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Physiology and Ecology of Dispersal Polymorphism in Insects

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Abstract: Studies of dispersal polymorphism in insects have played a pivotal role in advancing our understanding of population dynamics, life history evolution, and the physiological basis of adaptation. Comparative data on wing-dimorphic insects provide the most definitive evidence to date that habitat persistence selects for reduced dispersal capability. The increased fecundity of flightless females documents that a fitness trade-off exists between flight capability and reproduction. However, only recently have studies of nutrient consumption and allocation provided unequivocal evidence that this fitness trade-off results from a trade-off of internal resources. Recent studies involving wing-dimorphic insects document that flight capability imposes reproductive penalties in males as well as females. Direct information on hormone titers and their regulation implicates juvenile hormone and ecdysone in the control of wing-morph determination. However, detailed information is available for only one species, and the physiological regulation of wing-morph production remains poorly understood. Establishing a link between the ecological factors that influence dispersal and the proximate physiological mechanisms regulating dispersal ability in the same taxon remains as a key challenge for future research.

Keywords: wing polymorphism, life-history trade-off, reproduction, endocrine regulation, juvenile hormone, habitat persistence, flightlessness

Overview and Perspective

The ability to disperse by flight is an important feature of insects that has played a key role in their evolutionary success (99, 118). Numerous species

are polymorphic for dispersal capability by having discontinuous variation in wing length and/or flight-muscle mass (14, 53, 95, 127). Dispersal polymorphism has been intensively studied by ecologists, evolutionary biologists, and physiologists for decades (23, 25, 53, 69, 84, 95, 106, 121, 127). These studies have made important contributions to our understanding of dispersal per se in addition to advancing our understanding of population dynamics and species interactions (17, 20, 22, 67), life history evolution (23, 71, 95, 117), and the physiological basis of adaptation (50, 84, 127).

Wing polymorphism, by far, has been the most commonly studied type of dispersal polymorphism (53, 95) and is the focus of our review. Obligate flightless individuals (wingless or with reduced wings) can be visually identified in these species. Thus, inferences concerning dispersal capability can be made much more easily and reliably than for wing monomorphic species whose flight capability must be determined by tedious flight assays (25). Indeed, the ease of wing-morph identification has facilitated the first rigorous assessment of the relationship between the incidence of dispersal and habitat persistence (23).

Studies of wing polymorphism have also played a significant role in the development of ideas concerning the interaction between dispersal and other key life history traits such as fecundity, age at first reproduction, and diapause (18, 25, 61, 71, 95, 105, 111, 124, 127). In numerous wing-polymorphic species, flight capability (presence of fully developed wings and flight muscles) is negatively correlated with age at first reproduction and fecundity (14, 99, 115, 124). Such negative associations have led to the notion that flight capability and reproduction are energetically expensive and compete for internal resources, thus resulting in trade-offs (i.e. the flight-oogenesis syndrome) (18, 25, 61, 77, 95, 99, 127).

Insect physiologists also have been fascinated by the physiological mechanisms that regulate the development of radically different morphs of the same species, which are adapted for dispersal versus reproduction (50, 69, 84, 85, 121, 130). Wing-polymorphic insects have served as models for studies of both the endocrine regulation of morph development and the physiological mechanisms underlying the evolution of novel developmental pathways (e.g. heterochrony) (41, 72).

Dispersal polymorphism in general and wing polymorphism in particular were last comprehensively reviewed about a decade ago (50, 53, 89, 95). Since these reviews, new data have been obtained on important facets of this topic that previously were unavailable because of technological constraints or limited study. Our review focuses primarily on what we feel are the most recent advances in the physiology and ecology of dispersal polymorphism. First, we review general information on the types of dispersal polymorphism, their taxonomic distribution, and the genetic and environmental factors influencing morph production. Second, we update evidence for a trade-off between flight capability and reproduction in females and review new information documenting a similar trade-off in males. Third, we discuss recent physiological studies that provide strong evidence for an energetically based trade-off between dispersal capability and reproduction. Fourth, we review the endocrine regulation of morph determination with a special emphasis on the involvement of juvenile hormone. Fifth, we review new evidence that more rigorously documents the purported relationship between the evolution of dispersal, habitat persistence, and habitat dimensionality. Throughout, we integrate data on the physiology and ecology of dispersal polymorphism, which ultimately will allow for a deeper understanding of the mechanisms underlying the evolution of dispersal.

Taxonomic Distribution and Types of Dispersal Polymorphism

Dispersal polymorphism is a widespread phenomenon among the insects (18, 53, 95, 99), occurring in the Orthoptera (8, 95, 111, 129), Psocoptera (82), Thysanoptera (10), Homoptera (14, 18, 27, 28, 65, 100), Heteroptera (35, 40, 105, 108, 123, 124), Coleoptera (68, 114, 115), Diptera (109), Lepidoptera (64), and Hymenoptera (101).

