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MODE OF SWARMING IN RELATION TO REPRODUCTIVE ISOLATION IN MAYFLIES

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Abstract.—Mayfly males swarm, that is they fly in a fixed pattern by a specific object, the swarm marker. Females orientate to the same markers. *Leptophlebia marginata* mayflies were observed to orientate to two kinds of objects in a single locality in central Finland: to trees and to horizontal pale objects on the ground; when dispersed or moved to the other type of marker, they returned to their former orientation. Tree swarming is by far the most common mode of swarming, but some horizontally orientating populations were found. Sympatric populations are genetically and morphologically distinct, whereas other populations appear to have some gene flow between the swarming types. The tree-swarming mode appears to be primitive and the horizontal mode derived; wind rather than predation is the factor favoring swarming close to the ground. Swarming constitutes an effective mechanism of premating isolation in mayflies.

Key words.—*Leptophlebia*, mayflies, reproductive isolation.

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The nuptial flight or swarming of mayflies is a rhythmic phenomenon, which is of short duration but may attain spectacular dimensions. In the tropics it takes place at night. The short life span of the imagoes and their nocturnal habits represent an antipredator strategy.

In the temperate zone, predator pressure is less intense, and temperature may be more important in determining the time of swarming. The relaxation of predation allows daytime flight and an increase in complexity of swarming in the temperate zone in comparison with tropics (Edmunds and Edmunds 1980). Beyond the temperate, in the boreal zone, the study conditions become ideal, as darkness never interferes with observation.

Swarms of different mayflies may orientate to different objects, *swarm markers*, or different species may swarm at different times. This constitutes an effective isolating mechanism, as mayflies mate within the swarms (Savolainen 1978; Edmunds and Edmunds 1980). In central Europe, for example, *Ephemera vulgata* swarms in the morning and *E. danica* in the afternoon (Müller-Liebenau 1960). In Finland, swarming of *E. danica* takes place in the middle of the day in sunlight, whereas *E. vulgata* swarms in the evening or by day during cloudy weather (Savolainen and Saaristo 1981).

Two synchronous modes of behavior with regard to swarming sites and swarm markers were observed in a study of the swarming of *Leptophlebia marginata* at a locality in Outokumpu, central Finland (62°51'N, 28°52'E) (Savolainen 1978). The two types of mayflies swarmed at the same times of day; that is, they responded to changes of weather in the same fashion. Some swarmed beside trees as do *L. marginata* elsewhere. In a forest some swarmed at tree-top level; others swarmed at a low level (0.2 to 1.5 m) above swarm markers paler than the environment and directly exposed to sunlight, such as stones, patches of lichen, and experimentally introduced pieces of gray-and-white cardboard (fig. 1).

In an earlier study (Savolainen 1978), these behavioral differences were observed when individuals of one swarming mode and site were transferred to another site. Marked mayflies orientating to horizontal pale objects were transferred to tree-swarming sites as far as 15 km away from the original site; they always resumed swarming orientating to pale objects at the new site, where only mayflies orientating to trees were seen before. Individuals orientating to trees from the latter site resumed tree swarming when transferred to a site occupied by mayflies orientating to pale horizontal objects. In that study no mor-

phological differences were observed between the individuals with different swarming behavior. A preliminary electrophoretic study (Saura et al. 1979) showed that the two populations most probably are reproductively isolated. We have now collected a large amount of data from populations both to the north and south of the area of sympatry in central Finland. This is a morphometric and electrophoretic study on the sets of populations exhibiting the two swarming modes. As a reference we have used the closest northern European related species, *L. vespertina*, collected from the same localities.

MATERIAL AND METHODS

Leptophlebia marginata were collected from about 30 localities in Finland from 1976 to 1985. The collecting procedure and general background of *Leptophlebia* populations are described in detail elsewhere (Savolainen 1978). Only samples larger than 20 individuals are considered here; they make up a total of 2052 specimens. The collecting localities are shown in figure 2. Table 1 gives the grid coordinates for the samples, the mode of swarming (orientating to trees or horizontal objects), as well as the type of data available for each locality. Some sites, in particular number 3, Outokumpu, were sampled over 4 yr. *Leptophlebia vespertina* samples comprised 40–50 individuals from each site, and all were taken in 1985. Adults used in electrophoresis were stored in dry ice.

