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EVIDENCE FOR USE OF WATER BALLAST BY MONARCH BUTTERFLIES, *DANAUS PLEXIPPUS* (NYMPHALIDAE)

Additional key words: migration, flight stability, gliding, soaring, lipids.

To ensure stable flight characteristics, the Center of Gravity (CG) of an aircraft must be located relatively close to the center of lift (Falk & Matteson 1971; Anonymous 1991). This constraint also applies to gliding butterflies. Gibo and Pallett (1979) investigated aerodynamic characteristics of dried and weighted (i.e., ballasted with plasticine to a mass of 450 mg) *Danaus plexippus* L. (Nymphalidae: Danainae) and found that when the wings were set in the normal gliding configuration, stable flight was possible only if the CG was located slightly posterior to the metathorax. If the CG was ahead of this position, the butterflies pitched down into a dive; if behind, they pitched up, stalled, and fell (Gibo & Pallett unpubl. data).

Because *D. plexippus* usually migrate by soaring and gliding when conditions are favorable (Gibo 1986; Gibo & Pallett 1979; Schmidt-Koenig 1985), it seems reasonable that they must keep their CG close to the stable gliding position. Stabilizing the location of the CG may be a problem for the butterflies because each individual tends to accumulate more than 100 mg of lipid during the migration, most of which is deposited in the abdomen (Beall 1948; Walford 1980; Brown & Chippendale 1974; Gibo & McCurdy 1992). Unless the increase in lipid mass is compensated for, the CG's of the butterflies could shift into their abdomens, making the migrants less capable of stable gliding flight.

Loss of the ability to glide would be a serious handicap for migrating *D. plexippus.* Gibo and Pallett (1979) calculated that the butterflies had the capacity to glide for 1060 hours before depleting an average 140 mg lipid reserve, but would deplete it within only 44 hours if they migrated by cruising, flapping flight. Thus, flapping flight is approximately $1060/44 = 24$ times more costly than gliding and soaring flight. Other researchers have determined that flapping flight in *D. plexippus* can be 28 to 31 times more costly than gliding flight (Masters et al. 1988). Furthermore, even butterflies migrating primarily by flapping flight apparently reduce energy expenditures by alternating between bouts of flapping and gliding (Urquhart 1960). Considering that *D. plexippus* from eastern North America must migrate up to thousands of kilometers to overwintering sites in southern Mexico and must accumulate large lipid reserves along the way (Brower 1985; Masters et al. 1988), a significant reduction in the capacity for gliding flight would make it nearly impossible for the butterflies to succeed.

The butterflies could offset the effect of changes in lipid mass on the location of the CG by ballasting with water. If individuals with small lipid masses carried extra water in the abdomen, perhaps in their large crop, and eliminated it as lipid mass increased, they could keep their CG's at the optimal location. Surprisingly, the increased wing loading resulting from carrying extra water would tend to improve the gliding flight performance of the butterflies. An increase in wing loading raises gliding airspeed without changing the glide angle (Lighthill 1977; Piggott 1976; Welch et al. 1977). In other words, *D. plexippus* that carry ballast water are still able to glide as far as usual from a given height, approximately 3.5 m forward for every 1 m of descent (Gibo and Pallett 1979), but can fly faster. Because any increase in gliding airspeed allows the migrants to travel faster between thermals and to compensate for a greater range of crosswind and headwind conditions, butterflies with higher wing loading should be able to make faster progress towards the overwintering sites. Furthermore, if *D. plexippus* are adapted to glide most efficiently when carrying a moderate to large lipid mass, the normal condition for most of the migration (Beall 1948; Brown & Chippendale 1974; Cenedella 1971; Gibo & McCurdy 1992), then selection may have favored carrying extra water when lipid mass was small. Here we present evidence for the hypothesis that migrating monarchs use water as ballast to partially counteract the effects of changes in lipid mass.

