THE EVOLUTION OF FLIGHTLESSNESS IN INSECTS[1]

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Abstract.   Many pterygote (winged) insects have secondarily become flightless; why has this occurred? In this paper I test for an association between the frequency of flightlessness and (1) environmental heterogeneity, (2) geographic variables, (3) gender, (4) alternate modes of migration, and (5) taxonomic variation. Various authors have predicted that decreased environmental heterogeneity will favor the evolution of flightlessness. This hypothesis is consistent with a number of studies on the variation of wing dimorphism and flightlessness and with data analyzed in the present paper on the relationship between habitat type and wing morph in the North American Orthoptera. The incidence of flightlessness is also exceptionally high in woodlands, deserts, on the ocean surface, in specific habitats on the seashore (dunes and rock crevices but not the foreshore), in aquatic habitats, in the winter months, in hymenopteran and termite nests, and among ectoparasites of endotherms and parasites of arthropods. It is low in habitats bordering rivers, streams, ponds, etc. and in arboreal habitats. Some of these habitats can be classified as persistent, but others cannot be so designated or are too vaguely defined. The incidence of flightlessness increases with altitude and latitude but, contrary to "conventional" wisdom, it is not exceptionally high on oceanic islands compared to mainland areas. Several authors have hypothesized that the clinal variation in flightlessness is a consequence of clinal variation in habitat persistence. Though the available data are consistent with this hypothesis, other factors such as impairment of flight by low temperatures cannot be rejected, though considered unlikely. Flightlessness is more frequent than expected by chance among parthenogenetic species and more frequent among females than males. Furthermore, there is a significant negative association between female mobility and flightlessness in males. I suggest that loss of flight is favored in females because it permits greater allocation of resources to egg production, but that flight is retained in males because it increases the probability of finding a mate.

In some species alternate modes of migration, viz phoresy and ballooning, have evolved. Phoretic transport (i.e., via other animal species) may be important in those species in which it occurs, but it appears to have evolved relatively rarely. Among the Insecta ballooning occurs only in the larvae of Lepidoptera. Aptery (winglessness) is unusually frequent among Lepidoptera that eclose in the fall and winter months and live in woodlands and forests. I hypothesize that larval migration by ballooning, the large-scale spatiotemporal stability of woodlands, and the small-scale unpredictability of spring bud burst are primary factors favoring the evolution of flightlessness in these Lepidoptera.

The mode of metamorphosis is correlated with the frequency of flightlessness; hemimetabolous and holometabolous insects are rarely flightless, while it is common among paurometabolous insects. Two factors that may favor such an association are differences in relative mobility of the larvae and niche shifts between the adult and larval stage. In the holometabolous insects taxonomic families with at least one flightless species have more species than those with only winged species. A possible explanation for this is that the occurrence of the appropriate ecological conditions favoring flightlessness in holometabolous insects and the requisite mutations are both very rare events.

Key words: aptery; Darwin; dispersal; evolution; flightlessness; heterogeneity; Insecta; persistence; pterygomorphism; sexual dimorphism; wing dimorphism; wings.

INTRODUCTION

In North America alone there are > 300 000 species of pterygote insects, inhabiting practically all habitats (Arnett 1985). The enormous diversity and evolution-

ary success of insects can be attributed in part to the evolution of flight, which enables them to disperse widely and easily in search of mates, food, and new habitats. However, many originally winged species have become secondarily flightless. Darwin (1876) proposed a hypothesis to account for the loss of wings of insects on the island of Madeira, but in his original manuscript

he notes that his hypothesis is inadequate to explain "the fact, discussed by Mr. Westwood that in many parts of the world, there are insects belonging to various orders, of which individuals may be taken either winged or perfectly apterous; of this fact the common Bed-bug is a well known instance. . . . The facts anyhow plainly show that there is something in regard to the wings of insects, which we do not in the least understand" (Stauffer 1975: 293).

In the "Origin of Species" Darwin suggested that "If under changed conditions of life a structure, before useful, becomes less useful, its diminution will be favoured, for it will profit the individual not to have its nutriment wasted in building up a useless structure" (Darwin 1876: 117–118). Contrary to the assertion by Slater (1977), it is evident from Darwin's previous statement (see also *Geographic variation in flightlessness: Darwin's hypothesis and the evolution of flightlessness on oceanic islands,* below) that he did not consider this hypothesis applicable to the evolution of flightlessness. However, one possible advantage of wing loss is that it allows an insect to divert energy normally expended in wing and wing muscle development to some other use, such as increased fecundity, that would increase the female's fitness more than the advantages accruing from the ability to fly. Indeed, the wing muscles of insects are relatively massive structures, occupying, for example, 70% of the thoracic cavity in the Gerridae (Andersen 1973), and comprising 10–20% of the body mass in most insects (Greenewalt 1962). Such large muscles undoubtedly consume a significant portion of an insect's energy budget, and thus potentially decrease egg production. This is supported by the observation that many insects histolyze their wing muscles during egg production. Autolysis (self-digestion) of its flight muscles during egg production by the mosquito *Aedes communis* provides sufficient nitrogen for the development of 18 eggs, nearly one third of the average number developed (Hocking 1952). In the cricket species *Teleogryllus oceanicus* and *Gryllus firmus* there is a positive correlation between the degree of wing muscle histolysis and egg production (Roff 1988). Finally, in wing-dimorphic insect species the onset of egg laying is earlier and total fecundity higher in the flightless morph than the winged morph (Roff 1986a, Roff and Fairbairn 1990).

However, although fecundity and flight capability may be negatively correlated, we still require a mechanism (or mechanisms) that accounts for the maintenance of flight in some species but not others. In this paper I examine the statistical association between the incidence of flightlessness and various factors within the framework of hypotheses proposed to account for the evolution of flightlessness. The paper is organized into five sections based on correlations with (1) environmental heterogeneity, (2) geographic variation, (3) gender, (4) alternate modes of dispersal, and (5) taxonomic variation.

ENVIRONMENTAL HETEROGENEITY AND THE EVOLUTION OF FLIGHTLESSNESS

Theory

Loss of flight capability means, in general, a loss of ability to migrate distances greater than a few hundred metres. The definitions of "migration" and "dispersal" are controversial in the entomological literature (Taylor 1986); in this paper I shall use "migration" in the sense of movement from one spatial unit to another (Southwood 1962, 1981, Johnson 1969, Dingle 1972). The term "dispersal" has frequently been used in this sense although it has also been used to include movement within a habitat (Danthanarayana 1986). While arthropods $< \approx 1$ mm may be able to migrate aerially without the use of wings (Washburn and Washburn 1983), the vast majority of insects, whether they actively fly between habitats or passively migrate using wind currents of the upper atmosphere (the so called "aerial plankton"), are winged, including such small insects as aphids (Parry 1978, Tedders and Gottwald 1985), thrips (Lewis 1973), and many insect species < 1.5 cm ("micro-insects," Farrow 1986). A study of the evolution of flightlessness must, therefore, address the question of the adaptive significance of migration in insects.

Southwood (1962: 172) put forward the hypothesis that among terrestrial arthropods, "the prime evolutionary advantage of migratory movement lies in its enabling a species to keep pace with the changes in the locations of its habitats." The theoretical basis of this hypothesis has been investigated very extensively (see, for example, Reddingius and den Boer 1970, Van Valen 1971, Roff 1974 a, b, 1975, 1986a, Jarvinen 1976, Jarvinen and Vepsäläinen 1976, Fahrig 1990). The general results of these studies can be illustrated by the following simple model. Suppose there are two patches that persist (i.e., are suitable for growth and reproduction) from generation to generation with probability p. Consider two scenarios; firstly, that there is no migration between patches, and secondly, that some proportion of the population in each habitat migrates to the other patch at each generation. The probability that a patch lasts t generations is p^t; clearly, as t increases the probability that a patch persists for the specified time interval decreases. Extinction in the first scenario (no migration) requires only that both patches become unsuitable for growth and reproduction during the time interval t, while extinction in the second (migration) requires that both patches simultaneously become unsuitable. Therefore, the probability of a population persisting over some time interval t without migration is $1 - (1 - p^t)^2$, compared to $(1 - [1 - p]^2)^t$ when there is migration between patches. If $p = .95$ the migratory population is 66 times more likely to persist for 100 generations than the non-migratory population. In a highly unstable environment where $p = .9$ this likelihood is increased to 6890. Thus migration can have

very significant effects on the persistence of a species. Increasing the number of patches over which migration occurs further reduces the likelihood of extinction (Roff 1974b). Extinction does not require that a patch become absolutely unsuitable. Suppose population growth in patch i is governed by the recursion equation

$$N(t + 1, i) = \lambda N(t, i)$$

where $N(t, i)$ is the population size in patch i at time t and λ is a random variable >0 and with mean >1. Even though the arithmetic mean population size grows without bound the probability of extinction may become certain as time increases (Levins 1969, Lewontin and Cohen 1969, May 1971, 1973). Imposition of a carrying capacity increases the probability of extinction (May 1973, Roff 1974b). Numerical analysis has demonstrated that in both cases migration between patches may greatly increase persistence time (Roff 1974a, b).

The above models illustrate the advantage of migration. Therefore, why do not all organisms migrate? It has long been assumed that migration is costly because a large number of migrants probably fail to find new habitats (Elton 1927). A second reason is that migration may be energetically expensive and hence reduce fecundity or mating success. Flight reduces subsequent reproduction in several insect species (Roff 1977, Inglesfield and Begon 1983), though in others migration is a programmed part of the life cycle and reproduction will not commence until the insect has flown (Rankin et al. 1986). A winged insect does not have to fly, and hence selection favoring a reduction in migratory activity will not necessarily also favor the loss of flight capability. Such a loss will be favored if there is a cost to possessing the ability to fly regardless of whether or not the individual flies (Roff 1984). This hypothesis has been tested using wing-dimorphic insects. In such species some individuals have functional wings and are capable of flight, while others lack wing muscles and have reduced or no wings, and are thus incapable of flight. A large number of studies have demonstrated that in these species the individuals possessing functional wings start reproducing later and produce fewer eggs than the "short winged" morph (reviewed in Roff 1986a and in Roff and Fairbairn 1990). Thus the development and maintenance of the flight apparatus is reproductively costly, whether or not it is ever used.

Given that there is a cost to flight (be it increased mortality and/or reduced fecundity) the proportion of migrants maintained in the population will be a function of the trade-off between the long-term advantage accruing to migrants by virtue of the dispersal of their genes over many patches and the short-term individual cost of migration. This problem was investigated by Roff (1975) for a variety of genetic models of migration. In these models both the finite rate of increase, λ, and the carrying capacity, K, were allowed to vary randomly. Increasing the cost of migration or decreasing the mean value of λ decreases the proportion of migrants in the population. The effect of changing other parameters depends upon the migration function and/or the genetic basis of the trait; however, overall it appears that increasing the mean carrying capacity or decreasing the variances of either λ or K also decreases the proportion of migrants in the population (see Roff 1975: Table 10). The influence of the number of patches was not investigated in this study, but other studies have shown the intuitively reasonable result that decreasing the number of patches increases population fluctuations and the probability of extinction (Roff 1974b, Fahrig and Merriam 1985, Lefkovitch and Fahrig 1985). As the number of patches decreases there will be increased selection for migration, contingent on possible changes in the probability of migration beyond the boundary of the habitat. If the loss of migrants by emigration out of the region is high, selection will favor a reduction in migration rate. At some small region size an insufficient migration rate between patches will be sustained, the population will go extinct, and the area will be recolonized by immigration. Thus as region size decreases there may first be an increase in the frequency of migrants, then a decrease, and finally an increase again as the population repeatedly goes extinct and is restarted by incoming migrants.

To summarize, in a heterogeneous environment migration will evolve in accordance with the cost of migration, the number of habitat patches within the region, and the means and variances of λ and K.

Evidence

Southwood (1962) confined his analysis to two categories of habitat, "temporary" and "permanent." Specifically, he predicted that, "within a taxon one should find a higher level of migratory movement in those species associated with temporary habitats than in those with more permanent ones" (Southwood 1962: 172). Examples of permanent habitats are "rivers, lakes, perennial plants including trees of climax vegetation such as woodlands, salt marshes, heath lands and marshes fringing lakes and rivers" (Southwood 1962: 175), while temporary habitats include "dung, carrion, fungi, plant debris (i.e. logs, straw, hot-beds), and annual and perennial plants of seral communities (e.g. wastelands, fields) . . . Some ponds" (Southwood 1962: 175). There is a trend for permanent habitats, as defined by Southwood, to be extensive (large K), and for temporary habitats to be localized (small K), though in some cases small patches may have well defined borders and be highly persistent (e.g., caves).

Southwood's analysis, though based on an extensive survey of the literature, was largely qualitative, and no statistical tests were presented. Nevertheless, the evidence presented by Southwood (1962) does indicate a correlation between migratory tendency and habitat persistence (where sufficient data are given in Southwood's paper I have performed the appropriate statis-

tical test and, in general, there is a significant correlation in the predicted direction). Analysis of wing dimorphism and habitat characteristics in gerrids (Brinkhurst 1959, 1963, Vepsäläinen 1978, Dingle 1979, 1985), planthoppers (Denno 1978, 1979, Denno and Grissell 1979, Denno et al. 1980, 1990, McCoy and Rey 1981) and carabid beetles (den Boer 1970, 1971, den Boer et al. 1980) have all given further support to this hypothesis. Studies of carabid faunas in habitats at different stages of succession have also found that the frequency of flightless species increases as succession proceeds (den Boer et al. 1980, Ranta and Ås 1982). The same correlation has been demonstrated for the Heteroptera of Britain (Brown 1982), and the hemipteran, *Coranus subapterus* (Wallace 1953, analyzed in Roff 1990a).

To test the hypothesis further I analyzed the relationship between wing morph and habitat in the Orthoptera of North America using two monographs, one describing the fauna of eastern North America (Blatchley 1920) and the second the fauna of Canada and Alaska (Vickery and Kevan 1983). Based on these two monographs, species were assigned to one of 10 habitats. The distribution of species ordered by wing morphology (winged, wingless, or dimorphic) and habitat type are shown in Fig. 1, the habitats being ranked according to the descending frequency of occurrence of winged species in Blatchley's data. The 10 habitats so ranked are:

1) Pastures, meadows, scrubland and prairies;

2) Borders of, or within, swamps, lakes and streams outside of woods;

3) Arboreal;

4) Open dry areas, sandy sites and gravelly areas;

5) Woodland, not associated with water;

6) Same as 2, but within woods;

7) Under logs, stones and in burrows;

8) Caves;

9) Ant nests;

10) Alpine and tundra.

