

# The response of stonefly (Plecoptera) nymphs to seasonal increases in predation risk

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**Abstract:** The main objective of this study was to determine if predation risk accounted for the patterns of stonefly (Plecoptera) nymph abundance in the Maligne Valley watershed, Jasper National Park, Alberta. Seasonal declines in nymph density corresponded to increased use of the Maligne Lake Outlet and Lower Maligne River by harlequin ducks (*Histrionicus histrionicus*). Neither decline represented a shift from aperiodic to nocturnal use of surface rocks. Rather, rock use remained aperiodic throughout the season despite increases in risk. The decline that occurred in the Maligne Lake Outlet also did not represent a shift from small to large surface rocks. These results, when combined with the results of an odor experiment, suggest that nymphs tend to avoid surface rocks when in the presence of harlequin ducks. Nymph density did not decline seasonally in the Middle Maligne River, a site free of harlequin ducks but inhabited year-round by brook char (*Salvelinus fontinalis*) and rainbow trout (*Onchorhynchus mykiss*). Nymphs in this site as well as those exposed to char odor were nocturnally biased in their use of the substrate surface. Overall, predation risk appears to play a strong role in the patterns of stonefly nymph abundance in the Maligne Valley watershed, although not in the way originally expected.

**Résumé :** Le but principal de cette recherche est de déterminer si les risques de prédation peuvent expliquer l'abondance des larves de plécoptères (Plecoptera) dans le bassin hydrographique de la rivière Maligne dans le parc national de Jasper en Alberta. Les déclins saisonniers de l'abondance des larves correspondent à une augmentation de la fréquentation de l'émissaire du lac Maligne et de la rivière Maligne inférieure par l'arlequin plongeur (*Histrionicus histrionicus*) et ne sont pas dus au passage d'une utilisation aperiodique à une utilisation nocturne des pierres de surface par les insectes. L'utilisation des pierres reste aperiodique pendant toute la saison en dépit de l'augmentation des risques. Le déclin à l'émissaire du lac ne reflète pas non plus un passage des petites pierres à de grandes pierres. Ces résultats, combinés à ceux d'une expérience sur les odeurs, semblent indiquer que les larves ont tendance à éviter la surface des pierres en présence des arlequins. La densité des larves ne subit pas de diminution saisonnière dans la rivière Maligne moyenne qui n'est pas fréquentée par les arlequins, mais où habitent à l'année des ombles de fontaine (*Salvelinus fontinalis*) et des truites arc-en-ciel (*Onchorhynchus mykiss*). Les larves de ce site et celles qui sont exposées à des odeurs d'ombles ont tendance à faire une utilisation nocturne de la surface des substrats. De façon générale, les risques de prédation semblent jouer un rôle important dans la détermination des patterns d'abondance des larves de plécoptères du bassin de la rivière Maligne, mais de manière inattendue.

[Traduit par la Rédaction]

## Introduction

Prey may respond to their predators or the threat of predation by altering their foraging behavior, use of microhabitats, and activity within those microhabitats (e.g., Werner et al. 1983; Feltmate et al. 1986; Soluk and Collins 1988a, 1988b, 1988c; Feltmate and Williams 1989; Peckarsky and McIntosh 1998; Huhta et al. 1999). In a larger context, predators may account, directly or indirectly, for the spatial and temporal distribution and abundance of their prey (Werner et al. 1983; Skelly and Werner 1990; Douglas et al. 1994; review by Wooster and Sih 1995; Cowl et al. 1997). For example, harlequin ducks (*Histrionicus histrionicus*), brook char (*Salvelinus fontinalis*), and rainbow trout (*Oncorhynchus*

*mykiss*) may play crucial roles in the positioning behavior of stonefly (Plecoptera) nymphs in the Maligne Valley watershed, Jasper National Park, Alberta.

Nymphs are often found on or under rocks that make up the top layer of the river substrate (e.g., Hynes 1976; Peckarsky 1979; Hunt 1998). The use of surface rocks may be time-dependent, however, as risk from visual predators like ducks, char, and trout is highest during the day (e.g., Feltmate et al. 1986; Angradi and Griffith 1990; Flecker 1992). Harlequin ducks pick nymphs off the top and sides of rocks; they may also use their bills to dig around rocks and flip over smaller rocks to expose the nymphs underneath (personal observation). Similarly, char and trout pick nymphs off rocks and may overturn small rocks by fanning them with their tails (e.g., Feltmate et al. 1986). Nymphs can reduce this risk by restricting their use of surface rocks to nighttime.

