

## *Evolution of net-spinning caddisflies: a hypothetical mechanism for the reproductive isolation of conspecific competitors*

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Net-spinning caddisflies construct capture nets with a wide range of mesh sizes, although the ancestral net-spinner presumably spun large-meshed nets while inhabiting high current velocity microhabitats. Thorp proposed that the evolutionary diversification of mesh sizes resulted from the competitive displacement of some net-spinners into lower flow microhabitats where less water and therefore less food passed through their nets. As a result, smaller meshes were selectively advantageous because they captured smaller, more abundant food items. Although competition is often strongest between conspecifics, Thorp did not present a mechanism by which reproductive isolation, and ultimately speciation, would be achieved between the competitively inferior and superior individuals. One such mechanism may have been temporal isolation. Because the initially large-meshed nets of the competitively inferior caddisflies would have been inefficient in the lower flow microhabitats, these individuals would have theoretically grown slower and emerged as adults later than the competitively superior individuals, which in turn would have led to reduced gene flow between the two populations. Although temporal isolation may not have been their final reproductive isolating mechanism, it may have opened the door to the evolution of other isolating mechanisms.

Larval net-spinning caddisflies (Insecta: Trichoptera) construct silken catchnets to filter organic matter from streams. These catchnets are made with a wide range of mesh size openings; for example, mesh sizes in the most species rich net-spinning family, Hydropsychidae, range from  $\sim 100 \mu\text{m}^2$  in mature *Macrostemum transversum* (Walker) larvae to  $> 200000 \mu\text{m}^2$  in mature *Arctopsyche irrorata* Banks larvae (Wallace 1975). Despite this, species, and often instars within species, generally build nets with a specific mesh size, which in turn usually positively correlate to the water flow regime each inhabits (i.e., large mesh spinners primarily occur in high flow habitats and small mesh spinners occur in low flow habitats) (Wallace and Merritt 1980). This positive

correlation may occur largely because of two physical facts: (1) large-meshed nets are less efficient than small-meshed nets and therefore must filter more water to capture the same amount of food, and (2) fast currents transport more water than slow currents (Wallace et al. 1977). A generally held conception among Trichoptera biologists is that ancestral net-spinners inhabited high current velocity habitats in headwater streams and constructed large-meshed nets (Wallace et al. 1977). Therefore, a central question in the evolution of net-spinning caddisflies is: What was the selective force driving mesh size reduction to produce the diversity of meshes we see today? Three hypotheses regarding this macroevolutionary mesh down-sizing have been proposed (see below). However, as Thorp et al. (1986) emphasized, these hypotheses should not be confused with hypotheses explaining the contemporary distribution of net-spinners (e.g. Malas and Wallace 1977, Alstad 1987). Though the selective pressures responsible for diversifying mesh sizes may be similar to the pressures structuring net-spinner communities, these are nonetheless two distinct processes.

### **Hypotheses for mesh size reduction**

Although each of these hypotheses has strengths and weaknesses, an extensive treatment of them is beyond the scope of this paper. My intent is to simply outline each hypothesis as proposed and to identify any papers that present detracting arguments of them.

(1) The "capture-rate hypothesis" (developed by D.N. Alstad) is largely based on two general assumptions: (1) that food concentration progressively increases down the stream continuum, and (2) that water

flow velocity progressively decreases down the stream continuum (Alstad 1982). Therefore, although headwaters are resource depauperate, the high current velocity delivers more water per unit time than in downstream reaches. Large meshes may have been beneficial or even necessary for the ancestral net-spinners in these habitats because they minimize the drag associated with high velocity flow (Alstad 1982) and because they filter even more water per unit time than small meshes. Alstad (1982) suggested that as net-spinners progressively colonized downstream reaches, smaller meshes evolved in response to the greater food concentration and lower flow velocity. Although not clearly stated, the presumed selective advantage of these small meshes is that they attain the same filtration rate as large meshes in the resource poor upstream reaches (see Loudon and Alstad 1990). See Thorp (1983) and Thorp et al. (1986) for potential problems with the capture-rate hypothesis, and Alstad (1986) for responses to some of these contentions.

(2) The “competitive displacement hypothesis” (developed by J.H. Thorp) suggests that because high velocity flow delivers a lot of water per unit time and carries relatively large particles (which include high quality food items like drifting animals (Wallace et al. 1977)), ancestral net-spinning caddisflies inhabiting these microhabitats could “afford” to construct relatively inefficient, large-meshed nets to focus on high quality animal material. Because space within these high quality, high current velocity microhabitats is finite, Thorp (1983) proposed that net-spinners’ original impetus for venturing into lower current velocity microhabitats was competitive displacement by other net-spinning caddisflies. Since numerous flow microhabitats occur within a single stream reach (Hart et al. 1996), there presumably would have been no shortage of nearby low flow habitats to colonize. After being forced into progressively lower flow microhabitats, progressively smaller mesh openings were selectively advantageous because they captured smaller and more abundant, yet lower quality, food items. See Miller (1984) and Alstad (1986) for potential problems with the competitive displacement hypothesis, and Thorp (1984) and Thorp et al. (1986) for responses to these objections.

