Photoperiodic responses of phenologically aberrant populations of pierid butterflies (Lepidoptera)

Arthur M. Shapiro
University of California, Davis, California

Follow this and additional works at: https://scholarsarchive.byu.edu/gbn

Recommended Citation
Available at: https://scholarsarchive.byu.edu/gbn/vol35/iss3/7

This Article is brought to you for free and open access by the Western North American Naturalist Publications at BYU ScholarsArchive. It has been accepted for inclusion in Great Basin Naturalist by an authorized editor of BYU ScholarsArchive. For more information, please contact scholarsarchive@byu.edu, ellen_amatangelo@byu.edu.
PHOTOPERIODIC RESPONSES OF PHENOLOGICALLY ABERRANT POPULATIONS OF PIERID BUTTERFLIES (LEPIDOPTERA)

Arthur M. Shapiro

ABSTRACT—Two local pierid populations in western North America showing regionally aberrant phenologies were investigated in the laboratory. Neither a partially bivoltine Pieris napi from the Sierra Nevada foothills in El Dorado County, California (surrounded by univoltine populations), nor a vernal-univoltine P. occidentalis from a foothill outlier of the Colorado Front Range (below bivoltine populations) showed unusual responses to controlled developmental regimes in the laboratory. Their unusual phenologies are hypothesized to be the product of microclimate. Failure to undergo genetic adaptation to unusual microclimates is discussed with particular reference to the presence or absence of gene flow from nearby normal populations.

The timing of life-history phenomena in an insect population is determined by physiological responses to environmental stimuli. These proximate controls reflect a genetic basis believed to be the product of natural selection for seasonal cycles appropriate to the environment of the population. In the western United States topography has a dramatic impact on climate, and great differences may occur over short ground distances. How closely can insect populations adapt to their immediate climates on a microgeographic scale? Phenological adaptation is merely one case of the more general problem of population differentiation (cf. Ehrlich and Raven, 1969; Ehrlich et al., 1975). In most organisms, at least prior to the advent of electrophoretic genetics, population differentiation was assessed on the basis of visible phenotypic characters. Such characters, like the enzyme systems studied by electrophoresis, are often not translatable into specific selection pressures. In markedly seasonal climates the nature of selective pressures acting on phenology may be very apparent. Where local deviations from the broad geographic pattern of voltinism are observed in a species, the potential exists for the demonstration of microgeographic (or ecotypic) differentiation. This is the fourth paper in a series exploring the evolution of seasonality in the butterfly genus Pieris in western North America.

In various multivoltine Pieridace both phenotype and diapause are under photoperiodic control. The two sets of developmental options (diapause/direct development; vernal/estival phenotype) may be physiologically coupled (Pieris napi Linnaeus complex) or not (P. protodice Boisdalv & LeConte, P. occidentalis Reakirt). Recent studies have shown that univoltinism in both groups is derived from multivoltinism, accompanying invasion of a short-summer climate (P. occidentalis, Shapiro, 1975a) or persistence in a progressively drier one (P. napi, Shapiro, 1975b). Such patterns are defined over broad geographic areas. California P. napi, for example, is differentiated into a commonly bivoltine, heavily pigmented subspecies in the coastal summer-fog belt and a univoltine, more lightly marked subspecies in the interior, where summers are clear and hot. The transition between the subspecies appears to be in the form of a steep cline through the central Coast Ranges (Shapiro, in preparation).

Recently Lees and Archer (1974) have reported the existence of phenological differences among napi populations on a much finer scale. They have found apparently relict univoltine populations in suitable (bog-heath) habitats completely surrounded by multivoltine ones in the British Isles. Their preliminary interpretation of this situation is that it provides evidence for multiple invasions of Britain by napi stocks having different phenological characteristics and source regions. In the course of recent work on pierid phenology and evolution, the existence of regionally aberrant populations has been brought to my attention in both the napi and protodice-occidentalis groups. In both cases the populations appear to be unique, rather than forming a repeating pattern as in British P. napi. They would therefore seem to be good candidates for

1Department of Zoology. University of California, Davis, California 95616.
local genetic differentiation under atypical microclimate.

_Pieris napi_ in the Sierra Foothills

_Pieris napi_ from interior California are, as noted above, univoltine and monomorphic in nature. Under laboratory conditions they can be reared without diapause; then they produce the estival phenotype "castoria" virtually unknown in the wild in the interior (Shapiro, 1975b). In June 1974 Mr. William Patterson of Sacramento, California, took several wild "castoria" of both sexes in the canyon of the American River below Auburn in the Sierra Nevada foothills (El Dorado County, 650 feet). The occurrence of a second brood there was confirmed in 1975. _P. napi_ is common in the canyon, producing its usual vernal phenotype in March. The second brood, which is much scarcer, unlike the first is extremely localized within the canyon—at present being known from only two densely shaded ravines where the introduced cruciferous weed watercress (_Nasturtium officinale_ R. Br. = _Rorippa nasturtium-aquaticum_ Schinz. & Thell.) grows in permanent streams (Fig. 1). Most of the wild June butterflies are identical to laboratory-bred Sierran "castoria" (Fig. 2).

