The host associations and developmental plasticity of *Nemoria darwiniata*

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Introduction. Herbivorous insects and the green plants upon which they feed comprise over half of the macroscopic species on Earth (Farrell et al. 1991, Bernays and Chapman 1994) and much research has attempted to understand the important ecological and evolutionary interactions between insect herbivores and their plant hosts (Ehrlich and Raven 1964, Mitter et al. 1991, Thompson 1994, Funk et al. 1995, Farrell 1998). The diverse relationships between plants and their insect herbivores have existed for many millions of years, and thus form an important component of our planet's biodiversity.

Shifts in these ecological interactions, such as the movement of an insect species from one type of host plant to another, are a potential source of speciation (Futuyma 1979, Thompson 1994). However, herbivorous insects are generally perceived as being conservative in their host plant associations (Farrell et al. 1992), and unlikely to readily switch to a novel host. This is not to say that most herbivorous insect species interact with only one host; in fact, though some insects are found exclusively on a single plant species (extreme specialists), others may be found on several hosts from a broad range of plant families (generalists). Specialists and generalists are opposite ends of the ecological specialization spectrum (Futuyma and Moreno 1988), and a longstanding notion in evolutionary theory assumes that specialists are derived from generalists (Thompson 1994).

An example of a specialized herbivorous insect is *Nemoria arizonaria* (Grote). This geometrid caterpillar of the southwest United States feeds on only a few species of oaks in the genus *Quercus*. Furthermore, it has evolved a striking developmental polymorphism, whereby caterpillars eating the catkins (flowers) of the oaks turn into catkin-mimics, and caterpillars eating oak leaves develop into twig mimics (Mcfarland 1988, Greene 1989). Experiments controlling for diet (catkins and leaves), temperature,

photoperiod, and reflected light (yellow or green) revealed that diet alone is the cue that triggers this developmental response (Greene 1989, 1996). This species also possesses a specialized hiding behavior: the caterpillars of either morph will actively seek out its respective cryptic background if placed on another part of the plant (Greene 1989). The narrow host range of this species, along with selective forces such as predation have likely favored the evolution of such specialized traits (Greene 1999).

The developmental switch displayed by *Nemoria arizonaria* is an example of a polyphenism, in which an individual has the capacity to develop any of several discrete phenotypes depending on external, environmental or social conditions (Greene 1999). The evolution of polyphenisms, and phenotypic variation in general, "is emerging as one of the most exciting fields in biology" (Greene 1999), and may have strikingly contrasting predictions for specialists and generalists. Highly specialized organisms, such as *Nemoria arizonaria* or the dung beetle *Onthophagus acuminatus*, may display a threshold developmental response: discrete morphologies are produced from variation in diet. *Onthophagus acuminatus* males produce horns or do not produce horns on the basis of the amount and quality of dung they receive as larvae (Emlen 1994, 1996, 1997). Adult male morphology in turn affects an individual's mating strategy, with horned males guarding the tunnels of females and hornless males dig side tunnels that may bypass the guarding male.

If the environmental scenarios favoring the evolution of a threshold developmental response in specialists seem straightforward, then by contrast the developmental plasticity of generalists is relatively unclear. If we assume that specialists are derived generalists, then we might predict that phenotypic plasticity in a generalist is flexible, but perhaps the variation is more continuous rather than discrete. Furthermore, though the selection pressures experienced by a specialist and a generalist may be similar, the fact that a generalist experiences more environmental conditions than a specialist might preclude each phenotype's ability to fulfill its adaptive purpose. For example, in the case of our cryptic caterpillar, a similar generalist caterpillar might not "match" its background as well as the specialist. It should appear obvious then, that our appreciation and understanding of the diversity of examples, underlying mechanisms, and evolutionary and ecological reasons favoring phenotypic variation is truly just beginning.

In this study, I have examined the phenotypic variation expressed by an organism at the opposite end of the ecological specialization spectrum from *Nemoria arizonaria*, its generalist congener *Nemoria*

darwiniata (Dyar). The purpose of the study was threefold: to illuminate the biology and local host associations of a poorly known caterpillar; to conduct rearing experiments to determine if phenotypic plasticity exists, and whether this depends on the host plant; to see whether phenotypic plasticity, if present, is more continuous than in the specialist congener *Nemoria arizonaria.*

Nemoria darwiniata is a host generalist that's range covers the western United States (Fig.1). It is purported that the caterpillars feed on many broadleaf woody plants from several families, including Rhamnaceae (*Ceanothus* sp.)*,* Salicaceae (*Salix* sp.), Ericaceae, Anacardaceae (*Rhus* sp.) and Fagaceae (*Quercus* sp.) (Ferguson 1969, Ferguson 1985, Miller 1995). Miller (1995) also stated that caterpillars of *N. darwiniata* may be different colors, however no systematic studies had been undertaken to determine the influence of diet on larval development.

