

BODY BUILDING BY INSECTS: TRADE-OFFS IN
RESOURCE ALLOCATION WITH PARTICULAR
REFERENCE TO MIGRATORY SPECIES

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SYNOPSIS

Individuals of many species of insects inhabiting transient habitats exhibit migratory behavior and thereby escape deteriorating environmental conditions and colonize sites with favorable conditions. Limited food availability is one cue that may serve to induce migration, either by stimulating the adult to undertake migration, and/or by stimulating the larva to alter its resource allocation to "build" a migratory-form adult. Such changes in resource allocation often involve changes in lipid storage, body size, proportioning of wing size and body weight, and reproduction.

Detailed study of four species of presumed migratory noctuid moths indicated that the larvae retain the ability, when starved from various days in the last larval stadium, to pupate and metamorphose into adults. These adults have reduced body weights (from 12 to 24% of the weight of adults from fully fed larvae), and significantly lower wing loading ratios (i.e., body weight/wing area) than would be expected based on the predicted allometric relationship between body weight and wing area. We propose that this altered allocation of food to body weight and wing area is an adaptive response producing individuals with low wing loading ratios that presumably exhibit less energetically costly flight. This hypothesis is consistent with principles of flight energetics.

"The earth-bound early stages built enormous digestive tracts and hauled them around on caterpillar treads. Later in the life-history these assets could be liquidated and reinvested in the construction of an essentially new organism—a flying-machine devoted to sex." (C. M. Williams 1958)

". . . the central problem of evolutionary biology: to provide a general explanation for the design of organisms." (S. C. Stearns 1982)

INTRODUCTION

The liquidation and reinvestment of "assets" by insects during metamorphosis, mentioned in Williams' quote above, involves the allocation of acquired resources to building and maintaining the adult body. In addition, energy and nutrients are necessary for adult activities, including defense, dispersal and reproduction (Townsend and Calow 1981). We are in particular interested in the trade-offs of resource allocation among body-building, dispersal and reproduction.

Differences in resource allocation may be evident both among and within

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species. For example, an insect with a high-powered, hovering type of flight exhibits differently proportioned body and wings compared to an insect with a low-powered, gliding type of flight (Kammer and Heinrich 1978, Casey 1981a). Within a species, resource allocation may vary between generations. For example, individuals of certain seasonally migratory species respond to changing environmental conditions (e.g., photoperiod, food quality and quantity, and larval density) by altering their allocation of resources to body and wings, with consequent effects on fecundity (see below).

It is one goal of nutritional ecology to achieve an understanding of the patterns of resource allocation by species (Slansky 1982a, 1982b; see also Stearns 1982). In this paper we examine resource allocation to body building in insects, with particular reference to migratory species. Using data from the literature and our own unpublished data, we investigate the trade-offs among body weight, lipid content, wing size and reproduction. Our discussion is framed within the contexts of alteration of resource allocation in changing environments and the principles of flight energetics. In addition, we identify areas where more research is needed.

RESOURCE ALLOCATION TO BODY SIZE, PROPORTIONS AND COMPOSITION

Within a given environment, there will be some optimal adult body size (or sizes) for the individuals of a particular species that yields their maximal fitness. Selective forces acting at different times during an insect's life determine the evolution of optimal adult body size (Roff 1981, Ricklefs 1982). Such forces involve an individual's size-dependent relationships with food (Enders 1976, Wasserman and Mitter 1978, Mattson 1980), enemies (Hespenheide 1973, Enders 1975), competitors (Pearson and Stemberger 1980, Eberhard 1982) and the physical environment (Sweeney and Vannote 1978, Roff 1981), as well as the size-dependency of life history variables such as developmental time, fecundity and dispersal behavior (Dingle et al. 1980, Derr et al. 1981, Hinton 1981, Roff 1981, Ricklefs 1982, Stearns 1982).

Resource allocation to body building involves not only achieving a certain optimal size, but also, within the limits of that size, partitioning the resources among the various organs, structures and biochemical components of the body such that the insect will achieve its best performance (Calow 1977). One important feature of resource partitioning that is responsible for the different proportions of the various organs and structures to the body as a whole is allometric growth, whereby some tissues in the body grow at faster rates than others (Huxley 1972). Concentrations of the various biochemical components of the body (i.e., proteins, lipids, carbohydrates, amino acids, salts, etc.), also important to insect performance, result from the complex relationships of assimilation, anabolism, catabolism and excretion (Wigglesworth 1965, Gordon 1972, Rockstein 1978).

ADAPTIVE ALTERATION IN RESOURCE ALLOCATION: MIGRATORY INSECTS

Individuals of many species in habitats that can become adverse for reproduction or survival exhibit migratory behavior (Southwood 1977, Wellington 1980). These individuals can thereby escape deteriorating habitats and colonize favorable sites (Dingle 1978). The decision to migrate may be made either during the adult or larval stage.