There are two major categories of dispersal polymorphism: (*a*) wing polymorphism and (*b*) flight muscle polymorphism. Wing polymorphism involves discrete variation in the size of the wings and flight muscles, such as occurs in aphids and planthoppers (14, 27). Thus, in wing-polymorphic species, there is a flight-capable morph with fully developed wings (macropter or alate) and a flightless morph, either with reduced wings (brachypter) or without wings (apter). In contrast, flight-muscle polymorphism involves variation in the size of flight muscles (14, 53, 95). In this case, all individuals are macropterous and the morph with reduced flight muscles is flightless (89, 123). Furthermore, macropters of some wing-dimorphic aphids, water striders, and crickets also have the ability to histolyze their wing muscles, which transforms them into functional brachypters (28, 35, 62, 111). Flight muscle histolysis can also be triggered by wing shedding (dealation) (111, 112). Finally, variation in dispersal capability may result from behavioral differences in flight propensity in macropters (35, 90).

In addition to variation in wing length and flight-muscle mass, morphs consistently differ in a suite of correlated traits. For instance, the flightless morph typically exhibits enlarged ovaries, earlier ovarian development, and reduced stores of flight fuels (53, 95, 99, 127, 128).

Dispersal Capability of Wing Forms

With few exceptions (e.g. 112a), the macropter or alate is the only flight-capable wing form. Consequently, the macropter is primarily responsible for escaping deteriorating habitats and colonizing new ones (13, 23, 95, 99). The flight capability of the macropter is extraordinary in some species of planthoppers and aphids, whose migrations extend hundreds of kilometers (14, 27, 66). However, there is considerable intraspecific and interspecific variation in dispersal capability, with most macropterous individuals flying considerably shorter distances even in highly mobile species (14, 28). In waterstriders, both the flight threshold and the extent of wing muscle histolysis are negatively associated with the proportion of macropters in the population (32, 35, 99). Thus, the dispersal capability of the macropter should be reduced for species in which the proportion of macropters is low. This hypothesis is further supported by evidence from grasshoppers and bugs in which macropters are rare and those that do occur never fly (56, 93). Despite variation in the dispersal capability of the macropter, the ambit of the brachypter is often orders of magnitude smaller for most species because they disperse only by walking or hopping (14, 20, 27).

Wing-Morph Determination

Wing morph can result exclusively from variation in genotype [= genetic polymorphism, e.g. some weevils (58)], exclusively from environmental variation [= environmental polyphenism, e.g. some aphids (27, 50, 69)], or most commonly from a combination of both genetic and environmental variation [e.g. many crickets and planthoppers (73, 95)]. In cases where both environmental and genetic effects are involved, wing form can be viewed as determined by an environmentally sensitive switch that specifies the development of either a macropter/alate or a brachypter/apter (18, 53, 95, 99, 134). The sensitivity of the switch to environmental cues can be under either polygenic or monogenic control (21, 95, 99). Polygenic control systems are more prevalent in the Orthoptera, Dermaptera, Homoptera, and Heteroptera, and single-locus determination is most frequent in the Coleoptera and Hymenoptera (95, 99). Recent selection experiments have documented a significant heritability for wing morph in several cricket and planthopper species (70, 73, 79, 97). Selection experiments have also documented genetic correlations between various dispersal traits such as wing length, flight muscle reduction, and flight propensity (36). For wing-dimorphic insects, the morph-specifying developmental switch is thought to involve variation in the level of a hormone or hormones (34, 45, 50, 53, 84, 95, 130). However, direct physiological evidence in support of this notion exists for only one cricket species (130).

Various environmental cues such as crowding, host plant condition, temperature, and photoperiod influence wing form (14, 16, 19, 27, 28, 38, 53, 70, 80, 93, 132). In many species, the production of the macropter is density-dependent and is intensified by limited or nutritionally inadequate food (14, 27, 70). For these species, macropters are able to effectively escape deteriorating habitats and colonize better ones elsewhere (14, 23, 27). For a few aphids and crickets the opposite response occurs, whereby brachypters are produced under very stressful conditions (27, 103, 132). In such cases, there may be insufficient resources to produce a macropter capable of successful long-distance dispersal and colonization (27).

The switch that commits an individual to develop into a particular morph may occur at any one of several restricted periods of development (= sensitive stage). The sensitive stage can occur during (*a*) embryonic development (prenatal determination) or the early juvenile stadia (postnatal determination), as in several aphid species (27, 45, 50, 76); (*b*) the middle instars, as in some planthoppers (57, 65); or (*c*) as late as the last instar, as in many cricket species (103, 110, 132).

Trade-Offs between Dispersal Capability and Fitness Components

The widespread occurrence of flight polymorphism in insects strongly suggests that "fitness costs" are associated with the ability to fly (94). The energy used to construct wings and flight muscles (18, 27, 94, 105) is simply not available for reproductive investment (77, 111, 127). In general, strong support for a fitness trade-off between flight capability and reproduction is provided by comparative studies across a wide range of wing-polymorphic insects (18, 95, 96, 99). For instance, the macropterous form is significantly less fecund than the flightless morph in grasshoppers (93), crickets (77, 94), planthoppers (18), aphids (28), waterstriders and veliids (80, 124), water boatmen (123), seed bugs (105), and pea weevils (115). Furthermore, reproduction is often delayed in the migratory forms of grasshoppers (93), crickets (94, 111, 129), aphids and planthoppers (18, 28), waterstriders (33), true bugs (37, 105), and beetles (115). Other costs associated with flight capability in certain taxa include delayed development (28, 124), decreased longevity (18, 123), and reduced egg or offspring size (28, 102, 105). However, the only penalties consistently imposed on macropters across a wide variety of polymorphic taxa are reduced fecundity or delayed age at first reproduction (18, 99).