Wet mass, dry mass, water mass, lean dry mass, and lipid mass were determined for 234 specimens collected over a period of 8 weeks during the late summer migration in southern Ontario, Canada. Specimens were collected on 19 different days from mid August to early October, in open fields on the Erindale campus of the University of Toronto in Mississauga, Ontario, Canada. Specimens were collected from mid-to-late afternoon, corresponding to the period when migration usually ends for the day and the butterflies descend to forage and locate roosting sites (Urquhart 1960; Gibo 1986). Specimens were netted and transferred to small polyethylene bags. Within minutes of capture, each bagged specimen was placed on crushed ice in an insulated box. They were then brought to the lab and stored at −16°C until analysis. To minimize evaporative water loss when determining wet mass, each specimen was weighed immediately after being removed from the freezer. Dry mass was determined after the specimen had been dried at 60°C for 24

TABLE 1. Means and standard errors of *D. plexippus* Lipid Mass/Lean Dry Mass (LM/LDM) ratios and Water Mass/Lean Dry Mass (WM/LDM) ratios for the three phases of the migration. Sample size = 234.

Phase of migration	N	Mean ratio ± SE LM/LDM	 WM/LDM
Early	79	0.30 ± 0.01	1.54 ± 0.02
Middle	73	0.43 ± 0.02	1.44 ± 0.02
Late	82	0.23 ± 0.01	1.66 ± 0.02

hours. A standard protocol was used to measure lipid mass (Gibo & McCurdy 1992). Water mass was obtained for each specimen by subtracting dry mass from wet mass. Lean dry mass was obtained by subtracting lipid mass from dry mass.

A previous study showed that the migration in southern Ontario could be divided into 3 phases, an early phase (weeks 1–2 of the migration), a middle phase (weeks 3–4), and a late phase (weeks 5–8), and that median lipid mass peaked in the middle phase (Gibo & McCurdy 1992). If the butterflies were ballasting with water, then median water mass should show the opposite pattern and reach its minimum value in the middle phase of the migration. To control for size differences among individuals, Lipid Mass (LM) and Water Mass (WM) for each individual were expressed as ratios of the Lean Dry Mass (LDM). Thus, lipid mass ratios (LM/LDM) and water mass ratios (WM/LDM) were compared for different phases of the migration. The Kruskal-Wallis test (Stat View II 1991; Abacus Concepts, Inc., Berkeley, California, USA) was used to determine if the observed differences among the 3 groups were significant.

Table 1 shows that water mass ratio declined as lipid mass ratio increased, and increased

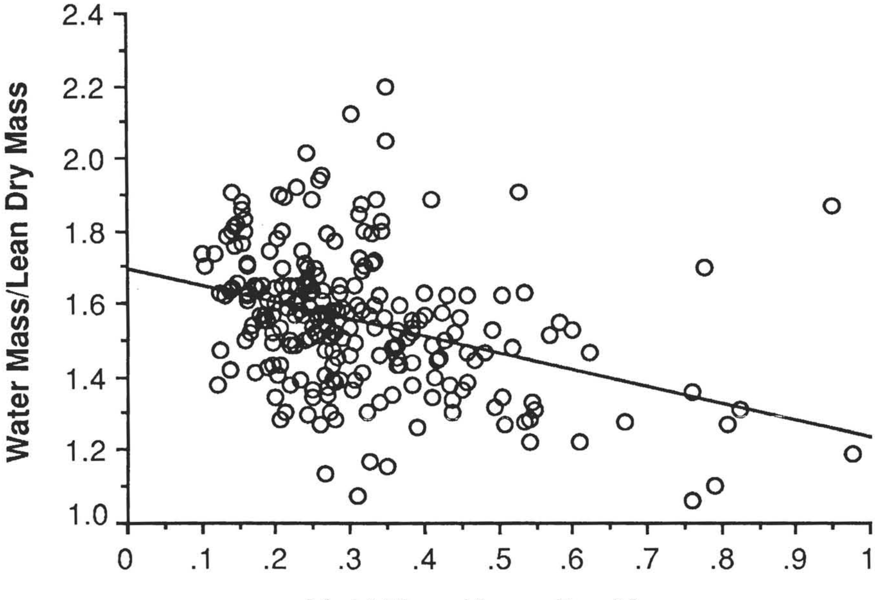

FIG. 1. Regression of *D. plexippus* lipid mass/lean dry mass (LM/LDM) ratios on water mass/lean dry mass (WM/LDM) ratios for the pooled data. Sample size = 254.