Adult insects may initiate a migratory response based on their evaluation

of environmental cues such as photoperiod, temperature, and food quality and quantity (see Slansky 1982a). Induction of reproductive diapause commonly is associated with the decision to migrate. The integration of reproductive and flight behaviors occurs at the neurohormonal level (DeWilde and DeLoof 1973, Rankin 1978) and involves the investment of resources in the flight system and its metabolism rather than in reproduction (Slansky 1980, Heinrich 1981).

The flight system is energetically costly to maintain and operate: metabolic rate during flight may be increased 50-100 times that at rest, and over 50% of an insect's resting metabolism may result from the metabolism of the resting flight muscles (Kammer and Heinrich 1978, Heinrich 1981). However, the extent to which metabolic costs of flight may divert energy away from other behaviors, and thus reduce reproduction and survival probability is not clear. Significant negative effects of flight duration on reproduction and survival have been found in tethered flight studies of only some of the species studied (for review see Slansky and Scriber 1984). Perhaps tethered flight techniques do not put as great a metabolic demand on a flying insect as does free flight. In addition, although there are few data available, insects may exhibit adaptations that reduce the potential negative effects of flight. For example, adequate storage of lipid reserves prior to long flight may satisfy the energetic demands of the flight muscles, such that sufficient energy stores remain for reproduction and survival; also, post-flight increases in food consumption may occur (see Slansky 1980). Reduction of metabolic costs may result from histolysis of flight in muscles in some situations where the flight system is no longer needed by the insect, such as after the mating flight in termites and when certain scolytid bark beetles have dispersed to and colonized a host tree (Atkins and Farris 1962, Johnson 1973; see also Solbreck and Pehrson 1979).

Whereas adults of some species may themselves decide to migrate, adults of other species may, under certain circumstances, produce offspring destined to exhibit migratory tendencies as adults. Larval (or nymphal) response to environmental cues also may influence adult migratory behavior. Because these responses occur before the adult stage, differential allocation of food during the larval and pupal stages may result in migratory forms being produced that differ from non-migratory adults in the size, proportions and biochemical composition of their body, as well as in other aspects of their biology (Johnson 1976, Wellington 1980; Table 1). Among the most dramatic examples of this phenomenon are aphids and locusts (see Dingle 1980).

Several species of aphids display alary polymorphism associated with an alteration between sexual and parthenogenetic generations (Dixon 1973). Production of the alate (winged) form may occur in response to dietary influence (Mittler and Sutherland 1969) or population density (Dixon 1973) and may depend upon the population age structure (MacKay and Lamb 1979). Differences in food consumption and fecundity between alate and apterous forms (Table 1) indicate further differences in resource allocation. In migratory locusts, individuals of the gregarious phase, produced in response to increased density, differ from solitary phase individuals in morphology and reproductive and migratory behavior. They are migratory throughout their lives, first as nymphs "marching" across the terrain en

TABLE 1. DIFFERENCES IN PERFORMANCE AND BODY STATE (SIZE, PROPORTIONS AND COMPOSITION) BETWEEN PRESUMED MIGRATORY AND NON-MIGRATORY INDIVIDUALS (REVISED FROM SLANSKY AND SCRIBER 1984).

Orders/Species	Performance/Body State Differences	References
Coleoptera <i>Dendroctonus pseudotsugae</i>	Individuals with higher lipid content show greater dispersal activity	Atkins (1966)
Diptera <i>Aedes taeniorhynchus</i>	Migrant phase lighter in dry weight with lower wing loading ratio and % lipid	Nayar and Sauerman (1969)
<i>Drosophila melanogaster</i>	Larger individuals of both sexes show greater probability of dispersal	Roff (1977)
Hemiptera <i>Oncopeltus fasciatus</i>	Higher % lipid and cytochrome c oxidase activity in migratory strain; delayed oviposition associated with increased flight	Holmes <i>et al.</i> (1979); Dingle (1968)
Homoptera <i>Acyrtosiphon pisum</i>	Alatae with longer preoviposition period, longer oviposition period, lower fecundity than apterae; same lifespan	MacKay and Wellington (1975)
<i>Aphis fabae</i>	Alatae less fecund than apterae but have higher reproductive rate	Dixon (1972)
<i>Cicadulina</i> sp.	Shorter body length associated with greater flight ability, less feeding and lower fecundity	Rose (1972)
<i>Drepanosiphum dixonii</i>	Macropterous alatae less fecund than brachypterous alatae	Dixon (1972)
<i>Myzus persicae</i>	Alate morph consumes more food	Raccah and Tahori (1971)

