

Best wishes,  
Lynda

## PATTERNS IN MAYFLY (EPHEMEROPTERA) WING LENGTH: ADAPTATION TO DISPERSAL?

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### Abstract

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Using regression analysis on data compiled from the literature, I compared relationships (forewing versus body length) of mayfly imagoes, as a measure of dispersal, between suborders (Schistonota and Pannota) and among habitat type (lotic, lentic, and mixed). There were no significant differences in slopes or intercepts of the regression lines between sexes. Forewing length changed less markedly with body size for species within the ancestral Schistonota than the Pannota. Regression lines for lake and river forms intersect at 7.85 mm (wing length) and 7.30 mm (body length). Small (body length < 7.3 mm) lentic mayflies have proportionately longer wings than small riverine forms. Large (body length > 7.3 mm) riverine mayflies have proportionately longer wings than lentic forms. Based on these relationships, small lake-dwelling mayflies and large riverine mayflies are best able to disperse. Mayfly species occurring in mixed (both rivers and lakes) habitats exhibited allometric relationships similar to mayflies restricted to rivers.

### Résumé

En me basant sur des régressions effectuées sur des données publiées, j'ai comparé la relation — longueur des ailes antérieures-longueur du corps—des imagos d'éphémères, afin de comparer leur capacité de dispersion entre sous-ordres (Schistonota et Pannota) et habitats (lotique, lentique et mixte). Il n'y avait pas de différence significative entre les sexes pour la pente ou le point d'interception des droites de régression. La longueur des ailes changeait moins avec la taille du corps chez les espèces du groupe ancien Schistonota, que chez celles des Pannota. Le point d'intersection des régressions pour les espèces de lacs et de rivières se situait à 7,85 mm (longueur des ailes) et 7,30 mm (longueur du corps). Les petits (longueur < 7,3 mm), éphémères lenticques ont les ailes proportionnellement plus longues que les petits éphémères des rivières. Les gros (longueur > 7,3 mm), éphémères des rivières ont les ailes proportionnellement plus longues que les formes lenticques. Sur la base de ces relations, les éphémères des lacs de petite taille et les grosses espèces des rivières auraient les meilleures capacités dispersives. Les éphémères d'habitats mixtes (lacs et rivières) ont des relations allométriques semblables aux éphémères limités aux rivières.

### Introduction

Insect wing length is frequently related to dispersal ability and fecundity such that individuals with long wings are typically good colonizers (Harrison 1980; McLachlan 1985). In this study, I examine the relationship between the ratio of wing to body length for mayflies that dwell in permanent habitats (rivers and lakes) to determine the likelihood of dispersal. Mayflies spend most of their lives as larvae in aquatic habitats, then emerge as winged forms (sub-imago and imago) to reproduce (Edmunds *et al.* 1976; Brittain 1982). Sexually mature adults (imagoes) do not feed (the alimentary tract inflates with air) and seldom live more than 3 days, during which time they may disperse, mate, and the females oviposit. Considering the brief duration of the adult stage, it is not surprising that mayflies have not colonized Antarctica or small oceanic islands despite the worldwide distribution of the order (Edmunds *et al.* 1976).

Dispersal in mayflies may vary with developmental stage (larva or imago), habitat (river or lake), or taxonomic level (e.g. suborder). Several mayfly workers (Ide 1955; Lehmkuhl 1976, 1980; Flannagan and Flannagan 1984) have suggested that the present-day macrodistribution of mayflies in North America resulted from dispersal by larvae (rather than imagoes) following the Wisconsin glaciation; changes in river courses provided

migration routes. Alternatively, wind-assisted flight may aid in dispersal of those imagoes possessing wings that are long relative to body size despite the short life of the imago and fragility of wings. With increased specialization, wings of mayflies have become longer and narrower, with the exception of those genera (e.g. *Caenis*, *Cloeon*, *Pseudocloeon*) having hind wings reduced or absent (Riek 1970).

Larval stages of most mayfly species develop only in running waters. During their development, these organisms may repeatedly participate in drift, i.e. downstream transport by the current. Müller (1954, 1982) proposed that adults of such species must disperse upstream to oviposit in headwaters and complete a colonization cycle. Most insects disperse by flight before reproduction occurs (Johnson 1969).