(3) The “predation hypothesis” (developed by J.C. Miller) proposes that mesh size reduction was initiated by some net-spinners that “wanted” to colonize lower flow microhabitats on the sides and bottoms of rocks. These microhabitats presumably require less energy and are less dangerous than high flow microhabitats because (1) movement around the substrate is easier, (2) drifting debris damages nets less often, and (3) dislodgment and subsequent predation by drift-feeding predators is less likely (Miller 1984). However, low velocity habitats also have a downside relative to high velocity habitats: more benthic-feeding predators (Miller 1984).

Therefore, Miller (1984) suggested that only those caddisflies that constructed their nets within protective retreats could successfully colonize the less catastrophic low flow habitats. However, moving their net inside a retreat forced net-spinners to reduce the overall size of the net, which made them less productive. To compensate for this reduced productivity, natural selection favored mesh size reduction in order to capture smaller, more abundant particles. Therefore, this hypothesis and the competitive displacement hypothesis have the same result – that meshes were down-sized as larvae moved from high to low velocity microhabitats within the same stream reach; they differ in the original impetus for colonizing the lower flow microhabitats and in the selective pressure causing the mesh size reduction (i.e., reduced water flow velocity in the competitive displacement hypothesis vs reduced net size in the predation hypothesis). See Thorp (1984) for potential problems with the predation hypothesis.

Because these hypotheses attempt to explain a macroevolutionary process, it is essentially impossible to know which of them, if any, were important in the mesh size diversification of net-spinning caddisflies. However, given the current knowledge and perception of net-spinner ecology and evolution, Thorp’s competitive displacement hypothesis is as viable as either of the others. Yet the competitive displacement hypothesis as proposed (Thorp 1983, 1984, Thorp et al. 1986) is incomplete for two related reasons: (1) competition is generally strongest between conspecifics (Darwin 1859), and (2) locally adapted phenotypes evolve most readily after assortative mating is initiated (Mayr 1963). Therefore, intraspecific competitive displacement would have likely played a role in the evolution of mesh size diversity under Thorp’s hypothetical scenario, although this diversification would have been most likely only after the displaced and the displacing individuals became reproductively isolated. Though Thorp (1983) alluded to the possibility of intraspecific competitive displacement, he only postulated a mechanism by which conspecific larvae became spatially isolated. However, if larvae were physically separated but adults were not (i.e., they continued to represent a panmictic population), then reproductive isolation would not have occurred (Mayr 1942). In other words, reproductive isolation, and in turn speciation, requires the physical isolation of adults.

### Temporal reproductive isolation

One possible reproductive isolating mechanism among competing net-spinning caddisflies may have been temporal separation of adults from different larval microhabitats. Specifically, larvae that were forced into inferior, low flow microhabitats where their nets were at

least initially maladapted would have theoretically developed more slowly than those individuals inhabiting prime, high flow microhabitats. In turn, the displaced larvae would have emerged as adults later in the year, thereby reducing gene flow between them and the competitively superior individuals. Food quantity and quality do influence the development and emergence time of some aquatic insects (see Sweeney 1984), thereby lending support to this possibility in larval net-spinners. Furthermore, if a larva's competitive ability was at least partly heritable, then the offspring of poor competitors were probably also poor competitors. As such, lineages presumably would have been assorted into high and low quality microhabitats generation after generation, which would have led to continual temporal isolation of the displaced and the displacing populations.

Though Thorp (1983) only applied his theory to the ancestral macroevolution of net-spinners, there is no reason to expect that competition for space is any less prevalent now than it has been in the past (e.g., *Cheumatopsyche pasella* Ross reaches densities of  $>45000$  individuals  $m^{-2}$  on snags in the Savannah River (Cudney and Wallace 1980)). Therefore, intraspecific microhabitat partitioning and subsequent temporal isolation may continue to be an important and creative force in the evolution of net-spinning caddisflies. However, I must note that certainly not every case of this hypothetical intraspecific competitive displacement would result in cladogenesis. In some cases the displaced individuals may not emerge later than the displacing individuals and as such the population remains panmictic (e.g., development may be cued to day length so that emergence time remains the same despite slower growth (see Butler 1984)). In other cases the displaced individuals may develop slower and emerge later than the displacing individuals but may be evolutionary dead-ends, going extinct before they fully diverge from the parental population (**PP**; i.e., the competitively displacing individuals). In yet other cases the population size in the high flow microhabitats may decline before the populations diverge so that the displaced individuals can re-inhabit the prime microhabitats. However, the remainder of this paper will only concern those theoretical cases that ultimately result in speciation.

