WHY ARE MOST INSECTS SHORT FLIERS?

Mark A. Davis
Department of Biology
Dartmouth College
Hanover, New Hampshire   03755

ABSTRACT.   Evolutionary and nonevolutionary explantions are offered
for the sharply skewed flight distributions obtained in laboratory
studies of insect flight.   The fact that there exists a genetic
component to flight duration suggests that selection might be
responsible for the preponderance of short fliers.   Several hypotheses
based on the predictability of the habitat in space and time and on
the reproductive cost of long flight can be constructed to show why
short fliers might be favored over long fliers.   Unfortunately, the
evolutionary arguments are entirely speculative since the empirical
data required to evaluate them is lacking.   Since flight is directly
dependent upon the physiological state of the individual, the
possibility that the skew is produced by the underlying physiological
mechanism of flight duration is considered.   In addition, an analysis
of the results of previous studies reveals that the skew is probably
partly an experimental artifact.

*   *   *

When the flight durations of insects are measured in tethering
experiments, the distributions are almost always sharply skewed
(Johnson 1976, Dingle 1966, Caldwell and Hegmann 1969, Rose 1972, M.
Davis 1980a, Rankin and Rankin 1980) (Fig. 1).   Mean flight durations
vary between closely related species (Dingle 1978), between
populations of the same species (Caldwell and Hegmann 1969, M. Davis
unpubl. data), and even within a single population during a season (M.
Davis 1980b).   In every case, however, short flights are significantly
more common than long flights.   To date, no one has attempted to
account for the skew, which is surprising given its ubiquity.   In this
paper, I present and evaluate 7 hypotheses in answer to the question,
'Why, when insects are flight tested, are most individuals short
fliers?'   The first 3 are evolutionary, the fourth is physiological,
and the last 2 are methodological.

I. THE SKEW IS THE PRODUCT OF NATURAL SELECTION

The fact that there exists a genetic component to flight duration
(Caldwell and Hegmann 1969, Dingle 1968, Rose 1972), suggests that
selection might be responsible for the preponderance of short fliers.
Theoretically, there are a number of reasons why short fliers might be
favored.

Ia.   Except in the case of habitat deterioration, short flights
are more likely to ensure that individuals will stay within an
area suitable for growth and reproduction.

In many cases, certainly when an environmental gradient is
involved, living conditions in adjacent areas will be more strongly
correlated with the departure site than will distant sites (Fig. 2A).