The trade-off to this restriction is that nymphs will have less time to search for food, which is typically most abundant on surface rocks (Brittain 1982; Peckarsky 1991; Culp and Scrimgeour 1993). For female nymphs, less food may ultimately mean lower reproductive output, as body size is directly related to egg number (Taylor et al. 1998). Conse-

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quently, positioning behavior may strongly depend on overall predation risk (e.g., Soluk and Collins 1988b). In the Maligne Lake Outlet (MLO) and Lower Maligne River, for example, predation risk increases from April to June as harlequin ducks arrive from their wintering grounds on the Pacific coast (Hunt and Ydenberg 2000; N.A. McCutchen, unpublished results). During the rest of the year, risk in both sites is either constant (MLO, which is used year-round by char and trout) or nonexistent (Lower Maligne River, where char and trout are absent because of natural barriers to colonization) (Sullivan 1989). When harlequin ducks are absent, nymphs may use surface stones aperiodically, as they are optimizing their food intake during times of relatively low risk. After harlequin ducks arrive, risk increases and it is expected that nymphs will shift from aperiodic to nocturnal use of surface rocks. Daytime refuges may be found among subsurface rocks (N.A. McCutchen, unpublished results) or under larger surface rocks, which are too heavy for fish and ducks to disturb. This shift in positioning behavior may explain why increases in harlequin ducks' use of the MLO and Lower Maligne River correspond to diurnal decreases in nymph biomass ( $\text{mg}/\text{m}^2$ ) on surface rocks (Hunt and Ydenberg 2000; N.A. McCutchen, unpublished results). Seasonal declines in nymph biomass are not observed in the Middle Maligne River, a site rarely used by harlequin ducks but inhabited year-round by young char and trout (Sullivan 1989; Hunt and Ydenberg 2000; N.A. McCutchen, unpublished results). Since risk does not change seasonally in this river, nymphs are not expected to alter their diel use of surface rocks, which should always be nocturnally biased.

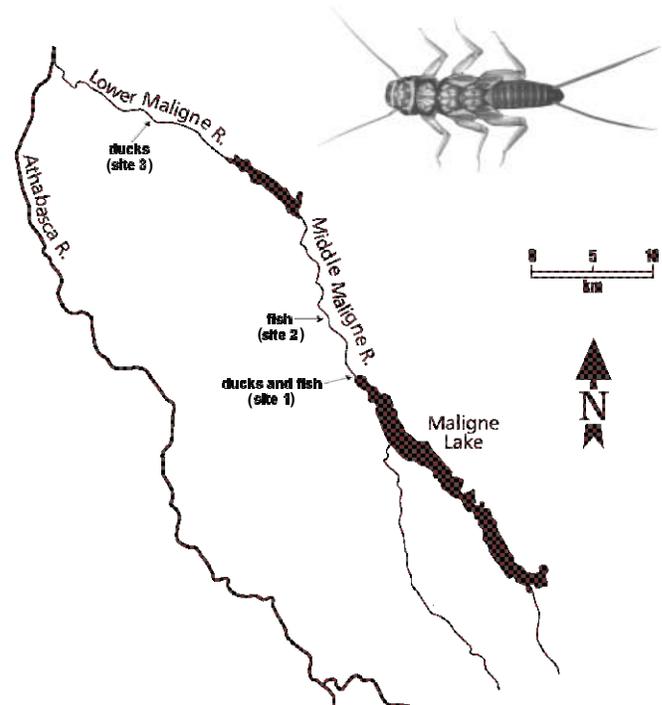
The main objective of this study was to determine if predation risk accounted for the seasonal patterns of stonefly nymph abundance in the Maligne Valley watershed (Fig. 1). In particular, I investigated whether (i) nymphs altered their diel use of surface rocks in sites where the risk was variable (harlequin ducks, MLO and Lower Maligne River) but not in sites where the risk was constant (fish, Middle Maligne River), and (ii) nymphs in the MLO moved from small to large rocks as the risk from harlequin ducks increased. Field surveys were complemented by a finer scale experiment that investigated how nymph positioning behavior changed in response to time of day and predator type.

