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Author(s): Hugh Dingle, Nigel R. Blakley and Elizabeth Ruth Miller

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VARIATION IN BODY SIZE AND FLIGHT PERFORMANCE IN MILKWEED BUGS (*ONCOPELTUS*)

HUGH DINGLE, NIGEL R. BLAKLEY[1], AND ELIZABETH RUTH MILLER
*Program in Evolutionary Ecology and Behavior, Department of Zoology,
University of Iowa, Iowa City, Iowa 52242*

In this paper we report observations on variation in flight performance and body size among tropical, temperate, and island milkweed bugs (*Oncopeltus*: Hemiptera: Lygaeidae). This is one of a series of papers on life history variation in *Oncopeltus*; photoperiodism is discussed in Dingle et al. (1980) and size dependent timing of metamorphosis in Blakley and Goodner (1978). Other papers are in preparation. The distribution of these bugs throughout much of the Western Hemisphere (Slater, 1964) allows comparison, both within and among species, of the selective forces acting on life histories. Various species occur in tropical and temperate regions and on islands throughout the Caribbean on milkweeds (Asclepiadaceae) and occasionally on plants of related families. One species, *Oncopeltus fasciatus,* is a long distance migrant to temperate North America (Dingle, 1968a et seq.), while the remainder are confined to the tropics and subtropics. General discussions of the ecology of these insects may be found in Blakley (1977), Dingle (1968a et seq.), Evans (1979), Ralph (1976, 1977), Root and Chaplin (1976), and Sauer and Feir (1973); a summary is included in Dingle et al. (1980) which also gives collecting sites for the populations discussed here. Migratory physiology is reviewed by Rankin (1978). All species discussed in this paper belong to the subgenus *Erythrischius* (Slater, 1964).

We found that flight performance differed considerably among species and populations of *Oncopeltus*. Dispersal abilities of insects vary with habitat (Southwood, 1962; Dingle, 1972), and many species occurring in isolated habitats, including islands, are apterous or brachypterous (Carlquist, 1974; Vepsäläinen, 1978). There are, however, only a few studies (e.g., Rose, 1972) which demonstrate that relatively shorter (as opposed to functionless) wings actually lead to reduced flight and none, so far as we know, demonstrating reduced flight in cases where it would be expected, for example, on islands, but where there is no obvious alteration in wing structure. In this report we demonstrate that reduced flight can occur with no apparent changes in wing morphology.

Body size has attracted considerable attention from evolutionary biologists. It is easy to measure, and it is associated with a number of other characteristics from life history statistics (Pianka, 1970; Stearns, 1976; Blueweiss et al., 1978) to an array of morphological and physiological traits (summarized by Pyke, 1978). Despite much effort by ecologists and others, however, the adaptive significance of body size is not well understood, and indeed there seems to be no general agreement on the most important selective factors (Pyke, 1978). Body size is also frequently influenced by proximate environmental conditions such as food availability, so that analysis is complex. Regardless of such phenotypic variability, the heritability of body size differences is more often assumed than demonstrated so that their adaptive nature falls short of proof. In this study we demonstrate heritable differences in body size between bugs of island

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[1] Present address: Institute for Behavioral Genetics, University of Colorado, Boulder, Colorado 80309.

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and mainland and of tropical and temperate origin by rearing insects in constant conditions in the laboratory.

Methods

Body Size Measurements

Laboratory bugs used for body size measurements were maintained at LD 14:10 and 23 C and were reared by first selecting 50 eggs, five each from ten randomly chosen clutches from stock cultures one generation removed from collection in the field. These groups of 50 eggs were placed in separate plastic boxes supplied with abundant fresh milkweed seed (*Asclepias syriaca*) and a water source. (A more detailed account of rearing, including a justification of using *A. syriaca* seed, is given in Dingle et al., 1980.) As a result of infertility, mortality from handling, and nymphal mortality, the number of adults eclosing in each box ranged from 25 to 35. From these boxes individuals of both sexes were randomly chosen, weighed at eclosion, and preserved in alcohol one week after adult eclosion for later measurement. Field collected bugs were preserved at the site of capture and returned to the laboratory. All measurements on alcohol preserved field and lab bugs were made after the bugs had been dried. Sample sizes are indicated in the appropriate tables and figures.

A number of body proportions were measured on both laboratory reared and field collected bugs and in laboratory bugs were regressed against body weight at eclosion. These regressions indicated that wing length (measured to the nearest .05 mm from the posterior notal process to the posterior margin) was linearly related to body weight and was the best and most convenient estimator of body size. Plots of wing length against weight at eclosion are displayed in Figure 1 using *O. fasciatus* and *O. cingulifer* as examples. For all species or populations within species, least squares regressions were significantly different from zero ($P < .05$ to $P < .001$); wing length is thus used as our measure of body size. Coefficients of determination

(r^2) ranged from .36 to .82 for these regressions. Weight itself was not used because high variances associated with fluctuations caused by egg production, feeding, and drinking confounded measurements in mature bugs, while measurements in bugs at eclosion resulted in high mortality from handling.

Some additional data were taken from museum specimens in the collection of the U.S. National Museum (Smithsonian) in Washington, D.C. Overall lengths of bugs were measured with calipers from the vertex of the anterior tip of the head to the posterior margin of the wings and recorded to the nearest 0.1 mm. Other measurements were not possible because the specimens were extremely fragile and therefore could not be handled.