Despite the widespread evidence in support of a trade-off between dispersal capability and reproduction, there are several notable exceptions. For example, the macropter produces more eggs than the flightless morph in one

moth (102) and several beetle species (2, 113). In one of these apparently exceptional cases, the brachypter actually has a greater reproductive effort than the macropter because it produces much larger eggs, even though it produces fewer of them (102). Also, minimal fitness differences between wing forms may occur in species in which macropters are rare and flightless (32, 56). In such cases, the reproductive penalties associated with macroptery are probably slight, possibly because macropters have reduced flight muscles and hence diminished maintenance costs (127).

Although inherent differences in reproduction between flight-capable and flightless wing forms often occur, certain circumstances can alter the realization of these differences (14, 18). For example, most assessments of fecundity are made in the laboratory, where survival is often maximized compared to that which occurs in nature. For insects that feed and reproduce continuously throughout adult life, macropters, if they live long enough, may be able to recover the inherent penalties imposed by flight capability and ultimately realize a life-time fecundity very similar to that of brachypters (18). Thus, fitness differences between morphs may be minimized in the laboratory, and this may explain why some studies have failed to find overall fitness differences between wing forms (18, 95, 99). However, in the context of reduced survival in the field, the reproductive delays and reduced initial fecundity of macropters should contribute to a lower realized fecundity compared to that of brachypters (18). In addition, the failure to identify functionally flightless macropters with histolyzed flight muscles can result in a substantial underestimate of the fitness cost of flight capability (AJ Zera & K Grudzinski, unpublished data).

Stress may exacerbate fitness differences between wing forms by disproportionally taxing the energy budget of the macropter, which bears the added cost of flight capability (14). For example, in a cricket species, the fecundity of the macropter is reduced to a much greater degree under conditions of food limitation compared to that of the brachypter (111). Similarly, brachypterous corixids were more fecund than their long-winged counterparts when food was limiting, but no fitness difference was observed when food was abundant (123). Also, reproduction is delayed to a greater degree in the macropter of some plant-hoppers when both wing forms are fed poor-quality host plants; this difference in age at first reproduction is minimized when both wing forms are fed high-quality plants (65). Finally, following extended diapause, brachypters of some planthoppers and waterstriders are much more fecund than macropters, but this difference is minimized in nondiapausing females that have fed continuously as adults (33, 65).

Although trade-offs between dispersal capability and reproduction have been studied extensively in females (18, 95, 99), the relationship between wing form and components of fitness has been almost completely neglected in

males (11, 14, 55, 88). Few studies have explored the possibility of a trade-off between dispersal capability and reproductive success in males, and those that have provide conflicting evidence for the existence of a fitness cost associated with macroptery. The cost may be leveled in terms of mate sensing and detection, sperm volume, or male attractiveness to the female, all of which could influence the number of offspring sired. Support for a phenotypic trade-off has been found in a few species of crickets, chinch bugs, pea weevils, and thrips, in which macropterous males exhibit decreased reproductive success compared to brachypterous males because of their delayed development, mating inferiority, or reduced weaponry used in fighting for females (10, 11, 39, 115). However, several other studies have failed to find any difference in mating success between the male wing forms of a planthopper (75) and two species of crickets (55, 99). Subsequent investigation (11) found a significant mating advantage for the brachypter of *Gryllus firmus*, whereas previous study failed to observe a difference in mating success between male wing forms (99).

Factors that influence the evolution of flightlessness in males are poorly understood and may differ from those influencing females (55). For instance, gender-related differences in the evolution of brachyptery might result from a differential cost of reproduction that is usually much lower for males (55, 88). Consequently, the cost-driven trade-off between dispersal and reproduction that occurs in females (77, 127) may be far less evident in males. This may explain in part why some studies have failed to find a difference in reproductive success between the male wing forms of polymorphic insects.

Alternatively, conditions under which mating success is usually assessed in the lab may mask inherent fitness differences between wing morphs (11). For example, if male wing morphs are differentially able to attract or locate females, then such differences may not be realized if individuals are enclosed in a confined space. One study conducted at a large spatial scale in the field showed a mating advantage for brachypterous males of the planthopper *Prokelisia dolus* because of their enhanced ability to locate females in a contiguous habitat (GA Langellotto & RF Denno, unpublished data). Fairbairn & Preziosi (35a) also report a mating advantage in the field for apterous males of the waterstrider, *Aquarius remigis*. Thus, evidence is accumulating for a trade-off between dispersal ability and reproduction in males that is so well documented for females.

In the dispersing morphs of insects, a suite of behaviors and characteristics has evolved that provides partial compensation for the inherent reproductive penalties associated with macroptery, as well as the cost of flight itself (90), and leads to a higher probability for the successful colonization of a new habitat (18). These include the following: (*a*) the selective colonization of nutrient-rich resources (9, 20), (*b*) large body size and correlated fecundity (14),

(*c*) trading off small egg size for increased egg number (28, 102, 105), (*d*) extensive feeding coupled with iteroparity or continuous reproduction following colonization (18), and (*e*) histolysis of wing muscles after arrival in the new habitat, with energy reallocation to reproduction (5, 28, 35, 111). Nevertheless, that these behaviors do not allow for total reproductive compensation is evident from the general observation that reproductive penalties do occur in macropters, even under conditions where food is often abundant (18, 95, 99, 111, 129).

