Flightlessness in Insects

David L. Wagner and James K. Liebherr

The evolution of wings is heralded as the most important event in the diversification of insects, yet flight-wing loss has occurred in nearly all pterygote insect orders. Flight loss is especially prevalent among taxa inhabiting historically stable habitats. Recent studies of wing-polymorphic species have revealed numerous selective trade-offs in the reproductive potentials of winged versus flightless forms. A diverse set of environmental factors, both biotic and abiotic, trigger flight loss in alary polyphenic taxa, presumably by influencing juvenile hormone titers. Phylogenetic comparisons promise to elucidate much about the historical contexts and consequences of flight loss.

> Wings have contributed more to the success of insects than any other anatomical structures...[1]

Although insects evolved in the Devonian, they did not become markedly successful until taxa capable of flight appeared in the lower Carboniferous. With this innovation came the great radiation of the class Insecta and enhanced ability to locate scattered resources such as food plants, mates and prey; to escape predators; and to disperse and migrate. Not only did wings provide for flight, but they also figured prominently in courtship, crypsis and mimicry, thermoregulation and water retention. Hence, it is not obvious why so many insect taxa have secondarily lost wings and/or the ability to fly (Table 1).

Flight loss has occurred in nearly all winged orders of insects, many times within most orders, and probably thousands of times within the Coleoptera. For example, in the carabid beetle genus *Nebria*, flight appears to have been lost independently at least 11 times among the 55 North American species[2].

The loss of flight may involve any manner and combination of fore- or hindwing modifications to which complex terminologies have been applied. In some taxa, flightlessness may not even be manifested exter-

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nally, as in those taxa where wings are present but the flight musculature is congenitally absent, inadequate or secondarily histolysed[3,4]. For simplicity, we refer to fully winged forms as macropterous or alate, flightless forms with reduced wings as brachypterous (Fig. 1), and those lacking wings as apterous (Figs 2 and 3). Loss of flight may occur seasonally, to which the terms cyclic, phasic and periodic alary polymorphism are applied. We refer to these environmentally triggered instances of flight loss as alary polyphenisms.

The study of flightlessness has proven especially interesting because it is linked to myriad morphological, physiological and behavioral components that are of both ecological and evolutionary significance. We first examine some general patterns of flightlessness, look at fitness trade-offs in species with both alate and flightless forms, and then conclude with some genetic and phylogenetic considerations.

Loss of flight

Wollaston's 1854 study of the insect fauna of the Madeiran island group, in which he estimated that some 200 of the 550 beetles lacked the ability to fly, was the first comprehensively to record and to explain instances of flightlessness[5]. Although early treatments tended to be monothetic, focusing on single factors to explain wing loss across both taxonomic and ecological boundaries[6], it is now evident that diverse sets of ecological and evolutionary circumstances lead to the loss of flight.

Stability

The most widely accepted explanation for flight loss relates to environmental stability, wherein dispersal is not essential for long-term survival of populations[7-9]. (We regard environmentally stable habitats as those where abiotic and biotic parameters – space, food, mates, etc. – allow populations to persist through many generations.) In his review of insect flightlessness, Roff[9] marshaled considerable data indicating that habitat stability accounts for most cases of flight loss

in insects. For example, beetles of geophilic habits are more often brachypterous than those of hydrophilic habits given similar geographic ranges, because dispersal is often necessary in freshwater habitats that periodically dry or flood[7]. Stable habitats with high rates of flight loss include mountains, tropical montane forests, Pleistocene refugia, caves and ocean surface[9]. Geologically and climatically stable portions of the southern continents that have persisted throughout the Tertiary are also reported to have high levels of brachyptery[10].

Isolation

Another hypothesis assumes that flightlessness evolves in isolated habitats because dispersers are likely to experience elevated levels of mortality. Darwin[6] favored this explanation for the evolution of flightlessness on oceanic islands. However, Roff[9] found that the proportion of flightless insects on islands was no higher than in continental areas. Habitats where isolation may affect the evolution of brachyptery include caves, inland sand dunes, and many high montane (especially arctic-alpine) and coastal strand communities (e.g. dunes, salt marshes, beaches and the intertidal zone).