Habitats are generally inclusive, i.e., species found in habitat category 1 are generally found in all of the described habitats within this category. In both data sets there is highly significant variation between habitats with respect to the frequency of wing morphs (omitting dimorphic species and habitats with too few observations; from Blatchley's data: $\chi^2 = 100$, df = 6, $P < .01$, and from Vickery and Kevan's: $\chi^2 = 128$, df = 6, $P < .01$; Fig. 1). Winged species predominate in habitats 1 to 4 whereas flightless species are in the majority in habitats 5 to 10. At least some of the components of each of habitats 1, 2, and 4 are transitional stages in succession and are temporary habitats as defined by Southwood (1962). Thus orthoperan species found on the prairies, which may or may not be heterogeneous in space and time (I have been unable to obtain sufficient data to test this possibility), are also found on early successional habitats such as pastures,

meadows, and scrubland (habitat 1). The high frequency of winged arboreal species (habitat 3) is explicable by the hypothesis that flight is required to move efficiently within a three-dimensional habitat (see next section, below). However, it should also be noted that many arboreal species of Orthoptera live in vines and shrubbery rather than trees, and are found in relatively early successional stages. Thus arboreal species of North American Orthoptera may be under selection for flight capability both because of the three-dimensional nature of their habitat and because their habitats are early- or mid-successional stages persisting for only a few decades. Southwood (1962) included woodlands within his permanent category and predicted that these will favor a nonmigratory lifestyle; this hypothesis is supported by the preponderance of flightless Orthoptera in woodland habitats (habitats 5 and 6).

Most Orthoptera found under logs and stones or in burrows (habitat 7) are flightless. However a subterranean lifestyle does not by itself appear sufficient to select for flightlessness, since the mole crickets, *Scapteriscus vicinus* and *S. acletus,* are highly modified for burrowing but are also excellent fliers. Both species inhabit open, temporary sites such as cultivated fields, turfs, and pastures (Matheny et al. 1983, Walker and Fritz 1983). All seven of the monomorphic winged species and two of the three dimorphic species occur in temporary habitats (habitats 1 and 2). Thirty-four of the flightless species occur in woodlands, as does the third dimorphic species, *Miogryllus verticalis,* in which the winged morph is rare. The habitat descriptions of the remaining eight flightless species are too vague for assignment. Omitting the dimorphic species, the distribution of winged and wingless Orthoptera in habitat 7 is significantly heterogeneous ($P < .0001$, Fisher exact test), and is in accord with the hypothesis that the evolution of flightlessness is a function of environmental heterogeneity.

The number of species found primarily, or only, in caves, ant nests, alpine areas, or tundra (habitats 8–10) are few in number, but are predominantly flightless (Fig. 1). Cave environments are relatively constant (Barr 1968) although some caves can experience seasonal flooding with concomitant drops in temperature (Barr 1967). There are few Orthoptera found in ant nests but these, like other myrmecophilous and termitophilous insects, tend to be flightless (see subsection *Hymenopteran and termite nests,* below). Why this should be so is not clear. Alpine and tundra habitats are persistent in the sense that rates of succession proceed extremely slowly in such areas.

The hypothesis that flightlessness will be favored by habitat persistence is broadly supported by the studies cited above and the present analysis of the association of pterygomorphism with habitat type among the North American Orthoptera. However, more quantitative data on the persistence times and patch sizes within the various habitat categories are needed.
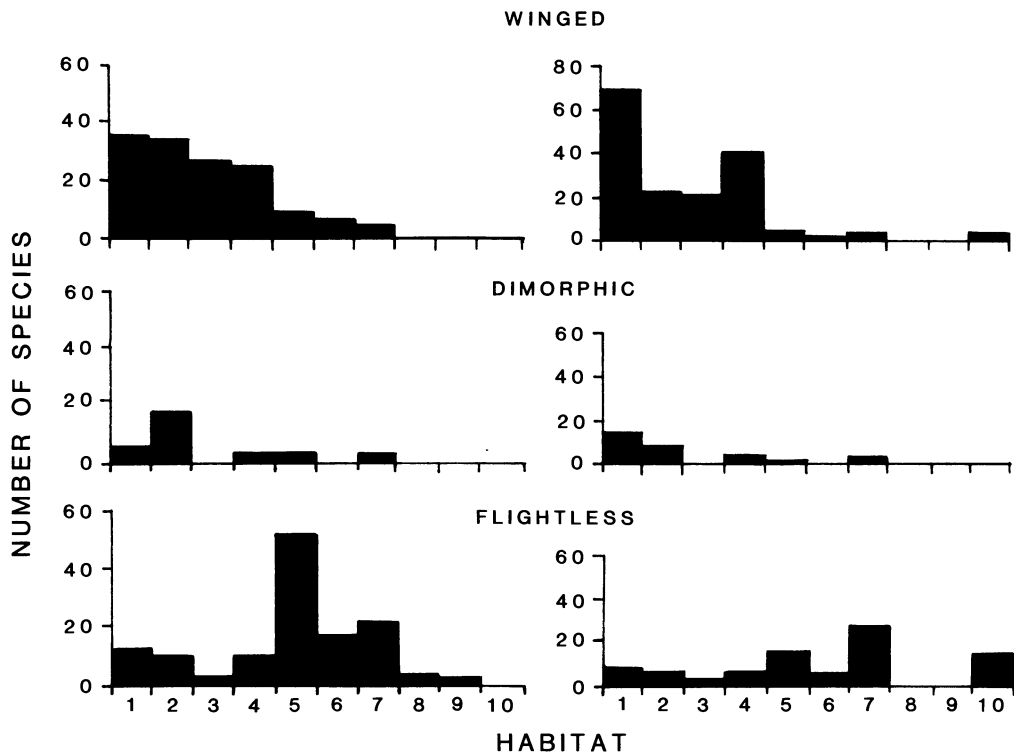
FIG. 1. Distribution of winged, dimorphic, and flightless North American Orthoptera among different habitats. Left panels: eastern North America (data from Blatchley 1920); Right panels: Alaska and Canada (data from Vickery and Kevan 1983). Habitat designations: 1. Pastures; 2. Borders of, or within, swamps, lakes and streams outside of woods; 3. Arboreal; 4. Open dry areas, sandy sites and gravelly areas; 5. Woodland, not associated with water; 6. Same as 2 but within woods; 7. Under logs or stones and in burrows; 8. Caves; 9. Ant nests; 10. Alpine and tundra.

Further observations on habitat and flightlessness

Based primarily on taxonomic surveys, various habitats have been cited as having inordinately high or low frequencies of flightless insects. The incidence of flightless insects within such habitats has frequently been explained on the basis of habitat persistence. Are such arguments justified? In the following analysis I include not only the evidence advanced in support of the proposed correlation between habitat type and incidence of flightlessness, which is frequently very scanty, but also data that I have gleaned from the literature (Table 1). High or low incidence of flightlessness was assessed at various taxonomic levels, depending on the available data; where the region is given (Table 1: column 3) the analysis pertains to the whole order within that region, otherwise to the taxonomic category indicated, the region either being worldwide or as indicated in the footnotes or brackets within the table.

Most of the data used in the present analysis and others within this paper were gleaned from taxonomic papers, and in many cases neither the original data nor statistical tests of associations were presented by the author. Furthermore, the condition of the wings is frequently not described in the taxonomic literature; this

is particularly true of the Coleoptera, Homoptera, and Hemiptera. For this reason one cannot always extract the relevant data from taxonomic reviews. I accepted only papers based on original data, or extensive reviews by noted experts of the taxonomic group in question. Where possible I verified all statements by the appropriate statistical analysis. Statements on associations were placed into one of 4 categories (Analysis column of Table 1): (1) my own statistical analysis, including both cases in which I statistically verified assertions by a particular author and cases in which I was able to compile data for a particular species or higher taxon; (2) statistical analysis by cited author; (3) review by cited author; and (4) observation by cited author. These cases were generally observations on particular species; for example, with regard to the cockroach *Ectobius africanus,* Rehn (1931: 352) noted "the reduction in alar length in the female sex is evident in no material with altitudinal data from below 1000 meters on Kibonoto, Kilimanjaro." While statistical significance cannot be precisely adduced from such statements it seems unreasonable to ignore or reject them. If no association generally existed we should expect to find an equal number of instances in which an opposite association was found.

TABLE 1.   Habitats commonly cited as containing higher- or lower-than-average frequencies of flightless species.

Habitat	Order	Taxon or Region	Incidence*	Analysis†	Reference‡
Woodland	Orthoptera	North America	+	1	...
		Acridoidea	+	3	1
	Coleoptera	Carabidae	+	2	2–4
		Scarabaeinae (Australia)	+	3	5
		Anotylus	+	3	6
		Pterostichus strenuus	+	2	7
	Lepidoptera	Europe	+	3	8, 9
		North America	+	1	30, 31
	Embioptera	Worldwide	−	3	10
Deserts	Blattodea	Worldwide	+	3	12–14
	Orthoptera	North Africa	+	2	15
		Worldwide	+	3	13
	Hemiptera	Reduviidae	+	3	16
	Coleoptera	Mexico and USA	+	3	17
		Namib Desert	+	2	18
		Tenebrionidae	+	3	19
		Trox	+	3	20
	Embioptera	Worldwide (males)	+	3	10
Ocean surface	Diptera	Chironomidae	+	1	a
	Hemiptera	Gerromorpha	+	1	b
Seashore	Hemiptera	Saldidae	−	1	c
	Coleoptera	Except Staphylinidae	+	1	d
		Blebius (Staphylinidae)	0	1	e
	Diptera	Worldwide	+/−	1	f
Freshwater	Plecoptera	Worldwide	−	1	g
	Hemiptera	United Kingdom and Canada	−	1	h, i
		Corixidae (United Kingdom)	−	3	9
	Coleoptera	England	+/−	1, 3	9, j
Margins of freshwater bodies	Coleoptera	Carabidae	−	3, 2	3, 21
	Orthoptera		+/−	1	k
	Hemiptera		+	1	l
Snow surface	Mecoptera	Worldwide	+	1, 3	22, m
	Diptera	*Chionea*	+	3	23, 24
	Insecta	Alpine	+	3	25
Caves	Blattodea	Worldwide	+	1, 3	11–13, n
	Orthoptera	Worldwide	+	3	13
	Coleoptera	Worldwide	+	3	19
		Ptiliidae	+	3	26
		Pseudanophthalmus spp.	+	3	27
		Aglyptinus dimorphicus	+	3	28
	Diptera	Worldwide	0	3	23
Hymenopteran and termite nests	Blattodea	Worldwide	+	3b	13, o
	Orthoptera	Worldwide	+	3	29
	Coleoptera	Various families	+	1	p
	Diptera	Worldwide	+	3	23
	Hymenoptera	Worldwide	+	1	q
Endotherm body surfaces (ectoparasites)	Dermaptera	Worldwide	+	1	r
	Hemiptera	Worldwide	+	1	s
	Diptera	Worldwide	+	1, 3	23, t
	Coleoptera	Worldwide	+	3	19
Arthropod tissues (parasites)	Diptera	North America	−	1	u
	Hymenoptera	Worldwide	+	1	v

* Incidence of flightlessness: + = greater than average, − = lower than average, 0 = no different from average, +/− = incidence depends on microhabitats.

† Categories of analysis: (1) My own statistical analysis, including both cases in which I statistically verified assertions by a particular author and cases in which I was able to compile data for a particular species or higher taxon; (2) statistical analysis by cited author; (3) review by cited author. For further details see *Environmental heterogeneity and the evolution of flightlessness: Further observations.* . . .

‡ References: (1) Jago 1973, (2) Greenslade 1968, (3) Thiele 1977, (4) Ranta and Ås 1982, (5) Matthews 1972, 1974, 1976, (6) Hammond 1976, (7) Den Boer 1971, (8) Hudson 1913, (9) Southwood 1962, (10) Ross 1970, (11) Rehn 1932*b*, (12) Chopard 1925, (13) Chopard 1938, (14) Schal et al. 1984, (15) Buxton 1923, (16) Poisson 1946, (17) Van Dyke 1929, 1933, (18) Holm and Scholtz 1980, (19) Crowson 1981, (20) Scholtz 1981, (21) Darlington 1943, (22) Byers 1954, (23) Hackman 1964, (24)

TABLE 1. Continued.

Byers 1969, (25) Mani and Giddings 1980, (26) Dybas 1960, (27) Barr 1967, (28) Peck 1968, (29) Chopard 1949, (30) Barbosa et al. 1989, (31) Covell 1984.

Additional reference information:

a) There are >5000 species of Chironomidae, 64 of which are marine (Hashimoto 1976). Only one freshwater species is flightless, and this occurs in the high Himalayas (Kohshima 1984), but 46% of marine species have flightless females, and in some species flightless males.

b) All 81 species of marine water striders are flightless. Other Gerromorpha found on the water surface in the intertidal region are the Veliidae (18 species, all flightless), the Mesoveliidae (3 species, all flightless), and the Hermatobatidae (9 species, all flightless; data for all groups are from Andersen and Polhemus 1976). In these families the freshwater species also tend to be flightless.

c) Flightless saldids occur, but all littoral forms have winged morphs capable of strong flight (Polhemus 1976).

d) Among the Coleoptera other than the Staphylinidae, there are ≥ 50 species that regularly spend a portion of their lives below the high tide line (Doyen 1976). Based on the 30 species for which wing morph data are available, 83% of these species are flightless (data from Walsh 1926, Doyen 1976). This is far higher than typical of the Coleoptera (see Table 8). In dunes abutting the shore, 71.4% of species within the carabid genus *Nebria* are flightless (Kavanaugh 1985).

e) There are ≈ 300 intertidal Staphylinidae (Moore and Legner 1976). I have been unable to obtain information on these species. However, only 4 of the 207 species of *Blebius,* a staphylinid genus found along the shores of the sea and saline lakes, are flightless (Herman 1986). This suggests that there is little or no evolutionary tendency for the intertidal Staphylinidae to become flightless.

f) Diptera found on the foreshore are almost entirely winged, while the fauna on the dunes abutting the shore have higher-than-usual frequencies of flightless species (Ardo 1957, Hackman 1964).

g) Almost all freshwater species (>90%, see Table 8) are winged, while all terrestrial species (≈ 10 species) are flightless (Illes 1968).

h) Among the freshwater Hemiptera of England 92.9% are winged compared to an overall incidence among British Hemiptera of 76.2% (data from Southwood and Leston 1959), while 96.8% of aquatic Canadian species listed by Scudder (1987) are winged. The difference in incidence between aquatic and non-aquatic species in England is statistically significant ($\chi^2 = 7.1$, df = 1, $P < .01$).

i) A significantly high frequency (57.5%, $n = 40$) of monomorphic winged, aquatic and semiaquatic species of Hemiptera occur, in Canada, on temporary ponds than species with flightless morphs (28.56%, $n = 14$; $\chi^2 = 3.47$, df = 1, $P < .05$, one-tailed test; data are from Scudder 1987).