Physiological Basis for the Trade-Off between Flight Capability and Reproduction

The most widely held physiological explanation for the elevated fecundity of the flightless morph is that flight capability has been "traded off" for increased reproduction. Thus, the physiology and development of the flightless morph has been altered, such that nutrients devoted to construction and maintenance of the flight apparatus in the long-winged morph are allocated to increased reproductive effort in the flightless morph (25, 53, 94, 111, 120, 127). Although this notion has attained the status of dogma, direct physiological evidence for this trade-off has been available only recently (77, 127).

Trade-Offs Involving Flight Muscles

Historically, the primary evidence supporting the trade-off hypothesis has been the strong negative correlation between flight-muscle mass and ovarian mass commonly observed in wing polymorphic species (89, 95). Fully grown flight muscles comprise a substantial proportion of total body weight of flight-capable adults, typically 10–20% (42, 77, 78; AJ Zera & K Grudzinski, unpublished data). These muscles are reduced in size by 40% or more in the brachypter (77, 78, 111; AJ Zera & K Grudzinski, unpublished data). Reduced flight-muscle mass results primarily from inhibition of muscle growth (77, 78, 104, 111).

The negative relationship between flight muscle and ovarian mass also exists in many nonpolymorphic species in which young adults initially have fully developed wings and flight muscles (63, 89). This relationship suggests that construction and maintenance of the flight apparatus competes with egg production for a limited internal nutrient pool in insects in general (25, 89, 90, 120). In macropterous species, flight-muscle reduction may result from either arrested growth or histolysis of fully grown muscles (6, 89, 111, 123; AJ Zera & K Grudzinki, unpublished data). Furthermore, histolysis typically occurs coincident with ovarian growth and may involve a transfer of nutrients from muscles to ovaries (81, 89).

Few quantitative data are available on either the relationship between flight muscle and ovarian masses in alternate wing morphs or on the degree to which reduction in flight-muscle mass accounts for increased egg production in the flightless morph (42, 77, 78, 111; AJ Zera & K Grudzinski, unpublished data). For example, in the cricket *Gryllus rubens*, the thoracic muscles of the brachypter weigh 24 mg less and the ovaries weigh 67 mg more than those of a macropter of approximately equal weight (77). These limited data indicate that reduction in flight-muscle mass can account for a significant proportion, but not all, of the increased ovarian mass in the flightless morph. Some ovarian growth may occur at the expense of organs other than flight muscle, although there are currently no data on trade-offs between ovarian growth and these "third-party" sources (77).

Reduction in nitrogen allocation to flight muscles in the brachypter appears to occur solely by reduction in total muscle mass and not by lowering the nitrogen content per unit mass (78, 127, 128). Also, reduction in wing mass does not appear to be important with respect to providing extra nutrients required for the enhanced reproduction of the flightless morph (128).

The smaller flight muscles of brachypters have reduced maintenance costs compared to the fully developed flight muscles of macropters. The importance of reduced maintenance in the evolution of the trade-off between flight muscle and ovarian mass has only recently attracted attention. General maintenance costs comprise a significant proportion (~30%) of the total energy budget of herbivorous insects (116). Energy conservation resulting from reduction in flight-muscle mass is thought to be the major factor responsible for the evolution of flightlessness in birds (74) and for the histolysis of flight muscle prior to overwintering in the Colorado potato beetle (30). Furthermore, respiration rates are significantly higher for isolated, fully developed flight muscles of macropters than they are for undeveloped muscles of brachypters of *G. firmus* (AJ Zera & J Sall, unpublished data). Also, the whole-organism respiration rate of flightless *Gryllus assimilis* with histolyzed muscles is significantly lower than that of flight-capable individuals (AJ Zera & J Potts, unpublished data). In summary, a growing body of information implicates flight-muscle maintenance as a significant energetic cost of flight capability (77, 127).

Trade-Offs Involving Flight Fuels

Many insects can fly uninterrupted for hours or even days during migration or tethered laboratory flight (44, 90, 129). Extended flight requires prior biosynthesis and storage of large quantities of flight fuel. For example, in *G. firmus, Callosobruchus maculatus*, and the phase-polymorphic *Spodoptera exempta*, triglycerides (the most likely flight fuel) account for 10–40% of total dry mass of the dispersing morph and are reduced by 30–80% in the reproductive morph (43, 87, 128). Triglycerides are very costly to biosynthesize (128), and thus the

energetic cost of flight fuel biosynthesis is likely to be a factor contributing to the reduced fecundity of the dispersing morph. However, it has yet to be established whether the lower lipid content in flightless individuals actually results from reduced biosynthesis instead of decreased acquisition (78, 128).

