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Short note

How does wing length relate to distribution patterns of stoneflies (Plecoptera) and mayflies (Ephemeroptera)?

Björn Malmqvist

Department of Ecology and Environmental Science, University of Umeå, SE-90187 Umeå, Sweden

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Abstract

Short wings, and hence a potential for reduced dispersal capacity, can be one of several reasons for rarity in freshwater insects. To test this hypothesis, I compared wing lengths, standardised for body length differences, of stoneflies and mayflies based on published Swedish material. Taking 25% presence as the limit between rare and not rare, rare species indeed had shorter wings than those that were classified as not rare. Wing length was not the sole explanation for rarity as seen in the presence of rare species along the entire range of wing to body lengths. In both stoneflies and mayflies wing lengths were positively related to range sizes. Occupancy showed a positive relationship with wing size in mayflies, whereas in stoneflies the relationship was not significant, probably because there was no difference in wing lengths over a range of occupancy values in the common species. Implications for conservation include the importance to identify poor dispersers among these groups and describe their habitats, since it can be expected that recolonisation by poor flyers can be very uncertain and slow after local extinction. Therefore, localities with rare, poorly-dispersing species should be protected but if extinction occurs, re-introduction might offer a possibility to re-establish such insects. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Rarity; Aquatic insects; Wing length; Occupancy; Range size

1. Introduction

Pertinent to the current biodiversity discussion are the questions why species are rare, how rarity is accomplished and how it relates to the risk of extinction. If these questions could readily be answered, this could be of avail in conservation work with respect to the protection of species and habitats, and thus be a desirable goal to achieve. The study of rarity, from a theoretical point of view, is a young branch of science manifested in recent texts like Gaston (1994) and Kunin and Gaston (1996), and although it might therefore be possible to make rapid progress, there are inherent difficulties in studying rarity, such as a general paucity of data rendering statistical analyses problematic. Therefore, it seems meaningful to study how rarity is expressed in known distribution patterns, including the full range of abundances or occupancies in comparative studies of entire taxonomic groups, which would also be easier, and perhaps more ethically correct, than adopting an experimental approach.

Two groups of factors, environmental variables and colonisation abilities, have been suggested to affect abundance and range size (Gaston, 1994). Colonisation ability is the combined capacity of dispersing to and establishing at a new site. It has been suggested that insects with long wings are good dispersers and thereby potentially good colonisers (den Boer, 1970; Harrison, 1980; McLachlan, 1985). With similar arguments, it could also be expected that rare species might be rare just because of poor colonisation ability. This could in turn be due to poor dispersal as a consequence of relatively short wings, a relationship which will be explored for two insect orders in this paper.

Aquatic insects show a striking variability in the morphology of the wing and its musculature, and hence, their flying ability (Harrison, 1980). This is perhaps most prominent in Hemiptera and Coleoptera, but also Plecoptera is well known for this (Brinck, 1949). In gerrids wing dimorphism appears related to habitat stability, e.g. the probability of their habitat drying up (Vepsäläinen, 1978), suggesting that habitat stability may be a

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E-mail address: bjorn.malmqvist@eg.umu.se (B. Malmqvist).

factor influencing the selection for dispersal (Roff, 1974; Hamilton and May, 1977). Similarly, temperature and elevation have been put forward concerning Plecoptera (Ward, 1992). The main argument for reduced flight capacity is the possibility to allocate more energy into egg production since wing production and fecundity depend on the same energy resource (Roff, 1977, 1990). In its extreme case, flightlessness, which occurs in Plecoptera, is a feature of males (Brinck, 1949). Recently, flightlessness has also been recorded in Ephemeroptera, where members of the Malagasy genus *Cheirogenesia* show strongly reduced wing surface area (Ruffieux et al., 1998). Curiously the wing length of these is not reduced, which is why they were classified as 'cryptic brachypterous'; the adults skim the water surface.

Stoneflies, and probably mayflies, originated in running waters and have subsequently invaded lentic habitats (Wootton, 1972), where they are among the most typical and widespread inhabitants (Hynes, 1970; Giller and Malmqvist, 1998). Whereas stoneflies have a single, but extended winged stage, mayflies sport both subimago and imago stages, with a combined duration of 1–2 h to a few days (Brittain, 1982). Does wing length reflect commonness and rarity in stoneflies and mayflies? How does wing length relate to occurrences of these insects? If weak dispersal is an important feature in rare species of these insects, how could we best protect them? In this study, I relate literature data on relative wing lengths to information on distribution patterns, including occupancy and distribution area.