## Materials and methods

### Relative estimates of nymph density on surface stones

Stonefly nymph density (number/ $\text{m}^2$ ) on surface rocks in the MLO and Lower and Middle Maligne rivers was estimated using "five-rock" sampling. In each site, an aquatic D-net was positioned just downstream of each of five haphazardly selected rocks (usually 8–12 cm wide, unless large rocks were sampled). Each rock was removed from the substrate surface and all invertebrates on and around each rock were washed into the net. Once it was cleaned of invertebrates, each rock was given to a field assistant who estimated its volume using water displacement. Sampled rocks were not returned to the river. The invertebrate sample was removed from the net, transferred to a sampling vial, and preserved with 70% ethanol. This procedure was repeated at five locations in each site, for a total of 5 five-rock samples,

**Fig. 1.** Map of the Maligne Valley watershed, Jasper National Park, Alberta ( $118^\circ\text{W}$ ,  $52^\circ\text{N}$ ), showing the sampling areas in the Maligne Lake Outlet (site 1; ducks and fish), Middle Maligne River (site 2; fish only), and Lower Maligne River (site 3; ducks only).



or 25 rocks per site, on each sampling day. The five rocks in each sample were approximately 1 m apart; replicates of each sample were approximately 10 m apart. Five-rock sampling was used in this study because the rocks in the watershed are typically too large for Surber or Hess sampling (Hunt 1998; personal observation).

In the laboratory, stonefly nymphs were removed from each sample and counted. Identifications were made to genus using Clifford (1991). Total rock volume for each sample was converted to surface area as follows: surface area =  $13.875 \cdot \log \text{volume}^{3.603}$ ,  $r^2 = 0.966$ . This function was determined by removing 40 rocks of various sizes from the river and wrapping each in plastic. Excess material was cut off and the remainder was weighed. Masses were converted to surface area using a previously established surface area–mass relationship (i.e., a  $6.25\text{-cm}^2$  piece of plastic weighed  $0.047 \pm 0.001$  g;  $n = 10$ ). Density (number/ $\text{m}^2$ ) estimates for each sample were log-transformed (i.e.,  $\ln(x + 1)$ ) to normalize the distributions (e.g., Elliott 1977).

### Diel patterns of nymph abundance

Nighttime and daytime five-rock samples were taken once a week in the MLO and biweekly in the Middle and Lower Maligne rivers from April to June in 1999. Nighttime sampling began about 1 h after sunset. All nighttime samples were taken within 2 d of the daytime samples. Density estimates were analyzed separately for each site using two-way ANOVAs with time of day (night and day) and month (April, May, and June) as the factors.

### **Abundance of nymphs under small and large rocks**

Paired large (15–20 cm wide) and small (8–12 cm wide) five-rock samples were taken once a week in the MLO from April to June in 2000. Density estimates were analyzed using a two-way ANOVA with rock size (large and small) and month (April, May, and June) as the factors.

### **Positioning response of nymphs to time of day and predator-odor cues**

To complement the field sampling, an experiment was designed in which I investigated how nymph positioning behavior changed in response to time of day and predator-odor cues. A flow-through aquarium was set up next to a predator-free creek that drains into Maligne Lake. Water was pumped into 2 “odor” tanks and 10 experimental tanks with a submersible pump. Each tank was 40 cm long  $\times$  28 cm wide  $\times$  12 cm high. Water from each odor tank was gravity-fed into five experimental tanks, while water from each of the experimental tanks drained into the creek downstream of the pump. Surface flow in the experimental tanks was approximately 20 cm/s (measured with a General Oceanics Mechanical Flowmeter model 2030).

This experiment was designed to test if nymphs used larger rocks as daytime refuges, and therefore, the experimental-tank habitats were very simple in structure. Each tank bottom was covered with gravel. Two small (5–8 cm wide, 0.25 m<sup>2</sup> total surface area) and 2 large (10–13 cm wide, 0.55 m<sup>2</sup> total surface area) rocks were then placed on the gravel surface. All rocks were dark, flat, and rough. Three MLO nymphs, the number expected given the number of rocks and their size, were placed in each experimental tank 24 h before each experimental run began. *Hesperoperla* spp. (Plecoptera: Perlidae) nymphs were used, as they are the most abundant type of nymph in the MLO (McCutchen 2001).