Enzyme Electrophoresis.—In order to ascertain the swarming mode, only males were sampled. A total of 16 enzyme systems were successfully assayed, namely, adenylate kinase, aldolase, esterase, fumarase, glutamate-oxaloacetate transaminase, α -glycerophosphate dehydrogenase, hexokinase, hydroxybutyrate dehydrogenase, isocitrate dehydrogenase, lactate dehydrogenase, malate dehydrogenase, malic enzyme, phosphoglucomutase, 6-phosphogluconate dehydrogenase, phosphoglucose isomerase, superoxide dimutase and triosephosphate isomerase (Saura et al. 1979). These systems code for over 40 loci, 5 of which proved to be polymorphic in *L. marginata*, namely, *Est-1*, *Pgi*, *Me*, and *α -Gpdh*. In addition, *Idh-2* was proven to be polymorphic by isoelectric focusing in some populations. As mentioned earlier (Saura et al. 1979), different alleles are fixed at this locus at locality number 3. Because distinguishing heterozygotes from homozygotes was not practical, *Idh-2* is discarded here.

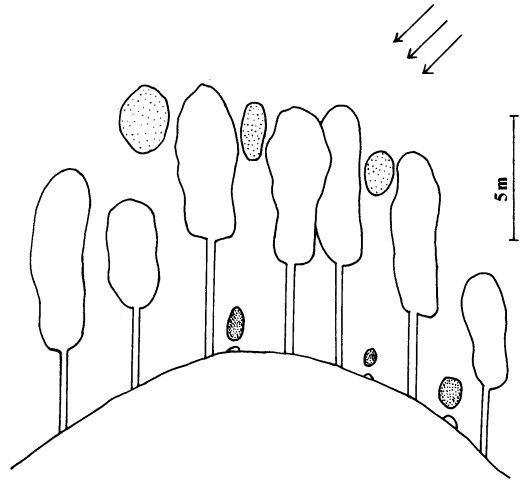


FIG. 1. The two modes of swarming of *Leptophlebia marginata*. Arrows indicate the direction of sunlight. The population orientating to trees swarmed high above the ground around tree tops on the shadow sides of the tree. The populations orientating to light horizontal objects on the ground (objects exposed to sun, e.g., lichen-covered stones) swarm in a dense cluster above such objects.

Morphometric Analysis.—The following measurements were taken from 552 individuals representing 15 populations: forewing length, forewing breadth, hindwing length, thorax length and thorax height. Locality number 3 was sampled over 4 yr. Only males were measured. All measurements were made with the ocular apparatus of a Wild M5 microscope. The data were subjected to principal-component analysis and discriminant analysis; in addition, an ANOVA was made on all samples of adequate size. Scanning electron microscopy was also attempted on the material, but no consistent differences were found between the tree swarmers and horizontal swarmers.

Allele frequencies and morphological data can be obtained from E. Savolainen.

RESULTS

Leptophlebia marginata orientating to trees (*tree swarmers*) showed no consistent morphological differences from those orientating to horizontal light objects on the ground (*horizontal swarmers*). Horizontal swarmers are, on the average, larger. To give some measures of mayflies from site number 3, Outokumpu, the mean forewing length is 9.4 for horizontal swarmers and 8.2 mm for tree swarmers. The values for hindwing length are 3.2 mm and 2.9 mm, respec-