Energetics

A third situation in which flight loss is prevalent is where the energetic cost of flight is high, e.g. in habitats with cold temperatures, high winds, or both. In numerous insect groups the incidence of brachyptery increases as one moves up in altitude or toward higher latitudes. Similarly, a great many of the flightless Lepidoptera and Diptera are winter-active taxa[11,12]. Both cool temperatures and high wind seem to come into play on the subantarctic islands where unparalleled proportions of the insect faunas are flightless (Fig. 1)[13]. The high costs of desiccation during flight might explain the numerous instances of flight loss among desert entomofaunas.

Parasitism

Vertebrate ectoparasites include several of the oldest and most diverse clades of flightless insects:

the Cimicidae and Polyctenidae (bedbugs and batbugs), the Phthiraptera (chewing and sucking lice) and the Siphonaptera (fleas). Although flightlessness is generally rare among flies (< 1%, Table 1), it occurs in five families of flies that are bat ectoparasites or inquilines: Calliphoridae, Chiropteromyxidae, Mormotomyiidae, Nycteribiidae and Streblidae. An indication that wings are a liability for a parasitic existence is provided by the blood-sucking hippoboscid flies, which shed their wings after locating a suitable host. Social insect parasites and inquilines are also prone to wing reduction or loss: included here are hundreds of termitophiles, myrmecophiles, and bee and wasp inquilines (Fig. 3).

Finally, and of course, flightless-ness occurs in ecological contexts that cannot be pigeonholed into any of the above: for example, many ant mimics (that do not live intimately with ants); and several cases where males are able to control access at female emergence sites[14,15].

Interrelationships

The ecological conditions that lead to brachyptery often are in-terrelated or reinforcing[8]. Moun-tains, for example (as argued by Darlington[7]), represent historically persistent habitats, because popu-lations can move upward or down-ward to minimize the impact of climatic fluctuations. Yet, it is also true that mountains are isolated and represent an energetically costly environment for flight. Similarly, caves tend to be environmentally stable as well as isolated and cool. Although flight loss in birds is associated with areas (such as islands) where predators are rare or absent, the importance to in-sect brachyptery of release from predators is not well studied.

Selective trade-offs

Wing-polymorphic taxa are excel-lent systems for studying problems of resource allocation, and in par-ticular, the reproductive perform-ance of winged versus wingless morphs. Advantages accrued by brachypterous water striders in-clude faster nymphal development and higher female fecundity[16]. Denno et al.[17] reported a syndrome

Table 1. Flightlessness in temperate pterygote insects[a]

Order	Described species[b] (worldwide)	Percentage flightless[c] (temperate)	Principal flightless sex
Ephemeroptera	2000	0	−
Odonata	4870	0	−
Plecoptera	1550	<10	Male
Embioptera	150	20–30	Female (all)
Phasmatodea	2000	90–100	Female
Orthoptera	12500	30–60	Both
Grylloblattodea	20	100	Both
Dermaptera	1100	20–40	Both
Mantodea	1500	0	−
Blattodea	4000	50–60	Female
Isoptera	1900	0	−
Zoraptera	24	100	Both
Psocoptera	2500	10–20	Female
Mallophaga	5000	100	Both
Anoplura	500	100	Both
Hemiptera	50000	20–30	Both
Homoptera	32000	>30	Both
Thysanoptera	4000	10–20	Male
Neuroptera	4670	<1	Female
Coleoptera	290000	<10	Both
Trichoptera	7000	<1	Both
Lepidoptera	112000	<1	Female
Mecoptera	480	20–30	Both
Hymenoptera	103000	<10	Female
Diptera	98500	<1	Female
Siphonaptera	2259	100	Both

[a]From Ref. 9, with permission.
[b]Taxonomy and estimates of ordinal species numbers from Ref. 41.
[c]Percentages include species with nonflying morphs.

of brachypterous advantages for *Prokelisia* leafhoppers, including greater fecundity, earlier age of first reproduction and longer adult life. The first two fitness advantages were also reported in *Chorthip-pus* grasshoppers[18] and *Gryllus* crickets[19]. In *Gryllus*, the age of first reproduction is genetically corre-lated with wing morph, establishing a pleiotropic connection between

genes for fitness and decreased dispersal.