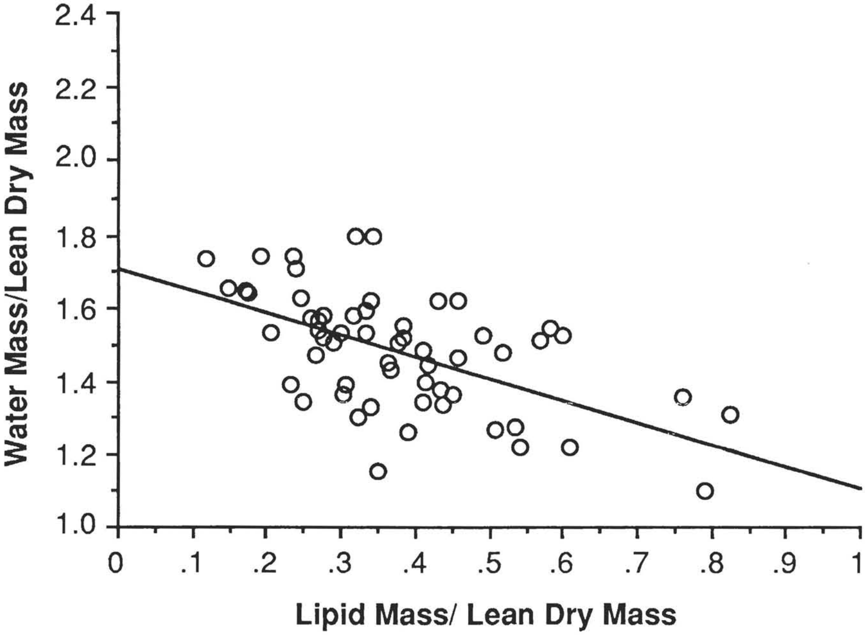

FIG. 2. Regression of *D. plexippus* lipid mass/lean dry mass (LM/LDM) ratios on water mass/lean dry mass (WM/LDM) ratios for the subgroup comprising the largest 25% of the specimens. All specimens in this subgroup had lean dry masses larger than 190 mg. Sample size = 59.

as lipid mass ratio decreased. As expected, maximum values for water mass ratio were observed in the early and late phases of the migration, while the value for lipid mass ratio peaked in the middle phase. The observed differences among the early, middle, and late lipid mass ratio groups were significant, with $n = 234$, $df = 2$, $H = 84.754$, and $P < 0.0001$. Observed differences among the early, middle, and late water mass ratio groups also were significant, with $n = 234$, $df = 2$, $H = 46.406$, and $P < 0.0001$.

Simple linear regression was used to model the relation between water mass ratio and lipid mass ratio for the pooled data ($n = 234$) and for a subgroup ($n = 59$) comprising the 25% of individuals with the greatest lean dry mass (i.e., >190 mg). The subgroup of large butterflies was analyzed separately because larger individuals are more likely to have difficulties stabilizing their CG with changes in lipid mass owing to the longer lever arm between the posterior of the metathorax and the center of mass for the abdomen. The large butterfly subgroup had a mean lipid mass ratio of 0.38 ± 0.02 and a mean water mass ratio of 1.48 ± 0.02. Figures 1 and 2 show that there was an inverse relationship between water mass ratio and lipid mass ratio for both the pooled data and the large butterfly subgroup. The regression was significant in each case, with $n = 234$, $b = -0.46$, $df = 1/232$, $F = 35.05$, $P < 0.0001$ for the pooled data, and $n = 59$, $b = -0.60$, $df = 1/57$, $F = 27.61$, $P < 0.0001$ for the large butterfly subgroup. The 95% confidence intervals for the slope were -0.31 and -0.62 for the pooled data and -0.37 and -0.84 for the large butterfly subgroup. Regression coefficients were 0.36 for the pooled data and 0.57 for the large butterfly subgroup. Consequently, the regression accounted for just 13% of the total variance observed for the pooled data and 33% of the variance for the large butterfly subgroup. As expected, the inverse relationship between lipid mass ratio and water mass ratio was stronger for larger individuals.

