speeds ranging from approximately 9 to 13 km/h, the theoretical maximum range, without pauses for feeding, would fall between 9500 and 13 800 km. In addition, because *D. plexippus* appears to restrict thermal soaring to days when the wind has a southern component, their maximum range is further extended. Even though soaring in thermals requires a great deal of flying in circles, it is obvious that this technique would allow individuals to fly much longer

and to cover much more ground between stops for feeding than would be possible by utilizing powered flight alone. Consequently, a *D. plexippus* adult leaving southern Ontario with approximately 140 mg of fat, encountering normal weather conditions (i.e. no extended periods of southern winds, rain, or low temperatures), making occasional stops for feeding, and utilizing tail winds and soaring flight, appears to have more than enough resources to migrate to Mexico. In fact the main problem facing *D. plexippus* may not be to accumulate sufficient resources for the trip, but to minimize the time and cost of the migration by finding the optimum balance between powered flight (which rapidly uses up energy sources), soaring (which requires particular weather conditions), and foraging or resting (which require time).

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