ECOLOGY OF PELTOPERLA ARCUATA AND TALLAPERLA MARIA (PLECOPTERA: PELTOPERLIDAE) AT THE FERNOW EXPERIMENTAL FOREST, TUCKER COUNTY, WEST VIRGINIA

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ABSTRACT

We examined the abundance, life history, and production of the stoneflies Peltoperla arcuata and Tallaperla maria (Plecoptera: Peltoperlidae) in four forested headwater streams at the Fernow Experimental Forest, Tucker County, West Virginia. Peltoperla arcuata was most abundant in the smallest watersheds (<100 ha), and was present at all sites. Tallaperla maria was most abundant in watersheds >200 hectares (ha), was restricted to sites with a baseflow alkalinity of >2 mg L-1 CaCO₃, and was the dominant peltoperlid only at sites with an alkalinity >15 mg L⁻¹. We conclude that water chemistry overrides stream size as a determinant of speciesspecific distribution of Fernow peltoperlids. Both taxa had semivoltine life cycles with an 18-month naiadal period following a 6-month egg diapause. Emergence was during May-July for both species. Peltoperla arcuata had about 15 instars; T. maria had about 14 instars. Peltoperlid production was highest (509 mg m-2 y-1) in a 128 ha watershed where only P. arcuata was collected; P. arcuata production was lowest (17 mg m⁻² y⁻¹) in a 4th order stream (1536 ha). Tallaperla maria production was highest (271 m⁻² y⁻¹) in a 257 ha watershed partially underlain by limestone. Production across streams was higher for *P. arcuata* (205 mg m⁻² y⁻¹) than for T. maria (91 mg m^{-2} y^{-1}).

Introduction

Stoneflies (Plecoptera) of the family Peltoperlidae are "shredder-detritivores" (Merritt and Cummins, 1996) which comminute

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leaves and other coarse allochthonous organic matter into finer particles that can be ingested by other macroinvertebrates in headwater streams. Shredders are therefore an important trophic link between terrestrial and aquatic components of forest ecosystems (Cummins, Wilzbach, Gates, Perry, and Taliaferro, 1989). Shredder assemblages in certain Appalachian headwater habitats, especially leaf packs in riffles, are often dominated by peltoperlids (Griffith, Perry, and Perry, 1994).

Peltoperlidae is one of the smallest families of Plecoptera, comprised of 14 genera and about 40 species (Stark and Stewart, 1981). Of the six Nearctic genera, three are eastern: Peltoperla, Tallaperla, and Viehoperla (Stewart and Stark, 1993). Naiads of Peltoperla and Tallaperla have identical gill formulae, and similar habitus and mouthparts. No species-specific characters were found for Peltoperla or Tallaperla naiads in early instars by Stark and Kondratieff (1987). The characteristic used to distinguish between naiads of the two genera is the presence of black spots on the pronota and mesonota of P. arcuata. Eastern peltoperlids have a very distinctive "roach-like" habitus. We speculate that this body shape is an adaptation for penetration between tightly appressed leaves comprising the leaf packs within which peltoperlids are often very abundant.

Both taxa are widespread in Appalachia (Stewart and Stark, 1993). At the Fernow Experimental Forest, Tucker County, West Virginia, *P. arcuata* and *T. maria* occur together at some sites; at other sites only one species is found. The basis for habitat segregation between these species is unknown.

The objectives of this study were to document the life history and secondary productivity of *P. arcuata* and *T. maria* on the Fernow Experimental Forest, and to examine habitat factors potentially underlying species-specific distribution patterns.