2. Materials and methods

I collected information on distributions primarily from a single published study (Degerman et al., 1994). This report contains extensive information on geographical distributions of macroinvertebrates and fish in Sweden based on >5000 sites distributed fairly evenly across the entire country (i.e. approximately between 55 and 69°N). This amounts to approximately one site every 10.4 km² and an average distance of 12.6 km between sites. Since the material is heterogeneous (Degerman et al., 1994), I have made additions based on my own studies over many years in southernmost and northern Sweden. Approximately 60% of the samples are from running waters, predominately streams < 10 m wide, but also ditches and large rivers, and the still water samples of the remaining 40% are primarily from pools and the margins of ponds and lakes, but also from larger lakes. The water quality of the sites ranges from very oligotrophic to eutrophic conditions and from very acid (pH < 4) to alkaline (pH > 8). Although desirable, information on the sites' habitat suitability for each species was not available. Obviously, all sites cannot have been suitable for all species.

Data on forewing lengths for Plecoptera were compiled from Lillehammer (1988) and for mayflies from Engblom (1996), Bengtsson (1912, 1914, 1917), Sowa (1975a,b), Söderström and Nilsson (1986), and Klapalek and Grünberg (1909). The value used concerning forewing length was the female mid value of the range reported. Other variables, such as wing loading and wing beat frequency as well as flight muscle size, also affect flight ability, but such data are difficult to find in the literature. The wing length of females was chosen because females are the dispersing sex, mating often taking place near the location of hatching. It was not possible to obtain data for all species present in Sweden. Those 31 stonefly and 26 mayfly species for which data were available are shown in Tables 1 and 2.

Since body size varies considerably across taxa an index of relative wing length was constructed, which simply equals the ratio of forewing to body length. Obtained values of relative wing length are shown in

Table 1

Data on female body and wing lengths (mid values), relative wing length (wing length/body length), occupancy (number of sites) and range size (number of 100×100 km squares) of 30 stonefly (Plecoptera) species in Sweden^a

Species	Body size (mm)	Wing length (mm)	Relative wing length	Number of sites	Number of squares
Amphinemura borealis	6.25	8.50	1.36	907	48
A. stanfussi	6.05	5.05	0.83	164	21
A. sulcicollis	6.40	7.45	1.16	1441	48
Arcynoteryx compacta	16.50	12.35	0.75	68	10
Brachyptera risi	10.00	12.15	1.22	730	41
Capnia atra	7.25	6.25	0.86	27	8
C. bifrons	8.85	7.40	0.83	10	4
C. pygmaea	5.75	7.00	1.22	6	6
Capnopsisi schilleri	4.90	6.30	1.29	30	21
Dinocras cephalotes	24.25	24.00	0.99	144	21
Diura bicaudata	16.00	12.60	0.79	87	26
D. nanseni	15.00	14.30	0.95	1201	38
Isogenus nubecula	16.25	15.65	0.96	12	10
Isopera difformis	15.65	11.05	0.71	221	31
I. grammatica	10.00	11.35	1.14	1241	52
I. obscura	10.25	10.90	1.06	314	40
Leuctra digitata	7.00	8.00	1.14	921	47
L. fusca	6.35	7.55	1.19	324	40
L. hippopus	6.65	6.60	0.99	236	37
L. nigra	6.00	8.30	1.38	465	39
Nemoura arctica	8.05	7.30	0.91	4	1
N. avicularis	8.40	10.00	1.19	193	31
N. cinerea	8.15	7.65	0.93	1725	56
N. dubitans	8.25	8.75	1.06	1	1
N. flexuosa	7.65	8.55	1.12	35	12
Nemurella picteti	8.70	9.05	1.04	418	39
Perlodes dispar	17.50	16.85	0.96	23	10
Protonemura meyeri	8.45	9.90	1.17	813	46
Siphonoperla burmeisteri	6.50	7.45	1.15	520	30
Taeniopteryx nebulosa	10.85	13.20	1.22	4.77	46

^a Nomenclature follows Lillehammer (1988).

Tables 1 and 2. No corrections for geographic location of measured animals nor season were made.

Distribution range size was estimated as the number of 100×100 km squares in which each species was found, derived from the maps in Degerman et al. (1994), with my own complementary information concerning range size of *Capnia bifrons* (in the province of Västerbotten) and *Ameletus inopinatus* (in the province of Halland), and occupancies as the tabulated number of sites with the species as reported in the same publication.