Flight Tests

Flight duration was measured by using the tethered flight technique previously developed (Dingle, 1965 et seq.). Bugs were attached at the pronotum to an applicator stick with a small amount of fast-drying glue. When lifted free of the substrate most flew immediately, although it was necessary with some to direct puffs of wind at the head to stimulate flight. Adult bugs, which were maintained as male-female pairs, were flight tested at 8, 10, and 12 days post-eclosion. Each flight test consisted of five successive flights, and the durations of these five flights were summed to give the total flight duration for the day. These daily totals were used to compare flight durations among populations and species (Tables 5 and 6). The tests began at eight days, when cuticle deposition is complete, because previous results had shown that little flight could be expected until then (Dingle, 1965 et seq.). Ambient temperatures during flight testing varied approximately from 25 to 27 C. Between flight tests, bugs were returned to the environmentally controlled chambers in which they were reared.

With one exception all species and populations used for flight testing were maintained at 23 C on a photoperiod of LD 14:10. These conditions were chosen for
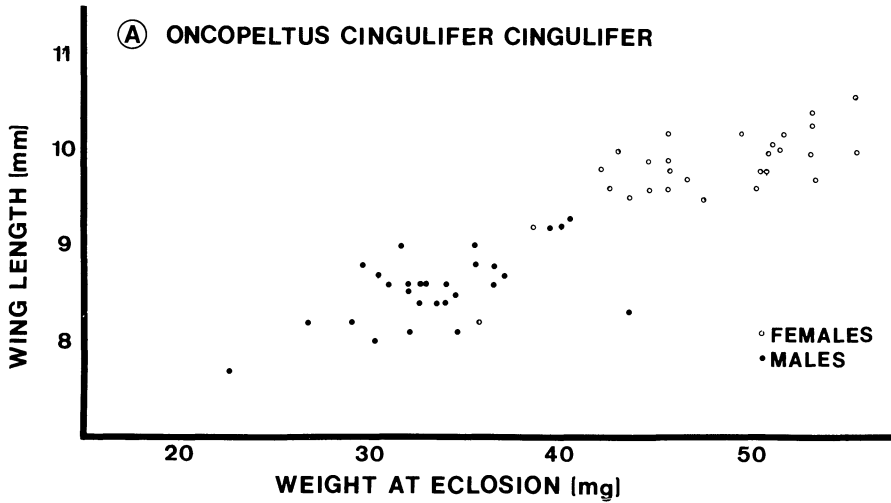
FIG. 1. Wing length as a function of weight at adult eclosion in A. *O. c. cingulifer* and B. *O. fasciatus*.

three reasons. First, they proved optimal for flight for *O. fasciatus* from north central North America (Dingle, 1965 et seq.). A temperature of 27 C suppressed flight in this population (Dingle, 1968*b*), while lower temperatures have adverse influ-

ences on reproduction (Dingle and Caldwell, 1971). Second, this photoperiod was approximately the upper extreme experienced by the various species over most of their ranges, and therefore likely to have the overall least potential of "normal"

FIG. 1B.

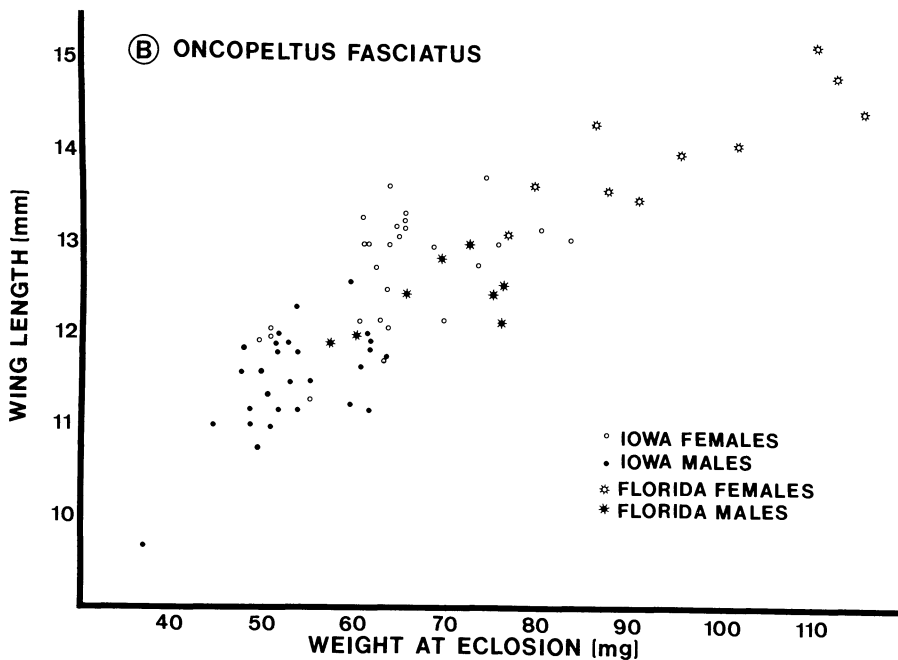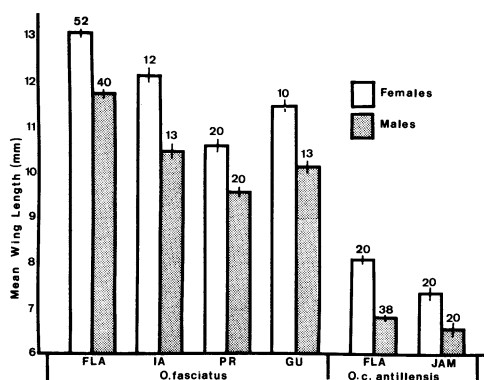FIG. 2.   Mean wing length for field collected samples of *O. fasciatus* and *O. c. antillensis*. Numbers above bars indicate respective sample sizes; lines indicate standard errors. FLA, Florida; IA, Iowa; PR, Puerto Rico; GU, Guadeloupe; JAM, Jamaica.

photoperiods to induce diapause (Dingle et al., 1980). Diapause is a possible confounding influence on flight (see below). Third, growth and reproduction at 23 C on both long and short days were, for all populations and species, comparable to that of *O. fasciatus* (Dingle, Miller, and Klausner, unpubl.). There was no evidence of suppressed responses in tropical bugs at what for them would be somewhat low daytime temperatures. Since flight and reproduction are intimately related (Rankin, 1978), we assume this temperature has no adverse influence on flight.