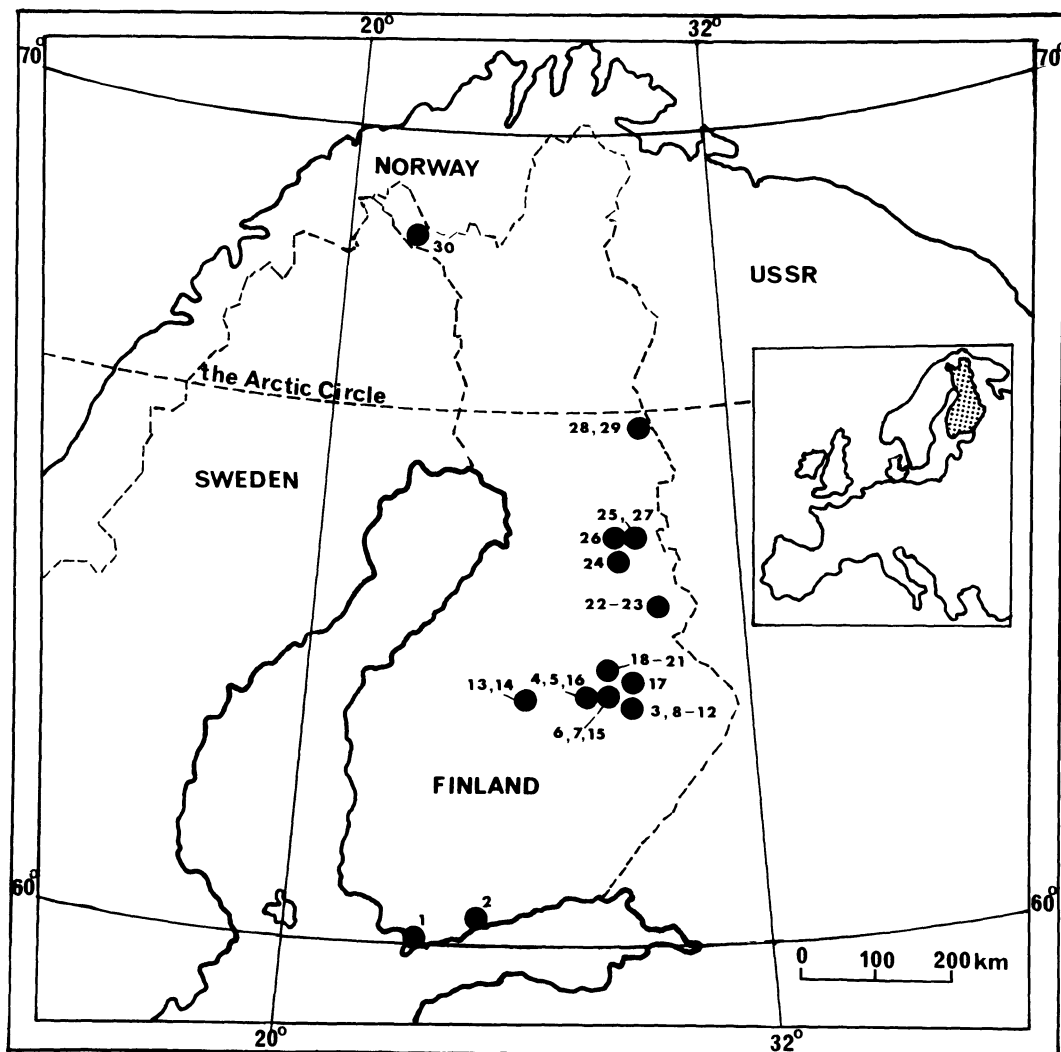


FIG. 2. The collection localities of the *Leptophlebia* samples.

tively. The tree swarmers constitute a morphologically uniform group. Morphological measures taken from this material showed no significant between-year and between-sample differences. No significant between-sample and between-year differences were present in the forewing-length and hindwing-length measures in the horizontal swarmer data; in the extensive horizontal-swarmer data from Outokumpu, between-year differences in thorax height were highly significant and differences in forewing breadth and thorax length were significant. All morphological comparisons between tree and horizontal swarmers showed highly significant differences. There is, however, some overlap in all measures.

This is best visualized in the principal-component plot (fig. 3). The first two principal components account for 92% of the variation in the data, with forewing length and hindwing length being the most important.

Inspection of figure 3 shows considerable overlap in the morphometric data. The extent of overlap does not suggest that two species need be involved. Discriminant functions were determined for tree and horizontal swarmers. The result is that about 18% of horizontal swarmers and 24% of tree swarmers would be misclassified.

One may also ask whether this group of misclassified observations constitutes a third group, given that tree and horizontal swarmers are real

TABLE 1. The localities of origin of the *Leptophlebia* data in Finland given in uniform grid coordinates, the name of the water course of origin and its nature, mode of swarming (whether Horizontal or Tree) and the type of data available. X, indicates electrophoretic data; asterisks, morphological data.