Methods. We captured *Nemoria darwiniata* moths at blacklights in the Rattlesnake Mountains and the Garnet Mountains near Missoula, Montana between 25 June and 4 August 2000. Gravid females were placed in separate vials and either remained in these vials until they laid their eggs, or were placed into separate flight cages for oviposition experiments.

To separate between maternal effects and the influence of food plant, we divided sibling groups of caterpillars and reared related individuals on different hosts. Each larva was placed in a separate plastic container with a sprig of fresh vegetation. Stems of the food plants were placed in aquapics to keep food fresh. Fresh vegetation was provided for larvae every second or third day as needed. Caterpillars were raised in the Health Sciences building on the University of Montana campus and at the Biological Research

Station at Fort Missoula. Larvae were examined on a regular basis during their development.

Because *Nemoria darwiniata* was reported to be a broad generalist from previous accounts (Miller 1995, Ferguson 1985, Ferguson 1969) we collected plants from a wide variety of plant families that were common where the adult moths were found, or that were in plant families that are known hosts of other closely related *Nemoria* species. The relative growth of each caterpillar was scored as follows: --, caterpillar did not eat or grow on treatment; +, caterpillar ate and grew on treatment, but did not pupate; +++, caterpillar ate, grew, and pupated on treatment.

Results. We captured thirteen gravid females (12 from Rattlesnake Mts., 1 from Garnet Mts.), and from the eggs raised 186 caterpillars on 30 species of plants (Table 1). Table 2 presents the number of larvae assigned to each treatment, their relative success on the treatment, and the general color(s) of the caterpillars assigned to the treatment. Caterpillars did not grow on 16 plant species, grew without pupating on nine plant species, and pupated on five plant species.

Caterpillars showed a remarkable range of coloration patterns, from ivory white to chocolatey brown, others were yellow, orange, tan, pale green, and silver (Plate 1). Generally, the color of the caterpillar matched its background well: an examination of figure 2 shows that most all of the lightest caterpillars (8/11) were fed the white or yellow flowers of *Ceanothus velutinus* or *Tilia* spp., most of the darkest caterpillars (4/7) were fed the leaves of *Crataegus douglasii* or *Amelanchier alnifolia*, and nearly all pale green or silver caterpillars (28/30) were fed the leaves of *Ceanothus velutinus*, *Salix scouleri*, or

Rhus glabra. Larvae that scored at least + were included in the statistical analysis regarding differences in color. For the purposes of the analysis, caterpillars were categorized as one of four colors: white, brown, pale green or silvery, or other. Caterpillars were also categorized by plant treatment; those placed on flowers were placed in group 1, those placed on *Crataegus douglasii* and *Amelanchier alnifolia* were placed in group 2, caterpillars eating the leaves of *Ceanothus velutinus, Salix scouleri,* and *Rhus glabra* were placed in group 3, and all others were placed in group 4. The differences in coloration due to plant treatment were significant well below the standard alpha level of 0.05 using a G-test: G-value= 101.42, with nine degrees of freedom.

Three general factors contributed to the overall appearance of the caterpillar: pigments beneath the epidermis throughout the caterpillar body, the pattern of darker pigments (likely to be melanins) present in the lateral surface the dorsolateral processes, and white "bumps" on the surface of the caterpillars skin (Fig. 2). These bumpy structures could create dramatic effects in the appearance of the caterpillars, highlighting the darker lateral pattern or obscuring it all together. The density and total number of bumps over the surface of the skin varied greatly between dark and light caterpillars. It is not known whether the white color of the bump is due to pigments or structural colors.

Discussion. The observed color variation in caterpillars of *Nemoria darwiniata* supported the prediction that a generalist will display both flexible and continuous phenotypic plasticity that does not match its background to the degree of a specialist congener. It should be noted that I treated color as a discrete variable in my statistical analysis; however, this does not imply that the variation in color was wholly discrete.

Rather, I was unable to develop a method that quantified the observed variation, and opted instead to lump similar-looking caterpillars into groups. The individuals within a group were not identical, but variation within a group was much lower than the variation between groups.

The larval color morphology of *Nemoria darwiniata* was found to be dependent of the larval diet, however the exact environmental cue conferring morph induction remains unknown. In *Nemoria arizonaria*, the diet was limited to two parts (leaves or catkins) of the same closely related plant species, and morph induction was determined by chemical cues within the diet. In the case of *Nemoria darwiniata*, caterpillars ate fourteen different plant species (including both the flowers and leaves of two) from ten plant families. It seems less probable that *Nemoria darwiniata* would be able to track the chemistry of such diverse host plants for use as a cue in morph induction, but that it might use a cue that is wholly different than its congener would be equally astonishing.