Range size and occupancy relationships were tested with relative wing length in regression analysis. Student's *t*-test was used to compare range sizes between rare species, defined as those 25% with the smallest estimated

Table 2

Data on female body and wing lengths (mid values), relative wing length (wing length/body length), occupancy (number of sites) and range size (number of 100×100 km squares) of 26 mayfly (Ephemeroptera) species^a

Species	Body size (mm)	Wing length (mm)	Relative wing length	Number of sites	Number of squares
Acentella	4.5	5.25	1.17	351	19
lapponica					
Ameletus	10	10	1.00	1000	33
inopinatus					
Baetis niger	6.25	7	1.12	1340	52
B. rhodani	7.25	12	1.66	2826	55
B. scambus	6.25	6.5	1.04	17	52
B. subalpinus	5.5	6	1.09	1153	41
B. vernus	6.75	8	1.19	86	26
Brachycercus harrisellus	6	5.75	0.96	5	5
Caenis macrura	3.25	3.5	1.08	3	1
Centroptilum	6	6.75	1.13	1223	54
luteolum					
Cloeon dipterum	9.5	7	1.03	20	4
C. inscriptum	7.5	8	1.07	515	32
C. praetextum	7.5	7.5	1.00	60	22
C. simile	9.5	10	1.05	12	3
Ephemera danica	19.5	19	0.97	281	38
E. glaucops	14	13	0.93	2	2
E. vulgata	18	21	1.17	5.6	45
Ephemerella ignita	8	9.25	1.16	466	45
Heptagenia sulphurea	10	12	1.14	918	53
Leptophlebia marginata	7.5	8	1.07	1374	54
Paraleptophlebia cincta	7.5	8.5	1.13	57	22
Parameletus chelifer ^b	10.0 ± 0.53	10.13 ± 0.53	1.01	70	19
P. $minor^b$	8.6 ± 0.71	9.3 ± 0.60	1.08	23	9
Rhithrogena	14	14	1.00	4	2
germanica					
Siphlonurus armatus	14.5	15.5	1.07	13	1
S. lacustris	13.5	13.5	1.00	716	36

^a Nomenclature follows Engblom (1996).

^b For the two *Parameletus* species means and one standard deviation are given since range values were not available.

range sizes (Gaston, 1994), and common species. Before testing, range size and occupancy data were log transformed. Statistical analyses were carried out using Statistica for Mac (Statsoft, release 4.1).

3. Results

Wing lengths of females were related to distribution patterns in species of both orders. The relationship was significant with respect to range size but a pattern existed also in occupancy relationships. Thus, concerning distributional ranges, both groups showed a significantly decreasing wing length with decreasing range size (Fig. 1; mayflies: $r^2 = 0.33$, p < 0.01; stoneflies: $r^2 = 0.13$, p < 0.05). Testing the difference between rare and not rare species showed that the relative wing length of both mayflies and stoneflies was indeed smaller in rare species (Table 3).

The occupancies of squares by mayflies showed a positive relationship with relative wing lengths (Fig. 2), which was due to relatively high values in common species $(r^2 = 0.27, p < 0.01)$. Stoneflies showed a similar but statistically non-significant relationship $(r^2 = 0.088, p > 0.05)$, primarily because several rare species also had long wings (Fig. 2). There was also a low wing length to body ratio for the most widely distributed species, *Nemoura cinerea*.

4. Discussion

The evolution of insect wings and other investments in flying is interesting for many reasons. In the context of conservation, the relationship between colonisation



Fig. 1. Range size (number of 100×100 km squares occupied) of stoneflies (top) and mayflies (bottom) in relation to wing length index (as ratio between wing and body lengths) in Sweden.

Table 3

Comparison of relative wing lengths (ratio between wing and body lengths) of rare Swedish mayfly and stonefly species (defined as those 25% with smallest range sizes) with not rare species, i.e. those with larger range sizes^a

Order		Relat	ive wing len	Significance		
		n	mean	t	р	
Mayflies						
	Rare	7	1.111			
	Not rare	19	0.96			
				3.99	0.0003	
Stoneflies						
	Rare	8	1.09			
	Not rare	22	0.94			
				2.14	0.020	

^a Significance was assessed in student's *t* tests (one tailed).



Fig. 2. Occupancy of stoneflies (top) and mayflies (bottom) in relation to wing length index (as ratio between wing and body lengths). Occupancy is the number of sites where each species was found in Sweden.

success and rarity is particularly important and the results shown in this paper suggest that flight ability can be one of several explanations for rarity. The observations show that, although with considerable variation, rare species frequently are relatively short-winged and that common species have long wings. It is also clear that rare species are found along the entire range of wing to body length ratios, which suggests that even if wing length influences rarity in some cases, it is not an exclusive explanation for rarity.