Locality	Coordinates	Water course	Type	<i>marginata</i>		<i>vespertina</i>
				Horiz.	Tree	Tree
1 Tenala	665:29	Vitsjön	lake		X*	
2 Espoo	668:37	Bodomjärvi	lake		X*	
3 Outokumpu	696:59	Munajärvi	lake	X*	X*	X
4 Kuopio	697:52	Suovu	lake		X	X
5 Kuopio	697:53	Kolmisoppi	lake		X	
6 Kuopio	697:55	Melavesi	lake		X	
7 Kuopio	697:56	Laatanlampi	lake		X	
8 Kaavi	697:59	Rikkavesi A	lake		X*	
9 Kaavi	697:59	Rikkavesi B	lake		X*	
10 Kaavi	697:59	Nälkölampi	tarn		X*	
11 Kaavi	697:59	Syrjäjoki	river		X	
12 Kaavi	697:59	Väärälampi	tarn		X*	
13 Vesanto	698:45	Keitele	lake		X	X
14 Vesanto	698:45	Vesijärvi	lake		X	
15 Kuopio	698:54	Jännevesi	lake			X
16 Siilinjärvi	699:53	Ahmo	lake		X	
17 Juuka	701:59	Vaikkojärvi	lake		X	
18 Varpaisjärvi	703:54	Väljoki	brook		X*	
19 Rautavaara	703:55	Syväkankainen	tarn		X	
20 Rautavaara	704:55	Älänne A	lake		X	
21 Rautavaara	704:55	Älänne B	lake		X	
22 Kuhmo	712:62	Lentuankoski	river	X		
23 Kuhmo	714:61	Kuusamonjärvi	lake	*		
24 Hyrynsalmi	716:57	Seitenjärvi	lake		X*	X
25 Suomussalmi	718:58	Sakarajärvi	lake	X		
26 Hyrynsalmi	719:56	Kaiskonjoki	river		X	
27 Suomussalmi	719:59	Alanteenjoki	lake		X	
28 Kuusamo	735:61	Oulankajoki A	river		X*	
29 Kuusamo	736:60	Oulankajoki B	river	X*		
30 Enontekiö	762:29	Saitsilampi	tarn	X*		

groups that are described effectively by the five observed variables. By using the principal-component equations from the first step one may conclude that the misclassified mayflies are unlikely to constitute another group. Tree swarmer have a wider spread along the first principal component (Prin 1) than do horizontal swarmer. The horizontals overlap with the last segment of the tree swarmer only. There is evidence for a continuum; the extent of the overlap also suggests that the five morphometric variables do not adequately discriminate between the two swarming behaviors. One way of interpreting the misclassified category suggests that some individuals might show both swarming behaviors, that is, alternative strategies.

Figure 3 showed a principal-component analysis over all populations. For locality number 3—that is, Outokumpu alone—where tree and horizontal swarmer are sympatric, there is much less overlap (fig. 4). With the exception of a few

individuals, nearly all specimens of this locality can be reliably assigned to swarming type by morphometrics alone.

As mentioned in the Materials and Methods, four loci were found to be polymorphic. Figure 5 shows a UPGMA phylogenetic tree based on the unbiased genetic distance of Nei (1978). The values for genetic distances between populations of *L. vespertina* versus *L. marginata* ranged from $D = 0.785$ to 3.183. Within *L. marginata*, D ranged from 0 to 0.419 (between Kolmisoppi and Enontekiö). The phylogenetic tree shows four main branches, the most distinct of which comprises the populations of *L. vespertina*.

The situation within *L. marginata* is interesting. There is an isolated tree-swarmer population (Kolmisoppi, number 5), a distinct branch comprising the repeatedly sampled horizontal swarming population number 3 from Outokumpu only, then a mixed group consisting of populations extending from northern horizontal