STUDY AREA

The Fernow Experimental Forest (USDA Forest Service) is located in Tucker County, West Virginia (39°03'N, 79°40'W). The 1900 hectare (ha) forest includes the entire watershed of Elklick Run, a fourth order tributary of the Black Fork of the Cheat River (Fig. 1). Located in the unglaciated Allegheny Plateau Province of the Central Appalachians, the Fernow Experimental Forest receives

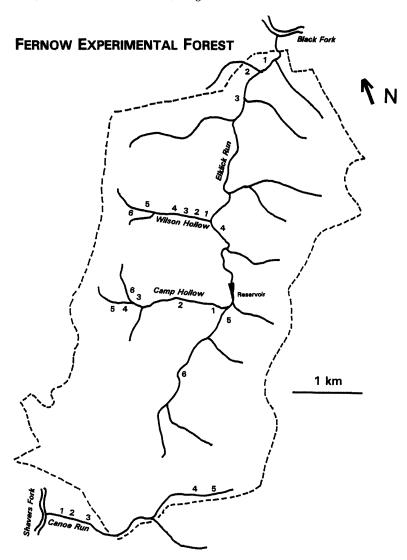


Fig. 1. Map of Fernow Experimental Forest, Tucker Co., WV. Numbers refer to study sites as described in Table 1.

about 150 cm of annual precipitation. Elevation ranges from 554 m to 1113 m.

The Fernow is primarily mixed deciduous second-growth forest. Important tree species include northern red oak (Quercus rubra L.), sugar maple (Acer saccharum Marsh.), yellow-poplar (Lirio-dendron tulipifera L.), American beech (Fagus grandifolia Ehrh.), black cherry (Prunus serotina Ehrh.), American basswood (Tilia americana L.), and white ash (Fraxinus americana L.).

The western half of the Fernow (roughly west of Elklick Run) is underlain by shales and sandstones of the Hampshire formation and the eastern half is underlain by limestones of the Greenbrier formation. Adams, Kochenderfer, Wood, Angradi, and Edwards (1994) present additional information about the Fernow Experimental Forest.

Four streams were sampled in this study: Elklick Run, Camp Hollow, Wilson Hollow, and Canoe Run (Fig. 1). Stream substratum is primarily flat, subangular sandstone cobble and gravel. Bedrock outcrops are common, especially in Elklick Run; large woody debris is abundant, especially in streams draining smaller watersheds.

MATERIALS AND METHODS

Peltoperlid naiads were collected from October 1993 to September 1994 using a Surber sampler (0.10 m², 0.25-mm mesh). Across the four streams, 23 sites were sampled approximately monthly with two samples taken at each site (Table 1, Fig. 1). Samples were preserved in 5% formalin plus a small amount of phloxine-B stain. Naiads were generally found in leaf packs in riffles; in summer when leaf packs were absent, naiads were found deeper in riffle substrates.

At each sample site during monthly collections, stream width and sample depth and velocity were measured. Electronic thermographs continuously recorded temperatures in each stream. Monthly water samples collected from selected sites on each stream were analyzed for pH, conductivity, alkalinity, calcium, and nitrate.

Naiads were measured using a computer digitizing system and measuring software (Java, Jandel Scientific). Naiads were placed under a video camera where their image was captured on a frame freezing monitor, and head width (widest portion posterior to eye) and total length (cerci excluded) were measured. Additional details are presented in Yokum (1995).

The number of instars for each species was estimated by the Janetschek (1967) method in which a sliding mean of three size classes was used to resolve positive peaks in the head-width frequency distribution. Positive peaks are putative instars. Stewart and Stark (1993) consider this method useful despite its shortcomings.

Selected specimens of known head width were dried (60°C, 48 h) and weighed to the nearest 0.001 mg. Dry mass of the remaining naiads was estimated using a least-squares regression of log-transformed dry mass on log-transformed head width. Because slopes of regressions were not different among streams, equations based on collections from all streams were used (Table 2). Secondary productivity was estimated for *P. arcuata* and *T. maria* in each stream (all sites combined) using the size-frequency method corrected for the cohort production interval (Benke, 1996).

RESULTS AND DISCUSSION

Habitat and water quality

For each stream, stream width, sample depth, and sample-point velocity, generally increased with increasing watershed area (Table 1). Among streams Elklick Run represents the largest stream sampled; Wilson Hollow was the smallest stream sampled. Physical habitat conditions at Camp Hollow and Canoe Run were similar.