Nemoria darwiniata is a broad host generalist with a broad geographic range, and separate populations of this species encounter different frequencies of their host plants in the local environment. In the Rattlesnake Mountains, *Nemoria darwiniata* was collected at a site where *Ceanothus velutinus* was an abundant shrub. The caterpillars reared from the eggs of females captured at this site performed well on both the flowers and plants of this species, but caterpillars from a site with a more abundant host may perform differently. Furthermore, if a mosaic of host performance and associations exists (see Thompson 1994 for the "Mosaic Theory of Coevolution"), there may also be a mosaic of cryptic color patterns. I think such an exploration of the geographic variation in *Nemoria*

darwiniata would shed brilliant light on the developmental plasticity possible for a broad host generalist.

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Table 1. Plant species offered to caterpillars of *Nemoria darwiniata*. Plants were identified using Kershaw et al. (1998). *Caterpillars were fed only leaves in this plant treatment; any flowers were removed from sprigs. **Caterpillars were fed only flowers in this plant treatment; leaves were removed from sprigs.

Family	Species
Coniferaceae	*Juniperus* spp.
	Pinus ponderosa
	Pseudotsuga mensizii
Saxifragaceae	*Ribes aureum*
	Ribes cereum
Salicaceae	*Populus trichocarpa*
	Salix scouleriana
Rhamnaceae	*Ceanothus velutinus,* leaves*
	Ceanothus velutinus, flowers**
Elaegraceae	*Sheperdia canadensis*
Rosaceae	*Amelanchier alnifolia*
	Crataegus douglasii
	Holodiscus discolor
	Physocarpus malvaceus
	Prunus virginiana
	Rosa woodsii
	Rubus parvifolia
Aceraceae	*Acer glabrum*
Ulmaceae	*Ulmus pumila*
Hydrangaceae	*Philadelphus lewisii*
Caprifoliaceae	*Lonicera* spp.
	Symphoricarpus albus
Fagaceae	*Quercus macrocarpa,* leaves*
	Quercus macrocarpa, catkins**
Juglandaceae	*Juglans major*
Betulaceae	*Alnus incana*
	Betula papyrifera
Malvaceae	*Tilia* spp., leaves*
	Tilia spp., flowers**

Anacardaceae	*Rhus glabra*
	Rhus trilobata
Ericaceae	*Arctostaphylos* spp.
	Vaccinium spp.

Table 2. The relative growth and observed color variation in *Nemoria darwiniata*. The first column describes the treatment the caterpillar received, the second column lists the number of individual larvae placed on each treatment (the number in parentheses describes the number of sibling groups represented in the treatment), the third column describes the maximum relative achieved by an individual within a treatment (scoring is detailed in the text), and the final category describes the general color developed by the caterpillars in the treatment (the colors are arranged in descending order beginning with the most frequently observed).

Treatment	N (N sibling groups)	Relative growth	Color(s)
Acer glabrum	3 (2)	--	N/A
Alnus incana	2 (2)	--	N/A
Amelanchier alnifolia	6 (5)	+	Brown
Arctostaphylos spp.	12 (8)	+++	Tan, brown, pale green, yellow
Betula papyrifera	4 (3)	+	Yellow, green
Ceanothus velutinus, flowers	5 (5)	+++	White
Ceanothus velutinus, leaves	21 (10)	+++	Silver, pale green, white, brown, orange
Crataegus douglasii	9 (5)	+++	Yellow, brown, tan, green
Holodiscus discolor	9 (6)	--	N/A
Juglans major	2 (2)	--	N/A
Juniperus spp.	1 (1)	--	N/A
Lonicera spp.	5 (4)	--	N/A
Philadelphus lewisii	8 (6)	--	N/A
Physocarpus malvaceus	5 (4)	--	N/A
Pinus ponderosa	3 (3)	--	N/A
Populus trichocarpa	6 (6)	+	Tan, yellow
Prunus virginiana	3 (3)	--	N/A
Pseudotsuga mensizii	7 (6)	--	N/A
Quercus	2 (2)	+	Tan

macrocarpa, catkins			
Quercus macrocarpa, leaves	2 (2)	--	N/A
Rhus glabra	6 (4)	+++	Pale green, yellow
Rhus trilobata	2 (1)	+	Tan
Ribes aureum	3 (3)	---	N/A
Ribes cereum	7 (6)	+	Yellow, brown
Rosa woodsii	7 (6)	+	Green, tan
Rubus parvifolia	2 (2)	--	N/A
Salix scouleriana	16 (8)	+++	Silver, pale green, white
Sheperdia Canadensis	6 (4)	--	N/A
Symphoricarpus albus	6 (5)	--	N/A
Tilia spp., flowers	4 (4)	+	White
Tilia spp., leaves	3 (2)	+	Yellow
Ulmus pumila	3 (3)	+	Tan, white
Vaccinium spp.	6 (4)	--	N/A