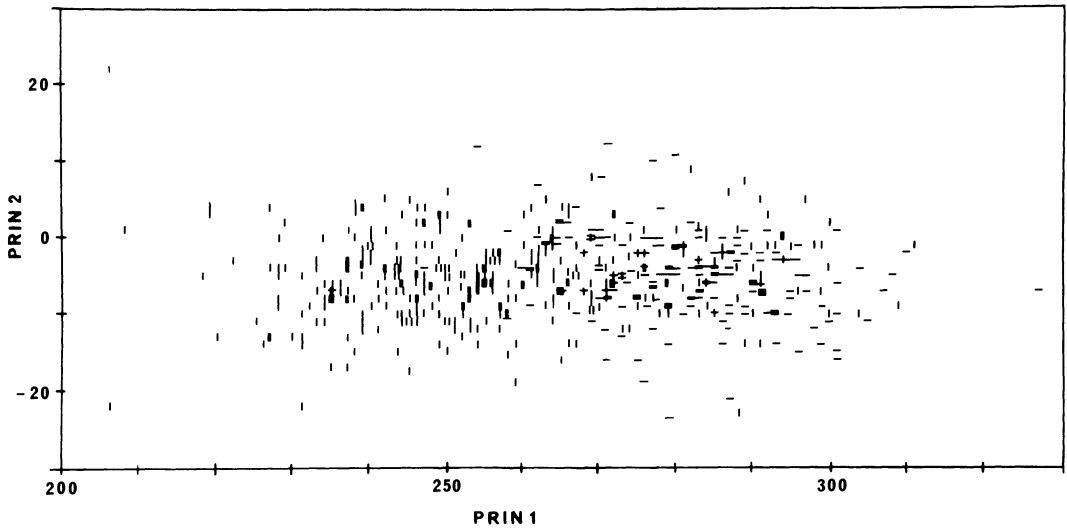


FIG. 3. Principal-component analysis plot (PRIN 1 \times PRIN 2) based on the morphometric data of the total *Leptophlebia marginata* material. Vertical bars, tree swarmer; horizontal bars, horizontal swarmer.

swarmer from Lapland, that is, a subarctic area where no adequate trees are available as swarmer markers, as well as the southernmost populations and a mixed lot in between. This includes representatives of both swarming modes as well as population 12 from Väärälampi, which exhibits somewhat atypical tree swarming. The last major branch consists of strict tree swarmer only, including the repeatedly sampled number 3 tree-swarming population of Outokumpu. As can be

seen, the last sample from this locality, from 1985, belongs to the other minor branch. This is, of course, completely permissible within the standard deviations.

DISCUSSION

The results indicate that locality 3, Outokumpu, has two reproductively isolated populations. These populations orientate to different swarmer markers and are genetically and morphologically

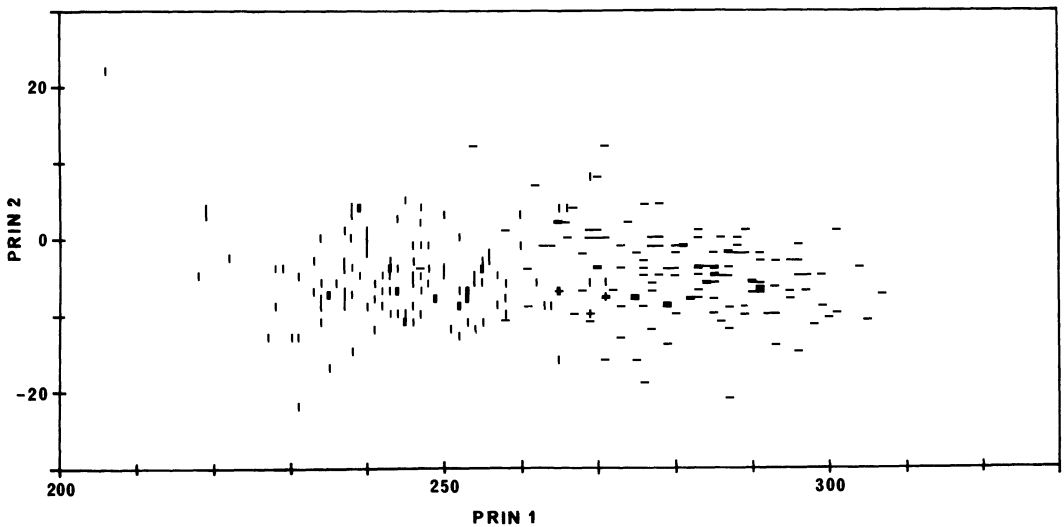


FIG. 4. Principal-component analysis based on locality 3, Outokumpu, where the horizontal and tree swarmer are sympatric.