Among-stream differences in pH, conductivity, alkalinity, and calcium concentration reflect watershed geology. Sites at Elklick Run and lower Canoe Run partially drain limestone geologic formations, and had pH values >7.0, alkalinities >15 mg L⁻¹, and calcium concentrations >7 mg L⁻¹ (Table 1). Other sites had pH values <7.0, and alkalinities < 7 mg L⁻¹. Nitrate concentrations and total degree days were similar among streams (Table 1). Weekly mean temperatures were similar among streams and sites (Fig. 2).

Abundance and Distribution

Peltoperlid abundance varied greatly among streams and among sites (Fig. 3). Mean annual abundance of peltoperlids was highest at Wilson Hollow (180 m⁻²), where only *P. arcuata* was collected. There was a trend towards increasing abundance at the more

Table 1. Physical habitat and water quality characteristics of study sites on the Fernow Experimental Forest. Values are means for the study period based on monthly samples. Water quality data were not collected at all sites.

			Sample	Sample	Stream			Alkalinity		i	Annual
Stream	Site	WS area (ha)	velocity (m s ⁻¹)	depth (cm)	width (m)	Ηd	Conductivity (µS cm ⁻¹)	$({ m mg~L^{-1}})$ ${ m CaCO_3}$	Calcium Nitrate $(mg\ L^{-1})\ (mg\ L^{-1})$	Nitrate (mg L ⁻¹)	degree days
Wilson Hollow	_	128	1.0	6	2.1	6.2	27	1.6	1.9	0.5	
	7	120	1.2	∞	2.9						
	3	108	6.0	∞	3.2	6.3	26	1.4	1.9	0.5	3276
	4	92	1.0	∞	2.8						
	5	49	0.4	9	1.2	6.2	20	1.4	1.3	0.1	
	9	18	9.0	5	1.2						
Camp Hollow	-	199	1.4	10	3.1	6.7	38	6.4	3.5	0.5	3315
•	7	182	1.3	6	2.4	6.7	37	6.0	3.4	0.5	
	3	78	1.1	7	1.6						
	4	41	6.0	7	2.0						
	5	32	8.0	7	1.4	6.2	28	1.7	1.9	0.2	
	9	34	1.1	∞	1.9	5.6^{a}	30	<1.0	1.8	1.5	

^a Stream drains experimentally acidified watershed.

Table 1. Continued

Stream	Site	WS area (ha)	Sample velocity (m s ⁻¹)	Sample depth (cm)	Stream width (m)	Hd	Conductivity (µS cm ⁻¹)	Alkalinity (mg L ⁻¹) CaCO ₃	Calcium Nitrate (mg L ⁻¹) (mg L ⁻¹)	Nitrate (mg L ⁻¹)	Annual degree days
Canoe Run	-	257	1.4	10	3.1						3285
	7	239	1.2	6	2.7						
	С	203	1.1	6	3.0	7.4	82	27.7	12.0	0.5	
	4	51	1.0	2	2.5						
	5	56	6.0	7	2.4	7.0	45	0.6	4.9	0.4	
Elklick Run	_	1536	1.6	11	5.8	7.2	29	20.6	8.9	0.5	
	7	1407	1.4	18	6.3						
	Э	1387	1.4	14	6.5	7.2	63	18.4	8.1	0.4	3364
	4	818	1.4	10	6.5	7.2	65	20.3	8.8	0.4	
	5	313	1.1	6	3.5						
	9	66	1.1	∞	3.5	7.1	58	18.4	7.6	0.2	

^a Stream drains experimentally acidified watershed.

Table 2. Regression equations for the relationships between log-transformed head width (HW, mm) and log-transformed dry weight (W, mg) for P. arcuata and T. maria on the Fernow Experimental Forest.