j) Among the aquatic Coleoptera there is significant heterogeneity in the frequency of flightless and "flight capable" species among habitats ($\chi^2 = 44.8$, df = 4, $P < .001$; data from Southwood 1962: Table 4), with the frequency of flightless species increasing with relative permanence of habitat (0%, 6.9%, 18.9%, 41.2%, and 81.3%, respectively).

k) See text, *Environmental heterogeneity and the evolution of flightlessness: Evidence,* above.

l) None of the British riparian Hemiptera are monomorphically apterous (Southwood and Leston 1959).

m) Of the 68 species of Mecoptera occurring in North America, 16 (possibly 17) have flightless females, of which 13 species are found on snowfields. All 13 flightless species found on snow belong to the family Boreidae (snow scorpions) and are wingless in both sexes (Byers 1954, Arnett 1985). In Australia only 1 of the 16 mecopteran species is wingless (*Apteropanorpa tasmanica*); this is apterous in both sexes and was collected on the snow (Riek 1970).

n) Roth and Willis (1954) describe 48 species of cockroach as cavernicolous. Of the 18 for which I was able to obtain wing lengths on the females 8 are winged, 10 are flightless and 1 is dimorphic. The proportion of flightless species (55.6%) is not significantly different from the proportion of (non-cavernicolous) flightless species in Texas (60.9%, $n = 23$, $\chi^2 = 0.1$, $P > .5$; data from Hebard 1943), but is significantly higher than the proportions in French Guiana (7.8%, $n = 65$, $\chi^2 = 21.4$, $P > .001$; data from Hebard 1926) or Africa and Malagasy (26.6%, $n = 86$, $\chi^2 = 6.3$, $P < .05$; data are from Rehn 1932a, 1937).

o) 100% ($n = 28$) of myrmecophilous and termitophilous cockroaches listed by Chopard (1938) are flightless.

p) Approximately 28.4% ($n = 81$) of termitophilous Staphylinidae are flightless (data from Seevers 1957, Kistner 1970a–f, Kistner and Pasteels 1970a, b, Kistner and Abdel-Galil 1986a, b), compared to only 2.3% ($n = 479$) of staphylinids found in other habitats (data are from Campbell 1976, Watrous 1980, Herman 1986). In the Ptinidae (Coleoptera) 82% of inquiline species are flightless (data from Lawrence and Reichardt 1969). Species within the coleopteran family Limulodidae (27 species, worldwide) are highly specialized beetles found in ant nests, and all are flightless (Arnett 1968). Larvae of blister beetles (Meloidae) feed on the provisions and larvae of wild bees (a few genera attack the egg cases of grasshoppers); of the 310 species in North America at least 20 species (6.5%) are flightless (Arnett 1985).

q) Wasps (Hymenoptera) are uncommon in ant and termite nests (Wheeler 1910, 1928, Kistner 1969). In two studies of the insects of ant nests (Brues 1902b, Mann 1914) eight species of wasps were collected, three of which were flightless. This is significantly more than expected by chance given the overall frequency of flightless Hymenoptera of 5.1% ($n = 39\,499$ species, data from Reid 1941). The Formicidae were omitted for obvious reasons. Also omitted was the Mutillidae, which comprises 3500–4000 species, all females of which are apterous. The larvae are largely parasitic on ants and bees, but the adults do not inhabit the nests of these.

r) Twelve species of Dermaptera (suborders Arixeniina and Hemimerina) are highly modified ectoparasites closely resembling lice in their appearance, and are likewise apterous (O'Toole 1986).

s) Ectoparasitism is uncommon among the Hemiptera, but in all cases the species are flightless. The Cimicidae (bedbugs), all species of which are flightless, are generally considered ectoparasites, although they do not remain on the host after feeding, residing instead in the nest of their host species. The hemipteran genus *Polyctenidae* comprise a small number (two in North America) of rare species that are flightless and ectoparasitic on bats (Miller 1971, Arnett 1985).

t) In North America there are between 40 and 50 dipteran species that are ectoparasites of birds and mammals. At least 26% of these insect species are flightless (data from Arnett 1985). This represents a considerable increase over the $\approx 1\%$ of flightless species in the Diptera (Table 8).

u) Dipteran species parasitic on arthropods comprise 12.5% of the dipteran fauna of North America; none are flightless (data are from Arnett 1985).

v) Flightless parasitic wasps occur in 13 families of the Hymenoptera (data from Arnett 1985), the frequency of flightless species ranging from 0.1% in the Braconidae to 100% in the highly speciose Mutillidae (Reid 1941).

Specific statistical tests of the relative incidence of flightlessness in each habitat are provided in the footnotes to Table 1, and only the conclusions and implications will be discussed here.

Woodlands.—Within woodlands a higher-than-average incidence of flightlessness is found in the Orthoptera, the Coleoptera, and the Lepidoptera, but not male Embioptera (females are universally apterous). As mentioned above (see Evidence), woodlands are both persistent and, frequently, spatially extensive (Southwood 1962).

Deserts.—Orders in which there is a high frequency of flightless desert species are the Blattodea, the Orthoptera, males of Embioptera, the Coleoptera, and the hemipteran family Reduviidae (Table 1).

Fusion of the elytra to prevent water loss has been suggested as the primary factor in the evolution of aptery in desert beetles (Brues 1902*a*, 1908, Hesse 1938, Scholtz 1981), though it also occurs in aquatic species (Jackson 1950, Doyen 1976). As such fusion does not occur in the other desert-dwelling orders it is probably a secondary adaptation that is contingent upon flightlessness first evolving as a consequence of some other factor.

The category of "desert" is broad and can encompass several types of habitat. For example, as noted by Southwood (1962), insects that feed on foliage produced during erratic rainfalls face an environment that may be highly variable in both space and time. However, due to the dryness, rates of decay are very slow and hence insects feeding on detritus, carcasses, or the persistent parts of desert plants live in a habitat that may be relatively persistent, though it seems unlikely that these patches persist for hundreds of years. Blattids are typically omnivorous, while embiopterans and many desert-dwelling apterous Coleoptera are detritovorous or necrophagic (e.g., Tenebrionidae: Holm and Edney 1973, Trogidae: Scholtz and Caveney 1988). Most Orthoptera feed on vegetation, and the desert fauna has a number of highly migratory species that take advantage of the ephemeral patches of grassland that arise following rainstorms (Southwood 1962), but I have been unable to ascertain the food or general habits of the apterous species. The Reduviidae are either predatory or bloodsucking (Arnett 1985). The diversity of desert habitats is too broad and quantitative data too scanty to describe the high incidence of flightlessness among some taxa as being primarily a consequence of habitat persistence or environmental heterogeneity in general.

Ocean surface.—Two groups of insects, the midges and water striders, have colonized the ocean surface, and in both groups flightlessness is extraordinarily high in the marine species (Table 1: footnotes a, b). This habitat is both long lasting and extensive, and dispersal can be accomplished by swimming or skating, but we lack data on the distribution of food sources. It is possible that the probability of finding either food or a mate by flight is so low that it is not worth the energy cost; the best strategy may be to keep together in localized swarms. Further research on the spatial distribution of marine midges and water striders is required to resolve this question.

Seashore.—Like deserts, the seashore comprises several different habitats. Most intertidal Coleoptera, other than the staphylinids, are crevice dwellers, and are predominantly flightless (Table 1: footnote d). Likewise, in the dune habitat flightless species are unusually prevalent in the Carabidae and Diptera. Contrariwise, insects found in or around seaweed thrown up on shore or on the sand (Diptera, Staphylinidae, and Saldidae) are predominantly winged (Table 1: footnote c).

Rock crevices are persistent but may become submerged at high tide. Most beetles found in this habitat can withstand at least short-term immersion in seawater (Doyen, 1976). Foredunes are also persistent, though major storms may destroy local habitats and move the dunes around. On the other hand, seaweed thrown up on shore is a temporary habitat inasmuch as it dries out and/or is removed by the incoming tide.

Freshwater.—Freshwater habitats range from small temporary pools and streams to large lakes and rivers. Insects that have aquatic larvae cannot migrate between water bodies except by flight or walking overland. The latter is not likely to be very successful, while the former permits not only the colonization of new sites but also the colonization of a variety of sites. Thus insects with aquatic larvae should be predominantly winged, and wingless species should occur only in relatively permanent bodies of water such as rivers and lakes (Southwood 1962).

Adults within the Ephemeroptera, Odonata, Plecoptera, Tripchoptera, and neuropteran suborder Megaloptera are virtually all winged (>90%, see Table 8) and have aquatic larvae. Though Plecoptera are typically winged, all terrestrial Plecoptera are flightless (Table 1: footnote g). The incidence of flightlessness increases with the relative permanence of the water body within the British Coleoptera (Table 1: footnote j), the Corixidae (Southwood 1962), the Gerridae (reviewed in Dingle 1980), and the aquatic Hemiptera of Canada (Table 1: footnote i).

Margins of freshwater bodies.—Flightlessness is rare among Carabidae and Hemiptera (Table 1: footnote l) that live along the margins of rivers, streams, etc. In the North American Orthoptera, species found on the margins of freshwater bodies that are outside of woodlands are predominantly winged, while those within woods are predominantly flightless (see Fig. 1). The margins of freshwater bodies are assumed to be relatively unstable habitats for carabids due to flooding and overgrowth of dense vegetation (den Boer 1970, Thiele 1977). I can find no data on rates of loss of habitat with which to test this hypothesis.

Snow surface.—High alpine faunas generally comprise a high frequency of flightless species (Mani and

Giddings 1980), while two orders, Mecoptera and Diptera, have genera containing inordinately high frequencies of flightless species found on snowfields (Table 1: footnote m). It is unlikely that snow-covered ground is the typical habitat of the nival species; a more likely scenario is that these insects wander onto the snow in search of the insect and plant debris that collects there. For example, nival wingless mecopterans feed on moss (Carpenter 1931, 1953), while species of the genus *Chionea* (Diptera) are scavengers and their typical habitat is deciduous woodland (Byers 1983). Many, if not most, insects found at high altitude are predators and scavengers feeding on arthropod fallout and windblown plant matter (Edwards 1987). The rates of succession in alpine areas are very low; this, in conjunction with the "blanket" nature of fallout, probably produces a relatively persistent and uniform habitat. It is also possible that low temperatures might impede flight and favor the evolution of flightlessness (see *Geographic variation in flightlessness: Temperature and flight impairment*, below).

Caves. — Flightlessness is unusually frequent among cavernicolous species within the Blattodea, Orthoptera, and Coleoptera, but not the Diptera (Table 1). Though not always extensive in space, caves are generally temporally stable and very persistent, as evidenced by high levels of endemic fauna (Barr 1967, 1968).

Hymenopteran and termite nests. — Many species of insects, belonging to a variety of different orders, have evolved to live within ant, bee, or termite nests, either as welcome or unwelcome "guests." A higher-than-average incidence of flightless species within this habitat occurs in the Blattodea (Table 1: footnote o), Orthoptera, Coleoptera (Table 1: footnote p), Diptera, and Hymenoptera (Table 1: footnote q). In some species only the larvae live within the nests (e.g., *Meloe*, Mutillidae), while other species (e.g., some Staphylinidae) are highly modified as adults and all parts of the life cycle remain within the nest.

Byers (1969) suggested that the loss of wings in species living in this type of habitat could result from wings being impediments to underground movement. However, as discussed in the case of mole crickets, a high degree of modification for a subterranean existence can occur without the loss of wings. Furthermore, aptery occurs in many Coleoptera, and in this order the wings are completely covered by the elytra when not in use; it seems unlikely that wings would be an impediment to underground movement for these species.

Ant and termite nests may be long lasting in some cases, but in others, such as in temperate regions, recolonization must occur each year. Location of a new nest may be by flight (in the winged species), walking, or phoresy. The evolution of flightlessness will depend upon the persistence of the nests, the distance between nests, and/or the evolution of an alternate means of transport (phoresy). There is, at present, too little in-

formation to assess the relative importance of these factors.

Endotherm body surfaces (ectoparasites). — In addition to the highly specialized orders of vertebrate ectoparasites, Malophaga, Anoplura, and Siphonaptera, ectoparasitic species also occur in the Dermaptera (Table 1: footnote r), Hemiptera (Table 1: footnote s), Coleoptera, and Diptera (Table 1: footnote t). There has been considerable convergent evolution in body form, the ectoparasitic Dermaptera, Hemiptera, Diptera, and Coleoptera frequently being "louse-like." It has been suggested that this specialization in body form could be responsible for the loss of wings (Byers 1969). But there is no evidence that such specialization should necessarily lead to loss of wings, and, as demonstrated by the mole crickets, considerable structural modification can occur without the loss of flight capability.

From the point of view of an insect, an endotherm is a highly persistent habitat: it is large relative to the insect, and "patches" come together at least during the mating season; hence migration between patches can be easily accomplished by hopping or walking from one animal to another (either mates or offspring). The extinction of the patch comes about upon death of the animal. This may be frequent in the case of small mammals, but this is offset by the relatively high frequency of encounters between hosts, either as a result of random encounters or high frequency of breeding.

Arthropod tissues. — This habitat has not previously been noted in regard to the incidence of flightlessness. In contrast to endothermic vertebrates, arthropods are a highly transient food source since each host can support only one generation of parasite, the host being killed by the parasite. Therefore, flightlessness should be unlikely to evolve in such cases. This prediction is supported by the Diptera, but not the Hymenoptera (Table 1: footnotes u, v). Further study is required on this problem.

Summary. — In some habitats the incidence of flightless species is greater than average within a particular order. The high incidence of flightlessness among six of these habitats (woodlands, the ocean surface, specific habitats of the seashore, various aquatic habitats, caves, and endotherm body surfaces) is consistent with the hypothesis of habit persistence. Many of these habitats are not only persistent but also extensive in space, enabling insects to disperse by alternate means such as walking, skating, or swimming. The relative importance of habitat persistence and/or other factors (flight impairment, phoresy, etc.) in the remaining five habitats (deserts, margins of freshwater bodies, the surface of snow, hymenopteran and termite nests, and arthropod tissues) requires further study. There is considerable vagueness in the various habitat designations, and, while habitat persistence cannot be rejected, considerably more detailed study of the population dynamics of insect populations in different habitats is required to assess how important habitat persistence is in re-

lation to other factors. In particular, more information is needed on the size and distribution of habitat patches, the costs of migration, and the spatiotemporal variation in λ and K.