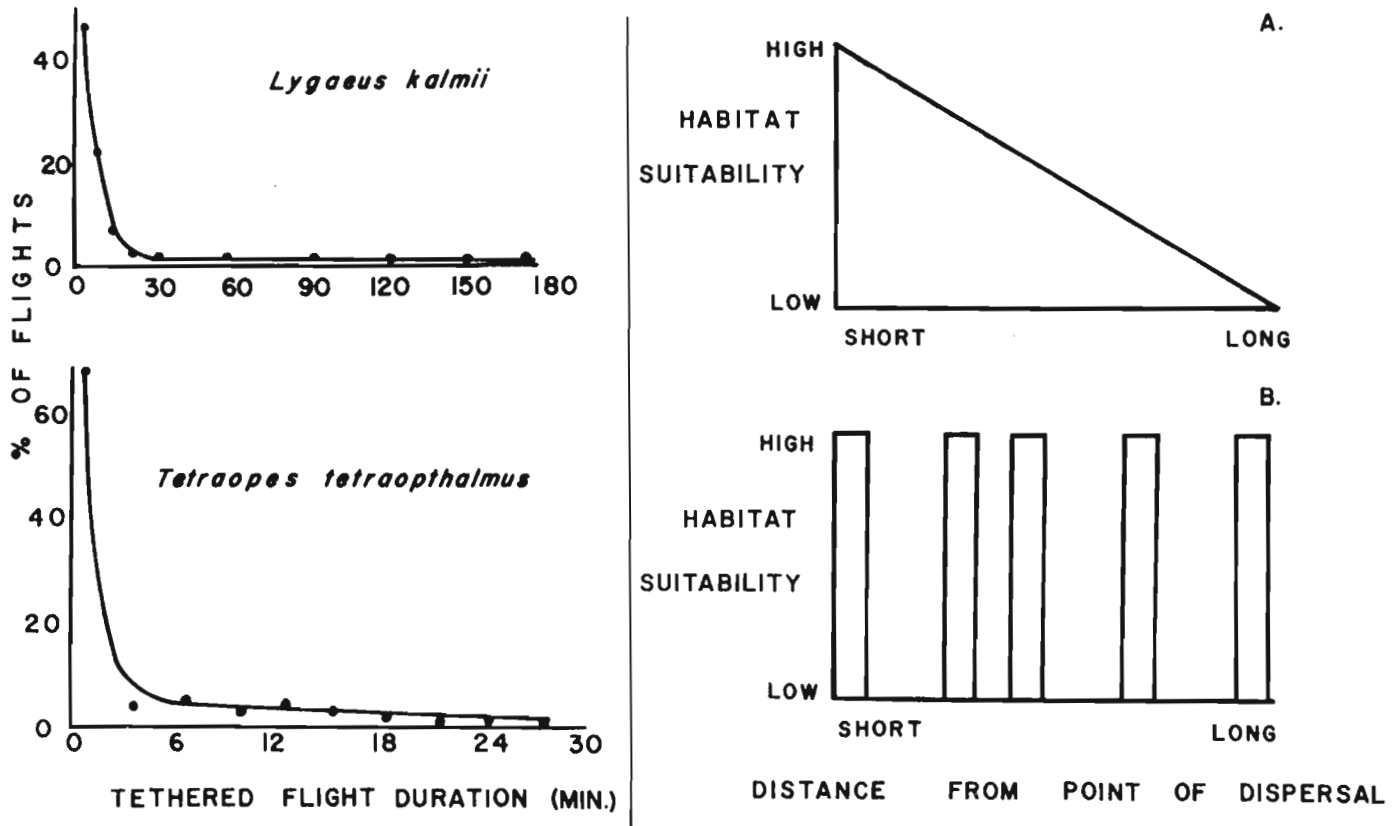*   *   *   *   *   *   *   *   *   *   *

Fig. 1. (left) Flight distributions for Lygaeus kalmii Stahl.
(Hemiptera: Lygaeidae) from Caldwell and Hegmann (1969), and Tetraopes
tetraopthalmus Forster (Coleoptera: Cerambycidae) from Davis (1980a).
The distribution for L. kalmii was obtained from 176 individuals which
were captured from the field and were flight tested once. The
distribution for T. tetraopthalmus was obtained from 12 individuals
which were captured from the field and were flight tested 13 times
each throughout their lives, i.e., 156 flights. Both species were
tested in the laboratory under laboratory conditions (25° C for L.
kalmii, 28° C for T. tetraopthalmus). A still air tethering technique
was used in both cases.

Fig. 2. (right) Idealized habitat suitability shown as a
function of the distance from the point of dispersal, assuming that
the disperser departs from an area of high habitat suitability. In
A., the habitat consists of an environmental gradient. In B., the
habitat consists of a series of discrete patches.
****
To the extent that the availability of food, mates, hiding
places, and oviposition sites decline with increasing distance from
the departure site, short fliers should be favored.