Species	n	Regression	r.2
P. arcuata	79	Ln(W) = -0.72+3.33 Ln(HW)	0.94
T. maria	53	Ln(W) = -0.77+3.09 Ln(HW)	0.96

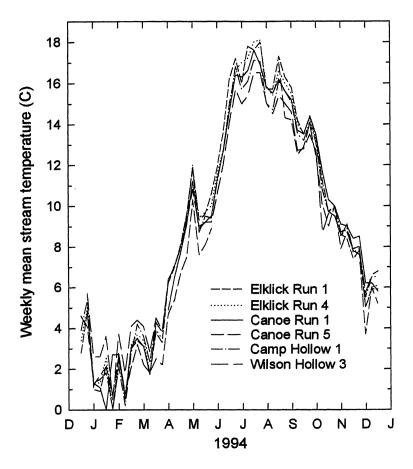


Fig. 2. Weekly mean temperature for Fernow study sites. Numbers in legend refer to study sites in Fig. 1 and Table 1.

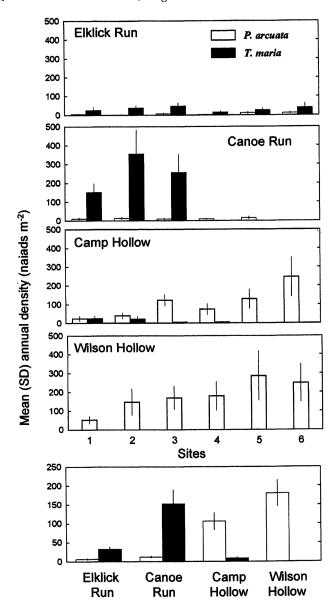


Fig. 3. Mean density of peltoperlid naiads at Fernow study sites and for sites at each stream combined. Sites are as in Fig. 1 and Table 1. There was no site 6 at Canoe Run.

upstream sites. Mean annual abundance of peltoperlids was lowest at Elklick Run (38 m⁻²), of which most (32 m⁻²) were *T. maria*. At Elklick Run, *Peltoperla arcuata* was relatively more abundant at the most upstream sites. At Camp Hollow there was also an upstream trend in abundance of *P. arcuata*. *Tallaperla maria* was common only at the two downstream sites at Camp Hollow. *Tallaperla maria* was abundant at the three downstream sites at Canoe Run. *Peltoperla arcuata* was rare but present at all Canoe Run sites, exclusively so at the most upstream sites (Fig. 3).

Because the largest streams, Elklick Run and Canoe Run, also had the highest baseflow alkalinities (Table 1), it is difficult to determine the relative importance of stream size and water chemistry in the distribution of peltoperlids in Fernow streams. At Elklick Run, T. maria and P. arcuata were both present with T. maria dominant at all sites despite great variation in stream size but with uniformly high alkalinity. At Canoe Run, T. maria was present only at the downstream, more alkaline sites. Peltoperla arcuata was present at the most upstream sites at Canoe Run, but did not thrive there as it did in similar sized sites at Wilson Hollow a few km away.

Across sites for which we have water quality data, the percent of total peltoperlid abundance comprised of *T. maria* (relative abundance) was strongly correlated with alkalinity (Fig. 4). Relative abundance of *T. maria* was also correlated with watershed area with two exceptions: at two similar-sized streams, lower Canoe Run and lower Camp Hollow, relative abundance of *T. maria* was greater at Canoe Run, the more alkaline stream (Figs. 3 and 4, Table 1); and *T. maria* was the dominant peltoperlid at the smallest Elklick Run site (99 ha); non-alkaline streams of a similar size are dominated by *P. arcuata* elsewhere on the Fernow.

We conclude that on streams of the Fernow Experimental Forest, *P. arcuata* thrives and is the dominant peltoperlid only in small streams (e.g., <200 ha) with low base flow alkalinity (e.g., < 2 mg L⁻¹), and *T. maria* is the dominant peltoperlid in more alkaline streams (>15 mg L⁻¹). At intermediate sites such as Camp Hollow sites 1 and 2 (182-199 ha, 6 mg L⁻¹ alkalinity), both species occurred but neither was abundant (Figs. 3 and 4). Fernow streams with a higher alkalinity (>30 mg L⁻¹) are overwhelmingly domi-