Relatively few mayfly species are restricted to lakes. Such lentic forms must either remain in the immediate vicinity to oviposit or must be capable of broader scale dispersal if they are to reach new habitats. In lentic species that swarm and oviposit at the same locale, I expect relative wing size (expressed as the ratio of forewing length to body length) to be reduced compared with riverine populations.

Recently, McCafferty and Edmunds (1979) introduced two suborders, Schistonota and Pannota, into the higher classification of extant Ephemeroptera based mainly on larval thoracic structure. Schistonota retain the ancestral condition wherein the larval thorax possesses forewing pads free from notal fusion for one-half or more of their length; Pannota evolved from the ancestral pattern and exhibit a fusion of larval wing pads and an enlarged mesonotum (McCafferty and Edmunds 1979). Because of the distinction in larval thoracic morphology, I expected that the relationship between forewing and body size of imagoes might also differ between suborders.

An assumption of this study was that organisms with a greater wing length to body length ratio were more likely to disperse than organisms with a lesser ratio. Here, I focussed on Johnson's (1969) class I dispersal, a "one-way journey by short-lived adults". I considered dispersal from present-day distributions, occurring from one generation to the next. Using regression analysis of data compiled from the literature, I examined allometric relationships between forewing length and total body length of nearctic mayfly species within the Schistonota and Pannota. I also compared allometric relationships among mayfly imagoes from running water, stillwater, and mixed (both rivers and lakes) habitats.

There are shortcomings to the approach presented here, whereby allometric relationships are sought among species within an order rather than among morphs within a species. My selection of wing length as a measure of dispersal is based on the large data set in the literature. Wing loading, wing beat frequency, and weight of flight muscle also contribute to flight performance (Greenewalt 1962); yet, information on these variables is less readily available. The premise of this paper is that the function of flight is to disperse along a horizontal path. Clearly, wing structure also is modified (e.g. fluting) for vertical flight observed in mating swarms of mayflies (c.f. Edmunds and Traver 1954; Savage 1983).

### Methods

I compared forewing and body (excluding cerci) lengths of male and female imagoes using data compiled from the literature. As hind wings are reduced in Ephemeroptera and even lacking in some species, relationships were based on forewing measurements. Where a size range was reported, the mid-point was selected so that a single value was obtained for each species. Data on corresponding forewing and body lengths for both sexes of each species were obtained from Gordon (1933), Ide (1954), Allen and Edmunds (1959, 1961, 1962a, 1962b, 1963a, 1963b, 1965), Kilgore and Allen (1973), Lehmkuhl (1976), Carle (1977, 1978), Carle and Lewis (1978), Berner (1978), Pescador and Peters (1980), Pescador and Berner (1981), Harper and Harper (1981), Harper and Hawkins (1984), and Kondratieff and Voshell (1984).

Table 1. Summary of regression equations for superfamilies within the Schistonota and Pannota where:  $A$  = intercept;  $B$  = slope;  $Y$  = dependent variable, forewing length;  $X$  = independent variable, body length; SE = standard error of the slope;  $p$  = probability;  $R^2$  = coefficient of determination. Data were transformed ( $\ln(X + 1)$ ) and fitted to the power function

Taxa	$n$	$\ln(A + 1)$	$B$	SE	$p$	$R^2$
Schistonota:	183	0.342	0.872	0.0184	<0.001	0.925
Baetoidea	143	0.325	0.885	0.0213	<0.001	0.924
Leptophleboidea	26	0.343	0.851	0.0707	<0.001	0.858
Ephemeroidea	14	3.032	0.737	0.0854	<0.001	0.861
Pannota:	74	0.128	0.969	0.0280	<0.001	0.943
Ephemerelloidea	57	0.325	1.024	0.0394	<0.001	0.925
Caenoidea	8	0.601	0.266	0.0202	<0.001	0.967
Prosopistomatoidea	9	0.837	0.680	0.1461	<0.010	0.756

If results indicated no difference in the slope of the regression lines between sexes, subsequent analysis could be based on measures of males alone, for which more data exist. Analysis of measures obtained from males was based mainly on data from Needham *et al.* (1935), Burks (1953), and Lewis (1974). Data from types that have fallen as junior synonyms (Edmunds *et al.* 1976) were included within the data range for the type description. Habitat designation for most specimens was obtained from Hubbard and Peters (1978).