For many insects, the habitat is not a gradient, but a series of
islands, eg., patches of a host plant that are distributed throughout
the environment (Fig. 2B). Under this situation, short fliers may
also be favored, since they will be more likely to stay within the
patch. Because the habitat suitability declines to zero once the
patch is left, and remains at zero until another patch is located,
individuals that do disperse from a patch should be capable of flying
a long distance. This can be illustrated by the following simple
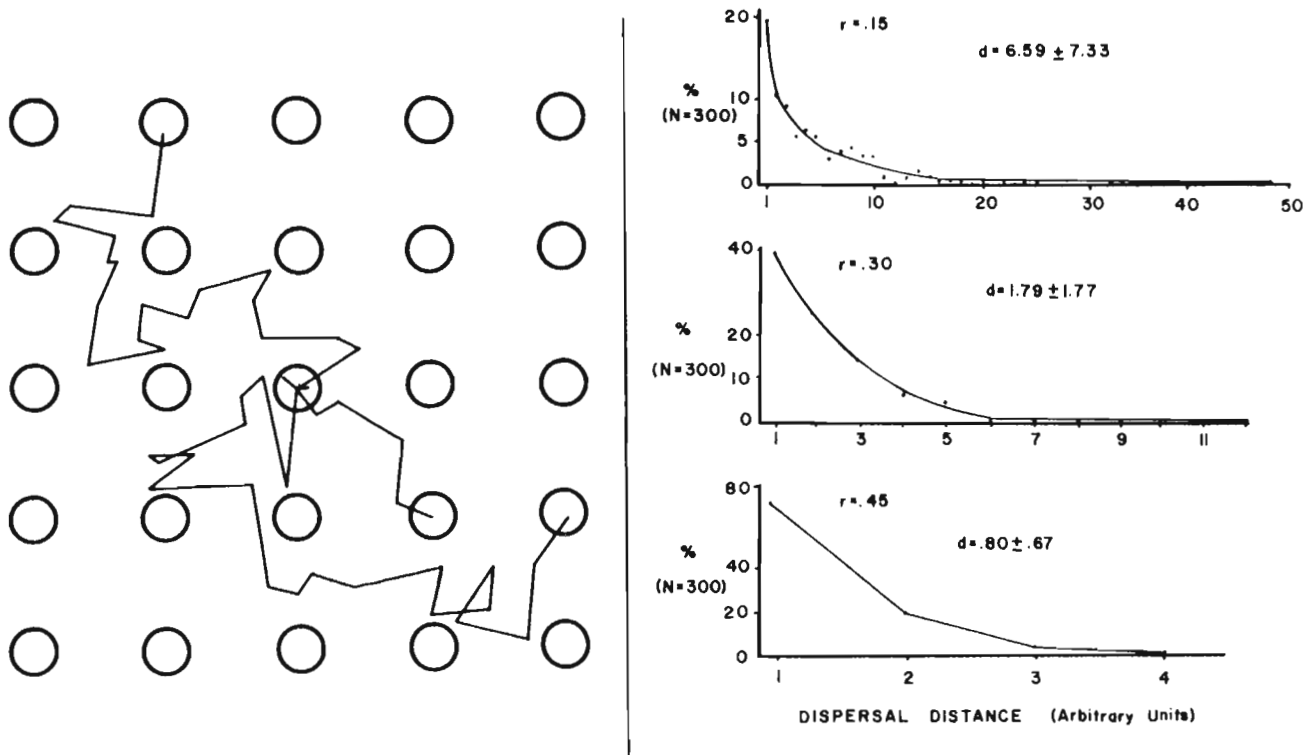computer model.

Fig. 3. (left) Shown is an environment consisting of a series of
habitat islands that are 1 distance unit apart. Organisms disperse in
a random walk fashion until they find themselves within one of the
habitat patches. Illustrated are the dispersal tracks of 5
individuals. The first step in the random walk of 2 of these is very
short, leaving the individual within the original patch.

Fig. 4. (right) The distribution of dispersal distances given a
habitat patch radius (r) of .15, .30, and .45 units. d=the mean
dispersal distance $\pm$ the standard deviation. Dispersal distances were
determined by a computer simulation described in the text. See also
Fig. 3. Note that the 3 graphs have different scales.
****
    Consider an environment containing patches of suitable habitat,
whose centers are 1 distance unit apart (see Fig. 3). Individual
insects take flight from the center of a patch and move in a random
walk fashion throughout the environment until they encounter a patch.
For each step of the random walk, a direction of movement (0-360) and
a distance (0-1 unit) are determined by a random number generator. An
individual that moves less than the radius of the patch on its first
step, in any direction, will have found a suitable patch already, the
one from which it left, and thus will stop. All other individuals
will have left the original patch and will continue to move until
another patch, or the original patch, is encountered.
    Fig. 4 shows that the results of the model yield a distribution
of dispersal distances which is sharply skewed. The largest group
group moves only a short distance, most of these being individuals
that stayed within the original patch. The long horizontal tail
indicates that leaving a patch is risky, since a long flight may be
necessary to locate another one.
    Based on this line of reasoning, one would predict that insects
living in habitat islands would exhibit either short or long flights,

but not flights of intermediate length, since the latter would tend to
leave individuals stranded between patches. In fact, this bimodal
distribution is precisely what has been found when such insects have
flight tested (Fig. 1). The sharply skewed flight distributions are
characterized by long horizontal tails indicating that once a flight
exceeds a certain minimum time, it will probably be sustained for a
long period.