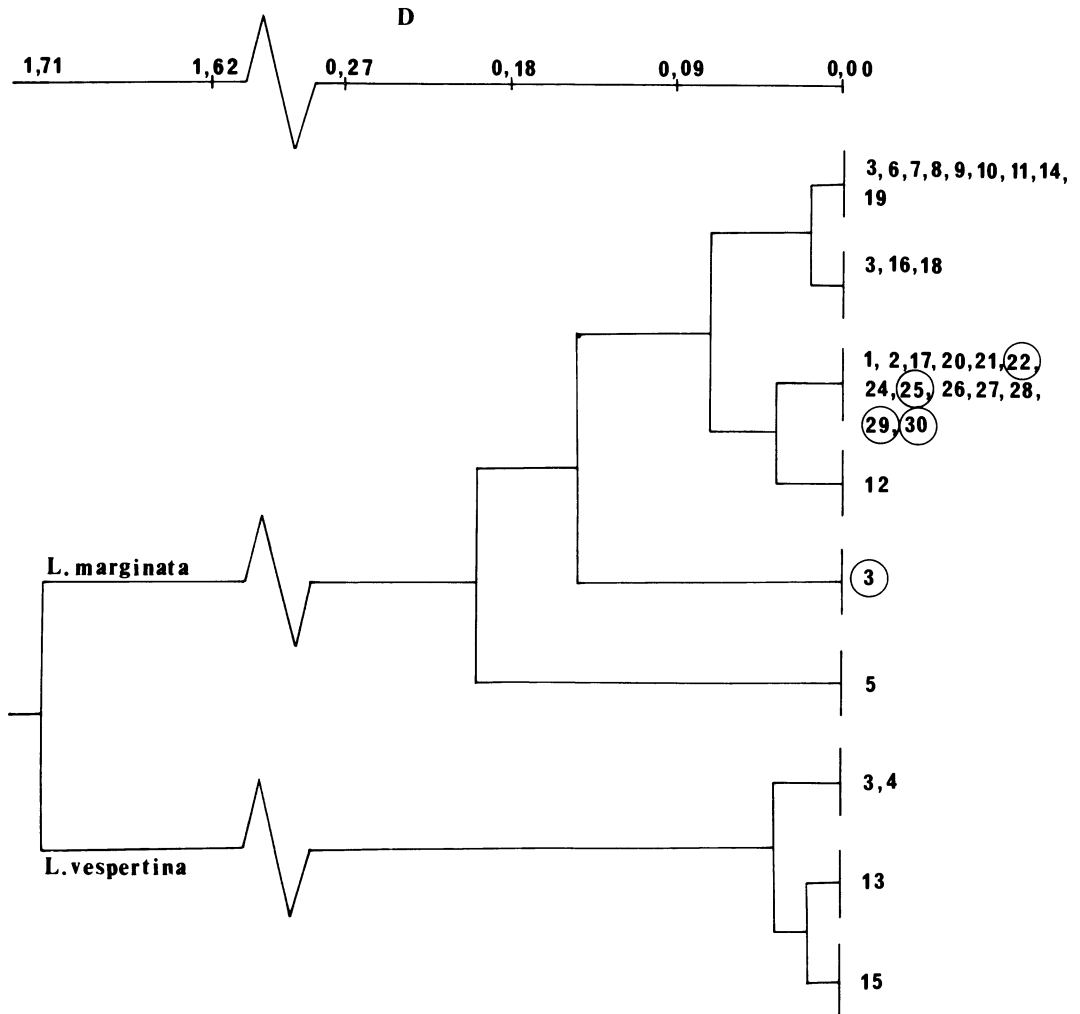


FIG. 5. An Unweighted Pair-Group Arithmetic Average (UPGMA) phylogenetic tree based on the genetic distances in the *Leptophlebia* material. The lowest branch represents *L. vespertina*, and the higher branches *L. marginata*. The numbers refer to the localities of origin. Horizontal swarmers are indicated by circled numbers; the rest are tree swarmers.

discrete. Much of the morphological overlap shown in figure 4 can be attributed to developmental malformations, for example, fused or missing leg segments. Malformed individuals are included in the primary data and account for most of the overlap in figure 4.

The horizontal and tree swarmers at Outokumpu are genetically distinct (fig. 5). In contrast, horizontal swarmers collected from other localities are genetically less distinct from tree swarmers. Interestingly, they are morphologically differentiated from the tree swarmers. When all populations are considered together, the tree swarmers spread over the right side of principal-

component 1 and overlap with horizontal swarmers within that area (fig. 3). The conclusion is that morphological and genetic differentiation is most pronounced at the only area of sympatry, that is, at Outokumpu.

Only a few samples have been collected from areas outside the known area of distribution of horizontal swarmers in eastern-central Finland. *Leptophlebia* swarm conspicuously and in the early spring, when no other mayflies are on the wing. The probability that we have missed individuals representing an alternative swarming type is, therefore, minimal. In particular, sites 4–16 and 28–30 were observed so intensely that

missing a swarming type there is highly improbable.

What might then be the original mode of swarming in *L. marginata*? When the species is considered as a whole, tree swarming is the prevalent mode, and horizontal swarming has been recorded only at localities sampled in this study. The only other *Leptophlebia* species found in Europe, *L. vespertina*, is a tree swarmer; in open terrain, they swarm over continuous vegetation. A single observation from Lapland indicates that in the absence of trees they orientate to fixed, light-colored small objects (Savolainen 1978). Other European leptophlebiids (see Tiensuu 1935) appear to swarm like *L. vespertina*.