Orders/Species	Performance/Body State Differences	References
Lepidoptera <i>Choristoneura fumiferana</i>	Smaller moths have lower wing-loading ratio; exhibit greater flight activity	Sanders and Lucuik (1975)
<i>Epiphyas postvittana</i>	Presumed migrants smaller with lower body length forewing length ⁻¹ ratio	Danthanarayana (1976)
<i>Parnara guttata</i>	Fall season individuals have high tethered-flight activity, lower fecundity, longer pre-oviposition period	Ono and Nakasuji (1980)
<i>Pieris brassicae</i>	Adults from crowded larvae lighter in fresh weight with lower wing loading ratio	Long (1959)
<i>Plusia gamma</i>	Adults from crowded larvae lighter in fresh weight with lower wing loading ratio	Long (1959)
<i>Plutella xylostella</i>	Presumed migrants larger with longer forewings, greater fecundity	Yamada and Umeya (1972)
<i>Spodoptera exempta</i>	Crowded larvae with higher % lipid; presumed migrants have longest wing lengths	Matthee (1945); Aidley and Lubega (1979)
Orthoptera <i>Locusta migratoria</i>	Longer wings, higher % lipid; lower fecundity in migratory phase.	Matthee (1945); Norris (1950)
<i>Pteronemobius taprobanensis</i>	Macropterous form with longer preoviposition period, lower fecundity, greater survival during starvation compared to micropterous form	Tanaka (1976)

masse, and then as adults forming large swarms that are carried for long distances by prevailing winds (see Rainey 1978).

Differences in lipid content, wing size, body weight and fecundity between presumed migratory and non-migratory individuals also occur in Coleoptera, Diptera, Lepidoptera and other insects (Table 1). Although these differences are generally less extreme than the examples cited previously, they nonetheless similarly indicate that alterations in the consumption and allocation of food have occurred during the "building" of the various adult forms.

Insect flight involves different channels of power output or cost (Figure 1). In simplified terms, the energy actually utilized for flight provides the mechanical power output; the remaining power input is lost through muscle inefficiency as heat. Of the mechanical power output, some is used by the insect to accelerate and decelerate its wing mass (i.e., inertial power) whereas the remainder is used to do work on the surrounding air (i.e., aerodynamic power). The three aerodynamic power output components of a flying insect are profile power, which overcomes the drag on the surface area of the wings, induced power, which is used to accelerate air across the wings at a velocity sufficient to overcome the force of gravity and parasite power, which is necessary to overcome the drag on the body (Figure 1; Casey 1981a, 1981b). The design of the adult, in particular the ratio

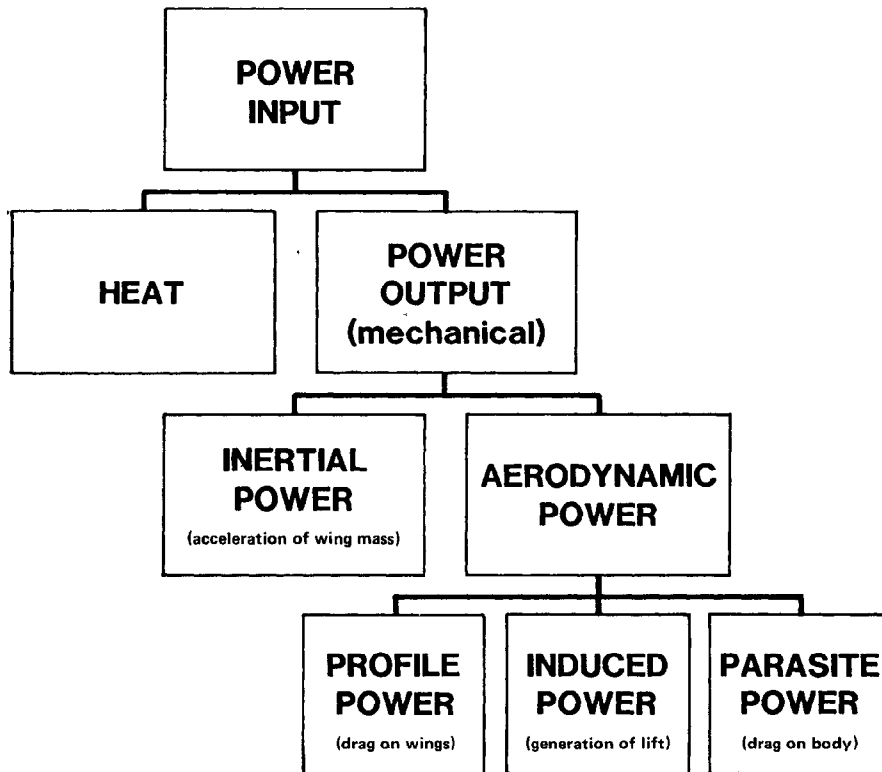


Fig. 1. Energy demands for power in flying insects (modified from Casey (1981b); see text for explanation).

between body weight and wing area (i.e., wing loading ratio), along with wing beat frequency and flight speed, in large part determine these power output demands.

A low wing loading ratio (i.e., large wing area relative to body weight), when coupled with a relatively slow wing beat frequency, would tend to minimize the power output demands of flight. Many insects presumed to be migratory exhibit low wing loading ratios compared to non-migratory individuals (Table 1), and many of these species seem to utilize air thermals and upper air currents to aid in their dispersal, thus presumably reducing the power output demands of their flight (Johnson 1969, Danthanarayana 1976, Gibo 1981).