For 26 intraspecific comparisons of wing-polymorphic species, Roff[20] found that 21 of these were characterized by more fecund brachypters, whereas only three had more fecund macropters. And in one of these seemingly exceptional cases – that involving the lymantriid vapourer moth, *Orgyia thyellina* –
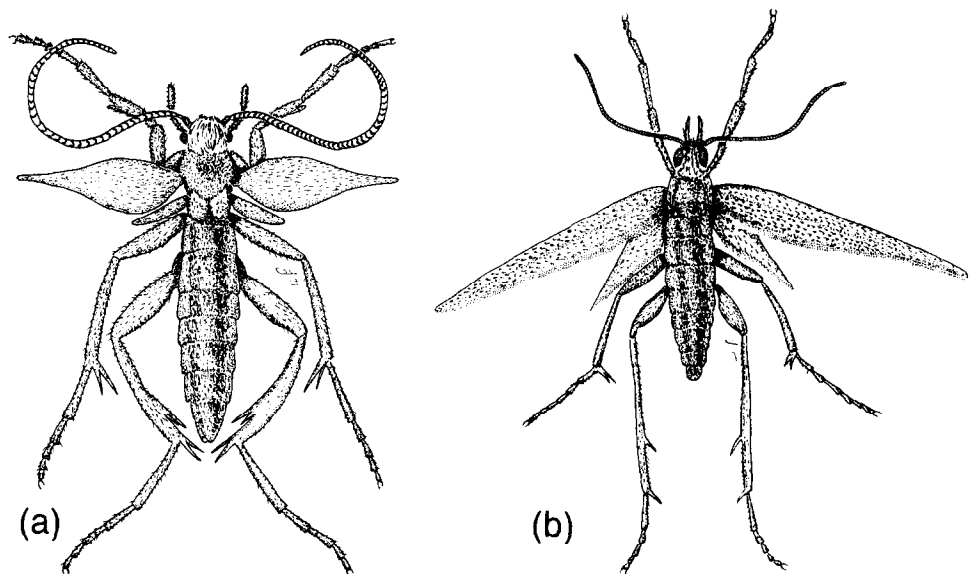
Fig. 1. Brachypterous moths from the subantarctic islands. (a) *Pringleophaga kerguelensis* (Tineidae) from Kerguelen Island. (b) *Exsilaracha graminea* (Pyralidae) from Campbell Island; the enlarged hind femora provide this moth with grasshopper-like jumping abilities. *From Ref. 13, with permission; redrawn by Julie Henry.*
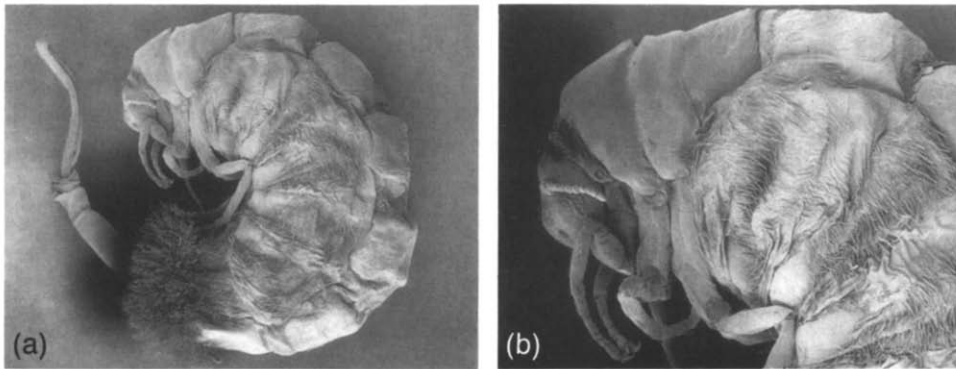
Fig. 2. Aptery in the case-bearing psychid moth, *Psyche casta*: (a) adult female; (b) detail of thoracic segments. Females have lost all external vestiges of wings; males are fully winged. Dispersal occurs via the first instars, which balloon on small strands of silk.