Relationships between forewing and body lengths were determined using least-squares regression analysis. Data were analyzed using linear,  $\ln$ /linear, and  $\ln/\ln$  transformed measures. Regression equations providing the best overall fit to the data are presented. Analysis of covariance (ANCOVA) was used to compare the slopes and intercepts of regression lines (Snedecor and Cochran 1967).

## Results

Results of the regression analyses of forewing length on body length showed that  $\ln/\ln$  transformation provided the best fit to the data ( $n = 78$ ) for female ( $R^2 = 0.86$ ) and male ( $R^2 = 0.88$ ) imagoes. Representatives of both Pannota ( $n = 37$ ) and Schistonota ( $n = 41$ ) were included in this analysis. Because there were no significant differences between either slopes ( $F_{1,152} = 0.166$ , ns) or intercepts ( $F_{1,153} = 3.819$ , ns) between sexes, subsequent analyses were based on measures of males.

**Taxonomic relationships.** Overall, relationships providing the best fit to the data followed the power equation,  $\ln Y = \ln A + B \ln X$  (Table 1). The slope for Pannota ( $0.97 \pm 0.028$ ) approached a line of isometry; i.e. forewing length increased linearly with increasing body size. The slope for Schistonota ( $0.87 \pm 0.018$ ) suggested that forewing length increased less markedly with increasing body size than in the Pannota. There were significant differences in slopes ( $F_{1,253} = 6.362$ ,  $p < 0.025$ ) between suborder, but not between intercepts ( $F_{1,254} = 0.347$ , ns) (Table 2). The distribution of wing lengths of both suborders was unimodal with the forewing length (mean  $\pm$  standard error) of Schistonota ( $9.55 \pm 0.243$  mm) larger than that of the Pannota ( $8.08 \pm 0.337$  mm). The largest Schistonota specimens were *Hexagenia* (Ephemeroidea, Ephemeridae).

Results from ANCOVA on transformed data ( $\ln(X + 1)$ ) showed no significant differences among slopes for superfamilies within each suborder ( $p > 0.05$ ) (Table 2). Significant differences, however, were noted among intercepts for superfamilies within each suborder (within Schistonota,  $F_{2,179} = 5.459$ ,  $p < 0.01$ ; within Pannota,  $F_{2,70} = 4.526$ ,  $p < 0.025$ ). Significant differences in intercepts reflect differences in size of mayflies within each suborder.

**Habitat.** Most mayfly species examined occupied rivers ( $n = 186$ ) or mixed habitats ( $n = 62$ ). Few species were restricted to lakes ( $n = 9$ ). This distributional pattern reflects

Table 2. Significance of analysis of covariance between suborders and among superfamilies within each suborder of mayfly imagoes. Taxa are listed in Table 1

Comparisons	Covariance			
	Test of slopes		Test of intercepts	
	$F_s$	$p$	$F_s$	$p$
Between suborders	6.362	<0.025	0.347	ns
Among Schistonota	0.690	ns	5.459	<0.01
Among Pannota	1.772	ns	4.526	<0.025

the natural occurrence of mayflies in the three habitat types throughout North America (Edmunds 1978). Eight of the nine lake species belong to the superfamily Baetoidea (Schistonota) and, of these, seven are Baetidae; the exception is *Ephemerella lacustris* Allen and Edmunds, a Pannota (Table 3) known from only two localities (Allen and Edmunds 1965; McCafferty 1985).

The regression equations for mayflies inhabiting each habitat type are presented in Table 3. Results of ANCOVA on transformed data ( $\ln(X+1)$ ) showed significant differences in slopes of the regression lines ( $F_{2,251} = 3.768, p < 0.05$ ); there were no significant differences among intercepts ( $F_{2,253} = 0.647, ns$ ). The wing lengths of river and mixed habitat mayflies were close to isometric with body length. The slope of the regression line for lake forms was much less than one. The regression lines for mayflies inhabiting lakes and rivers intersect (coordinates: wing length, 7.85 mm; body length, 7.30 mm) (Fig. 1). Thus, I used a body length of 7.3 mm to separate mayflies into small and large species. Small (body length < 7.3 mm), lentic mayflies have proportionately longer wings than do small riverine forms. Large (body length > 7.3 mm), riverine mayflies have proportionately longer wings than do large lentic forms. Thus, small lake-dwelling mayflies and large riverine mayflies are most likely to disperse. The regression line for mayflies occupying mixed habitats was similar to mayflies in lotic habitats.