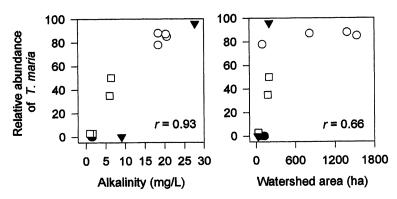


Fig. 4. Pearson correlations between relative abundance of T. maria (T. maria abundance + total peltoperlid abundance * 100) and baseflow alkalinity and between relative abundance of T. maria and watershed area. Symbols denote stream: (\bullet) Wilson Hollow, (\square) Camp Hollow, (∇) Canoe Run, (\bigcirc) Elklick Run. Some symbols hidden; n=13.

nated by the omnivorous amphipod Gammarus minus, and peltoperlids are uncommon (T. Angradi, unpublished data).

Miller and Kovalak (1979) speculated that density of *P. arcuata* increased in the upstream direction in a small Pennsylvania stream partly because smaller streams (with their smaller watersheds) were less subject to high flows which could scour naiads and the leaves on which they feed. They reasoned that although total organic matter was roughly equivalent in all channels on an annual basis, organic matter was retained longer in the smaller channels which are less subject to high spring flows. We accept this explanation for the increased abundance of *P. arcuata* with decreasing watershed area at Wilson Hollow and Camp Hollow, and we add that *P. arcuata* probably has adaptations for burrowing into the deep interstitial zone, because these upper stream reaches are usually without surface flow in late summer and autumn.

Life history

Peltoperla arcuata and T. maria exhibited semivoltine life cycles (Fig. 5). Peltoperla arcuata, for which we have the most data, had an approximately 18 month larval period following an egg diapause of about 6 months. Late instars of T. maria were rare in our collections, but we infer a life cycle similar to P. arcuata.

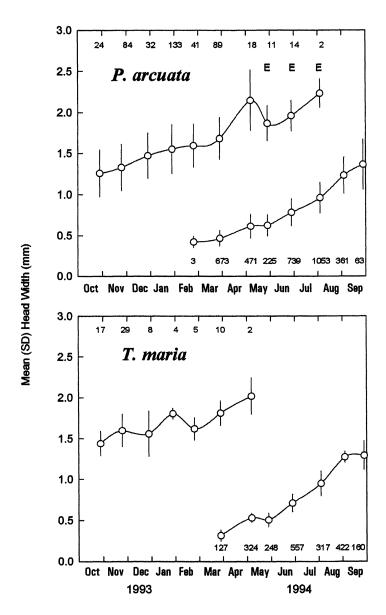


Fig. 5. Semivoltine life cycle of peltoperlids for all Fernow sites. Numbers adjacent to horizontal axes are sample sizes. E=emergence.

The mesh size of the net we used (0.25 mm; the smallest naiads we collected had head widths <0.2 mm) may have failed to adequately sample first instars which probably appear in November-January (O'Hop, Wallace, and Haefner, 1984; Elwood and Cushman, 1975). Overlapping cohorts of *T. maria* naiads were collected from March through April (Fig. 5); overlapping cohorts *P. arcuata* naiads were collected from February through July (Fig. 5).

Instar analysis suggested that *P. arcuata* had at least 15 instar peaks based on head width (Fig. 6), and *T. maria* had about 14 instar peaks. Final instar size was larger for *P. arcuata*. However,

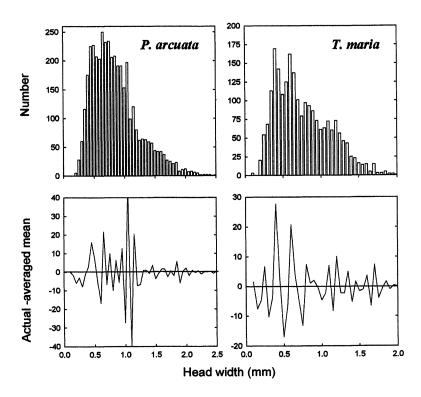


Fig. 6. Frequency distribution of peltoperlid naiads for all Fernow sites and (lower panels) instar analysis in which the actual number of naiads in each size class was subtracted from the sliding mean of the number of naiads in three size classes (mean of the size class in question and the next smallest and next largest size class). Positive peaks are putative instars.

as noted above, we collected few late instar *T. maria* naiads. Ruggles and Tarter (1991) estimated 10-12 instars for *P. tarteri*.