brachypterous females lay fewer eggs but these are larger, hence emphasizing egg provisioning over egg number. In contrast, Aukema[21] reported that long-winged females in three species of *Calathus* ground beetles are not only more fecund than short-winged morphs but may also produce more eggs over a longer period.

A related area of trade-offs concerns migratory polymorphism and the allocation of resources for flight or reproduction in migratory and nonmigratory individuals[22].

Flight apparatus development
Southwood[23], having been influenced by Wigglesworth's earlier work, proposed that insect juvenile hormone (JH) regulated flight-wing development, arguing that increased levels of JH lead to juvenile characters, i.e. brachyptery, and lower levels to adult character-

istics such as macroptery. Topical application of JH to *Gryllus* crickets during the ultimate or penultimate nymphal instar allowed Zera and Tiebel[24] to redirect development from macroptery to brachyptery. They went on to show that JH levels were higher in the hemolymph of short-winged than long-winged individuals[25]. The level of B-ecdysone, another morphogenetic hormone, also differed between the morphs.

In cases of alary polyphenism, abiotic environmental factors may influence the concentration of JH or other morph-determining hormones prior to adult eclosion. The most commonly reported stimulus affecting morph determination is photoperiod. Kimura and Masaki[26] found that the brachypterous form of the vapourer moth was prevalent at light:dark regimes between 12:12 and 14:10, whereas the macrop-

terous form was most common between 16:8 and 20:4. For water striders, in which the macropters overwinter, decreasing short-day photoperiods resulted in an increase in the relative frequency of macropterous individuals[27]. Temperature also influences wing development; in several *Ptinella* feather-winged beetles, for example, the highest percentage of alate individuals developed in laboratory cultures at 20°C (Ref. 28).

Biotic factors such as high population densities also induce alary polyphenisms, for example in migratory locusts, where the immatures of the sedentary solitary form are transformed into the swarming gregarious morph. Population density also increases the frequency of macropters in alary polyphenic homopterous insects such as *Prokelisia* planthoppers[29] and aphids[30].

Abiotic and biotic factors may interact to determine flight apparatus development. If the larvae of the carabid *Pterostichus oblongopunctatus* are starved and reared at photoperiods differing from natural field conditions, more individuals develop metathoracic flight muscles[31].

Several ground beetle and weevil species have wing development governed by a single gene that has two alleles, with the brachypterous allele dominant to the macropterous one[20]. Significant variation in genetic mechanism occurs even among closely related species. Polymorphism in the carabid *Calathus erythroderus* is determined via a mendelian two-allele system; in the related *C. melanocephalus* the expression of the long-winged morph can be modified by temperature and food supply[32]. Other more complex systems may be polygenically determined and also include an environmental component, as in *Limnoporus* water striders[16].