Nymphs were exposed to either harlequin duck odor ( $n = 25$ ), brook char odor ( $n = 25$ ), or a no-odor control ( $n = 25$ ). Harlequin duck odor was reproduced by adding 1 g of fresh duck feces to an odor tank; all feces contained stonefly parts. Brook char odor was reproduced by placing a live 20 cm long char in an odor tank. The char was angle-caught prior to the experiment and housed downstream of the aquarium when not in use. It was fed nymphs 3 days before and throughout the experiment. The no-odor control was produced by adding 10 mL of clean stream water to the odor tank. During each experimental run, 5 replicates of one treatment were randomly matched with 5 replicates of another.

“Odors” were added to the odor tanks 1 h before observations began and were not removed until the end of each run. Observations were made 1 h before sunset and repeated 1 h after sunset. During each observation period the nymphs visible on the substrate surface, under large rocks, and under small rocks were counted (rocks were flipped over to find the nymphs underneath). Nighttime observations were made with a red light, which nymphs cannot detect (e.g., Elliott 2000). After each run, nymphs were removed from the tanks, which were then thoroughly flushed and set up for the next treatment series. Data were analyzed with repeated-measures ANOVA in which the treatment effects (duck, char, or control) on nymph position (under large stones, un-

der small stones, or visible on the surface) during time 1 (day) and time 2 (night) were compared. Analysis of ranked and unranked data yielded the same results, therefore only the unranked data were used (Zar 1996). Multiple comparisons were made with Tukey’s honestly significant different (HSD) tests. This experiment was conducted from 3 to 11 July 2000.

## **Results**

### **Relative estimates of nymph density on surface rocks**

Four families of stonefly nymphs were identified in the Maligne Valley watershed: Perlidae, Chloroperlidae, Perlodidae, and Nemouridae (McCutchen 2001). All families were found in each site, but perlid (*Hesperoperla* spp.) nymphs were the most common in the MLO. Perlids (mostly *Claassenia* spp. with some *Hesperoperla* spp.) also dominated the Middle Maligne River, while nemourids (*Zapada* spp. and *Podmosta* spp.) were the most abundant nymphs in the Lower Maligne River.

### **Diel patterns of nymph abundance**

Mean nymph densities did not differ between nighttime and daytime in either the MLO (time:  $F_{[1]} = 0.002$ ,  $p = 0.996$ ) or the Lower Maligne River (time:  $F_{[1]} = 0.583$ ,  $p = 0.449$ ) during any part of the season (Fig. 2). However, overall mean nymph density declined from April to June in both sites (month, MLO:  $F_{[2]} = 26.042$ ,  $p < 0.001$ ; Lower Maligne River:  $F_{[2]} = 13.712$ ,  $p < 0.001$ ). In particular, mean daytime declines were matched by mean nighttime declines (time  $\times$  month, MLO:  $F_{[2]} = 0.598$ ,  $p = 0.552$ ; Lower Maligne River:  $F_{[2]} = 0.170$ ,  $p = 0.845$ ). Conversely, mean nymph density in the Middle Maligne was higher at night than in the day throughout the season (time:  $F_{[1]} = 4.233$ ,  $p = 0.046$ ). Furthermore, mean density did not change over the season (month:  $F_{[2]} = 0.222$ ,  $p = 0.802$ ) but remained constant both day and night (time  $\times$  month:  $F_{[2]} = 0.211$ ,  $p = 0.811$ ).

### **Nymph abundance under small and large rocks**

Mean nymph density was higher under large than small rocks in the MLO (rock size:  $F_{[1]} = 14.109$ ,  $p < 0.001$ ) (Fig. 3). However, mean density declined throughout the season (month:  $F_{[2]} = 27.032$ ,  $p < 0.001$ ) under rocks of both sizes (month  $\times$  rock size:  $F_{[2]} = 5.144$ ,  $p = 0.007$ ).