The exception to the LD 14:10 23 C rearing conditions was *O. cingulifer*. Here 50 of the 90 individuals flight tested were reared at LD 14:10 23 C, while the remaining 40 were reared at LD 14:10 27 C. This was done as a partial control in the event that higher temperature promoted flight in this tropical species. No difference in flight performance between the two *O. cingulifer* samples was detected. The data are therefore combined for presentation and analysis (Table 5).

Only days 8, 10, and 12 post-eclosion were used for flight tests because under some conditions and in some populations of *Oncopeltus fasciatus* individuals begin reproducing at around 15 days, while in

other populations some individuals enter reproductive diapause even at LD 14:10 (Dingle, 1978; Dingle et al., 1980). Since reproduction suppresses flight while diapause permits it (Dingle, 1978; Rankin, 1978), there is a potential confounding of influences in comparisons of older bugs. The 8–12 day period includes the time of migration even in early reproducing individuals (Dingle, 1965 et seq.) so long as migratory potential exists. The potential influence of diapause is thus removed by restricting flight test comparisons to this age interval.

RESULTS

Body Size

We collected sufficient numbers of adults of two species of milkweed bug, *Oncopeltus fasciatus* and *O. cingulifer antillensis*, from five locations for comparisons of body size differences among field populations. The data for mean wing lengths of both males and females of these samples are given in Figure 2. In the case of *O. fasciatus*, individuals from South Florida are conspicuously larger than those from Iowa. Furthermore mainland bugs are larger than island individuals, and Guadeloupe are larger than Puerto Rico (differences are significant at $P < .001$ and $P < .0001$). Differences in habitat or host plants do not account for the among-population body size differences. All samples were taken from roadsides and pastureland which contained stands of *Asclepias*. In Florida and the Caribbean this was *A. curassavica* so that the largest and smallest bugs, from Florida and Puerto Rico respectively, were both feeding on the same hosts as were both island populations. The intermediate sized Iowa insects were collected from *A. syriaca*, a plant with a much larger seed crop and fruit. All bugs were collected between June and September.

Populations of *O. cingulifer antillensis*, the subspecies occurring in the northern half of the range of this species (O'Rourke, 1977), were collected in South Florida (Hialeah, Everglades) and Jamaica (near

TABLE 1. *Mean wing lengths in millimeters ($\pm SE$) of laboratory reared* Oncopeltus cingulifer antillensis *(Florida, Jamaica) and* O. c. cingulifer *(Trinidad, St. Vincent) with associated* t *values for indicated comparisons.*

Location	Females	N	t	Males	N	t
Florida	9.11 ± .08	13		7.82 ± .10	15	
Jamaica	8.69 ± .13	20	2.39*	7.65 ± .04	20	1.56 N.S.
Trinidad	9.86 ± .08	20		8.33 ± .07	20	
St. Vincent	8.96 ± .08	14	8.08**	7.91 ± .08	18	3.92**

    * Significant at .01 level.
    ** Significant at .001 level.

Discovery Bay, Browns Town, and Ocho Rios), and the mean wing lengths are indicated in Figure 2. Florida females are significantly larger than Jamaica females ($P < .001$, $F_{1,38} = 23.50$), and Florida males are significantly larger than Jamaica males ($P < .02$, $F_{1,56} = 6.22$). As with *O. fasciatus,* the evidence from the field samples suggests that mainland bugs are larger than island bugs.

We made a sufficient number of collections from different locations with subsequent rearing of laboratory stocks to allow within-species among-population comparisons of body size in two species, *Oncopeltus fasciatus* and *O. cingulifer,* and among-species comparisons for these and two exclusively tropical species, *O. sandarachatus* and *O. unifasciatellus.* Data from lab reared *O. cingulifer antillensis* suggest that bugs of island origin are smaller than those of mainland origin (Table 1), thus confirming field data. The difference in mean wing length between Florida and Jamaica females indicates that Jamaica females are significantly smaller. The difference between males, while not statistically significant, is in the same direction.

The situation with *O. c. cingulifer* is somewhat more complicated. Here comparisons are made between populations originating in Trinidad, a relatively large continental island which at its nearest point is only 11 mi from the South American mainland, and St. Vincent a small mountainous relatively isolated oceanic island in the Lesser Antilles to the North of Trinidad. In both sexes, bugs originating from St. Vincent are significantly smaller,

suggesting a pattern of smaller bugs on smaller more isolated islands. Since Trinidad is so close to the mainland, however, there is some question as to whether it should be considered an island from the perspective of a milkweed bug. It might be viewed as an extension of the mainland and in this comparison as an analogue of Florida. Further support for this view comes from the fact that we found two species of *Oncopeltus* on Trinidad, *O. varicolor* and *O. unifasciatellus,* which are otherwise known only from mainland faunas.