### Discussion

Since Huxley (1932), allometric analysis has been used to study the dimensional relationships of organisms (Gould 1966). Greenewalt (1962) showed that the body weight of insects and birds is approximately proportional to the cube of wing length, with the ratio for insects falling below that of birds. Soaring birds have the greatest relative wing lengths. Insects, with body weight from <1 mg to  $10^4$  mg, showed much greater variation than birds in wing length to body weight ratio, reflecting a varied number of evolutionary lines (Greenewalt 1962). Dragonflies, butterflies, and crane flies had the highest ratios and bulky bumblebees had the lowest; mayflies were not considered in his analysis. As mayfly body weight is proportional to the cube of body length (exponent = 2.88; Smock 1980), the wing length to body length ratios for mayflies that I developed in this study correspond well with Greenewalt's (1962) relationships for other insects.

Table 3. Summary of regression equations for mayfly occurrence in lakes, rivers, and mixed habitats. Data were transformed ( $\ln(X+1)$ ) and fitted to the power function. Refer to Table 1 for explanation of abbreviations

Habitat	$n$	$\ln(A+1)$	$B$	SE	$p$	$R^2$
Lake *	9	0.802	0.652	0.1038	<0.001	0.849
Mixed	62	0.248	0.913	0.0275	<0.001	0.948
River	186	0.252	0.912	0.0186	<0.001	0.929

\*Species are as follows: Baetoidea: Baetidae, *Callibaetis brevicostatus* Daggy, *C. ferrugineus* (Walsh), *C. fluctuans* (Walsh), *C. skokianus* Needham, *Centropilum quaesitum* McDunnough, *Cloeon mendax* (Walsh), *Pseudocloeon dubium* (Walsh); Heptageniidae, *Heptagenia maculipennis* Walsh; and, Ephemerelloidea: Ephemerellidae, *Ephemerella lacustris* Allen and Edmunds.