Ontogenetic Considerations

The point in ontogeny when various energetic costs of flight capability are manifest will strongly influence whether these costs can be traded-off with reproduction. For example, in the crickets *G. rubens* and *G. firmus*, flight muscle growth does not occur during the adult stage, whereas in *Modicogryllus confirmatus*, substantial growth does occur (77, 78, 111). Thus, in the former two species there can be no direct trade-off between ovarian and flight muscle growth in adults, whereas in the latter species such a trade-off is possible. Similarly, for many macropterous species in which flight muscle histolysis occurs coincident with ovarian growth, a direct transfer of nutrients from flight muscles to ovaries is possible. In fact, uptake of flight-muscle protein by growing oocytes has been documented in *Dysdercus* bugs (81). In *Gryllus* species, flight-muscle growth during the juvenile stage could indirectly trade off with adult ovarian growth via the synthesis of storage proteins, which may be used by adults for egg production. However, this hypothetical scenario has yet to be investigated in any species. In addition, flight-muscle maintenance costs (basal metabolism and protein turnover) occur whenever muscles are present and can be directly traded off with ovarian growth during the adult stage (127). Similarly, the point in ontogeny when flight fuels are biosynthesized will determine the degree to which biosynthetic costs can reduce ovarian growth.

Physiological Evidence for a Cost to Flight Capability and Its Trade-Off with Reproduction

Recent nutritional studies on the consumption, assimilation, and allocation of nutrients provide the first direct evidence that alternate morphs differentially allocate (trade off) internal nutrients to reproduction. These nutritional studies, in conjunction with data on organ masses, respiration rates, and lipid levels in alternate morphs, strongly support the notion for an internal resource-based trade-off between flight capability and reproduction (77, 78, 111, 127).

In feeding trials, both wing morphs of adult *G. rubens* consumed the same amount of food, thus eliminating the possibility that the elevated fecundity of the brachypter simply results from increased food consumption (77). Surprisingly, only three other studies have either quantified or controlled for food consumption by alternate wing morphs in trade-off studies (78, 110a, 111). In general, failure to control or quantify food consumption has compromised most trade-off studies (77, 127).

Feeding trials in *G. rubens* also document that whole-organism respiration is elevated [efficiency of conversion of digested food to body matter (ECD) reduced] in the macropter (77, 127). This elevated respiratory metabolism is consistent with the higher maintenance and biosynthetic costs associated with flight capability in the macropter (77, 78, 127, 128). Similar studies with other cricket species also document an elevated, whole-organism respiration rate in the macropter compared to that of the flightless morph (78; AJ Zera, S Mole, & J Potts, unpublished data). Tanaka (111) also convincingly documents that internal resources are differentially allocated to flight muscle versus ovarian growth in the wing morphs of *M. confirmatus*. In summary, data are now available in several cricket species that strongly support the existence of a physiological cost to flight capability. In *G. rubens* and *M. confirmatus* this cost trades off with and reduces ovarian growth (78, 111, 127).

Feeding trials in crickets have not only documented the existence of a trade-off between flight capability and fecundity; they have also identified conditions under which increased food consumption can counteract the cost of flight capability and can obviate the expression of a potential trade-off (127). In *G. firmus*, increased consumption by the macropter counteracts its elevated respiratory metabolism and results in no significant reduction in ovarian biomass during the first two weeks of adulthood (78). In an analogous study involving actual flight in a phase-polymorphic moth, a negative relationship between flight duration and fecundity was observed when moths were given only water (43). However, this trade-off was not observed when moths were fed sugar. Thus, increased nutrient intake, either by virtue of elevated consumption or improved food quality, can ameliorate the energetic cost associated with flight capability. The several examples where fitness differences were observed between morphs under conditions of nutrient stress, but not when nutrients were abundant, are consistent with this notion (14, 65, 111, 123).

The Endocrine Regulation of Morph Determination

Juvenile Hormone and Wing-Morph Determination: The Classical Hypothesis

The physiological mechanisms that regulate the production of alternate wing morphs have been the subject of considerable experimentation and speculation for over three decades (50, 63, 69, 89, 121). Most studies have focused on the roles of juvenile hormone (JH) and 20-hydroxy ecdysone (20-OH ecdysone), two hormones that are major regulators of molting, growth, and differentiation in insects. Twenty-hydroxy ecdysone initiates the molt and, depending upon the concentration of JH, also initiates metamorphosis. If JH is

above some threshold level, metamorphosis is blocked and a juvenile-to-juvenile molt ensues. During the last larval stadium, the JH titer drops to a very low level and an elevated titer of 20-OH ecdysone initiates both metamorphosis and molting (84, 92, 121).

The most widely held endocrine hypothesis of wing-morph determination posits that an elevated level of JH during some critical period of development completely or partially blocks the normal morphogenesis of wings, flight muscles, and associated structures, resulting in a brachypterous or wingless morph (50, 84, 89, 121). Although this hypothesis has been discussed in the physiological and evolutionary literature for decades (34, 41, 72, 84, 85, 89, 95, 125, 130), it is supported by limited data obtained from a very few species.

Endocrine Basis of Wing-Morph Determination in Crickets

The only insect for which detailed information is available on the endocrine mechanisms underlying morph determination is the cricket, *G. rubens* (126, 130, 132, 133). JH-III applied to long-wing–destined *G. rubens* during the penultimate or last stadium redirected their development to the brachypterous morph, thus implicating the involvement of JH in morph determination (132). An elevated JH titer in nascent brachypters versus macropters during the last stadium, quantified by radioimmunoassay, further implicated a morph-determining role for JH (103). Finally, substantially higher activities of a degradative enzyme, juvenile hormone esterase (JHE), were observed in nascent macropters throughout the last stadium (133).