Finally, there is a size difference between the two subspecies, *O. c. antillensis* from the northern half of the species range and *O. c. cingulifer* from the southern half. The two subspecies are distinct with respect to color and pattern, probably as the result of Mendelian segregation. *Oncopeltus c. cingulifer* is also the larger of the two in areas of Central America where the two morphs overlap in range (O'Rourke, pers. comm.). Comparing size alone between the southern and northern Caribbean populations therefore seems inappropriate. Other considerations of morph differences are beyond the scope of this paper.

The mean wing lengths of the two exclusively tropical species, *O. unifasciatellus* and *O. sandarachatus,* are given in Table 2. *Oncopeltus unifasciatellus* was collected near Cali, Colombia (Dingle et al., 1980) and is smaller than either *O. cingulifer* or *O. sandarachatus* from Trinidad, the nearest most continental location for these species (see above and Table 1). These size differences are significant in

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TABLE 2. *Mean wing lengths in millimeters (±SE) of laboratory reared* Oncopeltus unifasciatellus *(Colombia) and* O. sandarachatus *(Barbados, Trinidad) with associated* t *values for indicated comparisons.*

Species	Females	N	t	Males	N	t
O. unifasciatellus	8.96 ± .11	20		7.72 ± .06	20	
O. sandarachatus (Barbados)	10.83 ± .14	20	3.21*	9.38 ± .13	20	1.14 N.S.
O. sandarachatus (Trinidad)	10.28 ± .10	20		9.22 ± .05	20	

* Significant at .01 level

both cases for males and females (*P* < .001 all comparisons). Comparisons between *O. sandarachatus* from Barbados and Trinidad indicate that bugs from the Barbados population are larger, although the difference is statistically significant only for females. These size differences are the reverse of those for *O. cingulifer* in that bugs from the more isolated island are larger, not smaller. The situation in Barbados is particularly interesting and is considered further in the Discussion section below.

The most extensive sampling of wing length variation among laboratory populations of differing geographical origin was done in *O. fasciatus* (Table 3). The significance levels of various contrasts among these populations using Mann-Whitney *U* tests (Siegel, 1956) are displayed in Table 4. First, it is apparent that temperate zone bugs (including Florida) are larger on the average than tropical bugs, with the single exception of Maryland females which are smaller than those from Mexico. Secondly, insects from Iowa and Maryland are smaller than their Georgia and Florida counterparts. Within

TABLE 3. *Mean wing lengths in millimeters (±SE) for laboratory reared* Oncopeltus fasciatus *populations.* N = 20 *for all examples except Maryland where* N = 33.

Location	Females	Males
Iowa	12.56 ± .07	11.51 ± .07
Maryland	11.73 ± .17	10.82 ± .13
Georgia	13.00 ± .15	11.51 ± .16
Florida	13.17 ± .09	12.04 ± .10
Mexico	12.16 ± .02	10.56 ± .02
Puerto Rico	10.95 ± .08	9.65 ± .07
Guadeloupe	11.26 ± .06	9.88 ± .08

these pairs Iowa bugs are significantly larger than Maryland, and Florida males are significantly larger than Georgia males; females of these latter two groups are not significantly different. The size differences between Iowa and Florida, especially in females, confirm size differences observed in field collections of these two groups (Fig. 2).

The size differences between island and mainland *O. fasciatus* found in field collections were also found in laboratory reared individuals. To avoid confounding by possible temperate vs. tropical influences, only tropical mainland bugs (from Mexico just south of Mexico City) are contrasted with the island populations, with the mainland insects found to be significantly larger. This observation again supports field data as does the observed difference between the insects originating in Puerto Rico and Guadeloupe. In this latter instance Guadeloupe females are significantly larger (*P* < .001); the difference between males is in the same direction but does not reach criterion of *P* < .05 (although close).

One further observation is of interest with respect to wing lengths in these populations. Note that in the Maryland and Georgia samples the highest standard errors occur, suggesting that these populations are more variable. This greater variability is confirmed by the coefficients of variation (8.3 for Maryland females, 5.2 for Georgia females, as opposed to 2.5 and 3.1 for Iowa and Florida females, respectively) but is best indicated by the total ranges of wing lengths found. Females of the Maryland population, for example, ranged from a minimum of 10.67 mm, almost the smallest female measured, to

TABLE 4. *Values of U (Mann-Whitney Statistic) and associated probability levels (P) for indicated contrasts of wing-lengths for different groupings of* O. fasciatus.

	Females		Males	
Contrast	U	P	U	P
Temperate (IA, MD, GA, FL) vs.				
Tropical (Mex., PR, Guad.)	1070.5	<.0001	481.0	<.0001
Iowa, Maryland vs. Georgia, Florida	311.5	<.0001	475.0	<.0001
Mexico vs. Puerto Rico, Guadeloupe	57.0	<.0001	98.0	<.0001
Georgia vs. Florida	182.0	>.6260	109.0	<.0140
Maryland vs. Iowa	125.0	<.0001	113.0	<.0001
Guadeloupe vs. Puerto Rico	82.5	<.0010	133.0	<.0690

14.35 mm, the largest bug encountered, a spread of 3.68 mm. Georgia females showed a spread of 2.48 mm (11.35–13.83 mm). In contrast Iowa and Florida females ranged over only 1.05 and 1.50 mm, respectively. Similar results can be demonstrated for males.