RESOURCE ALLOCATION IN "LESS THAN IDEAL" ENVIRONMENTS

Associated with the strongly determinant relationship between an individual's body size, proportions and composition (i.e., its body state), and its fitness, are adaptations that may allow the insect to attain its optimal body state under less than ideal environmental conditions. For example, a larva may alter its food intake in response to changes in the nutrient content of its food, consuming more of a food with a reduced nutrient content and thereby achieving a body weight and composition similar to that of a larva consuming a more nutrient-rich food (Slansky and Feeny 1977). Increased catabolism and excretion also may be exhibited in response to a nutrient imbalance in the food (Gordon 1972, Horie and Inokuchi 1978, Rockstein 1978). Another food-related response involves the induction of detoxication enzymes upon consumption of potentially toxic allelochemicals (Brattsten 1979). These compensatory responses may incur various costs that could reduce fitness (e.g. energetic costs of increased feeding, catabolism and detoxication, and increased exposure to predators and parasitoids while feeding). Thus, the "success" of a compensatory response will be determined by the extent to which its benefits outweigh its costs. Compensatory success, when defined as the degree to which the actual body state approaches the optimal body state) varies among individuals, situations and species, and may reflect different adaptive strategies (Scriber and Slansky 1981, Slansky 1982b). However, more research is necessary to determine the benefits and costs of compensatory responses and the extent to which compensatory ability reflects adaptive strategies.

The frequent occurrence of prolonged larval development (in some cases including an increase in the number of instars) under conditions of "poor" food quality or reduced food quantity (for references see Scriber and Slansky 1981) may be another response by which larvae attempt to get as close as possible to their optimal body state with minimal costs. If feeding conditions improve within a relatively short period of time, then the larva may be able to closely approach its optimal body state with only a short delay in the timing of pupation. However, the success of this response may be tempered, for example, by the subsequent delay in onset of reproduction resulting from the prolonged development. Thus in certain circumstances, rather than exhibiting a compensatory response, larvae may be "making the best of a bad situation", prolonging their development in order to achieve not their optimal state but their minimal state necessary to survive metamorphosis and produce a reproductively competent adult.

Minimal-weight-values, below which a starved immature insect does not

undergo successful metamorphosis to an adult, vary considerably among species (Table 2), but similar to the situation of the compensatory abilities discussed above, we have little understanding of the ecological and evolutionary relationships between minimal-weight-values and adaptive strategies. Questions such as "Are adults at the minimal weight reproductively competent?" and "Have species subject to frequent food limitation (e.g., because of the ephemeral nature of their food in relation to the duration of the larval stage) evolved as an adaptation minimal-weight-values that are a low percentage of their presumed optimal weights (e.g., *Drosophila melanogaster*, Table 2, and certain species of tree-boring Coleoptera; see Andersen and Nilssen 1983)?" remain to be answered.

A further adaptation involves the utilization of environmental cues by insects to facilitate their avoidance of or escape from a deteriorating environment. Poor food quality and starvation, as well as other environmental factors, may serve as cues to larvae of many species to produce migrant-form adults (see above) and as cues to adults to stimulate migratory flight behavior (Dingle 1968, 1978, Mittler and Sutherland 1969, Elsey 1974, Sanders and Lucuik 1975, Solbreck and Pehrson 1979, Duelli 1980). These inductive responses (Slansky 1982a) involve changes in resource allocation that alter the optimal body state of the non-migratory form to produce the optimal body state of the migratory form. As discussed above, this commonly involves changes in body size and weight, and in wing size.

LARVAL STARVATION AND RESOURCE ALLOCATION IN NOCTUID MOTHS

Assuming that changes in body weight and wing area with body size follow some theoretical relationship, then significant differences from this relationship should indicate that resources are being differentially allocated to body weight and wing area at different body sizes. By relating this differential allocation of resources to the flight behavior and other aspects of a species' lifestyle, one can infer whether this differential allocation has adaptive value.

We investigated resource allocation in four presumed migratory species of noctuid moths in response to larval starvation (Angelo and Slansky in prep.). Larvae were experimentally starved from various days of their last instar, and measurements were made of the body weight, wing area and lipid content of newly emerged adults. Because area is the square and weight is the cube of linear dimensions, a log-log plot of these as length changes yields a straight line with a slope of 0.67 (indicating that area and weight do not change in proportion to each other; if they changed proportionately, the slope would equal 1). We compared the slope values between body weight and wing area for the four species with the 0.67 value, as well as among themselves, in an effort to demonstrate differential allocation of resources during starvation. Furthermore, we related the observed changes to aspects of these species' lifestyles.

Use of such theoretical allometric relationships is common in comparisons of organism performance (e.g. metabolic rate) across a range of species with different body sizes; both the slope of the line and the extent to which the performance value for a particular species lies off the line have been used to draw conclusions of biological significance (Schmidt-Nielson 1970, Blueweiss et al. 1978, Greenstone and Bennett 1980). However, there seems to have been considerably less use of comparisons between predicted

TABLE 2. THE MINIMAL WEIGHT AT WHICH LARVAE WILL PUPATE WHEN SUBJECTED TO STARVATION, EXPRESSED AS A PERCENTAGE OF THE MAXIMAL WEIGHT ATTAINED WHEN FULLY FED. WHEN SUBJECTED TO STARVATION BELOW THIS MINIMAL WEIGHT, LARVAE STARVE TO DEATH. (REVISED FROM SLANSKY AND SCRIBER, 1984).