Habitat dimensionality and the evolution of flightlessness

Habitats that are transient but scattered over the ground can be reached by walking, but habitats that are scattered in three dimensions are much more difficult to locate and move between without flight. These considerations have led to the proposal that in arboreal insects, selection will favor the retention of flight capability. The most recent proponent of this hypothesis is Waloff (1983), although an association between arboreality and wings was suggested >70 yr ago by Marshall (1916). Arboreal insects are predominantly winged (Table 2), but in several taxa, most notably the Phasmatodea, Lepidoptera, and Coccoidea, the females of even arboreal species are predominantly or always flightless.

Stick insects (Phasmatodea) are leaf eaters and hence their food source is distributed widely about them: eggs are simply dropped to the forest floor and the nymphs, which resemble tiny adults, eat the same food as the adults (Arnett 1985). Among the Lepidoptera, the males of arboreal species are invariably winged, the flightless females do not feed, and the larvae migrate by ballooning (Hackman 1966; see *Alternative modes of migration and the evolution of flightlessness: Ballooning*, below, for a discussion of flightlessness and ballooning in Lepidoptera). Scale insects (Coccoidea) feed on sap and can be compared, in this respect, to the bloodsucking ectoparasites of endotherms: the larvae are highly mobile and migrate before metamorphosing into the sedentary adult female (aphids are also sap suckers, but in these migration is accomplished by the seasonal production of winged females [Dixon 1984]). In these three cases it is clear that foraging for food or egg dispersion has not favored retention of flight, while location of a mate may have been an important factor (discussed in *Gender variation in flightlessness*, below).

The habitat-dimensionality hypothesis applies not only to arboreal species but also to any insect that must move about in three-dimensional space. For example, flower patches are generally both clumped and distributed in three dimensions. Therefore, selection should favor the retention of wings in insects that forage for nectar and pollen. This mode of feeding is very common among the Coleoptera, Diptera and Lepidoptera. However, the evolutionary significance of nectar and pollen feeding is potentially confounded by the potential importance of spatial heterogeneity of larval habitat. The considerable coevolution between nectar-feeding insects and plants suggests that this source of food may be an important selective factor in preserving flight. To demonstrate this we require cases in which larval habitats are persistent and the insects first forage

and then return to their natal sites to breed, but I can find no such cases in these three orders and, therefore, the two hypotheses cannot be distinguished.

To conclude, the habitat dimensionality hypothesis is supported by the exceptionally high incidence of winged arboreal species, but its extension to other circumstances requires further study. Furthermore, the actual focus of selection, viz the importance of the foraging for food, the seeking for a mate, or the distribution of eggs, needs more detailed analysis.

GEOGRAPHIC VARIATION IN FLIGHTLESSNESS

Darwin's hypothesis and the evolution of flightlessness on oceanic islands

Darwin (1876) hypothesized that on oceanic islands a flightless morph would be more fit than a winged morph because it would be less likely to be accidentally blown or fly from the island (Wallace [1880] proposed a similar hypothesis for flightless birds):

> *Several facts—namely, that beetles in many parts of the world are frequently blown to sea and perish; that the beetles in Madeira, as observed by Mr. Wollaston, lie much concealed, until the wind lulls and the sun shines; that the proportion of wingless beetles is larger on the exposed Desertas than in Madeira itself; and especially the extraordinary fact, so strongly insisted on by Mr. Wollaston, that certain large groups of beetles, elsewhere excessively numerous, which absolutely require the use of their wings, are here almost entirely absent; these several considerations make me believe that the wingless condition of so many Madeira beetles is mainly due to the action of Natural Selection, combined probably with disuse. For during many successive generations each individual beetle which flew least, either from its wings having been ever so little less perfectly developed or from indolent habit, will have had the best chance of surviving from not being blown out to sea; and, on the other hand, those beetles which most readily took to flight would oftenest have been blown to sea, and thus destroyed* (Darwin 1876: 109).

On p. 401 he notes:

> *Again, an organ, useful under certain conditions, might become injurious under others, as with the wings of beetles living on small and exposed islands; and in this case Natural Selection will have aided in reducing the organ, until it was rendered harmless and rudimentary.*

In a section entitled "On the inhabitants of oceanic islands" Darwin (1876: 349) refers to "a useless appendage like the shrivelled wings under the soldered wing-covers of many insular beetles." From these statements a presumed association between oceanic islands and flightlessness in insects gained widespread

TABLE 2. Incidence of flightlessness among arboreal insects.

Order	Taxon or Region	Relative %*	Analysis†	Reference
Orthoptera	N America	−	1	‡
Phasmatodea	Australia	−§	3	Key 1970
Blattodea	Costa Rica	−	2	Schal and Bell 1986
Hemiptera	Britain	−	2	Waloff 1983
	Lygaeidae	−	3	Slater 1977
	Nabis	−	3	Zimmerman 1948b
Homoptera	Cicadellidae	−	2	Waloff 1983
	Coccoidea	+‖	1	¶
Thysanoptera	Worldwide	−	1	#
Coleoptera	Carabidae	−	2	Darlington 1943
	Curculionidae	−	3	Marshall 1916
Lepidoptera	Temperate	+‖	1	Hackman 1966
Hymenoptera	Symphyta	−	1	**

* + = greater than average proportion of flightless species; − = less than average.
† Categories of analysis: see Table 1 for explanation.
‡ See text, *Environmental heterogeneity and the evolution of flightlessness: Habitat dimensionality and the evolution of flightlessness.*
§ Males only; females typically flightless.
‖ Females only; males typically winged.
¶ See text, *Environmental heterogeneity and the evolution of flightlessness: Evidence.*
# From the habitat descriptions given by Stannard (1968) the female Thysanoptera of Illinois can be grouped as follows:

Wing form	Litter	Grass	Flowers	Shrubs and trees	Under bark
Winged	1	30	42	48	6
Dimorphic	17	17	6	3	14
Wingless	9	5	0	1	7

There is significant heterogeneity between habitats ($\chi^2 = 93.9$, df = 8, $P < .001$), with winged females predominating in shrubs and trees. Data from Watson (1923) and Cott (1956) show the same pattern.
** Only two species of this very large suborder are flightless (Naumann, 1984).

acceptance (Brues 1902a, Huxley 1942, Schmalhausen 1949, Hemmingsen 1956, Carlquist 1965, Mathews and Mathews 1970, Powell 1976, Davis 1986, Liebherr 1988). Nevertheless, a number of authors have questioned both the hypothesis and the presumed correlation (Bezzi 1916, Jackson 1928, Scott 1933, Darlington 1943, Byers 1969), though little data and no statistical analyses were presented by these authors.

In a heterogeneous environment there will be continual loss of winged individuals from a local patch; given that the mortality rate of migrants is likely to be greater than non-migrants, the proportion of the wingless form should increase over time until the habitat is extirpated by vagaries of the climate or by changes occuring as a result of successional changes. As noted previously, the mortality cost to migration comprises two components, loss due to mortality of migrants within the region and loss due to migration from the region. Darwin's hypothesis is based on the second source of mortality and hence is a component of the more general theory of the evolution of flightlessness. The change in the incidence of the winged morph following colonization of a small isolated patch has been modelled by Roff (1986b), who showed that the increase in the frequency of the flightless morph in a wing-dimorphic species can be very rapid. These results are supported by a study of Stein (1977) in which he monitored the temporal change in the proportion of the winged morph of four species of weevil in a recently seeded meadow (see Roff 1990a: Fig. 1). But

there is a considerable difference between the loss of winged individuals from a small meadow and the loss of individuals from an oceanic island.

The fundamental error in Darwin's hypothesis as applied to oceanic islands is that it does not correctly take into account the question of scale. This flaw in the argument can be illustrated by consideration of an experiment by l'Heritier et al. (1937) purporting to demonstrate Darwin's hypothesis experimentally. In this experiment, l'Heritier et al. (1937) placed an open vial containing both winged and vestigial *Drosophila melanogaster* on the deck of their research station. The location was subject to wind and, not surprisingly, in a relatively short time only the vestigial flies were left in the vial. They suggested, "que l'hypothèse de Darwin est entièrement justifiée par l'expérience." But this is not the case for the following reason. The perimeter of this "island" is large relative to its area (the perimeter can be considered an absorbing boundary since insects that move up to or beyond this boundary do not return). The population dynamics of a species in such a habitat depends upon the size of the absorbing boundary relative to the total area; as the total "island" area increases, the ratio of area to perimeter increases, and the probability of an organism moving across the absorbing boundary diminishes. To compare correctly this vial experiment with a realistic situation one would have to increase the number of vials by many orders of magnitude and distribute them over an area measured in hundreds or thousands of square kilometres

(Madeira, for example, is 829 km²). The probability that an insect from any patch a few kilometres removed from the island perimeter will be blown out to sea is likely to be small and the loss rate is likely to have negligible effects on the population. Therefore, while the loss of winged individuals from a small patch may be significant over time (Roff 1986b), the loss from many thousands of patches cannot be computed by multiplying the loss from a single isolated patch by the total number of patches.

Darwin's original manuscript shows that he was aware of the problem of scale:

> As the danger would be obviously greater, in the smaller & more exposed islets, I have ascertained through Mr. Wollaston's kindness, that on the Dezertas, a mountainous rock near Madeira, four miles long & about three-quarters in breadth, there are 54 Beetles; & that of these, 26 are winged & 28 wingless, which is a proportion one-fourth larger, than the Dezertas ought to have had in accordance with the proportions of the winged & and wingless coleoptera in the whole archipelago (Stauffer 1975: 292).

What rates of loss might we expect on an island the size of Madeira (≈829 km²) compared to an island the size of Dezertas (≈8 km²)? An approximate estimate can be obtained as follows: assume (1) that the density of suitable habitats is the same on both islands, (2) that the islands are circular, and (3) that insects migrate in a straight line until they locate a new habitat or pass beyond the island edge. If the probability that an insect starting from the center of a small island with radius r leaves the island is p, then the probability for an insect starting from the center of a large island with radius R is $p^{R/r}$. For islands the sizes of Madeira and the Dezertas this probability is approximately $p^{10.2}$. If the proportion lost from an island the size of Dezertas is 10%, the proportion lost from an island the size of Madeira is ≈6.6 × 10⁻⁹ %, a phenomenally small fraction. Even when 50% of the population is lost from Dezertas, only 0.086% is expected to be lost from Madeira. The actual loss rate from Dezertas would have to be enormously large for the loss rate on Madeira to be significant; in fact, it is extremely doubtful that any population could sustain this rate, and thus colonization of the island would itself be unlikely.

The conventional wisdom concerning geographic correlates of flightlessness includes other factors in addition to oceanic islands: Jackson (1928: 722) noted that it is:

> usually believed that apterous beetles predominate in certain restricted environments, as in oceanic islands, mountain tops, or in caves, but when one comes to examine the belief one finds that there is not always very much precise information available, and that comparative investigations in regard to the apterism of beetles in normal surroundings have rarely been made.

The same observation was made by Salt (1954) with regard to the presumed relationship between aptery and altitude. To date there has been no statistical treatment of the relationship between flightlessness and geographic variables such as island status or altitude. Darlington (1943, 1970, 1971) and Mani (1962, 1968) discussed the relationship between altitude and flightlessness in the Carabidae and the Himalayan insect fauna, respectively, and compared highland faunas with lowland, but did not statistically verify their conclusions.

It has been suggested that the presumed tendency for an increase in the proportion of flightless insects at high altitudes results from the same process postulated by Darwin (1876), viz, the blowing or straggling away of winged individuals, leading to the evolution of apterous species (Jackson 1928, Hynes 1941, Carlquist 1974). As discussed above (and in *Environmental heterogeneity and the evolution of flightlessness: Theory*, above), this hypothesis is a component of the environmental heterogeneity hypothesis and can be significant if the habitat patches are small and localized. Therefore, it is reasonable to suppose that this could be an important factor in such areas as mountain tops and very small islands. However, in order for this process to occur the habitat must be sufficiently persistent to permit the evolution of flightless species. If these habitats are indeed so persistent, then flightless species might be expected to evolve even if there were no loss by dispersal beyond the habitat perimeter; the importance of such loss may be to speed up the rate of evolution.

The above considerations suggest that flightlessness on oceanic islands should not, in general, occur because of the size of the island. Since Darwin's hypothesis is based on few data, it is first necessary to demonstrate that the phenomenon exists, i.e., that oceanic islands do have higher-than-expected incidences of flightlessness. Comparisons between oceanic and mainland regions may be confounded by such differences as climate, habitat variation, or topography. The available data are insufficient in most instances to take into account variations in climate and habitat directly, but latitude and altitude are available and hence can serve as crude surrogate measures for the effects of climate, habitat, topography, or other factors such as temperature, with which these two variables may be correlated. Therefore, before addressing the question of the relative incidence of flightlessness on oceanic islands we first test for correlations with altitude and latitude.

Is flightlessness correlated with altitude?

An increase in the incidence of flightlessness with increasing altitude has been observed both within and between species (Table 3). In 14 species the proportion of flightless morphs increases with altitude, and in 2 species no clinal variation was detected. There are 19 cases in which the percentage of flightless species is

TABLE 3. Studies reporting an increase (+), decrease (−) or no change (0) in the incidence of flightlessness with increasing altitude.

Order	Taxon	Cline	Analysis*	Reference
Intraspecific variation
Blattodea	*Ectobius africanus*	+	3	Rehn 1931, 1932a
Orthoptera	*Ageneotettix deorum*	+	3	Otte 1981
Plecoptera	*Leuctra hippopus*	+	4	Hynes 1941
	L. inermis	+	4	Hynes 1941
	Capnia logana	+	4	Nebeker and Gaufin 1965
	C. nana	0	4	Nebeker and Gaufin 1967
Hemiptera	*Saldula fucicola*	+	3	Lindskog 1974
	S. saltatoria	+	3	Lindskog 1974
	Microvelia gracillima	+	4	Hynes 1955
	M. major kilimandjaronis	+	4	Hynes 1955
	Nabis blackburni	+	4	Zimmerman 1948b
Coleoptera	*Aglyptinus dimorphicus*	+	1	†
	Zalobius nancyae	+	2	Herman 1977
	Z. spinicollis	0	2	‡
Diptera	*Tipula lobeliae*	+	4	Alexander 1962
Psocoptera	*Blaste nairobense*	+	1	§
Interspecific variation
Various	Insecta (Himalayas)	+	3	Mani 1962, 1968
Orthoptera	Orthoptera (general)	+	3	Chopard 1938
	Orthoptera (Alps)	+	2	Dreux 1961
	Orthoptera (N. America)	+	3	Otte 1979
	Acrididae (Africa)	+	3	Uvarov 1953
Plecoptera	Plecoptera (general)	+	3	Brinck 1949, Illies 1968 Zhiltsova 1978, Hynes 1941
Lepidoptera	Lepidoptera (general)	+	3	Hackman 1966
	Lepidoptera (European)	+	3	Dierl and Reichholf 1977
	Thyrocopa (Hawaii)	+	1	‖
Coleoptera	Coleoptera (Ethiopia)	+	4	Scott 1935, 1952
	Coleoptera (Madeira)	+	1	See text¶
	Carabidae (general)	+	1	See text¶
	Trechinae (general)	+	3	Jeannel 1926, 1927
	Curculionidae (India)	+	1	#
	Lucanidae (New Zealand)	−	3	Holloway 1963
	Galerita (S. America)	+	1	**
	Trox (general)	+	3	Scholtz 1981
	Nebria (general)	+	2	Kavanaugh 1985
Diptera	Diptera (general)	+	3	Bezzi 1916, Richards 1951
	Tipulidae (general)	+	1	††

* Categories of analysis: (1) My own statistical analysis; (2) statistical analysis by cited author; (3) review by cited author; (4) observation by cited author. For further details see *Environmental heterogeneity and the evolution of flightlessness: Further observations.* . . .