Attempts to compare among populations from different geographic areas using museum specimens suffered from three principal sources of error. First, since it was not possible to handle the fragile specimens, sex could not be readily determined and samples therefore contained an indeterminate amount of within species variance. Secondly, the museum collection was not a systematic field sample; some sites were represented by many individuals, others by only a few. Finally, bugs were collected haphazardly with respect to season, and our observations suggest that environmental conditions can exert significant influences on body size (Blakley and Goodner, 1978).

In spite of these difficulties, however, consistent differences in overall length (front of head to tip of wings) were apparent both within and among species in the tropics. Comparisons of mean overall lengths indicated that Bahamas *O. cayensis* (10.95 mm) were smaller than Jamaican and Puerto Rican *O. aulicus* (11.54 mm) which in turn were smaller than various species from mainland Central and South America (11.64–12.51 mm). Except for a local population of *O. cayensis* in South Florida, it and *O. aulicus* are known only from Caribbean islands (Slater, 1964). Within species, *O.*

fasciatus from Cuba, Hispaniola, and Puerto Rico ($\bar{x}$ = 12.81 mm) were smaller than those collected in Central America (14.87 mm). Similarly *O. c. cingulifer* from Grenada (9.70 mm) were smaller than their counterparts from Central America (10.67). No tests of significance were attempted because of the sampling problems outlined, but the trend is suggestive and indicates that island bugs are smaller than mainland, as already noted above for our field collected and laboratory reared samples.

Flight

Three tropical species, *O. c. cingulifer, O. sandarachatus,* and *O. unifasciatellus,* were tested for length of tethered flight. The number of individuals of each species whose summed totals of five flights (see Methods) reached 30 min, 5–30 min, or less than 5 min on at least one day or who never flew are indicated in Table 5. There was little long duration flight in any of these species. In laboratory reared bugs, no *O. unifasciatellus* and only 2% and 3%, respectively, of *O. cingulifer* and *O. sandarachatus* flew for more than 30 min, our previous operational definition of migratory flight (Dingle, 1965 et seq.); most flew for only a few seconds. The longest single flights for *O. cingulifer* and *O. sandarachatus* were 75 and 62 min, respectively, while the longest *O. unifasciatellus* flight was only 5 min 10 sec. It is perhaps worth noting in this connection that the *O. unifasciatellus* culture had been in the laboratory for several generations (Dingle et al., 1980), while the other two species

TABLE 5. *Distributions of longest daily tethered flight durations for different species of* Oncopeltus.

| Species | No flight | Number flying for | | | Total | Proportion flying >30 min |
		<5 min	5–30 min	>30 min		
O. cingulifer	0	80	8	2	90	.022
O. cingulifer (Trinidad)	0	(47)	–	8	55	.146
*O. sandarachatus**	0	50	8	2	60	.033
O. unifasciatellus	7	126	2	0	135	0

* Data for field collected bugs. Tethered flight in this test was divided into no flight, flight <30 min, and flight >30 min (see text for details).
** Flights of *O. sandarachatus* were slightly but significantly longer than those for laboratory populations of the other 2 species ($P < .05$, Mann-Whitney U tests).

had been recently collected in the field. Although long term laboratory maintenance does not depress flight in *O. fasciatus* (Dingle, 1965), an effect here on *O. unifasciatellus,* while unlikely, cannot be completely ruled out.

Although it did not differ significantly from either of the other species in the proportion of flights in each category, *O. sandarachatus* did display longer flights overall. When longest summed daily flights were ranked and compared between species, those of *O. sandarachatus* were significantly longer than those of either of the other two species ($P < .05$ for both comparisons using a Mann-Whitney U test). We therefore conclude that slightly but significantly longer flights occur in *O. sandarachatus.*

Table 5 also includes results from a Trinidad field population of *O. cingulifer.* These bugs were flight tested on the day they were collected in the field and were tested only once. The reproductive history of these bugs was followed for the next several days, and the data for onset of copulation and oviposition indicated that they were probably between 8 and 15 days post-eclosion at time of capture, well within the window for flight testing. They were collected by first removing all bugs from a well-defined milkweed patch and then capturing all new immigrants as they arrived. These particular individuals are therefore likely to be selected dispersers, and this is in fact suggested by the flight data. A higher proportion of these bugs, 14.6%, flew for over 30 min than of any other sample in Table 5. In spite of such selection, however, this population did not reach flight levels displayed by unselected (by us) temperate populations of *O. fasciatus.* The flight data thus suggest less migratory tendency in these tropical species even in a situation biased toward migrants by the method of collecting the bugs.

Both field and laboratory observations, on the other hand, indicate that northern populations of *O. fasciatus* are migratory and indeed are unable to survive the winters (Dingle, 1968a et seq.; Ralph, 1977).

TABLE 6. *Distributions of longest daily tethered flight durations for different populations of* Oncopeltus fasciatus.

| Population | No flight | Number flying for | | | Total | Proportion flying >30 min |
		<5 min	5–30 min	>30 min		
Michigan	0	193	44	74	311	.238
Iowa	0	114	27	44	185	.238
Maryland	0	33	7	13	53	.245
Georgia	0	91	7	6	104	.058
Florida	1	30	6	8	45	.178
Mexico	0	96	2	0	98	0
Puerto Rico	6	48	5	3	62	.048
Guadeloupe	13	28	1	2	44	.045

The migratory tendency is reflected in the flight performances of populations of this species originating in Iowa, Maryland, and Michigan (Table 6) in all of which approximately 24% flew at least once for over 30 min, a higher proportion than for any other species or population. The longest flights in these samples were for longer than 9 h nonstop which in the field would carry a bug some hundreds of kilometers, especially if wind-aided (Dingle, 1966). The longest single consecutive flight recorded was 36 h for an Iowa individual.