Emergence of *P. arcuata* occurred from late May through July based on the loss of the larger cohort naiads after April (Fig. 5). Emergence trap data collected in 1991 supports this conclusion (Michael Griffith, unpublished data). We did not collect mature *T. maria* naiads after April, but emergence probably occurred in May-June. In a Maryland stream at a latitude similar to the Fernow Experimental Forest, Duffield and Nelson (1990) reported emergence of *T. elisa* in May and June. Elwood and Cushman (1975) reported emergence of *T. maria* in April and May in a Tennessee stream. *T. maria* emerge in May at Coweeta in North Carolina (O'Hop et al., 1984).

Peltoperlids apparently exhibit indeterminant voltinism. Semi-voltinism of *T. maria* in North Carolina was reported by O'Hop et al. (1984) and Huryn and Wallace (1987), and in Tennessee by Elwood and Cushman (1975). Miller and Kovalak (1979) reported a univoltine life cycle for *P. arcuata* in Pennsylvania. Claassen (1931) reported a semivoltine life cycle in New York. In contrast to the semivoltine peltoperlids of the Fernow Experimental Forest, Ruggles and Tarter (1991) reported a univoltine life cycle for *P. tarteri* at Paint Creek in Fayette County, West Virginia. Emergence of *P. tarteri* occurred in June and naiads hatched in July. The naiads grew slowly until October and then rapidly through fall and winter. Univoltinism of *P. tarteri* may be related to higher stream temperatures or different food availability at the lower elevation stream examined by Ruggles and Tarter (1991).

At the Fernow Experimental Forest, stream flow is lowest in July-October. Surface flow ceases in many stream reaches in autumn. Also, leaf litter is scarce in perennial reaches by late summer (T. Angradi, unpublished data). Semivoltine life cycles with an egg diapause may allow *P. arcuata* and *T. maria* naiads to avoid these unfavorable environmental conditions in late summer and early autumn.

Production

Production was calculated using a cohort production interval (CPI) of 550 days because life cycles of both taxa were semivoltine (18 month larval period) (Table 3). For *T. maria*, production

Table 3. Secondary production estimates for Peltoperlidae at the Fernow Experimental Forest and at the Coweeta Hydrologic Laboratory, near Franklin, NC. CPI = 550 (Fernow) or 540 (Coweeta).

Stream	Taxa	WS area (ha)	Production (mg m ⁻² y ¹) ¹	Source
	Fernow	Experime	ntal Forest, V	vv
Elklick Run	T. maria	1536	79	This study
	P. arcuata		17	This study
Canoe Run	T. maria	257	271	This study
	P. arcuata		54	This study
Camp Hollow	T. maria	199	13	This study
•	P. arcuata		239	This study
Wilson Hollow	T. maria	128	0	This study
	P. arcuata		509	This study
WS 4 ²	P. arcuata	40	478^{3}	Griffith et al. 1994
WS 3	P. arcuata	38	370^{3}	Griffith et al. 1994
	Coweeta	Hydrolog	ic Laboratory	, NC
Upper Ball Creek	Peltoperlidae4	39	299	Huryn and Wallace 1987
Grady Branch	T. maria	13	496	O'Hop et al. 1984
Sawmill Branch	T. maria	9	560	O'Hop et al. 1984
C55	Peltoperlidae	8	735 ⁵	Lugthart and Wallace 1992

¹ Production values for Fernow are dry weight basis; Coweeta values are ash-free dry weight.

was highest in Canoe Run (271 mg m⁻² y⁻¹) and lowest in Camp Hollow (13 mg m⁻² y⁻¹; *T. maria* was not found at Wilson Hollow). For *P. arcuata*, production was highest at Wilson Hollow (509 mg m⁻² y⁻¹) and lowest at Elklick Run (17 mg m⁻² y⁻¹). Mean (±SD) production for all streams combined was higher for *P. arcuata* (205±195 mg m⁻² y⁻¹) than for *T. maria* (91±108 mg m⁻² y⁻¹). Total peltoperlid production was highest at Wilson Hollow where only *P. arcuata* occurred.