† Considering only insects collected in berlese funnels and, for adequate sample sizes, an altitudinal division of 0–600 m and >600 m we have, LW = 181, SW = 148 and LW = 43, SW = 130 where LW and SW are macropterous and micropterous specimens, respectively. $\chi^2 = 41.7$, df = 1, $P < .001$, indicating a higher frequency of SW at >600 m. Data are from Peck (1977).

‡ 41 specimens were collected over an altitude from 30 to 200 m, with only four specimens >100 m, and hence a failure to detect a decrease in % flightless individuals is not altogether surprising. Data are from Herman (1977).

§ Of 60 specimens none of the 6 wingless individuals were found below 3300 m and no winged individuals were found above this level; this difference is highly significant ($\chi^2 = 60$, df = 1, $P < .001$; significance level obtained using bootstrap technique described in Roff and Bentzen [1989]). Data are from Broadhead and Richards (1980).

‖ The only flightless species of Hawaiian *Thyrocopa* occurs above 2750 m while the 22 winged species occur no higher than 1500 m (data from Zimmerman 1978). Applying Dixon's outlier test to the distribution of the heights from which the types were collected (or midpoint of the range given) indicates that the flightless species is a significant outlier (test ratio = 0.75, $P < .01$).

¶ See text, *Geographic variation in flightlessness: Is flightlessness correlated with altitude?*

** Species are divided into those occurring above 900 m and those found below. Of the former there are 29 winged species and 55 wingless species (65% wingless), and of the latter 169 winged species and 87 wingless (34% wingless): this difference is highly significant ($\chi^2 = 25.8$, $P < .001$). Data are from Marshall (1916).

** Species are divided into those occurring at elevations 0–600 m and those >600 m. In the former range there are 28 winged species and 0 flightless species, and in the latter 0 winged species and 14 flightless species. $\chi^2 = 42$, df = 1, $P < .001$, indicating a higher frequency of flightless species at elevations >600 m. Data are from Reichardt (1967).

†† The distribution of the 90 flightless species of Tipulidae obtained from an extensive screening of the literature is as follows: 50 species occur above 1000 m (most above 1500 m); 1 species occurs below 600 m; 7 species occur at high latitudes (arctic and/or Siberia); 11 species are found on snow surfaces and the altitudinal range of 21 species is not given. Thus over one-half of the flightless tipulids occur at higher elevations. This family is exceedingly large (1517 species in North America alone [Arnett 1985]), and species occur commonly at low elevations. Therefore the high frequency of flightless species at high elevations cannot be ascribed to chance. Data are from Alexander (1917, 1918, 1919, 1923, 1932, 1940, 1941, 1943a, b, 1956a, b, 1962), Hemmingsen (1956, 1958), Tjeder (1963), and Byers (1982, 1985).

TABLE 4. Percentage of flightless carabid species (the few dimorphic species excluded) in adjacent lowland (<600 m) and highland (>600 m, generally >1000 m) regions. Data are from Darlington (1941, 1943, 1970, 1971). n = number of species.

Location	Lowland		Highland	
	%	n	%	n
New Hampshire	10.8	251	43.2	44
North Carolina	17.0	300	61.9	42
Santa Marta	1.5	134	73.3	14
Cuba	0.7	140	100.0	7
Jamaica	0.0	63	80.0	10
New Guinea	1.7	424	31.8	217

correlated with altitude and one case of a reversed cline. These results are clearly statistically significant.

The most comprehensive data set on pterygomorphism and altitude is that compiled by Darlington (1943, 1970, 1971) for the beetle family, Carabidae. From this data set I extracted data for adjacent lowland (<600 m) and highland regions (>600 m and generally >1000 m; Table 4). The percentage of flightless carabid species varies from 31 to 100% in highland regions, whereas in adjacent lowlands the range is from 0 to 17% (paired t = 4.12, n = 6, P < .01, arcsine-transformed data). A relatively low percentage of flightless carabid species has also been recorded from other lowland areas: Newfoundland, 23% (data from Lindroth 1955), Iceland, 16.7% (Darlington 1943), southwest Australia, 31% (Darlington 1943). In contrast to the low frequency in these lowland areas, the Carabidae of the Himalayas are predominantly flightless (71%, n = 41, data from Andrews 1930, Habu 1973, and Casale 1980), as are carabids from elevations >3000 m in New Guinea (95%, n = 21; Darlington 1971).

Of particular interest is the case of the Coleoptera of Madeira, the example that drew Darwin's attention to the problem of the evolution of flightlessness. From Wollaston's descriptions three altitudinal zones can be discriminated, low (0–300 m), intermediate (300–900 m) and lofty (>900 m) (Wollaston 1854). I excluded species considered by Wollaston to be recent introductions and species for which only one or two specimens were obtained. There is a highly significant difference among altitudinal zones (Table 5, χ^2 = 34.4, df = 4, P < .001), with the percentage of flightless species increasing with altitude.

Is flightlessness correlated with latitude?

An increase in the frequency of the flightless morph was observed in 14 species with no change or a decrease in 5 species, a difference that is statistically significant (Table 6; χ^2 = 4.26, df = 1, P < .05; I conservatively combined the groups "−" and "0"). At the interspecific level there are 10 cases in which the proportion of flightless species increases with latitude and 2 in which it decreases (χ^2 = 5.33, df = 1, P < .05; the 2 cases for

Gryllus were conservatively treated as a single datum). As with altitude, there is a statistically significant trend for the incidence of flightlessness in insects to increase with latitude.

Is flightlessness more frequent on oceanic islands?

The above analyses indicate that a comparison between the frequency of flightlessness on oceanic islands vs. mainland areas should take into account, where possible, differences in altitude and latitude. For the Carabidae, these two effects can be jointly tested by covariance analysis, dividing altitudinal range into two categories, 0–600 m and >600 m (Fig. 2). For mainland data there are significant effects due to latitude ($F_{1,17}$ = 9.7, P < .01) and altitude ($F_{1,17}$ = 32.5, P < .001), but no significant interaction ($F_{1,17}$ = 2.52, P > .05; dimorphic species were eliminated from this analysis, although there are generally so few that their inclusion in either category makes no difference). The data for oceanic islands cannot be easily divided into the two altitude categories, but we can consider islands of low and high relief (i.e., maximum elevation <600 m and maximum elevation >600 m). The effect of island status was then examined using a multiple regression model where the dependent variable was arcsine-transformed % flightless, and the independent variables were latitude, altitude (highland or lowland), island status (oceanic island or mainland), and all possible interaction terms (I also included distance from the mainland and island size as covariates, but these were not significant and are omitted from the present analysis). A stepwise analysis indicated that there is no significant reduction in explained variance with the addition of the "island status" variable or interaction terms. The lack of any effect is also evident from the plotted regressions (Fig. 2). I therefore conclude that, with respect to the Carabidae, there is no evidence of a correlation between the incidence of flightlessness and island status.

Though they give no statistical comparisons between mainland and oceanic islands, Richards (1951) and Hackman (1964) report that oceanic islands do not have higher frequencies of flightless dipteran species. Bradley (1958) makes a similar observation (again without statistical analysis) for the Lepidoptera, and Scott (1933) for the insects of the Seychelles. However,

TABLE 5. The altitudinal distribution of winged and wingless coleopteran species of Madeira. Data are from Wollaston (1854).

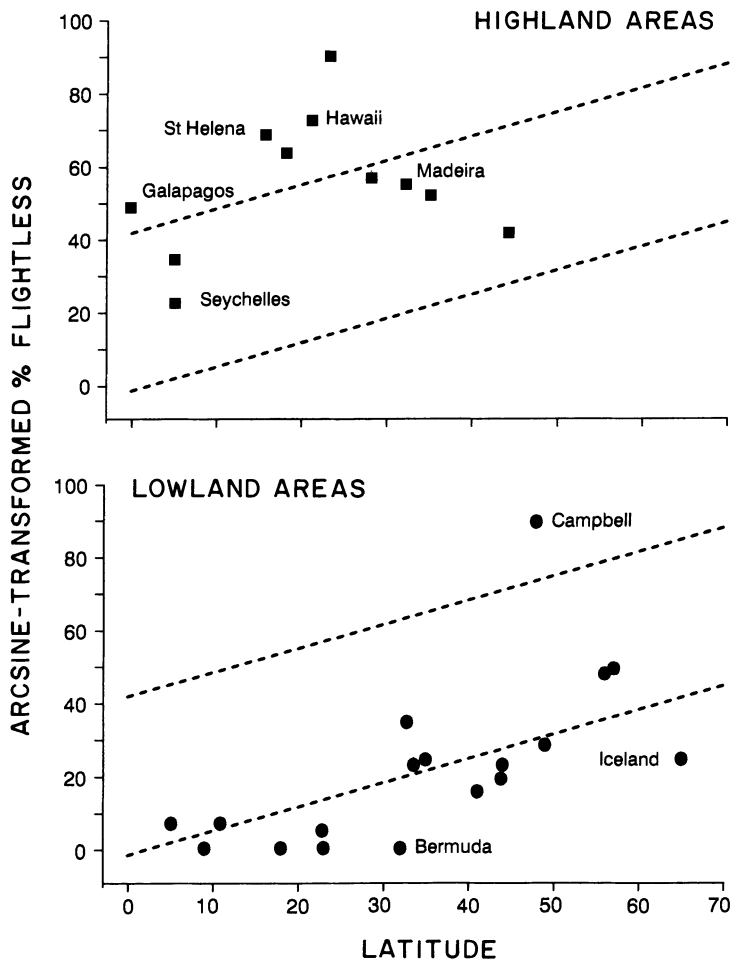| Altitude (m)	Number of species		
	Winged	Wingless	%
0–300	73	22	23.2
0–900	20	4	16.7
300–900	14	13	48.2
300–1800	22	24	52.2
900–1800	17	33	66.0

FIG. 2. Percentage of flightless carabids as a function of latitude and altitude. Regression lines (−−−) are shown for two categories of altitude (no significant interaction, see *Geographic variation in flightlessness: Is flightlessness more frequent on oceanic islands?* for details). Oceanic islands are divided according to relief (lowland = <600 m and highland = >600 m). Data from Wollaston (1854), Darlington (1941, 1943, 1970, 1971), and Van Dyke (1953).

in general, the insects of subantarctic islands do show particularly high incidences of flightlessness (Bradley 1958, Hackman 1964, Gressitt 1970). Since on the continent of Antarctica there is only one winged insect species (Gressitt 1970), the high incidence of flightlessness on the subantarctic islands is most probably due to characteristics of these islands and not solely, if at all, due to them being oceanic islands.

From the taxonomic literature I extracted data on faunas of oceanic and mainland areas (Fig. 3); these data could not be matched according to altitude, but where possible I selected data for mainland and oceanic islands at approximately the same latitude (in some cases several sites at approximately the same latitude were combined). The data comprise a wide variety of orders (Diptera, Orthoptera, Coleoptera, Hemiptera, Psocoptera, Neuroptera, and Thysanoptera), and there is no discernable tendency for oceanic islands to have higher frequencies of flightless species (Fig. 4). There

is a significant correlation between the incidence of flightlessness on oceanic islands and comparable mainland areas ($r = 0.50$, $n = 18$, $P = .017$; Fig. 4). The number of observations lying above (8) and below (10) the 1:1 line is no more than expected by chance ($P > .5$, sign test), and a paired t test indicates no significant difference between island and mainland faunas ($t = 0.14$, $P > .89$).

Thus, oceanic islands do not in general have higher-than-expected incidences of flightless insects. Therefore, Darwin's hypothesis is not required to explain the proposed correlation because it does not exist.

Habitat persistence and clinal variation in flightlessness

Various authors (Van Dyke 1929, Darlington 1943, 1970, 1971, Peck 1977, Walker and Sivinski 1986), have hypothesized that altitudinal and latitudinal clines in the proportion of flightless species result from clinal
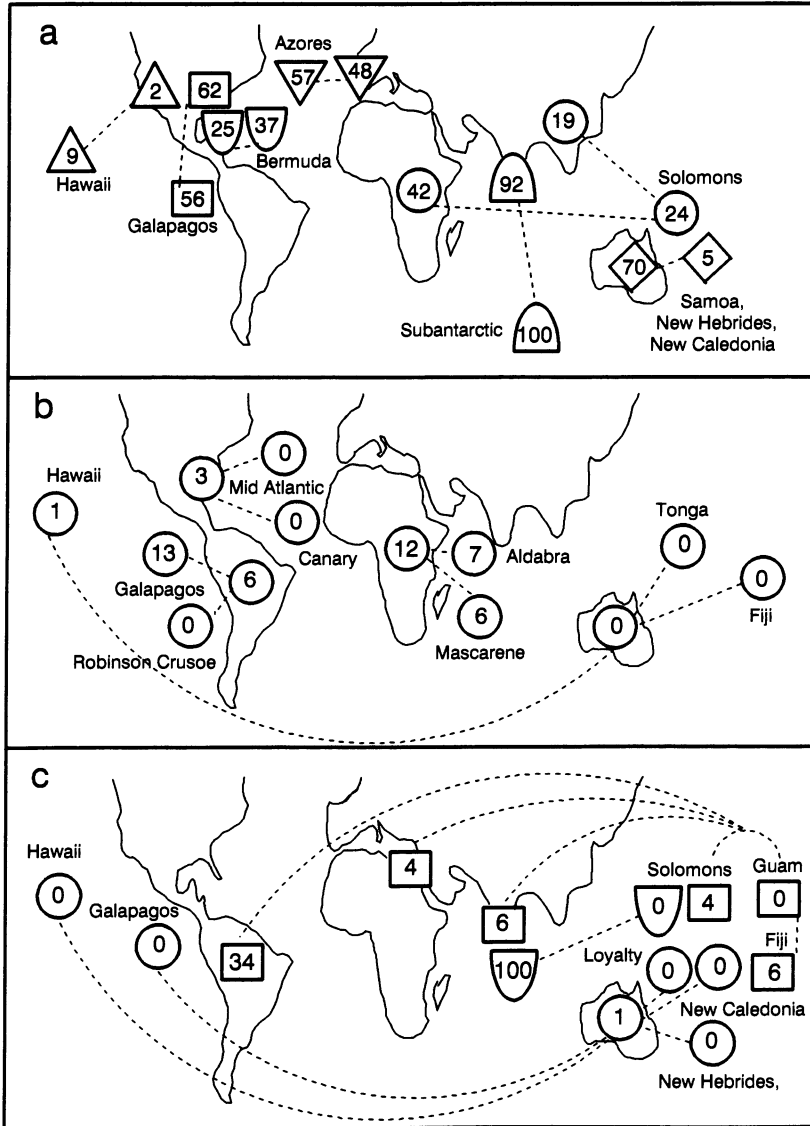
FIG. 3. Data used to test correlation between incidence of flightlessness on oceanic and mainland areas. Each symbol represents a different taxon, with the percentage of flightless forms shown inside. The mainland and oceanic sites for the same taxon are connected by dashed lines. To avoid the multiple use of mainland data some oceanic island data that are not significantly different have been combined as indicated.