> Ib. Unless habitats are very abundant and/or very ephemeral,
>   long flying dispersing individuals will probably suffer an
>   increased mortality rate and therefore will be less numerous
>   than short fliers.

To the extent that short fliers represent nondispersing
individuals, short fliers might come to predominate if dispersal is
very costly. The evolution and adaptive value of dispersal and
dispersal rates has been a frequent subject of theoretical studies in
recent years (Reddingius and den Boer 1968, Van Valen 1971, Gadgil
1971, Roff 1974, 1975, Comins et. al. 1980). Southwood (1962) argued
that migratory behavior "enables a species to keep pace with the
changes in the location of its habitat." More recently, models have
predicted that dispersal rates should be sensitive to the
predictability of the habitat in both space and time (Gadgil 1971, Van
Valen 1971, Roff 1975, Comins et. al. 1980).
     From a theoretical point of view, there seems to exist only a
small set of conditions which will favor a high dispersal rate. For
selection within a population to do anything other than minimize
dispersal, the fitness of dispersers must be as large as that of a
nondisperser (Van Valen 1971, Baker 1978). This seems unlikely, in
the short run at least, since, except for those species living in very
ephemeral and/or abundant habitats, dispersers probably suffer
increased mortality rates and lose time which could be used for
breeding (Roff 1977).

> Ic. Due to a flight/reproductive tradeoff, short fliers will
>   be favored by natural selection.

While features of the environment may exact a high cost to
dispersal, dispersers also may be at a disadvantage when it comes to
reproduction. Both the flight and reproductive systems of insects are
energy expensive and it appears that in many insects the development
of one system is usually at the expense of the other (Johnson 1969,
Dingle 1972). Studies of female insects have shown that development
of the reproductive system is usually postponed until after the
migratory or long distance flight period (Dingle 1968, Rankin 1974).
Johnson (1969) termed this phenomenon the oogenesis-flight syndrome,
and while it is not universal (Williams 1930, Popov 1954), it is very
widespread.
     There are 2 ways that a flight/reproductive trade off could
explain the relatively greater abundance of short fliers. First, egg
production may be reduced in long fliers, and second, the time to
reproduction in long fliers may be delayed. Data support both
possibilities. Roff (1977) showed that a negative correlation exists
between flight duration and egg production in Drosophila melanogaster.
Dingle (1968) found that reproduction was significantly delayed among
migrant Oncopeltus, and May (1975) found that brachypterous

individuals of the leafhopper, Stenocranus minutus, mature more
quickly and lay eggs sooner than macropterous individuals.

A flight/reproductive tradeoff may contribute to a skewed flight
distribution in two ways. Short fliers may predominate because it is
usually more adaptive to produce more offspring than to disperse, or
the short fliers may be more numerous simply due to their higher
fecundity. The first hypothesis is adaptationist in nature, but the
second represents an example of selection without adaptation (Gould
and Lewontin 1979).

II.   THE SKEW HAS A PHYSIOLOGICAL BASIS

It is possible that the skew is produced by the underlying
physiological mechanism of flight duration. A wide number of factors
are known to influence flight duration in insects, among them the
development of the flight musculature (Scudder 1971), the extent of
fuel reserves (Weis-Fogh 1952, Bursell 1963, Karuhize 1972), and the
presence of key enzymes (Johnson 1969) and hormones (Rankin 1974). In
addition, the motivational state of the insect is important, and this
can be influenced by the amount of food in the gut, its reproductive
state, time of day, and stimuli in its environment (Chapman 1959, Hans
and Thorsteinson 1961, Rankin and Rankin 1980). One hypothesis for
the heavily skewed flight distributions is that the full complement of
physiological and motivational factors necessary for long flight occur
infrequently during an individual's life. Under most conditions, most
individuals may exhibit only short flights because they are deficient
in one or more of the factors required for long flight.