Orders/Species	Sex	Minimal weight (% of maximal)	References
Diptera			
<i>Drosophila melanogaster</i>	♂	12% ¹	Beadle <i>et al.</i> (1938)
	♀	12% ¹	
	♂	19% ¹	Bakker (1959)
	♀	18% ¹	
Hemiptera			
<i>Oncopeltus cingulifer</i>	♀	44% ²	Blakley and Goodner (1978)
	♀	38% ²	
<i>O. fasciatus</i>	♀	51% ²	Nijhout (1979)
	♂	53% ²	
<i>Rhodnius prolixus</i>		25-43% ³	Friend <i>et al.</i> (1965)
Lepidoptera			
<i>Anticarsia gemmatalis</i>	♀	18% ¹	M. J. Angelo and F. Slansky (unpubl.)
	♂	12% ¹	
<i>Bombyx mori</i>		60% ⁴	Lees (1955)
<i>Choristoneura conflictana</i>	♀	32% ²	Beckwith (1970)
<i>Danaus chrysippus</i>		23% ¹	Mathavan and Muthukrishnan (1976)
		36% ⁴	
<i>Galleria mellonella</i>		36% ⁴	Lees (1955)
<i>Heliothis zea</i>	♀	14% ¹	M. J. Angelo and F. Slansky (unpubl.)
	♂	23% ¹	
<i>Lymantria dispar</i>		25% ²	Kopec (1924)
		45% ⁴	Lees (1955)
		50-60% ²	Nijhout (1975)
<i>Manduca sexta</i>		36-47% ²	Higgins and Pedigo (1979)
<i>Plathypena scabra</i>		26% ¹	Mukerji and Guppy (1970)
<i>Pseudaletia unipuncta</i>	♀	19% ¹	M. J. Angelo and F. Slansky (unpubl.)
	♂	24% ¹	
<i>Spodoptera frugiperda</i>	♀	19% ¹	M. J. Angelo and F. Slansky (unpubl.)
	♂	20% ¹	

¹Dry weight.

²Fresh weight.

³Minimal blood meal promoting molting in various instars.

⁴Time spent feeding in last instar.

and actual allometric relationships in interpreting differences in performance values among the individuals within a species (see, for example Casey 1976), and as a consequence, the significance of deviations of actual data from "expected" relationships is not as well understood. Nonetheless, we believe our logic is a good "first step" in interpreting the significance of

differential changes in body weight and wing area among the individuals within a species. In addition, we believe that between-species' comparisons of regression slopes for within-species' allometric relationships (such as that between wing area and body weight) can suggest meaningful differences between species (see, for example, Casey's (1976) study on sphinx moths) in how they respond to changes in their environment, as indicated in the following discussion.

The first species studied, the velvetbean caterpillar (VBC) *Anticarsia gemmatalis* is a presumed migratory insect that appears to fly northward each summer from overwintering sites in south Florida and elsewhere (Buschman et al. 1977, Greene 1979). When starved from various days in the last stadium, larvae of the VBC produce adults that are lighter in weight and have reduced wing area compared with fully fed larvae; the slope for these data (0.52) is significantly different from the theoretical value (Figure 2). Thus, as body weight is decreased due to starvation, moths are produced with significantly lower wing loading ratios than would be expected if the theoretical relationship is applicable. Smaller moths carry less weight per unit wing area than do larger moths, and the energetic cost of their flight is presumably reduced (Casey 1981a, Casey and Joos 1983; also see above).