A) (1) $\triangle$ = Tipulidae: Hawaii (Hardy 1960, Byers 1982,1985), California (Alexander 1967); (2) $\square$ = Acridoidea: Galapagos (Dirsch 1969), southern region of eastern North America (Blatchley 1920); (3) $\cup$ = *Gryllus firmus*: Bermuda (Kevan 1980), Florida (Veazey et al. 1980); (4) ∇ = *Rhyzobius litura*: Azores vs. Spain (Pope 1977); (5) $\bigcirc$ = Dermaptera: Solomons (Brindle 1970), Africa, and the Orient (Hincks 1959*a, b*); (6) $\cap$ = Curculionidae: Campbell Island (Kuschel 1964), India (Marshall 1916; since no trees are present on the subantarctic islands arboreal species within the Indian fauna have been omitted); (7) $\diamondsuit$ = *Pseudopachybrachius gutatus*: New Hebrides, New Caledonia, and Samoa vs. Australia (Malipatil 1979).

B) $\bigcirc$ = Psocoptera; (8) Psocoptera: Galapagos and Robinson Crusoe (Thornton and Woo 1973, Thornton and New 1981), South America (New and Thornton 1974); (9) Psocoptera: Hawaii, Tonga and Fiji (Thornton 1967,1981*a, b*), South Australia (Edwards 1949, New 1974); (10) Psocoptera: Aldabra and Mascarene Islands (Turner 1976, New 1977), East Africa (Broadhead and Richards 1980, 1982); (11) Psocoptera: the mid-Atlantic and the Canaries (Meinander 1966, 1973), Texas (Mockford and Gurney 1956).

C) (12) $\bigcirc$ = Neuroptera: Hawaii, Galapagos, New Hebrides, New Caledonia, Samoa (Zimmerman 1957, Kimmins 1958, Klimaszewski et al. 1987), Australia (Riek 1970); (13) $\square$ = Thysanoptera: Guam, Fiji, Solomons (Moulton 1942, 1944, Mound 1970), Brazil, Egypt, and India (Hood 1954, 1957, Priesner 1960, Ananthakrishnan, 1964); (14) $\cup$ = *Baphothrips leios,* Solomons vs. South India (Mound 1970); the remaining four values are not plotted on the map; (15) Carabidae: the averaged value for carabids from highland areas (Fig. 2: upper panel); (16) Carabidae: the averaged value for carabids from lowland areas at latitudes >30° (Fig. 2: lower panel; latitude cutoff based on latitudinal distribution of the three oceanic islands); (17) *Blebius*: Canaries, Cape Verde, Galapagos, Diego Garcia, and New Caledonia vs. mainland species, worldwide (Herman 1986); (18) Coccinellidae: Madeira (Wollaston 1854), worldwide (Pope 1977).

variation in habitat persistence. This hypothesis is composed of two distinct hypotheses; firstly, that the evolution of flightlessness is a consequence of environmental heterogeneity, a hypothesis discussed above (*Environmental heterogeneity and the evolution of flightlessness*), and secondly, that habitat persistence is a function of altitude and latitude. Under this hypothesis, clinal variation in the frequency of flightless species or morphs could reflect clinal variation in the frequency of different habitat types or in the persistence of the same habitat type at different locations. It is reasonable to hypothesize that, as temperature decreases, rates of succession will decrease and hence the duration of non-climax habitats will increase. Thus at higher altitudes habitat duration should increase and selection favor a decrease in the frequency of migrant forms (see *Environmental heterogeneity and the evolution of flightlessness: Theory,* above, and Roff 1975), but whether the persistence time of different types of habitats should vary with altitude is not obvious. Since temperature and habitat changes are similar along both latitude and altitudinal gradients (Ohsawa et al. 1985), the incidence of flightlessness is predicted to be generally correlated not only with altitude but also with latitude.

Clinal variation in patch size would also generate clinal variation in the incidence of flightless species. Certainly the tops of mountains may represent "island"-type habitats, but I see no reason to expect a general trend for patch size to decline with altitude or latitude. However, rates of succession should decrease more or less continuously with altitude and latitude, and hence the habitat persistence hypothesis predicts a relatively continuous and smooth relationship between the incidence of flightless insects and latitude or altitude. Though the scale of analysis is quite crude, the altitudinal clines presented in Table 3 do not appear to be a consequence of changes in the incidence of flightlessness only on mountain tops.

I tested the hypothesis that habitat persistence varies with latitude with data on the rates of succession on abandoned farmland. In the northerly states of the United States (Wisconsin, New Jersey, Illinois, and New York) shrubs appear only 10–20 yr after abandonment, and even after 40 yr succession does not proceed beyond a very open woodland/parkland condition (Thomson 1943, Bard 1952, Bazzaz 1968,1975, Mellinger and McNaughton 1975, Pickett 1982), while in the more southerly states of North Carolina, Tennessee, and Georgia a closed canopy is formed within 15–30 yr (Billings 1938, Oosting 1942, Quarterman 1957, Nicholson and Monk 1974, 1975, Lindsay and Bratton 1980). In the Mexican tropics invasion by trees occurs within the first 2 yr, and these may reach a height of 10 m within 5 yr (Purata 1986): in the upper Rio Negro region of the Amazon Basin a loose canopy of *Cecropia* spp. 5 m high was formed within 22 mo (Uhl et al. 1981).

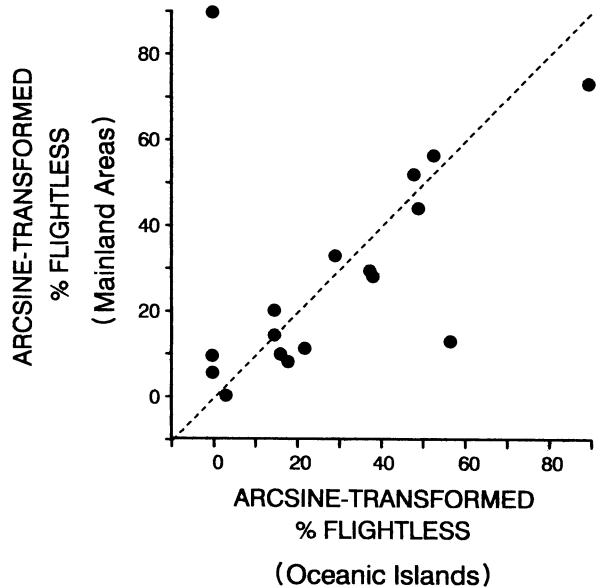Habitat persistence increases with altitude in two

FIG. 4. Relationship between incidence of flightlessness on oceanic and mainland areas (arcsine-transformed values). Data are given in Fig. 3. The dashed line indicates the line of equality.

ways; firstly, the number of successional stages may be reduced and a subalpine or alpine area may remain indefinitely at the meadow or grassland stage (Coe 1967, Billings 1969, Mark 1969, Frank and Moral 1986). Secondly, the rates of regeneration are greatly reduced (Hayward 1945, Grabherr 1982, Harmon et al. 1983, Hyland et al. 1987); for example, in the subalpine region of the Rocky Mountains, subalpine meadows may persist for 50–100 yr after disturbance, and young spruce–fir forest becomes established only after several centuries (Billings 1969).

The above data support the hypothesis that successional habitats of the same type persist longer at higher elevations and latitudes. However, this will only favor an increase in the frequency of a flightless species or morph if the increased persistence time is not offset by a decrease in the number of generations per year. Most of the species listed in Tables 3 and 6 are univoltine or bivoltine or take 2 yr to complete their life cycles, and they show little change in phenology across their distribution range.

The habitat-persistence hypothesis predicts that the frequency of flightless species will be correlated with habitat type, increasing with habitats of greater persistence. It is, however, insufficient to show that both habitat persistence and incidence of flightlessness vary clinally, since correlation does not imply causation. Greater weight can be given to the hypothesis of causation if it can be demonstrated that habitat persistence and incidence of flightlessness are correlated even when geographic variation in flightlessness is reversed from that generally observed.

In the coccinellid *Subcoccinella 24-subpunctata* geo-

graphic variation but no north–south clinal variation in the incidence of flightlessness was observed (see Table 6: footnote §). Pope (1977) suggested that the high incidence of fully winged individuals in southeast Europe and the Near East could be a consequence of high environmental instability due to cultivation practices that remove a large portion of the favored foodplant, Lucerne (*Medicago sativa*) several times during the year; since this occurs at a time when the temperature may reach 37°C, Pope (1977) hypothesized that the beetles suffer from both a loss of food and shade.

As described above, the Orthoptera of North America show a reversed cline (Table 5: footnote d). If the clinal variation in flightlessness is a consequence of clinal variation in habitat persistence, the reversal in the North American Orthoptera should be a consequence of a reversed cline in habitat persistence. Therefore, the correlation between the incidence of flightlessness and latitude should result from the more northerly region, Canada and Alaska, having more species within the relatively temporary habitats 1 to 4 (see *Environmental heterogeneity and the evolution of flightlessness: Evidence,* above, for a description of categories) than the "southern" region of eastern North America. Within the "northern region" 73.7% (188) of the species occur in habitats 1–4 compared to 60.1% (173) in the "southern" region, a difference that is statistically significant ($\chi^2 = 11.32$, df $= 1$, $P < .001$).

The data for the Orthoptera of North America are consistent with the hypothesis that latitudinal and altitudinal variation in the incidence of flightlessness is, in part at least, a consequence of variation in habitat persistence. However, more case studies are required before the hypothesis can be accepted as a general explanation of clinal variation in the incidence of flightlessness. Significantly more information is required on habitat characteristics of the relevant species and the relationship of the persistence of these habitats with latitude and altitude. Also, data on changes in scale, such as patch size, are needed to address the question of the effect of migrant loss as a factor.

Temperature and flight impairment

Several workers have suggested that since flight can be directly inhibited by cold temperatures, energy invested in wings and wing muscles may be wasted in cold regions, such as high latitudes and altitudes, and hence selection will favor the evolution of flightlessness in these areas (Hudson 1913, Darlington 1943, Downes 1964, Byers 1969, Carlquist 1974, Kimura and Masaki 1977).

In general, within a particular species flight appears to be possible only within a relatively narrow range of body temperatures (Hanegan and Heath 1970, Bartholomew and Heinrich 1973, May 1976, Heinrich and Casey 1978, Casey 1980). Some relatively large insects that fly at temperatures around 0°, such as bees and

moths, have morphological and behavioral adaptations to elevate their thoracic temperatures (Heinrich 1973, 1987, Heinrich and Mommsen 1985), but the reason why this is necessary has not yet been resolved. Once in flight, the thoracic temperatures of large insects such as honey bees, dragonflies, and many moths exceed ambient, and overheating may become a problem (Heinrich and Casey 1978, Kammer and Heinrich 1978, Unwin and Corbet 1984). It may not be possible to evolve an enzyme or muscle system that can operate across a wide range of temperatures (Kammer and Heinrich 1978), and hence flight at low ambient temperatures may be possible for large insects only if they evolve specific adaptations that permit them to elevate their temperatures in pre-flight warm-up and dissipate heat during flight. The body temperatures of small insects such as mosquitoes vary in flight with the ambient temperature (Kammer and Heinrich 1978, Unwin and Corbet 1984), and hence we might expect small insects to evolve the capability of flight at low temperatures more readily. Small insects are found flying at temperatures around 0° (Krogh and Zeuthen 1941, Downes 1965), but I have not been able to test the hypothesis satisfactorily. Without considerably more information on possible constraints due to the biochemical and/or physiological relationships between temperature range and flight capability, the hypothesis that the evolution of flightlessness is favored by the inhibitory effects of low temperature is impossible to test adequately. But I consider the hypothesis unlikely for three reasons. Firstly, in many species, particularly among the Diptera and Lepidoptera, it is only the female that is flightless. As the males fly readily it is unlikely that the loss of flight in the females is a consequence of their winged ancestors being incapable of flight (Prout 1916; the selective advantages of females but not males becoming flightless is discussed in the next section). The second reason for being skeptical of the flight-impairment hypothesis is that in many species pterygomorphism occurs across regions in which either very low temperatures do not occur, or the species matures at a time when individuals would not experience temperatures that might inhibit flight. Thirdly, reverse clines occur, and though these are relatively scarce (1 case for altitude and 3 for latitude), their occurrence is not expected if temperature per se is a major determinant. None of these arguments are sufficient grounds for rejecting the effects of low temperature, and there may be no conclusive means of testing it.

GENDER VARIATION IN FLIGHTLESSNESS

Before the distribution of eggs takes place mating must occur, unless the species is parthenogenetic. Given the potential difficulties of flightless insects locating mates, parthenogenesis should be particularly prevalent among flightless species, a prediction verified by Bell (1982).

TABLE 6.   Studies reporting an increase (+), decrease (−) or no change (0) in the incidence of flightlessness with increasing latitude.