If migrating *D. plexippus* use water as ballast, then an increase in lipid mass is not matched by an equivalent decrease in water mass. Both the regression equation for the population ($Y = -0.46X + 1.70$) and for the subgroup of large butterflies ($Y = -0.60X + 1.71$), indicate that for each 1.0 mg gain in lipid mass, the butterflies lost, on average, approximately 0.5 mg of water, and vice versa. In each case, the impact of changes in lipid mass on the location of the CG would have been reduced but not eliminated. With each gain or loss in lipid mass, the CG tended to shift about 50% of the distance that it would have moved if elimination or uptake of water had not occurred.

One possibility that should be considered is that ballasting may occur, in part, as an automatic consequence of nectaring, particularly if nectar is stored in the crop and the amount of expansion of the crop is largely determined by lipid mass. This is particularly likely to have been the case for the early and middle phases of the migration, from mid August to mid September, when conditions were favorable for the butterflies (Gibo & McCurdy 1992). However, during the late phase of the migration, from mid September to early October, weather conditions deteriorated. This period was characterized by frosts, a reduction in the amount of time that maximum daytime temperatures were above the flight threshold of the butterflies, and an increased frequency of periods of rain and overcast sky (Gibo & McCurdy 1992). As a result, late phase migrants, apparently experiencing a reduction in opportunities to forage and, perhaps, in availability of nectar, quickly lost lipid mass (Gibo & McCurdy 1992). Although late phase migrants may have accumulated their extra water mass through foraging and ingesting large amounts of presumably low quality nectar (the butterflies were losing lipid mass), drinking water from puddles and wet vegetation seems a more likely mechanism.

It is interesting to consider how partial ballasting would affect the aerodynamics of *D. plexippus*, particularly when compared to the effects of alternate methods of adjusting the location of the CG. Assuming that butterflies with small lipid masses achieve aerodynamic balance by carrying extra water as ballast, then their total mass will increase as lipid mass increases, although at a slower rate because of elimination of ballast water. As wing loading increases, their CGs will be shifted posterior to the stable gliding position. However, by sliding their forewings back over the hind wings, the butterflies should be able to move their centers of lift sufficiently close to their CGs to produce a new stable gliding configuration. Because this maneuver also reduces wing area, wing loading will increase faster than total mass and should result in a deterioration in flight performance. Although the combination of greater wing loading and reduced wing area should increase the gliding airspeed, it also should increase both the stall speed and the rate of sink as well as steepening the glide angle. Although the migrants would be able to glide faster between thermals, they would not be able to glide as far and would descend at a faster rate. Overall, these changes reduce the ability of the butterflies to soar cross-country and increase energy expenditures for flapping flight. Consequently, even with ballasting, migration should be more costly for *D. plexippus* with large lipid reserves. Presumably, increased costs of transport are offset by an increased probability of survival once the butterflies reach the overwintering sites.