Taken that tree swarming is the primitive leptophlebiid mode and horizontal swarming is the derived mode, which factors other than pure chance might account for it? *Leptophlebia marginata* swarms earlier in the spring than any other northern European mayfly, and its swarming period is also short (1–2 wk, whereas the other species swarm for periods longer than a month; Savolainen 1978). A northern early spring species is exposed to unpredictable weather. The spring is windy and temperatures may fall abruptly. At that time, daytime swarming is a preferred alternative for a short-lived adult insect. Because mayflies are poor fliers, they are very restricted by wind, and *L. marginata* is more sensitive to wind than any other northern species. Even a slight wind may effectively disrupt swarming, but a wind velocity greater than 1.0–1.5 m/s stops all *L. marginata* swarming (Savolainen 1978). Because both males and females orientate to the swarm marker and not to the swarm, a marker as common as a tree provides no sure clues for females to find the swarm dispersed by a gust of wind. Mayflies copulate within the swarm.

Swarming close to the ground inside the forest above a horizontal marker seems advantageous. It gives some protection against the wind, and pale, horizontal objects on the ground are more discrete and less common than trees in a forest.

Predator pressures figure very prominently as a causal factor in explaining mating and schooling aggregations of animals. In the case of *L. marginata*, predation seems to be of little consequence. Dragonflies are scarcely out in May; they represent young, teneral adults of small species at that time, and have not been observed preying on *L. marginata*. As for birds, the swarming site on pine barrens has low bird den-

sity, and bird predation has not been observed. Bats are of no consequence to daytime swarmers. Interestingly, the only predator of *L. marginata* is another swarming insect, *Empis borealis*. Empidid males capture insect prey and present these to females as nuptial gifts (Svensson and Petersson 1987). Empidids prey on low-flying insects and affect only the horizontal swarmers.

Given that tree swarming is the primitive mode and horizontal swarming the derived one and disruptive selection operates to maintain the reproductive isolation, one is tempted to invoke sympatric speciation (cf. Tauber and Tauber 1989). The only site, Outokumpu, where the reproductive isolation appears to be complete is an ecological extreme: an esker from 40 to 200 m wide between two lakes (Savolainen 1978, fig. 6). It is, accordingly, unusually exposed to the effect of wind. The other horizontally orientating populations extend from this site to the north; they are genetically less divergent, and tree swarmers have not been observed from these northern localities. The allopatric explanation is that the horizontal swarmers represent a western margin of distribution of an eastern species that is sympatric with *L. marginata* (described by Linnaeus from Sweden, where only tree swarmers are known) at least at Outokumpu.

There is some evidence against the allopatric hypothesis. First, the genetic and morphological divergence are clear-cut in the area of sympatry only. Secondly, a hypothetical horizontally swarming eastern species should have nearly uniform allele frequencies; that is, it should represent a single branch in the dendrogram. Interestingly, the horizontal swarmers are completely included within the major branch of tree swarmers in figure 5.

The allopatric hypothesis can be saved by introducing a third, reproductively isolated taxon, here represented by the horizontal swarmers at site 3, Outokumpu. They are morphologically and genetically differentiated from the tree swarmers at that site and also genetically, but not morphologically, differentiated from horizontal swarmers at other sites. Instead of two, we now have three forms, all isolated from each other to some degree. An explanation involving immigration from other locations and differentiation in allopatry can always be invoked to account for this pattern. The only effective counterargument that we have is that the distribution area of *L. marginata* in central-eastern Finland (i.e., the area with different swarming morphs) is most

thoroughly studied, and we know of no other cases. Other hypothetical cases may, of course, have died out.

Aerial swarming is a complicated behavior pattern that serves as a mechanism of premating isolation (Chiang 1963; Miehlibrand and Neumann 1976; Brittain 1990). As both sexes orientate to the same swarm markers, a change in this orientation leads to complete reproductive isolation. Mayfly males are not very discriminating but approach any flying object.

There is evidence for swarming intermediate between the two modes. *Leptophlebia marginata* mayflies at population number 12 (Väärälampi) exhibit an intermediate swarming. They are entered here as tree swarmer; morphologically they belong to the area of overlap with horizontal swarmer. They swarm near tall trees at a level lower than tree swarmer but higher than horizontal swarmer. Intermediate swarming may account for the origin of new morphs as well as for gene flow between swarming morphs.