On 20 March 1975 nine male and three female first-brood, vernal phenotype _napi_ were collected in one of these ravines. These included two copulating pairs in which the females were soft-winged, indicating that they had developed in the ravine itself. The eggs from these females were used in photoperiod experiments (Table 1). (Rearing methods are described in Shapiro, 1975a and 1975b.) The results are entirely typical for Sierran stock and do not suggest that American River material has a greater propensity to develop directly than do stocks from purely univoltine localities, at least under our laboratory regimes. However, this is not particularly surprising. The second brood of _napi_ in the American River gorge is much rarer than the first, indicating that is is only partial; its numbers also fluctuate from year to year.

---

Fig. 1. Locations of ravines ("B") where bivoltine _Pieris napi_ occur in the American River gorge; univoltine _napi_ are generally distributed at low density. USGS 7.5 minute "Auburn" quadrangle.
Table 1. Incidence of diapause (D) and non-diapause (ND) pupae in bivoltine (American River, 650') and univoltine (Placerville, 1800') Pieris napi from El Dorado Co., California, reared on watercress at 27 C under two photoperiods.

<table>
<thead>
<tr>
<th>Stock</th>
<th>Photophase: Continuous 15 hr</th>
<th>Pupae: D ND</th>
<th>D ND</th>
</tr>
</thead>
<tbody>
<tr>
<td>American River</td>
<td></td>
<td>15 29</td>
<td>16 6</td>
</tr>
<tr>
<td>Placerville</td>
<td></td>
<td>10 23</td>
<td>18 7</td>
</tr>
</tbody>
</table>

(In 1975 three trips by Patterson and Shapiro in season turned up only two males and one female. A later search of the host plant at the optimum time failed to turn up any napi immatures, although ten Pieris rapae larvae were found.) These circumstances suggest that the production of a second brood here is accidental, resulting from the peculiarly cool and moist conditions within the ravines. There is no evidence that the bivoltine sites are in any sense isolated from adjacent univoltine ones, nor is it clear that there is successful reproduction by the second brood in all years nor even that there is genetic continuity from year to year in the ravines; perhaps a few pu-

Fig. 2. Wild second-brood Pieris napi from the American River gorge, collected by W. Patterson in June 1974 (males at top; dorsal (left) and ventral (right) surfaces). The heavily marked female is atypical for an inland population.

Fig. 3. Phenotypes of representative lab-reared nondiapause Pieris napi from the American River stock. 27 C. continuous light; dorsal (left) and ventral (right).
pae will develop directly there whenever any female napi happens to colonize them. Experienced California collectors (R. L. Langston, B. Walsh) agree that even near the coast some localities produce second-brood napi every year and others only rarely or sporadically. Experiments have shown both developmental and phenotypic differences between coastal and inland stocks but not among the coastal stocks themselves.

Watercress is known to be host of P. napi in various Sierran sites up to about 5,000 feet (Shapiro, 1975c). The only other record of a Sierran "castoria" known to me is a fresh male taken flying among first-brood vernal napi at Lang Crossing, Nevada County, 4,500 feet, 9 June 1975. At this locality napi feeds on both watercress and native vernal crucifers. There are several possible explanations of this odd individual, but to test the hypothesis that watercress feeding itself inhibits diapause, split-brood experiments were conducted in 1975 using an Inner Coast Range stock (Gates Canyon) with no previous exposure to the plant. No evidence of a dietary influence on the incidence of diapause was found in this univoltine strain (Table 2).

### Table 2. Incidence of diapause (D) and non-diapause (ND) pupae in two split broods of a Bararea verna-feeding univoltine Pieris napi (Gates Canyon, Inner Coast Ranges, Solano Co., 750') reared at 27 C on continuous light. None of the differences was significant.

<table>
<thead>
<tr>
<th>Brood</th>
<th>Host</th>
<th>Pupae</th>
<th>D</th>
<th>ND</th>
<th>Mean ND developmental time in days</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Brassica kaber*</td>
<td>7</td>
<td>21</td>
<td>25.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Nasturtium officinale*</td>
<td>5</td>
<td>11</td>
<td>25.3</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Brassica kaber*</td>
<td>6</td>
<td>14</td>
<td>25.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lepidium latifolium*</td>
<td>5</td>
<td>16</td>
<td>24.6</td>
<td></td>
</tr>
</tbody>
</table>

Notes: (a) Tops. (b) Elongating rosettes. (c) In subsequent experiments mature tops did not support development. Butterflies in this brood were stunted.