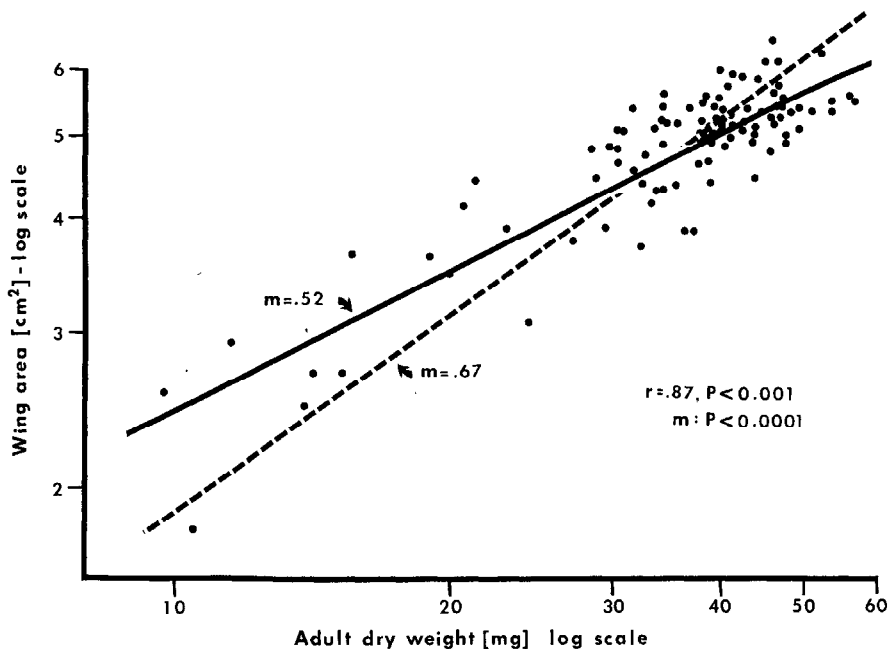


Fig. 2. Relationship between log wing area and log dry body weight. Dashed line: expected relationship based on area = the square and mass = the cube of linear dimensions. Solid line: actual relationship found for adult velvetbean caterpillar moths (both sexes) subjected to different durations of starvation during the last larval instar; regression is significant ($p < .001$). The slope of the VBC line ($m = 0.52$) is significantly different from the slope of the expected line ($m = 0.67$; t test, $p < .0001$), indicating that as body weight is reduced a relatively larger wing area is exhibited. Thus, smaller VBC moths have a lower than expected wing loading ratio (WLR = body weight/wing area) (from Angelo and Slansky in prep.).

Adult VBC, and many other species of insects, are presumably "passive" migrators, which, although maintaining active flight, are carried for long distances by upper air currents (see Rainey 1978, Rabb and Kennedy 1979, Walker 1980); a lower wing loading ratio may facilitate this type of movement (see above).

Migratory ability of VBC may have evolved to allow escape from seasonally unfavorable and/or food-depleted habitats, and colonization of seasonally favorable habitats containing suitable food. This ability to colonize and rapidly exploit new food sources undoubtedly contributes to its current status as a severe pest of soybean fields (see Barfield and O'Neil, this Symposium). In soybean fields (and perhaps when feeding on wild foodplants as well), starvation of VBC may frequently occur, especially due to high larval densities at certain times of the year (Herzog and Todd 1980, Linker 1980). If a relatively low minimal weight is an adaptation to frequent starvation as discussed above, then the low minimal-weight-values for VBC (Table 2) would further suggest the occurrence of frequent starvation in the field. If this is the case, then the lower than predicted wing loading ratio of the moths produced by starved larvae, involving a change in the allocation of food to body and wings, may be an adaptive response facilitating less costly flight in search of new larval foodplants.

Consistent with the reasoning above are the results from a similar starvation experiment with three other species of noctuid moths: the fall armyworm (FAW), *Spodoptera frugiperda*; the corn earworm (CEW), *Heliothis zea*; and another armyworm (SPLAT), *Spodoptera latifascia*. The FAW apparently has no diapause mechanism to allow survival during extended periods of low temperature, and therefore in the United States it is restricted to overwintering (with continuous generations) in subtropical areas of Florida and Texas (Mitchell 1979). Each spring and summer, FAW adults disperse throughout much of the United States as far north as Canada (Luginbill 1928). Adults of the CEW are also capable of dispersing over long distances (Phillips 1979). However, this species has a pupal diapause enabling it to survive cold winter temperatures throughout much of North America as far north as Canada (Hardwick 1965). Virtually nothing is known about the life history of SPLAT (Kovitvadi 1969).

The wing area to body weight relationships for VBC, FAW and SPLAT yield very small slopes (0.35, 0.22 and 0.22, respectively; Figure 3), consistent with the hypothesis that these migratory moths should achieve lower than theoretically predicted wing loading ratios at reduced body weights to facilitate less costly flight in search of new larval foodplants. The slope for CEW (0.59; Figure 3) also is smaller than the theoretical slope of 0.67, but it is substantially larger than that of the other species, suggesting that the CEW has evolved a somewhat different strategy of resource allocation than the other three species. This is further indicated by the substantially different slope of the relationship between % lipid and dry weight for the CEW (0.25) compared to those of the VBC and FAW, which are similar (0.52 and 0.57, respectively; Figure 4). The slope for SPLAT (0.15; Figure 4) is surprisingly more similar to that of the CEW, from which it differs in the wing area to body weight relationship, than to those of the VBC and FAW, to which it is very similar in the wing area to body weight relationship (Figure 3). Like the VBC, these three species exhibit relatively low minimal weights (Table 2).