Evolutionary correlates
The population genetic consequences of brachyptery would appear straightforward. A water strider species characterized by brachypterous populations is much more highly structured than a wing-polymorphic species[33]. However, in a comparison of five carabid beetles
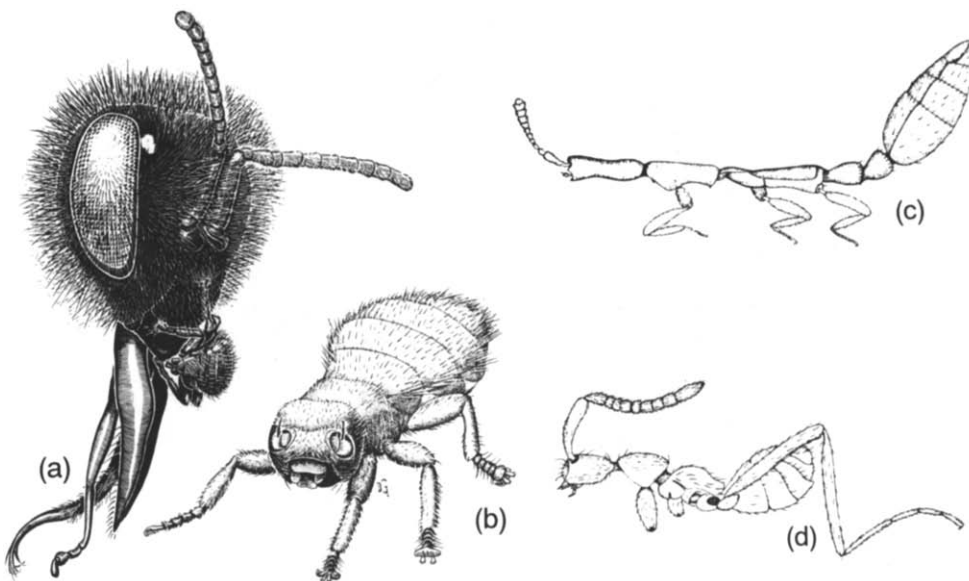
Fig. 3. Extreme cases of aptery and morphological specialization among social insect inquilines. (a, b) The bee louse, *Braula caeca*, is an unlikely-looking fly which lives on honeybees, apparently feeding on nectar and pollen around the bee's mouth; *illustrations supplied by David Grimaldi*. (c, d) Myrmecophilous rove beetles, *Mimanomma spectrum* (c) and *Mimeciton antennatum* (d), which live as guests in the columns of army ants; *reproduced from Ref. 42*.

having varying wing development, a fully winged species exhibited genetic heterogeneity comparable to that of one with vestigial wings[34]. Among these beetles, habitat subdivision was a much better predictor of genetic structure than flight apparatus, indicating that just because a taxon is macropterous, individuals do not necessarily disperse long distances.

Wide-ranging species often exhibit geographic variation in the frequency or degree of wing polymorphism. In the ground cricket *Allonemobius*, the incidence of macroptery varies among populations from 9 to 74%. Heritability for wing configuration averaged 0.52 for males and 0.72 for females, and did not differ significantly among populations, indicating that there is ample genetic variation for selection to influence morph incidence in all populations[35].

Flightlessness is often limited to one sex, typically females (Table 1). In the Lepidoptera, for example, brachyptery is restricted to females (Fig. 2), except on oceanic islands where both sexes may be flightless[36]. Exceptional systems in which males are brachypterous and females flighted include those involving predispersal mating, as occurs in tightly circumscribed spaces where males have access to emerging females. Examples include two groups of subcortical insects – scolytid ambrosia beetles[14] and aradid bugs[37] – and agaonid fig wasps[15].

Numerous morphological syndromes are associated with flight loss: reduced eye size[28], change in body shape due to reduction of portions of the thorax[3], enhancement of jumping ability[13], and phyletic size increase[38]. Any number of life history attributes are likely to be associated with flight loss; in forest Lepidoptera, for example, taxa with brachypterous females are often polyphagous and disperse as larvae[39]. It seems likely that many morphological and ecological syndromes involving flight loss await elucidation.

Future directions

Recent advances in the understanding of the evolution of flightlessness have come in several areas. The frontier between environmen-

tal induction and genetic control promises to be a fertile one, as many of the genetic programs studied thus far appear to be influenced by external stimuli. Correlations of morphological, behavioral and physiological characters into flightlessness syndromes indicate considerable pleiotropic effects among the responsible genes. Developmental control in these integrated systems remains poorly understood.