The southern populations of *O. fasciatus* all display less long duration flight than the northern, as indicated in Table 6 by the proportions flying over 30 min. The highest proportion of such flights, approximately 18%, occurred in the Florida population. The mean total daily flight durations of this sample were found to be significantly less ($z = 2.47$, $P < .007$, Mann-Whitney U test) than those of the Maryland bugs, the closest population known to be migratory. We conclude from this that our flight tests reveal less migratory tendency in the Florida sample than in the northern groups. Differences between northern bugs and the Georgia and tropical samples are even more apparent, with little tendency for long duration flight in the various southern populations.

Differences in flight performance were also noted among *O. fasciatus* of southern origin. Although displaying less long duration flight than northern bugs, the Florida sample showed more long flights than any of the other populations including that from relatively nearby Georgia. The low power-efficiency median test (Siegel, 1956) indicated differences significant at $P < .02$ to $P < .001$. Differences also existed among the three tropical samples (Mexico, Guadeloupe, Puerto Rico). A few of the island bugs displayed long flights, but several never flew, especially those from Guadeloupe. A comparison between Mexico and Puerto Rico showed that longer flights tended to occur with greater frequency in the Mexican sample ($z = 2.40$, $P < .008$, Mann-Whitney U) even though the longest flights were demonstrated by

Puerto Rican individuals. Note also that all Mexican bugs flew, if only for a few seconds, while six of the Puerto Rican never did, suggesting a higher threshold for flight in the latter. A higher threshold was quite apparent in the Guadeloupe population; not only did 13 bugs never fly, but several others required greater than normal stimulation to initiate flight (repeated tarsal release and puffs of wind on the head). A comparison of the distributions of flight durations for Guadeloupe and Puerto Rico (Table 6) indicates that a significantly higher proportion of the former flew only briefly or not at all ($\chi^2 = 7.27$, 2 d.f., $P < .03$). The data for southern populations of *O. fasciatus* (Table 6) thus suggest that flight tendency, presumably reflecting migratory behavior, declines along a geographical gradient from the continental mainland (Florida, Mexico) to the large island of Puerto Rico and finally to the smaller, more isolated island of Guadeloupe.

Discussion

A clear result of these studies is that the tropical species, *O. cingulifer, O. sandarachatus,* and *O. unifasciatellus,* and tropical and subtropical populations of *O. fasciatus* display less migratory behavior, as indexed by tethered flight, than temperate populations of *O. fasciatus* reared and tested under similar conditions of temperature and photoperiod. This is consistent with what is known of the natural history of these species. In the temperate zone *O. fasciatus* is a migrant which regularly travels long distances between seasons (Dingle, 1968a et seq.). In the tropics and subtropics movement is over a shifting mosaic of habitats brought about by asynchronous fruiting of the host plants (Root and Chaplin, 1976; Blakley, 1977 and unpubl.; Klausner, 1979) rather than over long distances as a consequence of changing seasons. There is in fact little seasonal variation in the milkweed habitat in the tropics (Blakley and Goodner, 1978; Dingle et al., 1980). The enhanced flight of northern *O. fasciatus* populations probably reflects increased selection for migra-

tion since these insects are incapable of surviving severe winters even in the adult reproductive diapause characteristic of the species (Dingle, 1968a).

A second result is that less flight occurs overall in *O. fasciatus* populations originating from islands, in spite of relatively long flights by a few individuals (Table 6). Bugs from Puerto Rico and Guadeloupe displayed generally shorter flights with higher thresholds than their conspecifics from Mexico or Florida. The highest flight thresholds occurred in bugs from Guadeloupe, the smaller and more isolated of the two islands. These data are consistent with other observations on the evolution of reduced flight and flightlessness on islands or in isolated habitats (Darlington, 1971; Carlquist, 1974; Järvinen and Vepsäläinen, 1976; Vepsäläinen, 1978; Dingle, 1980). There is probably selective advantage to retaining some flight on islands to facilitate local dispersal between milkweed patches which fruit asynchronously as they do on the tropical mainland (Blakley, 1977 and unpubl.; Blakley and Goodner, 1978). The island data otherwise seem consistent with a model which predicts gradual loss of dispersal genotypes in stable populations (Roff, 1975). This occurs because dispersal genotypes leave and are in general not replaced by immigration. As the number of dispersers becomes low, their descendants decrease in numbers relative to nondispersers, and the number of dispersing offspring is reduced by mating with nondispersers. Under a number of circumstances a stable dispersal polymorphism can also evolve. The generality of the model is discussed further by Dingle (1978) and by Järvinen and Vepsäläinen (1976) who extend it to the evolution of wing dimorphism in gerrids under density-dependent conditions.

If island bugs are the descendants of migrant colonizers, as seems likely, the reduced flight in the Puerto Rico and Guadeloupe *O. fasciatus* populations may have evolved in less than 400 years or approximately 2,400 generations (assuming 6 generations of 60 days each per year, a figure which seems reasonable based on

laboratory data). The only native species of *Asclepias* in the Caribbean is *A. nivea,* a relatively uncommon plant whose distribution is confined to the Greater Antilles (Woodson, 1954). The more common *A. curassavica,* now the principal host plant for *Oncopeltus,* was apparently introduced by man into the West Indies from South America because of its reputed medicinal properties. The earliest recorded introduction we have found is from Jamaica to Barbados in the early eighteenth century (Gooding et al., 1965; Watts, 1966). Thus we know the plant was well established in Jamaica by about 1700. Extrapolating backwards in time and considering the rates of communication between islands, it could not have been introduced from South America before the middle of the sixteenth century and probably reached Guadeloupe considerably later. *Oncopeltus fasciatus* may have occurred on the native *A. nivea* in Puerto Rico before the arrival of *A. curassavica,* but it could not have done so in Guadeloupe. Its evolution there must perforce have been recent.