Chironomid taxonomists have accepted the mode of swarming as a valid species criterion (Chiang 1963; Lindeberg 1967). Hawaiian *Drosophila* are a favorable subject for studies on the genetic mechanisms underlying ethological isolation (Carson 1978; Kaneshiro 1989). Mayflies are not as amenable as *Drosophila* for such studies, as rearing the nymphs is relatively cumbersome and the adults should be released in a space large enough to permit observation of their behavior.

This study gives evidence for a case of premating isolation emerging within mayflies. This may be a case of reinforcement within an area of sympatry, where the two forms behave as good species. Butlin (1989) argued that the term "reinforcement" should be used for the evolution of increased isolation resulting from selection against hybrids. An interaction between species causing divergence in mate-recognition systems should be called "reproductive character displacement." In areas of allopatry, the forms are less distinct and may exhibit intermediate behavior. Changing the mode of swarming can clearly be adaptive. This is shown by *L. vespertina* in Lapland, where it orientates to pale horizontal objects in the absence of trees (Savolainen 1978).

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LITERATURE CITED

- Brittain, J. E. 1990. Life history strategies in Ephemeroptera and Plecoptera. Pp. 1–12 in I. C. Campbell, ed. *Mayflies and stoneflies: life histories and biology*. Proceedings of the 5th International Ephemeroptera Conference and the 9th International Plecoptera Conference, Kluwer, Dordrecht.
- Butlin, R. 1989. Reinforcement of premating isolation. Pp. 158–179 in D. Otte and J. A. Endler, eds. *Speciation and its consequences*. Sinauer, Sunderland, Mass.
- Carson, H. L. 1978. Speciation and sexual selection in Hawaiian *Drosophila*. Pp. 93–107 in P. F. Brusard, ed. *Ecological genetics: the interface*. Springer, New York.
- Chiang, H. C. 1963. Ecology of insect swarms. IV. Comparison of the swarms of two closely related midges, *Anarete johnsoni* and *A. sp. near johnsoni* (Diptera: Cecidomyiidae). *Annals of the Entomological Society of America* 56:748–751.
- Edmunds, G. F., and Ch. H. Edmunds. 1980. Predation, climate, and emergence and mating of mayflies. Pp. 277–285 in J. F. Flannagan and K. E. Marshall, eds. *Advances in Ephemeroptera biology*. Plenum Press, New York.
- Kaneshiro, K. Y. 1989. The dynamics of sexual selection and founder effects of species formation. Pp. 278–313 in L. V. Giddings, K. Y. Kaneshiro and W. W. Anderson, eds. *Genetics, speciation and the founder principle*. Oxford University Press, New York.
- Lindeberg, B. 1967. Sibling species delimitation in the *Tanytarsus lestagei* aggregate (Diptera, Chironomidae). *Annales Zoologici Fennici* 4:45–86.
- Miehlibrand, J., and D. Neumann. 1976. Reproductive Isolation durch optische Schwarmmarken bei den sympatrischen *Chironomus thummi* und *Ch. piger*. *Behaviour* 58:272–297.
- Müller-Liebenau, I. 1960. Eintagsfliegen aus der Eifel (Insecta, Ephemeroptera). *Gewässer und Abwässer* 27:55–79.
- Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89:583–590.
- Saura, A., J. Lokki, and E. Savolainen. 1979. Ethological isolation and genetic diversity. *Aquilo Ser Zoologica* 20:13–16.
- Savolainen, E. 1978. Swarming in Ephemeroptera: the mechanism of swarming and the effects of illumination and weather. *Annales Zoologici Fennici* 15:17–52.
- Savolainen, E., and M. I. Saaristo. 1981. Distribution of mayflies (Ephemeroptera) in the biological province of Kuusamo (Ks), Finland. *Notulae Entomologicae* 61:117–124.

- Svensson, B. G., and E. Petersson. 1987. Sex-role reversed courtship behaviour, sexual dimorphism and nuptial gifts in the dance fly *Empis borealis* (L.). *Annales Zoologici Fennici* 24:323–334.
- Tauber, C. A., and M. J. Tauber. 1989. Sympatric speciation in insects: perception and perspective. Pp. 307–365 in D. Otte and J. A. Endler, eds. *Speciation and its consequences*. Sinauer, Sunderland, Mass.
- Tiensuu, L. 1935. On the Ephemeroptera-fauna of Laatokan Karjala (Karelia Ladogensis). *Annales Entomologici Fennici* 1:3–23.

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