Over the past ten years, substantial and wide-ranging fitness differences between brachypterous and macropterous forms have been demonstrated. Virtually all studies to date have focused on the fitness trade-offs in females, with little or no attention paid to those of males. Within-species studies should be especially helpful in revealing selective pressures acting to establish patterns of alary polymorphisms. Comparisons with migratory and nonmigratory individuals of fully winged insects, or even winged and unwinged reproductive propagules in plants, will help to establish still more general patterns regarding resource allocation and the selective trade-offs between dispersal and reproductive performance. Heritability studies are needed on more systems to quantify the genetic variation available to selection in different situations supporting flight loss.

Phylogenetic studies promise to reveal much about the evolution of brachyptery. Cladograms can be employed to track the evolutionary fate (e.g. relative rates of speciation and extinction) of brachypterous and macropterous sister groups. Moreover, cladograms provide the basis for making phylogenetically independent statistical comparisons among lineages or species – correlation tests involving flight loss have, by necessity, assumed that even sister species or taxa represent independent data (e.g. Ref. 9). For example, if wing loss occurring in a common ancestor results in an accelerated rate of speciation – perhaps due to greater population subdivision in flightless taxa – patterns attributed to adaptation may actually be nonadaptive at the species level (cf. Vrba's effect hypothesis[40]).

Although correlation tests may

be gainfully employed to reveal general ecological and evolutionary patterns, they do not provide information about the sequence of specializations associated with flight loss. By knowing where characters change within a lineage, one can determine which attributes are likely to be evolutionary prerequisites for flightlessness. For example, character mappings could show that the evolution of polyphagy in brachypterous moths almost invariably precedes flight loss. Conversely, one could determine whether other derivations – such as enhanced saltational or cursorial abilities, or elaboration of cryptic behaviors or other defensive attributes – are likely to follow the evolution of flightlessness.

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Nitrogen Cycling and Nitrogen Saturation in Temperate Forest Ecosystems

John D. Aber

The last decade has seen a dramatic shift in the focus of nitrogen cycling research in forest ecosystems. Concerns over nitrogen deficiencies and effects of removal in harvest have given way to concerns over excess nitrogen availability and the potential for forest decline and surface water pollution. Driving this paradigm shift is the increase in atmospheric deposition of nitrogen to forests due to industrial and agricultural activity. At the core of the new paradigm is the concept of 'nitrogen saturation' of forest ecosystems. The purpose of this review is to synthesize recent advances in research relating to nitrogen deposition effects on temperate zone forest ecosystems, and the further effects of nitrogen saturation on environmental quality.

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The concept of nitrogen saturation was apparently unknown before 1981, when Ingestad *et al.*[1] presented a very simple model of N nutrition based on the nutrient flux density and N productivity concepts. This model was used to predict when N additions would be sufficient to remove all N limitations on forest growth under typical conditions in Sweden[2]. Simultaneously, van Breemen *et al.*[3] reported ex-

treme soil acidification and increased aluminium mobility due to very high levels of ammonium (NH_4^+) deposition in the Netherlands. Nihlgard[4] brought together data from both soils and plant research suggesting that excess N availability was a serious concern for both forest decline and soil and stream-water acidification. His 'ammonium hypothesis' marks the beginning of the focused discussion of the potential environmental dangers of excessive N deposition.

Several definitions of N saturation have been proposed[5,6]. Some are based on the absence of a growth response from the vegetation[7], and some on either the initiation of nitrate leaching[8], or on an equivalence between N losses and N inputs (no further N retention[9]). All of these definitions describe stages of declining ability of an ecosystem to retain added N. Processes that contribute to N retention include plant uptake and accumulation, microbial uptake and incorporation into soil organic matter, and physical–chemical processes such as cation exchange and abiotic incorporation of mineral N into soil organic matter. We need not think of N saturation as occurring at a specific point in time, but as a

set of changes in critical ecosystem processes which represent the integrated response of a system to increased N availability[6,8].