Although microhabitat mediated temporal isolation may independently divide a net-spinner population into two genetically distinct (sub)populations and eventually species, the mechanism outlined above is probably an over-simplified representation of this process in most cases. In all likelihood gene flow would occur between the daughter population (**DP**; i.e., the competitively displaced individuals) and the **PP**, though at a less than panmictic rate, primarily due to one or both of the following phenomena: (1) a persistence of the environmental conditions that allowed the **PP** to grow larger than prime microhabitats could support, and (2) a

concerted relationship between three life history traits: (i) the phenotypic variability in emergence time over the population as a whole, (ii) the average adult life span, and (iii) the mean difference in emergence time between populations. Both of these situations will be considered in greater detail below.

### Environmental persistence

A unidirectional flow of genes from the **PP** to the **DP** would potentially continue as long as **PP** individuals are competitively displaced from high current velocity microhabitats and emerge later in the year with the **DP**. The importance of this gene flow for the persistence of the **DP** greatly depends on whether its realized niche shifts to a new ecological dimension within (Fig. 1a) or outside (Fig. 1b) the **PP**'s fundamental niche. A population's fundamental niche is the  $n$ -dimensional volume in ecological space (the axes of which are all the potentially encountered environmental variables) where its growth rate,  $\bar{R}$ , is  $\geq 1$  (i.e., births at least equal deaths) in the absence of interspecific competition while the population's realized niche is the ecological volume it actually inhabits (Hutchinson 1958, Holt and Gaines 1992). Therefore, if the **DP**'s realized niche remains within the **PP**'s fundamental niche (Fig. 1a), then the **DP** can potentially exist indefinitely without immigration because  $\bar{R} \geq 1$ . This is not true, however, if the **DP**'s realized niche is outside the **PP**'s fundamental niche (Fig. 1b), which is an example of a source-sink population (Pulliam 1988). Because  $\bar{R}$  is  $< 1$  outside the fundamental niche, the **DP** will presumably go extinct in the absence of immigration unless the population evolves so that  $\bar{R}$  is  $< 1$ . However, theoretical work by Holt and Gaines (1992) suggests that in source-sink structured populations, selection should favor adaptive honing of species to their primary niche (= source population) rather than adaptation to new niches (= sink population). The reason is that competition, and therefore selection, is usually strongest in areas with the largest population and the highest mean individual fitness, both of which generally occur in the source rather than the sink (Holt and Gaines 1992). Therefore, unless competitive displacement from the prime microhabitats is extensive such that many potentially beneficial mutants are "tested" in the new niche, speciation by this mechanism may be unlikely in source-sink populations (Holt 1996).

The eventual cessation of this gene flow, regardless of whether the **DP**'s realized niche is inside or outside the **PP**'s fundamental niche, would likely result from either: (1) an environmental change that eliminates competitive displacement from the prime microhabitats long enough for each population to begin projecting down distinct evolutionary paths; once displacement stopped, intrinsic reproductive isolating mechanisms could po-

tentially evolve rapidly between the populations (Avice 1994), (2) the evolution of prezygotic reproductive isolating barriers in response to selection against inferior hybrids, i.e., reinforcement (e.g., Sætre

et al. 1997, Rundle and Schluter 1998); since gene flow can swamp out local adaptation and produce less fit offspring (Storfer and Sih 1998), any gene that reduces hybridization may have a selective advantage in both populations, (3) the evolution of different phenotypic character states which increase each population's mean fitness but which secondarily act to prezygotically isolate the populations, i.e., differential pleiotropic character selection (e.g., Johannesson et al. 1995, Nagel and Schluter 1998), or (4) the evolution of unique secondary sexual characters (Lande 1981) or mate/gamete recognition genes (e.g., Ferris et al. 1997, Swanson and Vacquier 1998) in the DP to which PP individuals do not respond, or vice versa.