Other methods of adjusting the CG that do not involve partial ballasting are feasible, but would either prevent the butterflies from enhancing their flight performance through higher wing loading or would lower flight performance. One method would be for *D. plexippus* with small lipid masses and CG's located anterior of the stable gliding position to slide their forewings forward. This maneuver would shift the center of lift sufficiently close to CG to produce a stable gliding configuration. However, because this maneuver increases wing area, it also increases drag and reduces flight performance. Gibo and Pallett (1979) found that a swept forward wing configuration resulting in an approximately 20% increase in wing area was associated with a 40% reduction in gliding airspeed and a steeper glide angle. Butterflies with wings swept forward should not be able to fly as fast, glide as far, or compensate for as great a range of unfavorable winds, as those that maintain the standard wing configuration and adjust their CG with ballast water. On the other hand, migrants could adjust their CG without changes in wing configuration by either extending the abdomen or by inflating their crop with air to push their internal organs to the posterior of the abdomen. However, they would not achieve the increased gliding flight performance associated with greater wing loading. Finally, monarchs with large lipid masses that did not eliminate water, but simply bent their abdomen up or down to bring the center of mass closer to the center of lift, also should experience a deterioration in flight performance. The bent abdomen would protrude into the airflow, resulting in increased drag and a tendency to pitch the butterfly up or down, depending upon whether it is held above or below the wings. The increased drag would result in a steeper glide angle, an increased rate of sink, and a lower airspeed, while the pitching moment may make stable gliding flight impossible without further compensatory changes in wing configuration. Although these other methods may be used, carrying water ballast seems to be the most effective means for migrating *D. plexippus* to adjust the position of their CG to compensate for changes in lipid mass, particularly since the resulting increase in wing loading should enhance flight performance. Nevertheless, because our evidence is correlative, ballasting by migrating *D. plexippus* in response to changes in CG remains a hypothesis. Finally, since gliding and soaring flight have been reported for other migratory insects, including *Nymphalis antiopa* L. (Nymphalidae) (Gibo 1981b), *Vanessa cardui* L. (Nymphalidae) (Myres 1985), six members of the odonate genera *Tramea* and *Pantala* in the family Libellulidae (Gibo 1981a; Walker & Corbet 1975), and the desert locust *Schistocerca gregaria* Forsk (Acrididae) (Roffey 1963), these species also should be considered candidates for employing ballast to adjust their CG.

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NOTES ON *DANAUS GILIPPUS STRIGOSUS* (NYMPHALIDAE: DANAINAE) IN SOUTHERN CALIFORNIA

Additional key words: Asclepiadaceae, *Asclepias*, milkweed, host plant, distribution, striated queen.

The striated queen, *Danaus gilippus strigosus* (Bates), is a widespread butterfly that breeds throughout much of southwestern United States and northwestern Mexico (Howe 1975); it is common throughout the Colorado Desert in California (Emmel & Emmel 1973). Although adults are found regularly along the Pacific coast of California from Santa Barbara to San Diego and in the adjacent coastal mountains during autumn of most years (Coolidge 1926; Emmel & Emmel 1973), they are considerably less common in the coastal region during the spring and summer (e.g., Orsak 1977). Most late summer and fall records of this species from the coast likely represent adults that have dispersed from the desert; however, some small populations may be established in coastal San Diego County (e.g., Mission Gorge, Otay River Valley) or elsewhere where larval hosts are available (J. Brown pers. comm.). The purposes of this note are to present records of new larval hosts and document the colonization by *D. gilippus* of the coastal region of southern California.

Coolidge (1926) and Emmel and Emmel (1973) reported climbing milkweed, *Sarcostemma hirtellum* (R. Holm) (Asclepiadaceae), as the primary larval host of *D. gilippus* in the desert areas of southern California, and Emmel and Emmel (1973) suggested that purple climbing milkweed, *Sarcostemma cyanchoides* ssp. *hartwegii* (R. Holm), may be used as well. Emmel and Emmel (1973) also reported that larvae of *D. gilippus* have been taken on *Asclepias albicans* (Wats.) and *A. erosa* (Torr.), both of which occur in the Colorado Desert (Munz 1974). Comstock (1927) and Coolidge (1926) reported intro-