Many stream insects live in habitats that dry up from time to time. The frequency of complete drought is variable and is related to many different factors including climate, geographical location and channel size. Winged stages allow recolonisation of habitats that have lost populations due to drought and serve as a very important route to recruitment not only within streams but also between systems (Bunn and Hughes, 1997). Relatively long wings would be advantageous for such dispersal. Corkum (1987) found particularly long forewings in small lentic species of mayflies but also in large riverine ones and she therefore suggested that these two categories might be strong dispersers.

It can be expected that the successful dispersal of poorflying species will depend on the distance between sites. The estimated average distance between sites was greater than 10 km. Since the habitat at each site is not likely to be suitable for any species, the flight distance needed could be far greater, but on the other hand, there are unsampled locations between the sites. Even 10 km is probably a very long flight distance rarely exceeded by a mayfly or stonefly (Hershey et al., 1993; Bunn and Hughes, 1997). Long-distance wind transport of insects might also take place which can offset the influence of wing size. It is likely to be most important in species which fly well clear of the ground for courtship, foraging and host-finding (Ashmole and Ashmole, 1988) and at seasons when sudden strong winds can develop. Members of Plecoptera generally fly only to a limited extent (Hynes, 1976). In contrast, many mayflies swarm but this behaviour is prevented even at wind velocities of $< 2 \text{ m s}^{-1}$, and when there is a wind the swarms do not extend as high up as when it is calm (Savolainen, 1978).

Species tolerant to desiccation, flooding or pollution can endure periods of disturbance better than other species and therefore their dispersal capacity may be less important; once they have reached a suitable site they will remain there at lower risk of going extinct than less tolerant species. This could be one explanation why the widely distributed and tolerant *Nemoura cinerea* showed an unexpectedly low wing to body length ratio, although the dispersal capacity of this species has been reported as good (Hynes, 1958, 1970). In addition, the most common mayfly, *Baetis rhodani*, has only moderately long wings.

Measures of the size of species and their attributes vary according to geographic location and season, probably as a result of temperature during larval development (Vannote and Sweeney, 1980). For instance, some mayfly species have more generations per year in the southern part of their range than further north because of a significant difference in climate, and it is well known that body size differs between generation. Not only do individuals from the summer generation emerge at a smaller size than other generations, the average size of mayflies also tends to be smaller the later in the season they emerge (Ward, 1992). It is also likely that the relative wing length is affected by these changes in body size. Stoneflies are never multivoltine, and development may take one or several years depending on temperature and stream permanence (Hynes, 1976; Stewart and Stark, 1988). The data used in this study did not account for variation caused by voltinism -

only information on the range of wing lengths was available — although it is unlikely that the patterns observed would be present if the relationship was not real. Further studies, with an approach beyond the national scale including information about generation and time of emergence within the emergence period, are recommended for verifying the generality of these observations, although distribution data can be valuable despite being incomplete (Fagan and Kareiva, 1997).

4.1. Implications for conservation

Although there are many studies showing that the spatial distributions of organisms are limited by their dispersal ability, it is clear that there may also be many other explanations (Gaston, 1994). The observations in this study therefore do not show more than one of several possible mechanisms. The correlative nature holds that even a trend suggesting causality might have other rationales, including the opposite of the suggested one, namely that species may disperse poorly just because they are rare (Gaston, 1994). With this reservation, the implication for conservation would be primarily to identify poor dispersers among these insect orders and to describe their habitats with respect to stability. In contrast to more widely distributed species, recolonisation by poor flyers after local extinction can be very uncertain and slow. Natural recolonisation can have become more difficult because of increased distances between undisturbed systems where the insects breed (Zwick, 1992). Primarily, it is therefore important to protect known habitats of such insects from man-made perturbations. In the event of local extinction, artificial introduction could be one way to re-populate habitats that have lost rare stoneflies and mayflies with reduced dispersal capacity, but any introductions should always be carefully considered.

Clearly, it is only under an extinction threat that the suggested relationship between rarity and dispersal becomes a meaningful issue for conservation. Despite the fact that several of the rare species in this study are listed as endangered, the exact threats are seldom well understood. Other data sets would allow testing whether flight ability is coupled to rarity also in threatened species, and if so, whether the relationship is stronger when habitat suitability is accounted for. Metrics associated with flight ability in addition to wing lengths should be tested to determine their relative contribution. Moreover, future studies could well be extended to include other taxa than those used here and it would also be useful to conduct test introductions.

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