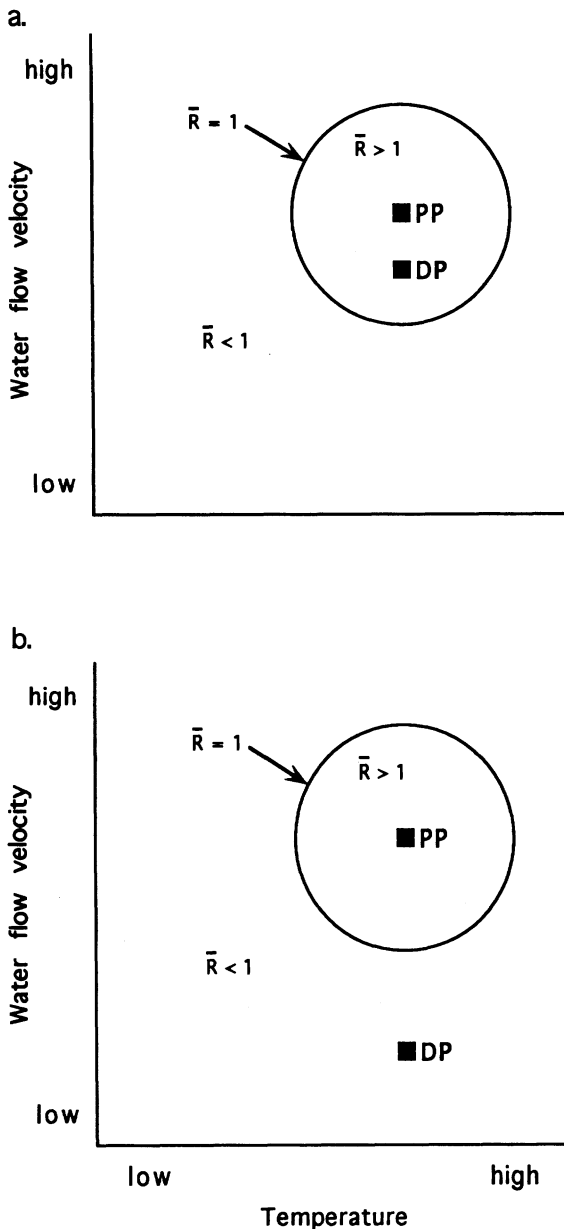


Fig. 1. The hypothetical fundamental and realized niches of a parental population (PP), and the realized niche of a daughter population (DP) (a) within and (b) outside the PP's fundamental niche. The PP's fundamental niche is the area in ecological space (in this example the two-dimensional circular area defined by water flow velocity and temperature) in which the population's growth rate,  $\bar{R}$ , is = 1 in the absence of interspecific competition, whereas each populations' realized niche is the actual ecological space that each occupies (signified by solid squares). [This figure is amended from Fig. 1 of Holt and Gaines (1992).]

### Coordination of life history traits

Unless the PP and the DP both episodically mass emerge from the stream, each presumably exhibits variation in emergence time caused by differential egg hatching times or maturation rates. If the temporal disparity in mean emergence time between populations is also relatively short or if the adult life span is relatively long, then early emergent individuals from the DP may overlap and mate with the PP while late emergent individuals from the PP may overlap and mate with the DP, thus resulting in bidirectional interpopulation gene flow. However, Stam (1983) and Butlin (1990) modeled similar situations using sympatric plant populations (with slightly different flowering times) and sympatric phytophagous insect host races (with slightly different emergence times), respectively, and found that despite the gene flow between populations, this situation could eventually lead to substantial reproductive isolation between them. In short, if some of the variation in emergence time is heritable, then this mechanism may induce a preferential flow of early emergence genes out of the DP and into the PP and late emergence genes out of the PP and into the DP, thereby causing the mean emergence time of each population to evolve in opposite directions. As Stam (1983) noted, this isolating mechanism is somewhat unique because it is initiated by an environmental difference between populations and not by disruptive selection (if the (sub)populations are considered as a single element, then any allele frequency change in one part of the population is compensated with an opposite change in the other part of the population), which is considered mandatory in most sympatric speciation models (see Futuyama 1998). However, this mechanism does require substantial genetic variability in emergence time and little temporal overlap between early (i.e., PP) and late (i.e., DP) emerging individuals for reproductive isolation to be realized (Stam 1983).

## Conclusions

Under the hypothetical cladogenic scenarios proposed above, the initial temporal isolation between inferior and superior net-spinner competitors is of utmost importance because two populations cannot begin evolving down independent paths until assortative mating is initiated; i.e., speciation cannot occur in a panmictic population (Mayr 1942). Therefore, although gene flow would likely continue between the two populations after the temporal separation originates, speciation may be unlikely without this separation. Consequently, if Thorp's competitive displacement hypothesis was indeed a mechanism by which net-spinning caddisfly meshes diversified, then temporal isolation of differentially skilled conspecific competitors may have played an integral role in this diversification.

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## Erratum.

Plague, G. R. 1999. Evolution of net-spinning caddisflies: a hypothetical mechanism for the reproductive isolation of conspecific competitors. – *Oikos* 87: 204–208.

Line number 32 on the second column of page 206, which currently reads:

evolves so that  $\bar{R}$  is  $< 1$ . However, theoretical work by  
should be changed to:

evolves so that  $\bar{R}$  is  $\geq 1$ . However, theoretical work by

*Ed.*