These data led Zera and coworkers to propose the following: (*a*) JH degradation is reduced during the early-to-middle last stadium in individuals destined to become brachypters, (*b*) reduced degradation delays the drop in the JH titer, and (*c*) prolongation of an elevated JH titer inhibits the metamorphosis of wings and flight muscles, resulting in a brachypter. This hypothesis was further substantiated by the following: (*a*) the strong cosegregation between high JHE activity and long wings in crosses between macropterous and brachypterous strains, (*b*) a higher rate of in vivo JH degradation in presumptive macropters, and (*c*) the absence of differences in JH biosynthesis between nascent morphs (126, 130, 133, 135). These data are currently the only direct evidence that an elevated JH titer exists in presumptive brachypters, and they are among the few data available on processes that may modulate the JH titer in developing morphs. Similar morph-specific differences in JHE activity have recently been reported in the crickets *G. firmus* and *M. confirmatus* (122, 131), although no information is available at present on JH degradation or titer in these species.

Although the endocrine data obtained for *G. rubens* are consistent with the classical JH-morph determination hypothesis, other interpretations cannot be ruled out. Most importantly, the JH titer differences between morphs are small, and thus their functional significance can be questioned (130). Thus, even though the endocrine regulation of wing-morph development is the most intensively studied in *G. rubens*, only the broad outlines of this regulation have been identified, and it is not certain that JH is the most important factor involved.

JH and Wing Polymorphism in Aphids and Planthoppers

Although the involvement of JH in wing-morph determination has been studied in aphids since the 1960s, much less definitive information is available for this taxon than for crickets. Several factors contribute to this discrepancy. First, several different juvenile hormones exist in insects, and the major juvenile hormone has yet to be identified in the Hemiptera (4, 48, 66a). This limitation has substantially hampered quantification of hormone titers in nascent wing morphs in Hemiptera (48). Furthermore, the small size of aphids and planthoppers also precludes many standard surgical manipulations used in insect endocrinology. Because of these limitations, endocrine studies have relied almost exclusively on indirect data resulting from the effect of topically applied JH or JH analogues on morph development. As noted by numerous workers, results of these manipulations are often difficult to interpret in the absence of other types of experimental data (49, 50, 85, 132). This problem is exacerbated in aphids because of the telescoping of generations in which a single female may contain three generations of aphids, each of which may have independently functioning corpora allata, the glands that produce JH (50, 54). These difficulties notwithstanding, some experiments do support the view that JH regulates morph determination. The most convincing cases involve the role of JH in photoperiodically mediated wing polyphenism in *Aphis fabae* (45) and density-mediated wing polyphenism in the planthopper *Nilaparvata lugens* (57). In both of these species, topically applied JH strongly redirected development from the macropterous to the flightless morph, and the stages most sensitive to JH were those that were also most sensitive to photoperiod or insect density. On the other hand, numerous other aphid species are not apterized or brachypterized by exogenous JH when it is applied during known critical periods of morph determination (50, 76). Indeed, some studies suggest that JH or some other cephalic factor has a macropterizing effect (50, 59, 60).

Precocenes, chromene derivatives that partially or totally destroy the JH-synthesizing corpora allata (7), have been used to investigate the endocrine basis of morph determination in aphids and planthoppers. If JH is involved in wing morph determination, treatment with precocenes should redirect development from the flightless to the macropterous morph. Early studies provided results consistent with this view (50, 76). However, recent studies in-

dicate that, although precocenes promote the induction of the fully winged morph in some aphids, the mechanism does not appear to involve a reduction in the JH titer (46, 47, 49). This finding implies that JH is not an endogenous regulator of wing dimorphism in these aphids. In contrast, precocene II strongly induced macropters in the planthopper *N. lugens*, and its effect was deterred by exogenous JH (3; O Ayoade, personal communication). These results are consistent with the earlier finding that JH induces brachyptery in *N. lugens* (57).

In summary, topical application experiments suggest that JH is involved in wing morph determination in *A. fabae* and *N. lugens*. However, until more direct data are obtained on JH titers or rates of hormone biosynthesis and degradation in these species, the involvement of JH in morph determination can only be regarded as suggestive. Finally, even if JH is involved in morph determination in these species, it is unclear whether these cases are rare exceptions or a common occurrence in the Hemiptera.

Role of Ecdysteroids and Neurohormones on Morph Determination

The only direct evidence for the involvement of ecdysteroids in morph determination has been obtained in *G. rubens* (130). Compared to macropters, nascent brachypters exhibited a significantly reduced ecdysteroid peak during the last stadium and a peak of shorter duration during the penultimate stadium (130). Because ecdysteroids promote differentiation (92), these reduced titers are consistent with the involvement of ecdysteroids in morph determination. Indeed, nascent morphs differ much more dramatically in the ecdysteroid titer than in the JH titer. The elevated JH and reduced ecdysteroid titers in presumptive brachypters should each have an inhibitory effect on morphogenesis. Thus, morph determination in *G. rubens* may be regulated by covariation in both the JH and the ecdysteroid titer (130). In contrast, ecdysteroids fed to an aphid had no effect on morph determination (1).