Similar reasoning can be applied to the evolution of body size differences, at least in the island populations of *O. fasciatus.* These differences are not the spurious result of reduced wing lengths resulting from selection for reduced flight. Careful examination of the insects indicated that wing lengths relative to body lengths remained unchanged, that is, there was an overall and uniform reduction in body size. The question then remains, what selective forces influence body size in these species of *Oncopeltus?*

Several hypotheses have been advanced to explain size differences in animals (summarized in Pyke, 1978). Briefly, the most relevant of these and the reasons for rejecting them for *Oncopeltus* are as follows: (1) Competition occurs involving either character displacement (Brown and Wilson, 1956; Hutchinson, 1959) or competitive gradients whereby larger can exclude smaller (Brooks and Dodson, 1965). Neither model applies to *Oncopeltus* species which when sympatric use the same resource (*A. curassavica*) and fre-

quently converge in size (e.g., *O. cingulifer* is larger on Trinidad, where it overlaps the larger *O. sandarachatus,* than on St. Vincent, where it occurs alone). There is also no evidence for replacement of smaller by larger species. (2) Size convergence may be expected where efficiency of resource utilization would result (Schoener, 1969, 1970). This hypothesis depends on changes in size of food items so is inapplicable to *Oncopeltus* since the same host plant, *A. curassavica,* occurs over most of the range of the genus. Where the host plant is *A. syriaca,* with thicker pods, one would expect the largest bugs (Iowa, Maryland). In fact Florida bugs, which feed on *A. curassavica,* are the largest. The lack of correlation between husk thickness and size also implies no optimum size for foraging efficiency (Pyke, 1978). (3) Size changes latitudinally, for example, Bergmann's rule. There is no consistent latitudinal variation in *Oncopeltus,* and all possible clinal variation in size seems to occur, for example, in *O. fasciatus* Florida > Iowa > Mexico > Maryland. (4) Insects are larger in the tropics presumably, because of a longer growing season (Schoener and Janzen, 1968). In multivoltine species, there may be multimodal latitudinal gradients (Masaki, 1978). There is no consistent relationship between length of growing season and size in *Oncopeltus* or for that matter, between size and growth rate (Blakley and Goodner, 1978).

The most reasonable hypothesis for *Oncopeltus* is that there is an association between body size and migration-diapause strategy. Comparisons among species indicate that the two largest of this study, *O. fasciatus* and *O. sandarachatus* and especially the former, display more flight than the two smaller species tested (Tables 5 and 6). Similar relationships occur in other insects. *Dysdercus fasciatus,* the largest of three African cotton strainers (Heteroptera: Pyrrhocoridae) studied, was the most migratory (Dingle and Arora, 1973). In the New World the most migratory of several species examined was *D. bimaculatus,* also the largest (Derr, 1977

and unpubl.; Derr, Alden, and Dingle, unpubl.). The migratory monarch butterfly, *Danaus plexippus* (Urquhart, 1960), is larger than the nonmigratory queen, *D. chrysippus.* In New England *Notonecta* (backswimmers, Heteroptera) the largest species is the migratory one most common in temporary habitats (Streams and Newfield, 1972). And finally, in his now classic discussion of character displacement in water boatmen (Heteroptera, *Corixa*), Hutchinson (1959) indicates that one of the largest species is a "fugitive species." Such a relation among species would explain why presumably nonmigratory island species of *Oncopeltus* (*O. aulicus, O. cayensis*), are generally small as suggested by measurements on museum specimens.

A similar overall relationship between size and flight is evident within *O. fasciatus,* but the situation is considerably more complex. Certainly body sizes of the two island populations (Puerto Rico, Guadeloupe) which fly the least are the smallest, but the slightly more active Puerto Rican bugs are the smaller of this pair. Likewise migratory North American invididuals are relatively large although the migratory Maryland sample is smaller on the average than Florida and Georgia bugs which fly less. In view of the variance in size in the Maryland population (Table 3), which contained both the largest and almost the smallest specimens examined, it would be interesting to know the correlation between size and flight both in these bugs and in samples from other geographic origins; such experiments are planned.

If a correlation between body size and migratory capability exists in *O. sandarachatus,* it suggests a reason why we found bugs of this species originating in Barbados larger than those from Trinidad, contrary to expectation. The host plant, *A. curassavica,* is almost completely consumed on Barbados by caterpillars of the monarch butterfly with the result that the bugs are unable to complete their life cycles there (Blakley and Dingle, 1978). The bugs captured on this island are therefore likely to be migrants from elsewhere, and on the assumption of a

positive relation between size and flight, as a consequence, large. As with *O. fasciatus,* this within species association of size with flight is in need of a direct test.