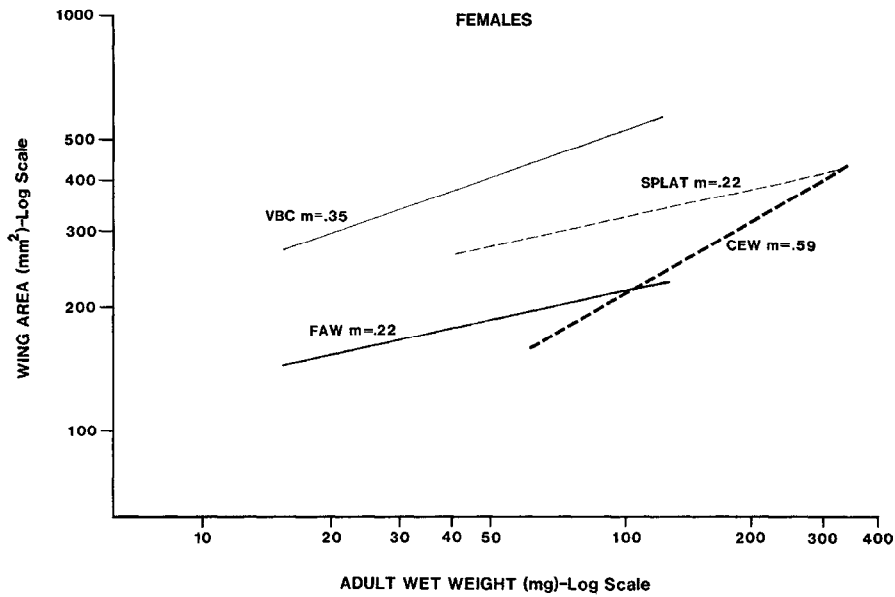


Fig. 3. Relationship between log wing area and log fresh weight for four species of noctuid moths subjected to different durations of starvation during the last larval instar. VBC = velvetbean caterpillar ($n = 24$), FAW = fall armyworm ($n = 27$), CEW = corn earworm ($n = 18$) and SPLAT = the armyworm *Spodoptera latifascia* ($n = 25$). Linear regression lines and slopes (m) are presented for females only; males were similar. Analysis of covariance indicated significant differences between some of the slopes (from Angelo and Slansky in prep.).

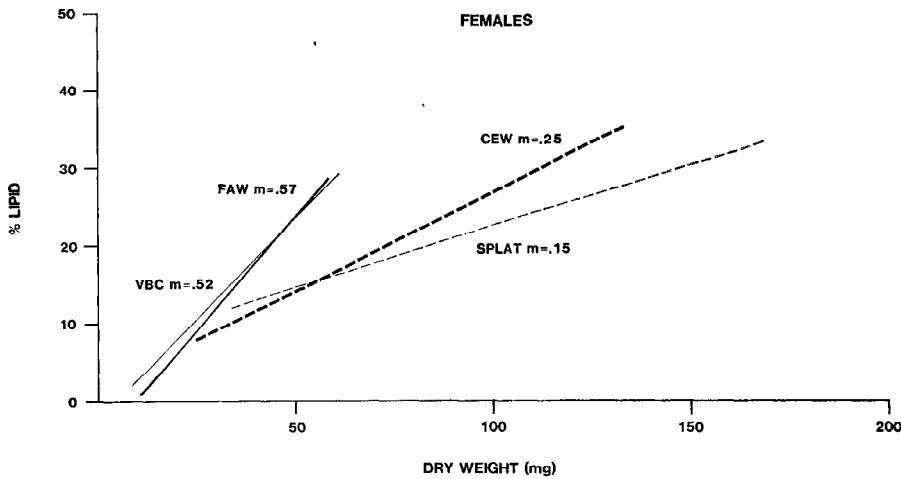


Fig. 4. Relationship between % lipid (dry weight) and dry body weight for four species of noctuid moths (see Figure 3 for explanation of abbreviations). Linear regression lines and slopes (m) are presented for females only; males were similar. VBC ($n = 31$), FAW ($n = 28$), CEW ($n = 18$) and SPLAT ($n = 25$). Analysis of covariance indicated significant differences between some of the slopes (from Angelo and Slansky in prep.).

CEW (and SPLAT) thus exhibit less reduction in lipid when starved as larvae compared with VBC and FAW. Perhaps it is important for larvae of the CEW to maintain a relatively high lipid content (i.e., a relatively high metabolic fuel reserve) throughout their last instar in the event an overwintering pupal diapause is required. For VBC and FAW, however, which apparently lack an overwintering diapause, to be able to produce adults with reduced wing loading ratios, facilitating less costly flight in search of more favorable habitats, seems to take precedence over maintaining their lipid content. When starved, individuals of SPLAT substantially reduce their wing loading ratio and maintain a relatively high lipid content, but how this relates to their biology in the field is unknown.

In addition, the maintenance of a relatively high lipid content by CEW may provide it with the metabolic fuel source for a more highly powered migratory flight. The relatively high wing loading ratio and steeper slope for the wing area to body weight relationship for CEW compared with the other three species (Figure 3) could indicate that CEW does undergo a more highly powered flight. Although more energetically costly per unit time, perhaps the high wing loading ratio of a high-powered flier would allow greater flight speed with the cost of transport (energy cost per unit distance travelled) actually being similar to that of a more passive flier with a lower wing loading ratio. Because cost of transport is dependent on both the metabolic cost and the speed of flight, it would seem possible that a migratory insect could reduce its cost of transport by reducing the former or increasing the latter. Use of upper air currents by many migratory insects (see above) may increase their speed of flight with little or no increase in metabolic cost, thus reducing their cost of transport.