The long horizontal tails of the distributions could be explained
by the existence of a motivational threshold for long flight. In this
case, once the threshold was exceeded, due to the appropriate
combination of physiological and environmental factors, and an insect
embarked on an extended flight, a medium ranged flight would be not
much more likely than a very long flight. Stopping would simply be
the result of encountering a particular stimulus (Hans and
Thorsteinson 1961, Jones 1979), which may be due more or less to
chance. In this light, Wallace's (1966) comment is particularly
interesting, "Immigrants form a small fraction of any population but,
given that an individual is an immigrant, he is very nearly likely to
have come from any one distance as from another."

III.   THE SKEW IS AN EXPERIMENTAL ARTIFACT

There is good evidence to suggest that experimental procedures
have contributed to the skew in the flight distributions. Two
distinct flight classes have emerged in studies in which insects were
flight tested more than once (Dingle 1966, Rose 1972, Davis 1980a).
Some individuals never flew for an extended period of time on any test
day, while others flew for extended periods on some, but
significantly, not all test days. The significance of this day to day
variation as a source for sampling bias was pointed out by Davis
(1980a). He showed that the proportion of long fliers actually
identified as long fliers increases with each additional test day
according to the function $1 - (1 - p)^n$,where n = the number of test
days, and p = the probability that a long flying individual will
exhibit a long flight on a given test day. Davis concluded that
studies could seriously underestimate the number of long fliers in a

population, perhaps by as much as 50% or more, if individuals are flight tested only once.

A second sampling bias may involve the age at which individuals are flight tested. Flight durations peak early in the life of most insects (Johnson 1969). Therefore, if field populations are sampled and flight tested, a skew may be produced or exaggerated by the inclusion of very young, and particularly, very old individuals, both of which are usually relatively short fliers. Davis (1980b) found that the number of long fliers in a population declined markedly during the second half of the season due to an increased number of old individuals. This source of error is probably less important than the error resulting from flight testing individuals only once, since in many of the studies the insects tested are of known and uniform ages (Dingle 1965, Rose 1972, Roff 1977). However, this information usually can be obtained only when the individuals have been reared in the laboratory.

EVALUATION OF THE THREE HYPOTHESES

Since flight, like any other activity of an insect, is directly dependent upon the individual's physiological state, the observed distribution of flights necessarily has a physiological basis. However, if the explanation for the skew is simply that the necessary combination of physiological factors occur infrequently, the original question is not really answered, only replaced by a comparable one, 'Why, when insects are flight tested, do so few individuals exhibit the full complement of physiological factors required for long flight?'

It is clear that sampling error accounts for part of the skew. Long flights are more likely early in the life of an insect, but even then significant day to day variation occurs. Therefore a skewed flight distribution would be the expected outcome of a single testing of a group of individuals of mixed ages, even though all individuals might exhibit long flights at some time during their lives. It should not be difficult to eliminate the sampling biases. Individuals of known ages can be flight tested more than once, preferably at least 4 or 5 times early in life. If after such tests the mean flight duration is used, the skew should be reduced. If the single longest flight duration is plotted, the skew could be reduced even further (Davis 1980a).

While there can be little doubt that the skew is partly an experimental artifact, experiments conducted to control for the sampling error have shown with equal definitude that most insects exhibit short flights most of the time. Might short flight be adaptive after all?

By themselves, each of the three evolutionary arguments may not be persuasive. However, it is significant that the three different lines of reasoning complement one another and are consistent in suggesting that natural selection should favor short fliers. The only difficulty is that currently the arguments are entirely theoretical.

For example, it is true that a striking similarity exists between the flight distributions and the dispersal distances of insects. When known the dispersal distances of insects, and other animals as well, follow a strongly leptokurtic distribution. That is, most individuals are quite restricted in their movements, while a few disperse very long distances (Bateman 1950, Wallace 1966, Endler 1977). It is very

tempting to assume that the experimentally measured flight distributions, which are likewise characterized by a preponderance of short flights, and also exhibit long horizontal tails, correspond to the dispersal distances in the field. Unfortunately, the extent to which laboratory tested long fliers actually represent the migrants or long distance dispersers of a population is not known for any insect species.