Several studies with aphids have implicated neurohormones (biogenic amines) in the regulation of morph determination. Microinjection of various biogenic amines into adult or young juvenile *Myzus persicae* strongly affected alate production (51). A subsequent study showed that radiolabelled amines, injected into adult females during a sensitive period of prenatal morph determination, were incorporated into the brains of nascent apterous embryos but not nascent alate embryos (52). Although these studies have been criticized for lacking proper controls (50), they are intriguing and deserve reinvestigation. On the other hand, there was no difference in the level of the neuromodulator octopamine between apterous and alate producers of an aphid (J Hardie, personal communication).

Endocrine Influences on the Timing of Morph Determination

The timing of morph determination in the life cycle of an insect and the selective pressures that bear on this timing are key issues in dispersal polymorphism, which have been poorly investigated. The advantage of early-stage determination is that greater commitments to either flight capability or reproduction can accrue, and more efficient morphs result (27). The advantage of late-stage morph determination lies in the ability of the individual to develop into a morph that is adapted to current environmental conditions (27). However, this flexibility may come at the price of devoting energy to the growth of inappropriate structures. For example, some crickets have the flexibility to alter development from the macropter to the brachypter as late as the last juvenile stadium (103, 131, 132). However, some of these brachypters have developed partially grown but useless flight muscles (131).

Although selection may favor morph determination during a particular stage in the life cycle, physiological and developmental processes may preclude morph determination from occurring at that stage. This issue of developmental constraint is an important but poorly understood aspect of dispersal polymorphism in particular and life history evolution in general. The few available data provide a contradictory picture of the importance of developmental constraint on the timing of morph determination. As mentioned previously, JH is a major regulator of insect metamorphosis and is also thought to be involved in morph determination (34, 50, 130). The dual roles of JH in both of these processes purportedly require that morph determination and metamorphosis occur during different developmental stages (50). Thus, the elevated JH titer required to specify brachyptery may disrupt metamorphosis if the timing of morph determination and metamorphosis coincide (50). Aphid investigators have used this argument to explain why morph determination occurs in advance of metamorphosis (50).

In contrast, recent studies in crickets have documented variation between nascent morphs in JH and ecdysteroid titers late in juvenile development, at a time when all individuals are undergoing metamorphosis (130). This suggests that the variation in the JH and/or ecdysteroid titer necessary to specify the different morphs does not necessarily disrupt adult metamorphosis (130). Thus, the restriction of morph determination in aphids to early development may not be a necessary consequence of the dual roles of JH in metamorphosis and morph determination. Rather, when generation time is short (27), wing-form determination early in aphid ontogeny will allow for both the production of highly specialized morphs and the accurate tracking of changing resources (27, 50). Thus, predictions concerning the timing of morph determination in relation to habitat stability must take into account the generation time of the organism as well as developmental constraints. Presently there are too few data for rigorous assessment of this issue.

Habitat Factors Influencing the Evolution and Maintenance of Dispersal Capability

The reproductive penalties associated with flight capability should minimize dispersal, unless wings are essential for tracking changing resources (23, 96). Thus, dispersal should be essential for the success of insect species exploiting temporary habitats, but it should be minimized in persistent habitats (106). Despite the abundance of theory that predicts elevated levels of dispersal in ephemeral/patchy habitats (31, 95, 96, 106), most assessments of the relationship between habitat persistence and the incidence of dispersal in insects have been qualitative in nature (12, 62, 86, 106, 117), have relied heavily on interspecific comparisons (96), and are possibly confounded by phylogenetic nonindependence (23, 118). Nonetheless, most of these studies provide evidence for diminished dispersal in persistent habitats (96).

Recently, wing-polymorphic insects have provided the most rigorous support for the habitat persistence–dispersal hypothesis through quantification of both habitat age and the incidence of dispersal (23). For 35 species of planthoppers inhabiting low-profile vegetation, there was a significant negative relationship between dispersal capability (% macroptery) and the persistence of their habitats (maximum number of generations attainable). The same result was obtained by using phylogenetically independent contrasts between congeners, suggesting that habitat persistence influences levels of dispersal independent of common ancestry (23). A negative relationship between dispersal capability and habitat persistence was also found when using geographically different populations of the same planthopper species (24).

Habitat persistence also influences the availability of mates and thus bears on the evolution of flight in the context of mate location (15, 23, 96). For instance, the frequency of macroptery is higher in males than females for planthopper species inhabiting temporary habitats, whereas the sexes are similarly macropterous for species in persistent habitats. In temporary habitats, wings are apparently favored in males to locate females at low colonizing densities, and they are favored in both sexes for reasons of habitat escape. In two-dimensional persistent habitats, wings are rarely required for mate location and they are much less necessary for habitat escape. As a consequence, and because flight capability imposes a reproductive penalty, flightlessness is favored. These data from planthoppers suggest that habitat persistence influences dispersal capability not only by selecting against habitat escape but also by dictating the availability of mates (15, 23).