Much more research is needed to critically evaluate these hypotheses. Laboratory studies indicate apparent differences in flight behavior among these noctuid moths, with VBC and CEW exhibiting greater degrees of nocturnal activity than FAW (Leppa et al. 1979); adults of SPLAT also seem relatively sedentary in the laboratory (N. C. Leppa, personal comm.). However, the extent to which these species differ in their flight behavior, both when searching within a habitat for adult food, mates and larval food-plants and when migrating between habitats remains to be determined. The similarity in body weight between the small-sized adult VBC produced in our experiments by larval starvation and the smallest field caught specimens (Angelo and Slansky in prep.) suggests that we are dealing with adults within the natural size range in our experiments and that the small adults are at least flight-worthy. However, whether these small-sized adults are reproductively competent, and whether they exhibit migratory flight are interesting questions that remain to be answered. In addition, we lack detailed information on how flight behavior, metabolic costs of flight, longevity and reproduction vary as a function of body size, and on the impact of flight behavior on fitness.

CONCLUSIONS

The way in which the individuals of a species allocate their resources is intimately associated with the evolved lifestyle of the species. Some of the more evident differences in resource allocation are manifested in the variety of sizes, shapes and colors of different species of insects. Differences in the relative abundance of different species also are often very obvious

(e.g. the extremely numerous larvae of a particular moth species defoliating much of a crop versus that "rare" species still absent from a devoted lepidopterist's collection) and may reflect interspecific differences in resource allocation to production of offspring and defense from enemies.

Less obvious but nonetheless important differences in resource allocation appear in the different body compositions, proportions of body parts, and behaviors of species. As research progresses, we are finding that insects differ in how they respond, through changes in resource allocation, to changes in environmental conditions. Two significant features of the environment that frequently exhibit changes are the quality and quantity of food. Obtaining a sufficient quantity of adequate quality food seems to be a common dilemma among animals (White 1978), and for insects flight is a common means of dispersal in search of food. Some species exhibit dramatic shifts between wingless and winged forms depending on the environment; individuals of other species are always winged, but they may exhibit alterations in the relationship between body weight and wing area (i.e., wing loading ratio), among other changes.

Of the four species of noctuid moths that we studied, all altered the allocation of their resources under larval starvation to produce adults with relatively larger wings and low wing loading ratios, even lower than the presumed theoretical prediction (i.e., the slopes of the relationship between wing area and body weight were all less than 0.67). This response seems to have adaptive value, associated with the apparent "passive" mode of long distance dispersal of these species, whereby individuals are blown along by upper air currents while maintaining active flight.

In contrast to the above species, some animals with a more energy-demanding flight, such as hummingbirds and euglossine bees, exhibit relatively small wings and high wing loading ratios, even at low body weights. This is indicated by values for the slope of the relationship between wing area and body weight that are greater than 0.67 (the slope for hummingbirds is 0.75 (Greenewalt 1962) and for euglossine bees is about one (Casey et al. 1984)). For animals like these with high-powered flight (i.e., relatively high wing beat frequency), a strategy of producing relatively larger wings at smaller body weights (i.e., reducing wing loading ratio like the noctuid moths studied here), would undoubtedly increase, rather than decrease, the energy cost of their style of flight due in part to the increase in drag over the surface of the wings as they became larger (see Kammer and Heinrich 1978, Casey 1981a).

Support for this hypothesis of increased energy requirements associated with larger wings in species with a high-energy-demanding mode of flight comes from data for two species of sphinx moths, *Manduca sexta* and *Hyles lineata*. Individuals of these species exhibit a very energy-demanding mode of flight, both because they have relatively high wing loading ratios (ranging from approximately 5 to 80 times those found for the noctuid moths in our study) and because they exhibit hovering flight (Casey 1976). The slope of the relationship between log wing area and log body weight for these two species is *negative*, indicating that individuals lighter in weight have larger wings (on an absolute scale) than heavier individuals. Associated with this is a greater weight-specific power requirement for the moths that are lighter in weight (Casey 1976). Why these species produce larger (rather than smaller) wings at reduced body sizes is not clear.

Before the adaptive significance of the various alterations in resource allocation seen among species in response to environmental changes can be understood, more information on the consequences of such alterations is required. Thus, questions pertaining to the significance of interspecific differences in ability to achieve optimal weights, in minimal weight values, in changes in wing loading ratio and so forth must be answered within the context of the species' lifestyle in nature, in terms of trade-offs between reproduction, dispersal and mortality. This is a difficult task requiring detailed behavioral observations and quantitative measurements; it is clear that considerable research in nutritional ecology remains to be done.

In addition to the goal of understanding the evolution of species' lifestyles, there is a pragmatic side to research in nutritional ecology. If the factors influencing the behavior (including resource allocation) of insect pests, both in terms of their relative impact and their mechanisms of action are understood, then better methods of altering the behavior of pest species to their detriment may be devised (see Barfield and Stimac 1980). For example, many insect pests apparently exhibit long distance migration, as well as dispersal between and within crops (Stinner et al. 1983). Field-level control measures often overlook this fact; successful pest management must include a broader view of pest behavior, in this case attempting to identify "source areas" and influence the pest in these before it moves into the crop fields (see Barfield and O'Neil, this Symposium). Thus it can be seen that research on resource allocation is a valuable approach to understanding flight behavior and other features of insect lifestyles that have a significant bearing on crop production.

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