The possible advantages of larger size to a migrant insect range from robustness to withstand the rigors of flight to enhanced reproductive potential at the time of colonization (Dingle, 1972, 1974, 1980). In some dipterans energetic costs of flight do depress egg production (Rygg, 1966; Roff, 1977). These costs are evidently mitigated by increased body size, and dispersers in *Drosophila melanogaster,* at least, are larger than nondispersers (Roff, 1977). The situation is less clear in *O. fasciatus* where tethered flight per se failed to reduce fecundity, but a period of starvation, as might occur during migration, did (F. Slansky, Jr., unpubl.).

Large size does apparently mitigate starvation, at least within some species. Larger individuals of *O. fasciatus* and *O. cingulifer* are better able to survive starvation than smaller insects. There was, however, no difference between the two species, even though *O. fasciatus* is considerably larger. Factors other than body size alone thus influence survival when food is scarce.

In *O. fasciatus* the ability to survive starvation could be an advantage during long periods of diapause when feeding is reduced. North American populations all consist of relatively large bugs and all display long-term diapause. In Iowa this delay of reproduction in the fall is necessary to permit migration (Dingle, 1978). The occurrence of flight with diapause suggests that increased size can be associated with both behaviors (hence a migration-diapause strategy). What we do not know is how long migratory Iowa bugs are likely to be in diapause in nature before resumption of feeding on a suitable food source. The still larger Florida bugs display diapause under more experimental conditions, and in some individuals for longer periods, than northern bugs, probably in response to unpredictable seasons and environments (Klausner, 1979; Dingle et al., 1980). The large Georgia bugs also diapause under more conditions than those from Iowa.

The Maryland *O. fasciatus* are puzzling. The mean size is small relative to other North American bugs, but at the same time the Maryland population contained the largest bugs measured, and the variance for size is high. Such size variance is likely to be a function of temporal variability (Roff, 1978) which may be considerable in Maryland. The climate is maritime, with an autumn season which frequently, but not always, permits the production of a full second generation at the end of the breeding season (Ralph, 1977). Why the majority of individuals should be small, however, is unclear and probably the result of other factors.

These other potential factors include the interaction between adult size and nymphal growth rate. Optimal adult size is apparently a compromise between selection for larger adults but for smaller nymphs, in order to complete the nymphal period more rapidly (Blakley, 1977 and unpubl.; Blakley and Goodner, 1978). Clearly the relation between size, reproduction, growth, diapause, and migration is complex and is under active study in this laboratory.

We can conclude from these studies that body size differences in both *O. fasciatus* and *O. cingulifer* are heritable. That this is the case is indicated by rearing the insects in the laboratory where size differences observed in field samples were confirmed when all bugs matured under similar environmental conditions. Differences are therefore presumably adaptive whatever the relevant selective forces. Heritability estimates (narrow sense) for Iowa *O. fasciatus* based on an extensive sib analyses are on the order of .4–.5, indicating sufficient additive genetic variance for fairly rapid responses to differences in selection (Dingle, Klausner, and Hegmann, unpubl.). Whether differences in additive genetic variance for body size exist among populations, as suggested by differences in phenotypic variance observed under constant laboratory conditions, remains to be tested.

From our data these characteristics of *Oncopeltus* populations and species emerge. Tropical bugs under the conditions of these experiments, are less migratory and smaller than temperate and also display no diapause (Dingle et al., 1980), apparently as a response to the relatively predictable, at least temporally, tropical environment. Isolation on islands further reduces flight and, apparently, size. Northern populations of *O. fasciatus,* the only species to invade the temperate zone, are relatively large and display migration and diapause, both obvious adaptations to more severe climates. The intermediate populations are more variable on one or more counts apparently in response to less predictable conditions. The genetic and environmental sources of that variability are under investigation.

SUMMARY

Both within and among species of milkweed bugs, *Oncopeltus* (subgenus *Erythrischius*), tropical forms are smaller than temperate and island are smaller then mainland. These differences were determined from measurements on field collected and laboratory reared bugs and from museum specimens. Laboratory rearing in constant environments indicated that the differences observed among populations and species are heritable and presumably adaptive. Variation in size between island and among continental populations of *O. fasciatus* were not always in predicted directions and are presumably influenced by local conditions, especially environmental heterogeneity (temporal and spatial variability).

Tests for flight potential using tethered insects also indicated significant differences among species and populations. Tropical species and tropical populations of *O. fasciatus* flew less than temperate populations of *O. fasciatus*. These generally low flight performances of the tropical bugs presumably reflect adaptation to relatively equable and predictable habitats with little selection for long-distance migration. In contrast, migration is a neces-

sity for temperate zone bugs since they cannot survive the winter. Intermediate levels of flight were observed in bugs of Florida origin and, along with a variable diapause (Dingle et al., 1980), is probably a reflection of unpredictability in Florida climate and habitats. The least flight was recorded in bugs from the islands of Puerto Rico and Guadeloupe, consistent with many observations of flightlessness in island insects.

In general there was an association between larger size and longer flight. Of the tropical species, the largest is *O. sandarachatus* which also displays the longest flights. Since this species cannot survive on Barbados because of the destruction of its host plants (Blakley and Dingle, 1978), bugs captured there were probably migrants, accounting for their large size relative to a Trinidad sample. Northern and migrant *O. fasciatus* are also generally larger, but large Florida and on the average small, but highly variable, Maryland bugs are evidently strongly influenced by local conditions which confound general trends. A number of competition, convergence, or clinal models fail to explain size differences in *Oncopeltus*. Larger bugs survive starvation longer (Blakley, 1977) suggesting that large size may be an advantage during food deprivation and other stresses arising during migration or diapause. A direct association between size and flight with populations of the same geographic origin remains to be tested.

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Corresponding Editor: D. B. Wake