Order	Taxon	Cline	Anal-ysis*	Reference
		Intraspecific variation		
Orthoptera	*Gryllus pennsylvanicus*	+	4	†
	Allonemobius fasciatus	+	1	‡
	Anaxipha exigua	+	4	Vickery and Kevan 1983
	Pteronemobius fascipes	+	2	Masaki 1973
	Paratettix texanus	+	4	Chopard 1938
	Orchelium concinnum	+	4	Thomas and Alexander 1962
	O. delicatum	0	4	Thomas and Alexander 1962
	O. campestre	0	4	Thomas and Alexander 1962
Hemiptera	*Hydrometra* spp.	+	4	Krogh and Zeuthen 1941
	Saldula fucicola	+	4	Lindskog 1974
	S. saltatoria	+	4	Lindskog 1974
	Pasira basiptera	+	3	Poisson 1946
	Gerris naja	+	3	Poisson 1946
	Reduvius minutus	−	3	Poisson 1946
Homoptera	*Megadelphax sordidula*	+	2	Raatikainen and Vasarainen 1976
	Proklesia marginata	−	2	Denno and Grissell 1979
Coleoptera	*Sitona hispidula*	+	4	Jackson 1933
	Subcoccinella 24-punctata	0	1	§
Diptera	*Tipula laccata*	+	4	Hemmingsen 1956
		Interspecific variation		
Orthoptera	Orthoptera (N. America)	−	1	‖
	Acrididae (N. America)	−	2	Otte 1979
	Gryllus (E. N. America)	+	1	¶
	Gryllus (open field spp. N. America)	+	3	Walker and Sivinski 1986
Plecoptera	Plecoptera (general)	+	3	Zhiltsova 1978
Lepidoptera	Lepidoptera (general)	+	3	Hackman 1966, Dierl and Reichholf 1977
Hemiptera	Gerridae	+	1	#
	Rhyparochrominae	+	2	Sweet 1963
Homoptera	Cicadellidae (Finland)	+	2	**
Coleoptera	Carabidae	+	1	††
	Brachinus (N. America)	+	2	Juliano 1983
Diptera	Tipulidae	+	3	Alexander 1919, 1943a, b, Byers 1969; see also Table 1: footnote ‡:(b)
	Tipula	+	4	Hemmingsen and Jensen 1960

* Categories of analysis: See Table 3 for explanation.

† Winged morphs are rare in southern Canada (<1%), but my own collecting and the data of Harrison (1979) indicate an increasing frequency southward.

‡ In Southern Canada (Montreal region) the frequency of winged morphs is <1% (based on the collection of several hundred specimens, but actual numbers not explicitly noted), but south of North Carolina winged individuals are quite common (T. Mousseau, *personal communication*). There is significant heterogeneity in the frequency of winged individuals between latitudes 47° N and 42° N, with the frequency of flightlessness increasing at the higher latitudes ($\chi^2 = 87.4$, df = 3, $P < .001$; data are from Tanaka 1986).

§ χ^2 analysis of data from Tables 4 and 5 of Pope (1977) indicates significant geographic variation ($\chi^2 = 750$, df = 4, $P < .001$), but this does not conform to a north–south cline.

‖ Within Canada and Alaska 38% of the orthopteran species are flightless (74 flightless, 24 dimorphic, 157 winged. Species in which the description did not clearly indicate wing condition were omitted; data are from Vickery and Kevan 1983), whereas in the more southern region of eastern North America, comprising the area within the United States east of the Mississippi River and in Canada east of the 90th meridian, 51% of the orthopteran species are flightless (120 flightless, 28 dimorphic, 142 winged; data are from Blatchley 1920). This difference is highly significant ($\chi^2 = 9.8$, df = 2, $P < .01$) and is minimal since the area considered by Blatchley includes part of the northern region. Eliminating all species not found south of North Carolina increases the frequency of flightless species in the southern region to 74%.

¶ Lutz (1908) collected data on the frequency of flightless morphs among *Gryllus* species of eastern North America but did not distinguish between species. There is a significant correlation between latitude and % wingless individuals (for females, Spearman rank correlation $r_s = 0.79$, $n = 12$, $P < .002$; for males $r_s = 0.66$, $P < .05$).

There is significant correlation between % flightless morphs within a species and mean latitude of species distribution (Pearson product-moment correlation $r = 0.30$, $P < .02$; Spearman rank correlation $r_s = 0.30$, $P < .02$; data are from Calabrese 1980).

** Sahlberg (1871), cited by Raatikainen and Vasarainen (1976).

†† To eliminate possible effects due to altitude or oceanic island status only areas below 600 m and not on oceanic islands were considered. There is a significant correlation between the percentage (arcsine transformed) of flightless carabid species and latitude (Pearson product-moment correlation $r = 0.85$, $n = 15$, $P < .001$; Spearman rank correlation $r_s = 0.80$, $P < .001$; data are from Darlington 1941, 1943, 1970, 1971, Lindroth 1955 and Greenslade 1968. The few dimorphic species were excluded from the analysis).

Incidence of flightlessness in males and females

Among those orders in which both winged and flightless species occur, both sexes are most frequently flightless in six orders, females in nine orders, and in two orders the male is the predominant flightless sex (Hemiptera excluded, see Table 8: footnote ‡). The male is more frequently flightless than the female (81.8% and 18.2% respectively, significantly different from a 1:1 ratio: $\chi^2 = 4.45, P < .05$). In sexual species, females invest more energy in eggs than males do in sperm (Trivers 1972), although the cost of sperm production may not be negligible (Dewsbury 1982). It is perhaps, therefore, not surprising to find that flightlessness is most frequently found in the female sex, males retaining flight to locate mates.

Male flightlessness and female mobility

I classified 52 families from the orders Coleoptera, Lepidoptera, and Diptera according to female mobility and wing morph of males. Females were designated as "not mobile" if they were larviform (e.g., Phengodidae and some Dermestidae) or showed clear evidence of not being able to move around freely; for example, among the North American Lepidoptera only one species, *Areniscythris brachypteris,* has a highly ambulatory female (Powell 1976), all other species being either totally immobile (e.g., Psychidae) or being very robust and sedentary (e.g., Geometridae; Hackman 1966). Among the North American Lepidoptera only the male of the highly mobile *A. brachypteris* is flightless (Powell 1976). There is a highly significant association between the mobility of the female and the wing morph of the male (Table 7, $\chi^2 = 34.7$, df = 1, $P < .001$), females that are relatively immobile being associated with males that are winged.

ALTERNATIVE MODES OF MIGRATION AND THE EVOLUTION OF FLIGHTLESSNESS

Phoretic transport of the female by the male

Among the hymenopteran families Bethylidae, Thiphiidae, and Mutillidae phoretic copulation has evolved, the males carrying the wingless females suspended from their genitalia, sometimes for considerable periods of time (Evans 1969). Phoretic transport of the wingless female also occurs in a few Diptera (Hackman 1964). While this may result in the migration of the female, the primary purpose in the Hymenoptera appears to be to transport the female to a feeding site (Given 1954, Clausen 1976). Phoresy in these species has removed the necessity of the female having to expend energy in foraging for food. The energy saved can be reallocated into fecundity (Given 1954). However, biomechanical factors will limit the relative size of the female and restrict her fecundity (Roff 1990*b*), and in the more "advanced" Hymen-

TABLE 7. Relationship between female mobility and male flightlessness in three orders of insects: Coleoptera (C), Lepidoptera (L), and Diptera (D).*

| | Females | | | |
| | Mobile | | Not mobile | |
Males	Total	(C, L, D)	Total	(C, L, D)
Flightless	35	(23, 1, 11)	1	(1, 0, 0)
Winged	3	(2, 0, 1)	13	(4, 5, 4)

* Families with flightless females are classified according to the mobility of the female and the flight capability of the male. Females not mobile are larviform or incapable of moving fast; mobile females have long legs and can run rapidly. Within one of the coleopteran families some species are flightless only in the female sex, others in both sexes; this has been placed in the category "males winged, females mobile." Data are from Arnett (1968, 1985; North American Coleoptera and Lepidoptera) and Hackman (1964; Diptera, worldwide).

optera the male has evolved complex modifications of the head that permit it to carry food back to the female (Given 1954).

Phoretic transport of the adult on another species

Some adult flightless insects inhabiting ant nests migrate between nests by attaching themselves to an ant, or are actively carried by the ant (Crowson 1981). The incidence with which this occurs is not known. A few hymenopteran egg parasites exhibit a phoretic relationship with their host, but in only one case reported by Clausen (1976) is the female wingless.

Phoretic transport of the larvae on another species

Approximately 2% (473 spp.) of the North American Coleoptera have larvae that are parasitic or prey upon Hymenoptera (data from Arnett 1985), and in these species phoretic transport serves to take the larvae to the nest of their host (Clausen 1976). The first-instar larvae show considerable morphological modifications, enabling them to actively climb perches where they can attach themselves to a passing bee, wasp, or ant (Crowson 1981). At least 28% of the species have wingless females, which is considerably more than the incidence of flightlessness among the order Coleoptera (<10%, Table 8). Phoretic transport of larvae also occurs in some Hymenoptera (Eucharitidae, Ichneumonidae, Trigonalidae, Perilampidae) and the neuropteran family Mantispidae (Clausen 1976), but so far as I can ascertain all these species are winged.

Ballooning

An alternate mode of migration by larvae is ballooning, which among the Insecta occurs only in the Lepidoptera. The larvae of both winged and flightless lepidopteran species balloon, but the phenomenon has been little studied, and even its frequency of occurrence is unclear.

TABLE 8. Percentage of flightless (including dimorphic) species in temperate regions, with a categorical assessment for the world fauna.

Order	No. of species	% flightless or dimorphic		Principal† sex
		Temperate	World*	
Group A. Hemimetabolous (gradual metamorphosis with a naiiad)				
Ephemeroptera	2000	0	0	...
Odonata	4870	0	0	...
Plecoptera	1550	<10	R	Male
Group B. Paurometabolous (gradual metamorphosis with a nymph)				
Gryllobattodea	20	100	100	...
Orthoptera	12 500	30–60	C	Both
Phasmatodea	2000	90–100	V	Female
Blattodea	4000	50–60	V	Female
Mantodea	1500	0	C	Female
Isoptera	1900	0	R	...
Dermaptera	1100	20–40	C	Both
Embioptera	800	20–30	C	Female (100%)
Zoraptera	24	100	V	Both
Psocoptera	2500	10–20	C	Female
Mallophaga	5000	100	100	...
Anoplura	500	100	100	...
Hemiptera	50 000	20–30	C	Both, female‡
Homoptera	32 000	>30	C	Both
Thysanoptera	4000	10–20	C	Male
Group C. Holometabolous (complete metamorphosis)				
Neuroptera	4670	<1	R	Female
Coleoptera	29 000	<10	U	Both
Trichoptera	7000	<1	R	Both
Lepidoptera	112 000	<1	R	Female
Mecoptera	480	20–30	U	Both
Hymenoptera	103 000	<10	R	Female
Diptera	98 500	<1	R	Female
Siphonoptera	2259	100	100	...

* R (rare) < 5%; 5% < U (uncommon) < 10%; 10% < C (common) < 50%; V (very common) > 50%.
† Sex which is most frequently flightless.
‡ Insufficient data to differentiate.
References: The following comprise only the more important references used. For further references see other tables. All orders (Grassé 1949, 1951, Brues et al. 1954, CSIRO 1970, 1974, Borror et al. 1976, Arnett 1985); Ephemeroptera (Hubbard 1979); Plecoptera (Needham and Claasen 1925, Brinck 1949, Illes 1968, Ross and Ricker 1971, Hynes 1976); Orthoptera (Blatchley 1920, Chopard 1938, 1949, Vickery and Kevan 1983); Blattodea (Rehn 1932*b*, Roth and Willis 1954); Mantodea (Edmunds 1972, 1976); Dermaptera (Hincks 1959*a*, *b*); Embioptera (Davis 1938, 1940*a–e*, 1942, 1943, 1944, Ross 1940, 1944, 1948, 1966, 1970); Zoraptera (Gurney 1938); Psocoptera (Mockford and Gurney 1956, Mockford 1965); Hemiptera (Southwood and Leston 1959, Miller 1971); Thysanoptera (Stannard 1968, Lewis 1973); Neuroptera (Killington 1936, 1937, Rehn 1939, Adams 1967, Riek 1970, Meinander 1972); Coleoptera (Arnett 1968, Crowson 1981, Hammond 1985); Lepidoptera (Hudson 1928, 1939, Southwood 1962, Hackman 1966, Covell 1984); Hymenoptera (Reid 1941); Diptera (Bezzi 1916, Hackman 1964).

Ballooning in Lepidoptera does not generally lead to long-distance migration; for example, migration distances, as measured in the gypsy moth, *Lymantria dispar*, average only a few hundred metres (Mason and McManus 1981), though a few percent may travel up to several tens of kilometres (Fosberg and Peterson 1986, Taylor and Reling 1986). In the bagworm *Thrydopteryx ephemeraeformis* the maximum migration distance is only ≈75 m (Cox and Potter 1986). But virtually all apterous moths are woodland species, feeding on a wide range of tree species (Hudson 1913, Southwood 1962, Dierl and Reicholf 1977; all 14 North American flightless species listed by Covell [1984] feed on tree foliage). Long-distance migration is, therefore, not generally required since woodlands are persistent and extensive (Southwood 1962).

In his review of the incidence of flightlessness among the Lepidoptera, Hackman (1966) suggested that wing reduction is particularly common among cold-season Lepidoptera in temperate climates. There is a significant trend for flightless species of moths to eclose in the fall–winter months, though it may be confined primarily to the family Geometridae (Table 9). In the bivoltine species *Orgia thyellina*, the fall generation of females is flightless but the summer generation winged (Kimura and Masaki 1977), further suggesting that the evolution of aptery in the Lepidoptera may be favored, in part, by fall emergence.

In the Lepidoptera that eclose in the fall and winter (hereafter simply referred to as "FW"), the eggs hatch in early spring at the time of first flush of foliage. Growth and survival of the larvae is critically dependent upon

TABLE 9. Percentage of adults eclosing in the fall–winter months in winged and wingless Lepidoptera. n = number of species.

Taxon	Region	Winged		Flightless		Data source* and test result
		%	n	%	n	
Lepidoptera	Central Europe	Not given		69.7	33	1, no test
Lepidoptera	Britain	5.1	743	57.1	14	2, $P < .01$†
Geometridae	Britain	4.6	284	72.7	11	2, $P < .01$†
	North America	0.6	174	42.9	7	3, $P < .01$†
	New Zealand	0.3	756	100.0	1	4, $P < .01$‡
	Greenland	0.0	4	100.0	1	5, no test
Lymantridae	Britain	0.0	7	0.0	3	2, NS
	North America	0.0	7	0.0	4	3, NS
Tineidae	New Zealand	8.6	255	25.0	4	4, NS
Arctiidae	New Zealand	Not calc.		0.0	3	4, NS

* References: (1) Dierl and Reichholf 1977; (2) Skinner 1984; (3) Covell 1984; (4) Hudson 1928, 1939; (5) Wolff 1964. NS = not significant.
  † Probability level obtained using method of Roff and Bentzen (1989).
  ‡ Based on the distribution of winged moths, the probability of one flightless species being in the fall–winter eclosure category by chance is $\approx P = 2/756 = .002$ (where the denominator is the number of species).

the age of the foliage (Feeny 1970, Hough and Pimentel 1978, Schneider 1980, Holliday 1985). If larvae emerge too early on a particular tree and leaves are not yet available, or they emerge too late and the leaves are too mature, the first-instar larvae spin a silken thread and migrate to neighboring trees by ballooning.