Excluding Elklick Run, the range of values for peltoperlid production (Table 3) was similar to what has been reported for two small streams in the headwaters of Camp Hollow by Griffith et al. (1994). At both the Fernow Experimental Forest and at the

² WS 3 and WS 4 roughly correspond to Camp Hollow sites 5 and 6.

³ Values adjusted for a CPI of 550 days.

⁴ Includes T. maria, T. anna, and Viehoperla ada.

⁵ Mean of two years.

Coweeta Hydrologic Laboratory in North Carolina, there is a trend towards higher peltoperlid production in smaller streams. Direct comparisons among studies are not feasible because of differences in taxonomic resolution, sampling methods, and units in which production is reported. However, it is clear that *T. maria* is the dominant peltoperlid in much smaller streams at Coweeta than on the Fernow, and that production of *T. maria* at Coweeta is within the range of production values for *P. arcuata* in the most productive Fernow stream (Wilson Hollow). The apparent replacement of *P. arcuata* by *T. maria* in small streams at Coweeta might reflect a more southerly center of distribution for *T. maria* then *P. arcuata* (Stewart and Stark, 1993).

Factors underlying species-specific distributions of Fernow peltoperlids

In headwater streams, frequency of flow-related natural disturbances are a function of watershed area. Compared to larger streams like Elklick Run and lower Canoe Run, channel dewaterings are more frequent and sediment scouring flood flows are less frequent in streams draining smaller Fernow watersheds (T. Angradi, personal observation). If behavioral responses to seasonal drought (e.g., burrowing) or floods/displacement (e.g., refuge seeking, oviposition flight behavior) differ between the species, segregation would be maintained on the basis of watershed area alone. However, this explanation is unsatisfactory since *T. maria* thrives in very small watersheds at Coweeta Hydrologic Laboratory in North Carolina (e.g., Table 3).

Apparent effects of stream size resulting from differences between streams in water temperature or food quality seem unlikely because water temperature did not vary much among streams or sites, and food preference experiments and gut analysis showed that the species prefer the same leaf species, and that their overall diets are similar (Yokum, Johnson, Tipton, Tarter, and Angradi, 1994).

We found a more consistent relationship between relative abundance of *T. maria* and alkalinity than between relative abundance of *T. maria* and watershed area (Fig. 4) and we conclude that water chemistry plays a greater role than stream size, *per se*, in maintaining separation between the two species in Fernow streams. Physiological responses to alkalinity (or a correlate) might result in

different inherent chemical preferenda for the two species. Griffith et al. (1994) have shown that baseflow alkalinity influences the relative abundance of plecopteran shredders in Fernow and nearby streams. Our data suggest, for example, that *Peltoperla arcuata* is more tolerant of poorly buffered water than *T. maria*. At Coweeta, *T. maria* was the dominant peltoperlid in Grady Branch and Sawmill Branch (O'Hop et al. 1984), streams comparable in size to the uppermost sites at Wilson Hollow (Table 3) where we found only *P. arcuata*. However the Coweeta streams had a higher pH (6.7) and alkalinity (4.5 mg L⁻¹, Wayne Swank, personal communication). *P. arcuata* tolerates higher alkalinities—they were collected at every Fernow site—but is at an apparent disadvantage to *T. maria* at higher alkalinities. High baseflow alkalinity might also confer an advantage to *T. maria* if they are better able to compete with *Gammarus minus* than are *P. arcuata*.

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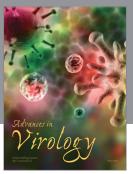
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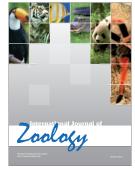


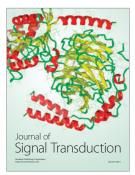














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