Although habitat persistence prevails as the primary factor influencing the evolution of dispersal capability, habitat dimensionality can be important as well (14, 15, 96, 98, 118). For example, wings may function in the negotiation of complex three-dimensional habitats (15). Mate finding and relocation of feeding sites following escape from a predator may prove difficult for flightless brachypters in trees. On the other hand, the consequences of falling from a host plant in two-dimensional habitats close to the ground are minimal because resources can often be relocated by walking. Consequently, selection may favor the retention of flight capability in arboreal species even if their habitats are persistent. This so-called habitat dimensionality–flight capability hypothesis was first proposed in rough form by Reuter (91). Recent studies with leafhoppers, aphids (26, 119), and planthoppers (15) have rigorously tested the hypothesis and confirmed that wing polymorphic and flightless species are rare in trees and occur far more frequently in low-profile habitats. A similar pattern is also suggested for Heteroptera (107) and Psocoptera (83). All of these relatively small, actively foraging insects apparently retain wings in order to effectively negotiate arboreal habitats (15).

Summary, Synthesis, and Future Directions

During the past decade, a wealth of new information has been obtained on the physiology and ecology of dispersal polymorphism. In some cases, this information provides more rigorous support for longstanding but poorly resolved issues, and in other cases new insights on various aspects of dispersal polymorphism have been obtained. Rigorous assessments of the relationship between habitat stability and dispersal capability, the trade-off between flight capability and reproduction (and the physiological basis for such a trade-off), and the endocrine control of flight capability have been conducted using wing-dimorphic insects (18, 23, 95, 111, 127). Discontinuous variation in flight capability and the ease with which volant and flightless morphs are recognized has facilitated such studies (23). Nevertheless, wing-dimorphic insects are not fundamentally different from wing-monomorphic ones in which there is continuous variation in flight capability (95). Thus, the general conclusions drawn from studies of wing-dimorphic insects are broadly applicable.

Studies of habitat stability and dispersal capability in wing polymorphic insects have provided the most definitive support for the hypothesis that the incidence of dispersal is inversely related to habitat persistence (15, 23, 24, 98). Moreover, additional field studies have shown that other factors such as habitat dimensionality and mate availability can also have a strong effect on the evolution of dispersal (15, 23).

There is extensive support in the life history literature for fitness trade-offs between flight capability and reproduction (18, 27, 95, 99). The notion that such fitness trade-offs result from the differential allocation of nutrients also has been a widely held view (18, 95, 127). However, only recently have physiological studies of nutrient acquisition and allocation provided direct evi-

dence for a nutrient-based trade-off between flight capability and reproduction (77, 78, 111, 127, 128). These studies implicate the maintenance of flight muscles and possibly biosynthesis of flight fuels as important energetic costs of flight capability.

A significant new finding of nutritional studies is that altered nutrient intake can either ameliorate (increased consumption) or exacerbate (starvation) the degree to which the cost of flight capability taxes the energy budget and hence reduces reproductive effort in the flight-capable morph (65, 78, 111, 123, 127). These nutritional studies provide a physiological explanation for the observation that reproduction is most adversely affected in macropters under conditions of nutrient limitation or stress (14, 111, 123).

Alternatively, if the flight-capable morph lives long enough and has adequate food, it may be able to compensate for its inherent reproductive penalty with increased feeding (14, 18). Also, flight allows macropters to locate more effectively nutrient-rich food, a behavior that may moderate the potential reproductive penalties imposed by flight capability (14, 20). Thus, in order to fully understand the factors underlying the effect of flight capability on reproduction, one needs to account not only for differences in energy allocation between wing forms but also for differences in food acquisition. However, there are risks (predation and parasitism) associated with extended feeding and search for nutrient-rich resources (29), which may offset the extent to which feeding may compensate for the reproductive costs imposed by flight capability. Failure to take such indirect costs (predation) and benefits (feeding compensation) into account may lead to erroneous conclusions regarding the existence of an energetic cost of flight capability and its effects on all components of fitness.

Our review confirms that there is a paucity of research on flight capability in males and its consequences for their reproductive success. However, a handful of recent studies provide evidence that flight capability imposes reproductive penalties in males (11, 14, 39), a phenomenon that has been extensively documented in females (18, 95, 99). Future research should focus on the degree and prevalence of this trade-off in males and on how habitat factors and the mating system interact to influence dispersal capability.

For the first time detailed information is available on the endocrinology of morph determination; however, these data exist only for one species of cricket (125, 130, 133). We are still largely ignorant of the hormones involved in morph determination, the endocrine mechanisms that regulate differential morph development, and the endocrine basis for differences in reproduction between morphs.

Perhaps the most difficult gap to bridge concerns the link between the ecological factors influencing the evolution of dispersal and the underlying physiological basis for wing-morph determination. Presently, the most rigorous assessments of the effects of habitat features on dispersal involve hemipteroid

insects (15, 23). However, virtually all of the detailed work on the physiological mechanisms underlying morph determination and the physiological basis for a trade-off between flight capability and reproduction has been conducted on crickets (77, 78, 111, 127, 128). Thus, for no taxon is there a complete picture of the ultimate causes influencing the evolution of dispersal and the proximate physiological mechanisms underlying and constraining dispersal capability. Currently, progress is seriously impaired by our failure to identify the major JH in the Hemiptera. Likewise, decisive studies of the habitat determinants of dispersal capability in the crickets are few and far between (95, 96). For us to narrow this existing gap and integrate our knowledge on the ecology and physiology of dispersal in general, and dispersal polymorphisms in particular, we must obtain detailed physiological and ecological data for the same species. Nevertheless, studies on wing-dimorphic insects have played a pivotal role in the advancement of our understanding of the ecology, evolution, and physiology of dispersal, life histories, and multitrait polymorphism.

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