### **Positioning response of nymphs to time of day and predator-odor cues**

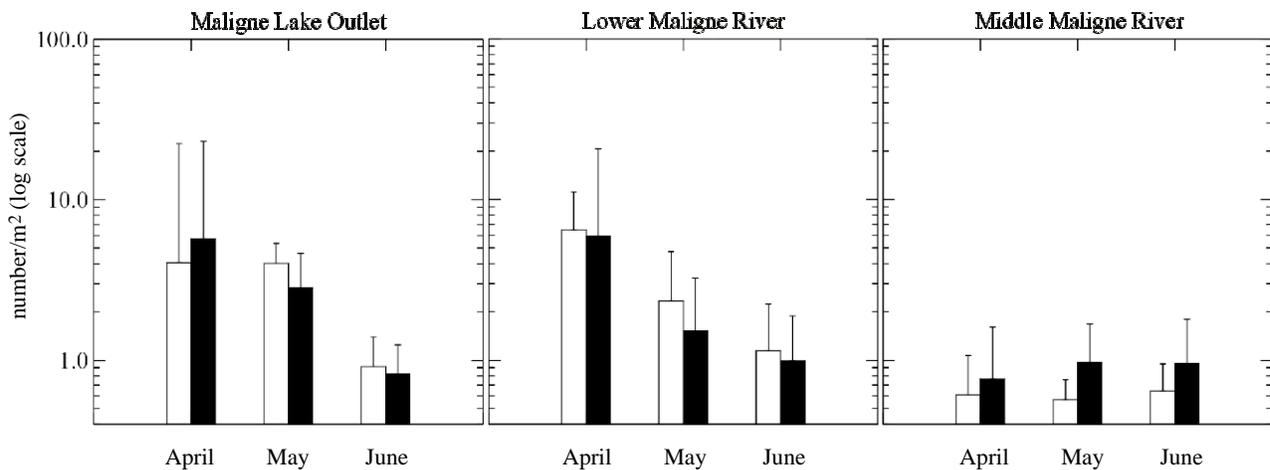
Mean nymph positioning behavior was strongly affected by time of day ( $F_{[5]} = 74.592$ ,  $p < 0.001$ ) and the interaction between time of day and treatment ( $F_{[10]} = 4.447$ ,  $p < 0.001$ ). General patterns of behavior were the same regardless of treatment, however (treatment:  $F_{[2]} = 0.207$ ,  $p = 0.814$ ). One hour before sunset, most of the nymphs were found under large stones, although more so in the control and char treatments than the duck treatment (Tukey’s HSD test,  $p = 0.035$ ) (Table 1). One hour after sunset, nymphs were visible on the substrate surface. However, the proportion of nymphs that were visible was predator-dependent. Relative to one another, char-treatment nymphs were more likely be visible on the substrate surface (Tukey’s HSD test,  $p = 0.001$ ), whereas

**Table 1.** Mean percentages of *Hesperoperla* spp. nymphs under large rocks, under small rocks, and visible on the substrate surface during different times of day and under different predator-odor regimes ( $n = 25$  for each treatment).

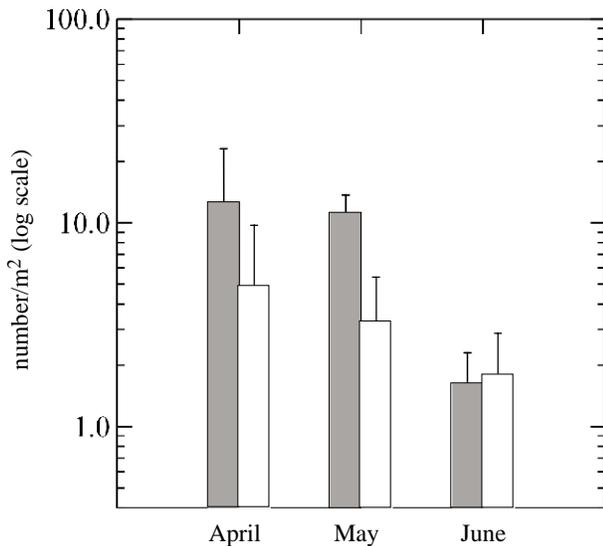
Treatment	Under large rocks		Under small rocks		Visible on the surface		
	Mean	95% CI	Mean	95% CI	Mean	95% CI	
Daytime	Control	94.0	9.1	6.0	9.1	0.0	0.0
	Harlequin duck odor	70.7	17.9	28.0	17.6	1.3	2.7
	Char odor	90.7	10.1	9.3	10.1	0.0	0.0
Nighttime	Control	48.6	15.9	3.3	4.9	48.1	16.0
	Harlequin duck odor	46.6	14.6	17.9	10.7	35.3	15.6
	Char odor	23.3	12.9	7.3	9.3	69.4	15.6

Note: CI, confidence interval.