The general problem faced by the FW female moth is that, unlike the summer-emerging moth in which present foliage is that which the larvae will encounter, she has no index by which to assess the time of foliage flush in the next spring, except inasmuch as there may be an autocorrelation in time of flush on the tree upon which she developed, or neighboring trees of the same species. Mitter et al. (1979) suggested that in the fall cankerworm, *Alsophila pometaria,* aptery and parthenogenesis are adaptations to ensure the evolution of close synchrony between egg hatch and leaf flush.

Three tactics are available to FW Lepidoptera: firstly, the female could fly around depositing her eggs at random over a number of sites so that at least some larvae will hatch in synchrony with the leaf flush; secondly, the female could deposit all her eggs on the single tree, increasing her total fecundity by virtue of the extra energy not used for the production and maintenance of wing muscles and flight, and leave the larvae to do all the migrating; and, thirdly, by using a combination of the above, the female distributing her eggs and larvae also ballooning. At present we have an insufficient theoretical basis to predict what factors will favor a particular strategy.

Flight impairment because of low temperatures has been suggested to be an important factor in the evolution of aptery in Lepidoptera (Hudson 1913, Kimura and Masaki 1977). However, since only the female is flightless the hypothesis does not seem reasonable (Prout 1916). Furthermore, while the female gypsy moth, *Lymantria dispar,* is typically flightless, females of the asian race fly and their larvae do not balloon. Such a situation is not predicted by the flight-impairment hy-

pothesis but may occur in the model described above (e.g., if mortality of ballooning larvae is very high).

To summarize, the above analyses suggest that (1) the ability of larvae to migrate by ballooning, (2) the large-scale spatiotemporal stability of woodlands, and (3) the small-scale unpredictability of future bud flush, are of primary significance in the evolution of aptery in the FW Lepidoptera (Barbosa et al. 1989).

TAXONOMIC VARIATION IN FLIGHTLESSNESS

Mode of metamorphosis

Both hemimetabolous and paurometabolous insects undergo gradual metamorphosis, the former with a naiiad, the latter with a nymph, while holometabolous insects undergo a complete metamorphosis (Arnett 1985). Hemimetabolous insects comprise the three orders Ephemeroptera (mayflies), Odonata (dragonflies and damselflies), and Plecoptera (stoneflies). Except for a few terrestrial stoneflies (<10 species), the larvae of hemimetabolous insects are entirely aquatic (Illes 1968). Although the naiiads can move around actively in the water, they are subject to downstream drift in streams (Muller 1982) and to loss of habitat when water bodies dry up or are eliminated by overgrowth of vegetation. Since they are unable to travel overland, the larvae of hemimetabolous insects have only a limited ability to colonize new habitats.

The larvae of paurometabolous insects (e.g., Orthoptera, Hemiptera), in general, can be described as small wingless adults, and have a relatively high degree of mobility (Southwood and Leston 1959, Arnett 1985). A few exceptions are found within the Homoptera; nymphs of the Cicadidae (cicadas) live in the soil and are relatively immobile (all adults are winged), while the nymphs of species within the superfamily Coccoidea (scale insects), "have legs and are active; in many species, however, these are soon lost, and the nymphs like the adult females are sedentary" (Arnett 1985: 232; most adult males are winged).

TABLE 10. Statistical comparison within the four orders, Hymenoptera, Lepidoptera, Diptera, and Coleoptera, of the mean number of species per family after division into families with ≥ 1 and with no (0) flightless species. Families of uncertain status are omitted (data are from Arnett 1968, 1985). Because of differences in variance and skew, the groups were compared with a Kruskal-Wallis test (one-tailed).

	Hymenoptera		Lepidoptera		Diptera		Coleoptera	
	0	≥ 1	0	≥ 1	0	≥ 1	0	≥ 1
	Number of species per family							
Lowest	1	1	1	26	1	1	1	3
Highest	1199	8322	1211	1404	1277	1517	1369	2864
Mean	170	1015	84	778	110	372	110	497
Median	19	421	52	1053	29	127	35	100
Sample size	39	12	69	5	87	20	59	30
H	6.58		4.73		4.86		6.72	
P	<.0125		<.025		<.025		<.005	

The majority of holometabolous insects (most Coleoptera, Diptera, Mecoptera, Hymenoptera, and Siphonoptera) have a wormlike immature stage that has very limited powers of movement, and frequently occupies a habitat different from that of the adult (Borror et al. 1976, Arnett 1985). Larvae of Trichoptera, some Neuroptera, and many Coleoptera and Diptera are aquatic. Most larvae of the suborder Planipennia (Neuroptera) are terrestrial, have relatively good ambulatory powers and, like the adults, feed on insects such as aphids and scale insects. Similar mobile larvae are found in some Coleopteran families (e.g., Coccinellidae). The most mobile larvae with holometabolous metamorphosis are the "caterpillar" larvae of Lepidoptera and Symphyta (sawflies), a suborder of the Hymenoptera (Arnett 1985). These larvae are virtually all herbivorous while the adults feed on nectar and pollen.

Insects with paurometabolous metamorphosis differ from insects having the other two types of metamorphosis in being relatively mobile as immatures and generally having the same feeding habits as larvae and adults. Therefore, as adults there is no change in their habitat or foraging mode. On the other hand, insects with hemimetabolous or holometabolous metamorphosis cannot, in most cases, migrate as immatures, and the adults have different food requirements from the larvae. Furthermore, many of these adults feed on material, such as pollen and nectar, that is most easily obtained by flight. These factors suggest that flightlessness may be more common in paurometabolous insects than holometabolous or hemimetabolous insects.

For each insect order, I assessed the incidence of flightlessness quantitatively for the temperate regions and qualitatively for the entire world (Table 8). The incidence of flightlessness is rare (<5%) among hemimetabolous insects (in fact, flightlessness is known only among the Plecoptera). Except for the Isoptera (termites), flightlessness is common (10%-50%) to very common (>50%) in paurometobolous species, but with the exception of the Siphonoptera (fleas), flightlessness

is rare to uncommon (5%-10%) in holometabolous insects. I combined hemimetabolous and holometabolous orders, and, because of sample size, the categories "rare" and "uncommon," and the categories "common" and "very common." The results for the predicted "flightless" group (paurometabolous) are 1 family (rare-uncommon) and 14 families (common-very common), while for the predicted "winged" group, 10 families fall in the category "rare-uncommon" and only 1 in the category "common-very common." These data are significantly heterogeneous ($\chi^2 = 18.45$, df = 1, $P < .0001$), and indicate that insects with paurometabolic metamorphosis are more likely to be flightless than insects that have hemimetabolous or holometabolous metamorphosis.

Lineage size and flightlessness

Flightlessness among the holometabolous insects is a relatively rare phenomenon (<10%, Table 8). This may be a consequence of the rarity with which holometabolous insects occupy niches that favor the evolution of flightlessness and/or the infrequency with which flightless morphs arise in populations of winged holometabolous insects. Providing the ecologies of species within a taxon are reasonably diverse, these two factors should favor the evolution of flightlessness primarily in taxa containing large numbers of species.

On the basis of available data I was able to classify insect families of the orders Hymenoptera, Diptera, Lepidoptera, and Coleoptera of North America into those in which at least one species is flightless and those in which all species are winged. The ecologies of the species in most families are too varied to consider them statistically as a factor in the analysis; therefore, the present test only considers the effect of the number of species within a family. It is possible that there is a correlation between habitat and the number of species within a family, but this cannot be tested given the very qualitative information on the ecology of species within different families. Families comprising only winged species contain significantly fewer species, on average, than those containing at least one flightless

species (Table 10). This is consistent with the hypothesis that chance may play an important role in the evolution of flightless species.

Conclusions

In an environment that is spatially and temporally heterogeneous there will be a large selective premium on the ability to keep pace with the changing location of habitats suitable for growth and reproduction. Flight clearly confers exceptional mobility on an insect, and, conversely, the lack of flight generally greatly restricts the area over which an insect can search for oviposition sites or food sources. Therefore it is reasonable to expect that selection will favor the retention of flight in a highly variable environment, and that nonmigratory life histories will most likely evolve in very persistent habitats. However, while a loss of migratory activity is to be expected in spatially and temporally homogeneous environments, the loss of wings will occur only if there is a cost to being winged. Studies of wing-dimorphic species have shown that there is a reproductive cost to being winged (Roff 1986a, Roff and Fairbairn 1990), and, hence, selection favoring a decrease in the incidence of migratory activity will also favor the evolution of flightless forms (Roff 1986a).

A major problem with testing the hypothesis of habitat persistence is that few data are available on the spatiotemporal patterning of environments. As a consequence, analyses have in general been restricted to very broad categories; nevertheless, there is good evidence that flightless species, or morphs in the case of wing-dimorphic species, are found in higher frequency in persistent habitats such as late successional stages (see *Environmental heterogeneity and the evolution of flightlessness: Evidence*, above). Exceptionally high incidences of flightlessness also occur in a variety of habitats (see *Environmental heterogeneity . . . : Further observations . . .*) that may be broadly defined as persistent (woodlands, the ocean surface, specific habitats on the seashore, various aquatic habitats, caves, and ectoparasites of endotherms), and in others that are too vaguely defined for their persistence time to be evaluated (deserts, riparian, nival). In two other habitats (hymenopteran and termite nests, parasites of arthropods) factors other than habitat persistence are probably critical. It is important to stress that while the correlation between habitat type and incidence of flightlessness may be established, there is still considerable scope and need for further research connecting the biology of a species to its environment.

Another aspect of environmental heterogeneity is the dimensionality of the habitat; in three-dimensional space, flight will likely be a considerable asset, and hence selection will favor the retention of flight capability in insects that are arboreal or forage among many plants for pollen and nectar. There is a significant association between arboreality and flightlessness (Table 2), but foraging mode is confounded with possible spa-

tial and temporal heterogeneity in the larval habitat (see *Environmental heterogeneity . . . : Habitat dimensionality . . .*).

Three geographic variables, insularity, latitude and altitude have been claimed to be correlated with the incidence of flightlessness (see *Geographic variation in flightlessness*). There is considerable evidence for an increase in flightlessness with altitude (Tables 3, 4, and 5) and latitude (Table 6), but oceanic islands, contrary to "conventional wisdom," do not have higher incidences of flightless insects than comparable mainland sites (Figs. 2, 3, and 4). Darwin (1876) hypothesized that insects on islands would tend to be flightless because of the probability of being blown from, or accidently migrating from, the island. While such a process may be important for small patches such as isolated meadows or mountain tops, the large size of oceanic islands makes such a process unlikely to be of great selective significance on these (see *Geographic variation in flightlessness: Darwin's hypothesis . . .*), and it is, therefore, not surprising to find that oceanic islands do not have exceptionally high frequencies of flightless insects.

Rates of succession proceed more slowly at higher latitudes and altitudes (see *Geographic variation . . . : Habitat persistence . . .*), thereby potentially leading to positive correlations between persistence of habitats and these two variables. Based on such a relationship it has been suggested that clinal variation in the proportion of flightless insects might be a consequence of clinal variation in habitat persistence. Little direct support for this hypothesis can be found. Flightlessness among the Orthoptera of North America is correlated with habitat persistence (see *Environmental heterogeneity . . . : Evidence*), but shows a reversed latitudinal cline in the incidence of flightlessness (see *Geographic variation . . . : Habitat persistence . . .*). As predicted by the hypothesis that habitat persistence generates the clinal variation, the proportion of species in temporary habitats is higher in the northern region of North America than the southern. This result is encouraging but insufficient to accept the hypothesis as a general explanation. An alternative hypothesis, that flightlessness is favored because low temperatures inhibit flight, cannot be rejected, but is unlikely because flightlessness is frequently restricted to only one sex, and because clinal variation occurs across regions in which temperatures are not likely to inhibit flight (see *Geographic variation . . . : Temperature and flight impairment*).

Flightlessness is correlated with parthenogenesis and gender, the female being more frequently flightless than the male (see *Gender variation in flightlessness*). This division may be favorable because it permits the female to allocate more energy to reproduction and the male to locate mates. In this respect it is significant that flightless but mobile females are associated with flightless males while flightless, immobile females are associated with winged males (Table 7). In some spe-

cies the winged male carries the flightless female (see *Alternative modes of migration and the evolution of flightlessness: Phoretic transport of the female by the male*), or both sexes may be transported by another species, either deliberately or unwittingly (see *Alternative modes . . . : Phoretic transport of the adult on another species*). While phoretic transport may be of considerable significance for some species in which it occurs, it does not appear to be a factor involved in the evolution of flightlessness in most species. A second method of migration without flight is ballooning, found among the Insecta only in the Lepidoptera (see *Alternative modes . . . : Ballooning*). This occurs in the larval stage, and among the flightless Lepidoptera is correlated with spring hatching and forest habitats (see *Alternative modes . . . : Ballooning*, Table 9). The evolution of aptery in these Lepidoptera may be favored because it leads to increased egg production and because there is no advantage to distributing eggs across a number of trees when there are no cues to the timing of bud burst in the following year; under these circumstances a better strategy may be to lay an increased number of eggs and let the larvae do the migration. In some cases parthenogenesis and aptery may enhance the evolution of clones that are particularly well adapted to trees in which bud burst at the level of the individual tree is predictable (Mitter et al. 1979).

The frequency of flightless species is more common among paurometabolous insects than those with either hemimetabolous or holometabolous metamorphosis (Table 8). I argue (see *Taxonomic variation in flightlessness: Mode of metamorphosis*) that this is a consequence of the relative mobility of the nymphs of paurometabolous insects, and because insects with the other two types of metamorphosis frequently undergo niche shifts from larvae to adult. In the holometabolous insects the probability that a flightless species will occur within the lineage, measured by the taxonomic grouping of family, is a function of the number of species within the family (Table 10). One explanation for this is that the frequency with which the appropriate combination of ecological characteristics and mutations occur is rare among these insects. Therefore, providing there is ecological diversity among species at the taxonomic level of family, the likelihood of finding the appropriate combination will increase as the number of species, and hence combinations, increases.

A common theme in the data and hypotheses on the evolution of flightlessness in insects is the importance of habitat heterogeneity. It is quite reasonable to suppose that flightlessness will most likely evolve in circumstances where movement on a large scale is not required, i.e., in a spatially homogeneous and temporally stable environment. However, while the evidence is convincing in some cases, the vast bulk of the evidence is correlational and based on very crude estimates of habitat variability. For this reason I consider the data, in general, to be consistent with the hypothesis of habitat heterogeneity but insufficient to adequately address the importance of other factors that may favor the evolution of flightlessness. Thus the question of what factors favor the evolution of flightlessness is far from being answered.

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