Data regarding migration and dispersal rates is also lacking owing to the difficulty of documenting these rates in natural populations. It is not sufficient simply to document removal rates, since predation and natural death produce the same effect. Dispersing individuals must actually be recorded, and it is doubtful whether any trapping systems capture any more than a small fraction of the individuals leaving a population (eg., B. Davis 1975, Barney et al. 1978). Finally, while the short term reproductive costs to long flight have been documented in some species, it is difficult to say what effect long flight has on the long term fitness of individuals. The initial reduction in fecundity might be compensated by benefits that could accrue if an empty habitat is colonized, eg., lack of intraspecific competition.

It is clear that two types of information are required before the evolutionary hypotheses can be evaluated. First, the relationship between laboratory determined flight duration and dispersal tendency in the field must be established. And second, the rate of dispersal in natural populations must be documented. Until these data are obtained, any evolutionary arguments will remain entirely speculative.

CONCLUSION

Insect flight duration has a physiological basis, and therefore the skewed flight distributions observed in laboratory studies are most directly due to the fact that on any given test day, relatively few individuals possess the necessary combination of the many physiological factors necessary for long flight. The skew can be considerably reduced if individuals of known ages are flight tested several times. Although the number of individuals capable of exhibiting long flight may be greater than previous studies have shown, it, nevertheless, is still true that considerable variation in flight ability exists within a species and within populations. Some individuals are more likely to exhibit long flight than others, and many individuals never exhibit a long flight at any time during their life time. What is the significance of this variation?

Although the existence of variation in no way necessarily implicates natural selection, it seems likely that an individual's flight capacity would have some effect on its fitness, i.e., through colonizing potential or fecundity. That flight duration has been shown to be heritable adds to the suspicion that the skewed flight distributions has an adaptive basis. Dingle (1966) suggested that short fliers maintain a center of dispersal in an area favorable for growth, while the long fliers colonize new habitats. To the extent that both benefits and costs accrue to long flight, it may behoove an individual to produce both dispersing and nondispersing offspring (Van Valen 1971, Gadgil 1971, Roff 1975). And as described in this paper, hypotheses based on the predictability of the habitat in space and time, and on the reproductive cost of long flight, suggest reasons why short fliers might be favored over long fliers.

The problem is that all of the evolutionary arguments are entirely theoretical. It is true there is a tantalizing similarity between the measured flight distributions and the observed distribution of dispersal distances in the field. And the evolutionary explanations for the skewed flight distributions are persuasive in their consonance. However, the plain truth is that there is yet no empirical data to support any evolutionary hypothesis. Until a link is established between flight duration and dispersal tendency, and actual dispersal rates are documented, one can only speculate about the potential adaptive basis for the skewed flight distributions.

ACKNOWLEDGMENTS

REFERENCES CITED

Baker, R. R. (1978) The Evolutionary Ecology of Animal Migration. Holmes and Meier Publishers Inc., New York.

Barney, R. J., S. J. Roberts, R. D. Pausch, and E. J. Armbrust (1978) Fall termination of aestivation and field dispersal of the alfalfa weevil (Coleoptera: Curculionidae) in Illinois. The Great Lakes Entomol. 11:255-259.

Bateman, A. J. (1950) Is gene dispersion normal? Heredity 4:353-363.

Bursell, E. (1963) Aspects of the metabolism of amino acids in the tsetse fly Glossina (Diptera). J. Ins. Physiol. 9:439-452.

Caldwell, R. L. and J. P. Hegmann (1969) Heritability of flight duration in the milkweed bug Lygaeus kalmii. Nature 223:91-92.

Chapman, R. F. (1969) Observations on the flight activity of the Red Locust Nomadacris septemfasciata (Serville). Behavior 14:300-334.

Comins, R. F., W. D. Hamilton, and R. M. May (1980) Evolutionary stable dispersal strategies. J. Theor. Biol. 82:205-230.

Davis, B. N. K. (1975) The colonization of isolated patches of nettles (Urtica dioica L.) by insects. J. Appl. Ecol. 12:1-14.

Davis, M. (1980a) Variation in flight duration among individual milkweed beetles: implications for studies of insect flight. J. Insect Physiol. (In press).

Davis, M. (1980b) Seasonal variation in the vagility of populations of the red milkweed beetle, Tetraopes tetraopthalmus. Envir. Entomol. (In press).