**Fig. 2.** Mean densities of stonefly nymphs on surface rocks during the day (□) and night (■) in the Maligne Lake Outlet, Lower Maligne River, and Middle Maligne River from April to June in 1999. Rock size was  $0.87 \pm 0.04 \text{ m}^2$  in the Maligne Lake Outlet,  $0.84 \pm 0.03 \text{ m}^2$  in the Lower Maligne River, and  $0.85 \pm 0.03 \text{ m}^2$  in the Middle Maligne River. Error bars represent 95% confidence intervals.



**Fig. 3.** Mean densities of stonefly nymphs under large (dark bars) and small (light bars) surface rocks in the MLO from April to June in 2000. Large rock size was  $1.44 \pm 0.04 \text{ m}^2$  and small rock size was  $0.66 \pm 0.12 \text{ m}^2$ . Error bars represent 95% confidence intervals.



duck-treatment nymphs were more likely to remain under the large rocks (Tukey's HSD test,  $p = 0.035$ ).

### Discussion

The intent of this study was to determine if predation risk accounted for the patterns of stonefly nymph abundance on surface rocks in the Maligne Valley watershed. It was of particular interest to determine if the seasonal declines observed in the MLO and Lower Maligne River represented a shift from aperiodic to nocturnal use of surface rocks as overall risk in each site increased. However, there was no evidence for a diel shift in rock use. Nevertheless, it is interesting that nighttime and daytime densities were matched and that nymphs exposed to harlequin duck odor cues tended to remain in refuge at night. Both results are noteworthy, as nymphs are often more visible on the substrate surface at night because it is the least riskiest time to be active (Allan 1978; Williams 1986; Soluk and Collins 1988a; Flecker 1992; Culp and Scrimgeour 1993; Douglas et al. 1994; Peckarsky and McIntosh 1998; Huhta et al. 1999; McIntosh and Peckarsky 1999; Elliott 2000). This more typical response was observed in the Middle Maligne River, a site where nymph densities did not change seasonally and also where risk was consistent year-round. Nymphs exposed to char odor were also most visible on the substrate surface at night.

It is possible that nymphs do not change their temporal use of surface stones when overall risk increases, but change their spatial use of surface stones instead. The declines in density, therefore, may have represented a shift from small to large rocks as overall risk in the MLO increased. However, there was no evidence for a spatial shift in surface-rock use even though nymphs were always more abundant under large than small rocks. Experimental results also revealed a strong preference for large rocks, regardless of treatment. Large rocks are likely preferred over small ones because they are harder for vertebrate predators to disturb and thus provide a safe refuge (Rabeni and Minshall 1977; Reice 1980; Feltmate et al. 1986; Quinn and Hickey 1990; Peckarsky 1991). Resources, both invertebrate prey and plant/alga matter, are also more abundant under larger rocks (Quinn and Hickey 1990; N.A. McCutchen, unpublished results).

It remains unclear why harlequin duck odor suppresses the nocturnal activity of nymphs when harlequin ducks are visual predators. Harlequin ducks are relatively unpredictable, however, as their use of sites varies seasonally and annually (Hunt and Ydenberg 2000; N.A. McCutchen, unpublished results). Nymphs may respond to this unpredictability by taking the most prudent course of action, which would be to remain under rocks at all times (e.g., Richardson 2001). This may be only a short-term response, however. Harlequin ducks are only present for a few months of the year (Hunt and Ydenberg 2000; N.A. McCutchen, unpublished results). For the long-lived nymph (1–3 years; Hynes 1976), the best long-term option may be to expend the energy required to move to a site free of harlequin ducks rather than remain in a high-risk area. It is also possible that nymphs remain in the harlequin duck site but shift farther down into the substrate (N.A. McCutchen, unpublished results).

This study strongly suggests that predators and the type of risk they represent account for the different patterns of stonefly nymph abundance in the Maligne Valley watershed, although not in the ways expected. Only further investigation into the interactions between nymphs and their vertebrate predators will illuminate exactly how these patterns are facilitated.

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