Implications of N saturation

Nitrogen saturation has at least three serious environmental impacts: (1) on soil chemistry and water quality, (2) on forest composition and productivity, and (3) on fluxes of radiatively active (or 'greenhouse') gases.

Negative impacts on water quality derive from the induction of nitrification in acid soils. Net nitrification (the conversion of NH_4^+ to NO_3^-) is generally very low to nonexistent in acid forest soils in the absence of elevated N deposition or N-fixing species[10]. However, nitrification can occur at low pH in the presence of elevated NH_4^+ concentrations, and is now common in heavily affected European and North American sites[11–13]. Nitrification appears to increase with increasing cumulative N deposition and storage in soils[14–16].

As an anion, nitrate is very mobile in temperate zone soils and tends to leach rapidly in the absence of plant uptake. By charge balance, this results in cation removal as well, with the nutrient cations tending to be drawn down first, followed by an increase in the concentration and mobility of hydrogen ions and inorganic aluminium[12,17,18]. Increases in nitrate concentration in surface waters have been reported for Scandinavia (Refs 19, 20 and see Ref. 21), and correlate with increased deposition in central Europe[22]. Increasing nitrate concentrations in

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In their excellent review of flight-lessness in insects, Wagner and Liebherr[1] do less than justice to the Mantodea: their Table 1 gives zero temperate mantids as being flight-less. Tropical mantids, however, very often have reduced wings; in Ghana, for example, out of 37 genera examined, eight have brachypterous and two have apter-ous females[2]. For temperate man-tids, a recent field guide to European insects[3] lists four species that are fully winged in both sexes, three with winged males and brachypterous females, and one species in which both sexes are apterous. Clearly, wing reduction is widespread in the Mantodea. The reasons why wing reduction has occurred in mantids are also not covered in Wagner and Liebherr's review. While other factors may also be involved, I have argued else-where[2] that wings are probably a feature by which visually oriented predators recognise mantids, and

that therefore in some species selection has favoured individuals with reduced wings. Females live much longer than males and can lay several oothecae from a single mat-ing, so selection has led to females reducing their wings but to males retaining theirs for dispersal and for finding mates. So why have females not lost their wings completely? The reason appears to be that in the larger species wings are also important in a deimatic display directed against predatory birds[2]. So there is a selective trade-off between small wings for better camouflage and large wings for more effective display. A similar trade-off occurs in many of the larger stick insects[4].

However, there are also some mantids in which both sexes have completely lost their wings. These are mostly small, very active species that rely for escape on speed and agility of running rather than on flight. In small species, deimatic displays are not very effec-

tive deterrents against birds, and escape by either flight or running is far more likely to be successful. My impression is that these cursorial mantids are found in arid environ-ments where high body tempera-ture enables them to move with more agility than is possible in cooler or more shady places, but this theory has not been tested.

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Reply from Liebherr and Wagner

Edmunds is right to mention the flight-wing dimorphism in mantids, as it appears to have originated numerous times during the evol-ution of the order[1]. Wing reduction and flight loss occur predominantly in female mantids, presumably in exchange for enhanced reproduc-tive output, as Edmunds suggests.

Edmunds also notes that brachyp-terous female mantids may retain wings for deimatic displays to ward off birds. Yet another group of aerial predators, the bats, appears to have influenced evolution in the Mantodea. Winged mantids possess

a mid-line thoracic ear that is sensi-tive to the ultrasonic frequencies of echolocating bats[2]. Flightless fe-male mantids often show losses in function of this ear[1], while conspe-cific males retain fully functional ears. Yager notes several additional instances of auditory dimorphism in night-flying wing-polymorphic insect taxa, where the flightless females have reduced auditory capacities[1]. These cases further sup-port arguments that bat predation has greatly influenced the mor-phology and behavior of many noc-turnal insects.

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