Dingle, H. (1965) The relation between age and flight activity in the milkweed bug, (Oncopeltus). J. Exp. Biol. 42:269-283.

Dingle, H. (1966) Some factors affecting flight activity in individual milkweed bugs (Oncopeltus). J. Exp. Biol. 44:335-343.

Dingle, H. (1968) The influence of environment and heredity on flight activity in the milkweed bug, Oncopeltus. J. Exp. Biol. 48:175-184.

Dingle, H. (1972) Migration strategies of insects. Science 175:1327-1335.

Dingle, H. (1978) Migration and diapause in tropical, temperate, and island milkweed bugs. Pages 254-276 in Hugh Dingle ed. Evolution of Insect Migration and Diapause. Springer-Verlag, New York.

Endler, J. A. (1977) Geographic Variation, Speciation, and Clines. Princeton University Press, Princeton, N. J.

Gadgil, M. (1971) Dispersal: Population consequences and evolution. Ecology 52:253-261.

Gould, S. J. and R. C. Lewontin (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. Royal Soc., Lond. B205:581-598.

Hans, H. and A. J. Thorsteinson (1961) The influence of physical factors and host plant odor on the induction and termination of dispersal flights in Sitona cylindricollis (Fahr.). Entomol. Exp. et Appl. 4:165-177.

Johnson, C. G. (1969) Migration and Dispersal of Insects by Flight. Methuen, London.

Johnson, C. G. (1976) Lability of the flight system: a context for functional adaptation. Pages 217-234 in R. C. Rainey ed. Insect Flight. Blackwell Scientific Publications, London.

Jones, R. E. (1977) Movement patterns and egg distribution in cabbage butterflies. J. Animal Ecol. 46:195-212.

Karuhize, C. R. (1972) Utilization of fat reserve substances by Homorocoryphus (Orthoptera: Tettigonidae) during flight. Comp. Biochem. Physiol. 43B:563-569.

May, Y. Y. (1975) Study of two forms of the adult Stenocratus minutus. Trans. Royal Entomol. Soc., Lond. 127:241-254.

Popov, G. B. (1954) Notes on the behavior of swarms of the Desert Locust (Schistocerca gregaria Forskal) during oviposition in Iran. Trans. Royal Entomol. Soc., Lond. 105:65-67.

Rankin, M. A. (1974) The hormonal control of flight in the Milkweed Bug, Oncopeltus fasciatus. Pages 317-328 in L. Barton Browne ed. Experimental Analysis of Insect Behavior. Springer-Verlag, New York.

Rankin, M. A. and S. Rankin (1980) Some factors affecting presumed migratory flight activity of the convergent ladybeetle, Hippodamia convergens (Coccinelidae Coleoptera). Biol. Bull. 158:356-369.

Reddingius, J. and P. J. den Boer (1970) Simulation experiments illustrating stabilization of animal numbers by spreading of risk. Oecologia 5:240-284

Roff, D. (1974) The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. Oecologia 15:259-275

Roff, D. (1975) Population instability and the evolution of dispersal in a heterogeneous environment. Oecologia 19:217-237.

Roff, D. (1977) Dispersal in Dipterans: its costs and consequences. J. Animal Ecol. 46:443-456.

Rose, D. J. W. (1972) Dispersal and quality in populations of Cicadulina species (Cicadellidae). J. Animal Ecol. 41:589-609.

Scudder, G. G. E. (1971) The post-embryonic development of the indirect flight muscles in Cenocorixa bifida (Hung.) (Hemiptera: Corixidae). Can. J. Zool. 49:1387-1398.

Southwood, T. R. E. (1962) Migration of terrestrial arthropods in relation to habitat. Biol. Rev. 37:171-214.

Van Valen, L. (1971) Group selection and the evolution of dispersal. Evolution 25:591-598.

Wallace, B. (1966) On the dispersal of Drosophila. The Am. Nat. 100:551-563.

Weis-Fogh, T. (1952) Fat combustion and metabolic rate of flying locusts (S. gregaria Forskal). Phil. Trans. Royal Soc., Lond. B237:1-36.

Williams, C. B. (1930) The Migration of Butterflies. Oliver & Boyd, Edinburgh.