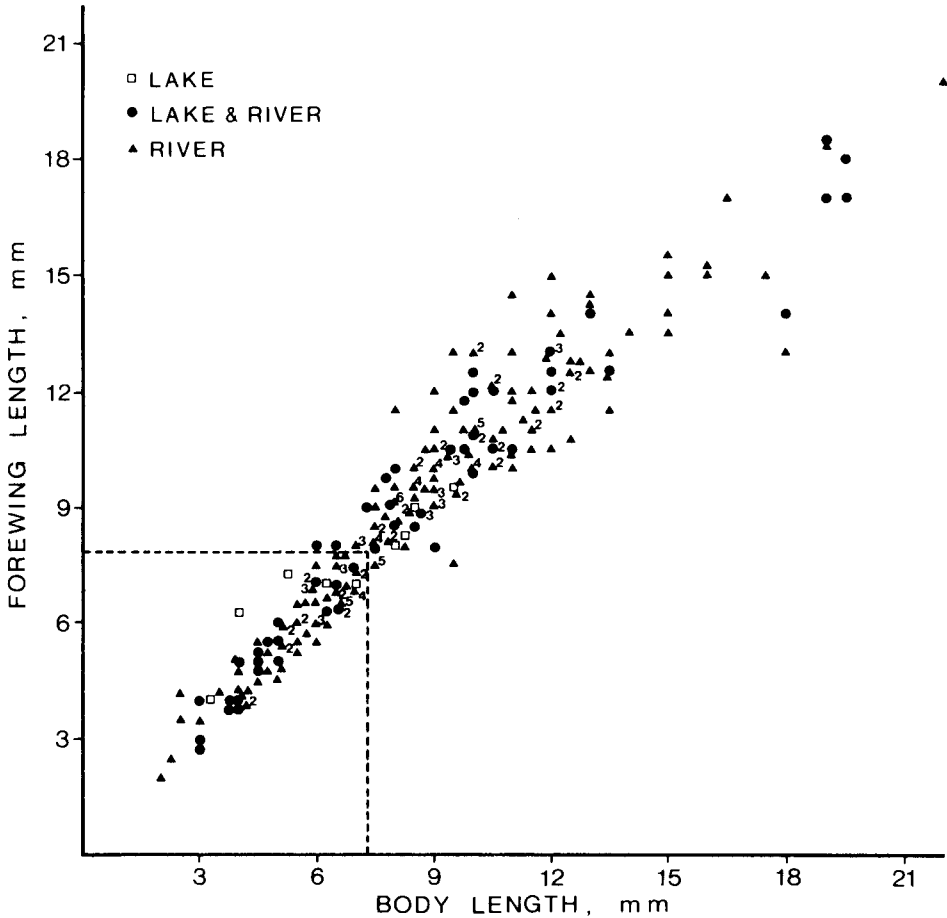


FIG. 1. The relationship between forewing length and body length for mayflies occurring in lakes, lakes and rivers, and rivers. The regression lines for mayflies inhabiting lakes and rivers intersect at 7.85 mm (wing length) and 7.30 mm (body length). Species occurring within the delineated box are considered to be small.

I examined forewing length to body length relationships among mayflies to compare the likelihood of dispersal between suborders and among habitats. No differences between forewing and body lengths were found between sexes. The increase in ratio of forewing length to body length was greater in Pannota than in the ancestral Schistonota. Moreover, the allometric relationship of mayflies occupying different habitats showed that small lentic and large riverine mayflies are more likely to disperse than other mayflies. The regression line of mayflies occupying mixed habitats is similar to the relationship exhibited by mayflies restricted to rivers. As variability within species was not considered in this analysis, the results represent only broad trends within the Ephemeroptera.

McCafferty and Edmunds (1979) present phyletic relationships of suborders and superfamilies of extant Ephemeroptera that rely on mesonotum and wing pad development of the larvae. Adults of the Schistonota and Pannota were not as easily distinguished as the larvae because adult thoracic morphology evidently evolved many times in relation to body and wing size modifications and flight behavior (McCafferty and Edmunds 1979). My study results showed significant relationships between forewing and body lengths of male imagoes for each suborder and significant differences in slopes between the two

groups. Because wing length varies as a function of both environmental [particularly temperature (Sweeney and Vannote 1978; McCafferty and Pereira 1984)] and genetic condition (Harrison 1980), the allometric relationships presented here were expected to vary among species with expanded emergence periods and among multivoltine species with cohorts emerging in different seasons (cf. Smock 1980).

Results showed that small lentic and large lotic mayflies are best able to disperse based on the allometric relationships. Riverine mayflies are known to fly upstream from slow-flowing areas where adults emerge to oviposition sites in riffle areas (Needham *et al.* 1935). This upstream flight need not be to headwaters, but merely to the nearest riffle area. The allometric relationship for large (body length > 7.3 mm) riverine mayflies (particularly, the Pannota) is consistent with Müller's (1954) colonization hypothesis. Upstream colonization by imagoes has been reported for selected mayfly species of both suborders [Schönemund 1930 (cited in Roos 1957); Roos 1957; Madsen *et al.* 1977].

As mayflies originated in cool, fast-flowing waters (Edmunds *et al.* 1976), it would appear maladaptive for the group to leave permanent running waters and enter lake habitats which may eventually disappear. As an imago leaving one habitat may not find another equally suitable habitat, why risk dispersal (Brown 1951)? The diminutive mayfly genera frequently found in lakes (e.g. *Baetis*, *Caenis*) are aerially buoyant and can be carried to great heights and, via horizontal air currents, great distances (Berner 1950). Several genera that can occur in lakes lack hind wings (*Caenis*, *Pseudocloeon*, *Cloeon*) and possess triangular or rounded forewings (Riek 1970). Small mayfly imagoes on lakes have a greater forewing to body length ratio than their riverine confamilials and probably are recent arrivals (in geological time). Larger lake-dwelling mayflies may have developed short wings (evidenced by a lower wing to body length ratio) due to selection to stay on the home lake. Donald and Patriquin (1983) suggested that when populations of Plecoptera (another typically riverine insect group) become established in lakes, selection for brachyptery occurs and subsequent dispersal is probably unsuccessful.

Although my premise is that selection is acting on dispersal ability, one might consider alternate advantages exhibited by large lentic and small lotic species. Indeed, Edmunds *et al.* (1976) stressed that the sole function of mayfly adults is to reproduce and that every adaptation has been directed towards this process. Perhaps mayfly species were selected for maneuverability in mating swarms over waterbodies in forested areas where short broad wings would be advantageous. Clearly, field tests of these allometric relationships are needed.

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