Haystack Mountain (5,589 feet) is an isolated hill eight miles northeast of Boulder, Boulder County, Colorado (Fig. 4), where Dr. Ray E. Stanford of Denver has for several years taken small, dark vernal "calyce" phenotypes of *Pieris occidentalis* indistinguishable from the single brood above treeline in midsummer (Fig. 5). He has no summer records of *P. occidentalis* from Haystack Mountain but finds its lowland sibling *P. protodice* there in summer instead. Because *P. protodice* winters only very locally but colonizes widely in summer, this is not surprising; it does however, raise the possibility that *P. occidentalis* has undergone a phenological shift to univoltinism in

Fig. 4. Location of Haystack Mountain, Boulder County, Colorado. USGS 7.5-minute "Boulder" and "Niwot" quadrangles.
response to competition from *P. protodice* (although no such phenomenon is known at other localities where the two are sympatric). Haystack Mountain is probably the lowest elevational record for *P. occidentalis* in Colorado. In the Rockies proper it is bivoltine at middle elevations (perhaps locally trivoltine) and univoltine in the Alpine zone (cf. Brown, Eff, and Rotger, 1957) and has two seasonal phenotypes (Shapiro, 1975d).

A laboratory stock was established from ova laid by five females collected by Stanford on 6 April 1975. Under laboratory conditions their developmental and phenotypic responses (Table 3 and Fig. 6) were identical to both Sierran multivoltine and Colorado Alpine stocks (Shapiro 1974, 1975d). Once again we have no experimental evidence for the evolution of a phenological ecotype and are therefore forced to look for microclimatic explanations. Since Haystack Mountain is effectively in the Great Plains climatic regime, which is hotter and drier than the usual regime of *P. occidentalis*, it may not be surprising that conditions there would be associated with summer dormancy. This question can be settled only by laboratory duplication of Haystack Mountain conditions or by testing the developmental responses of multivoltine *P. occidentalis* stock from elsewhere reared at Haystack Mountain. We hope to carry out such experiments within the next couple of seasons.

Phenological differences are known between plains and lower montane populations of a number of Colorado butterflies (J.A. Scott, R.E. Stanford, pers. comm.), but they may go in a direction opposite to those observed in *Pieris occidentalis*. Two species (*Colias alexandra* Edwards, Pieridae; *Plebeius icarioides* complex, Lycaenidae, both legume feeders) are bivoltine on the plains and univoltine in the mountains. The basis for these differences is uninvestigated.

With no evidence for genetic differentiation of Haystack Mountain *occidentalis*, the attractive hypothesis of competitive

<table>
<thead>
<tr>
<th>Stock</th>
<th>Photophase</th>
<th>Continuous</th>
<th>Pupae:</th>
<th>15 hr</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haystack Mountain, 1975</td>
<td>0</td>
<td>0</td>
<td>22</td>
<td>0</td>
</tr>
<tr>
<td>Donner Pass, 1973</td>
<td>0</td>
<td>16</td>
<td>2</td>
<td>18</td>
</tr>
</tbody>
</table>
seasonal displacement with \textit{protodice} must be set aside. The host plants of both species on Haystack Mountain are unidentified. Both prefer species of peppergrass, \textit{Lepidium}, throughout their ranges. On the plains most crucifers are vernal species, as in lowland California.

\textbf{Discussion}

Many instances are on record of ecotypic differentiation on a microgeographic scale, particularly in plants, which have more versatility in developing isolating mechanisms than do animals (Jain and Bradshaw, 1966).

As noted above, the lack of a genetic basis for biovoltinism in Sierran \textit{Pieris napi} is not very surprising, granted the extremely restricted habitat and the extensive distribution of univoltine butterflies, with ample opportunity for gene flow. The failure of the Haystack Mountain \textit{P. occidentalis} to differentiate is more intriguing. It is, of course, possible that it has differentiated and that the lab rearing regimes were too crude or inappropriately selected to show it. It is certain that experiments to date, involving simple manipulation of constant rearing temperatures and unchanging daylengths, have given an oversimplified picture of the developmental versatility of pierids in the field. If microclimate determines aberrant voltinism in these stocks, it is very likely that humidity, for example, may interact with photoperiod and temperature in controlling development in natural populations. The same genetic information may allow \textit{Pieris occidentalis} to respond appropriately to regimes as diverse as those at Haystack Mountain (5,589 feet) and Loveland Pass (12,400 feet).

Given such plasticity, we may wonder whether the Baldwin effect (Simpson, 1953) might not come into play in populations in extreme environments. Briefly, the Baldwin effect postulates the buildup by selection of a genetically obligate basis for the adaptations produced via developmental plasticity. In an atypical but predictable climate like Haystack Mountain, might not the developmental flexibility characteristic of montane populations be lost? (Alaskan \textit{Pieris occidentalis nelsoni} seem to be evolving in this direction; Shapiro, 1975a.) One important counter-
vailing force would be gene flow, which is almost certainly operating on high-elevation univoltine *occidentalis* in Colorado (Shapiro, 1975d). Havstack Mountain is about 30 air miles from timberline and much closer than that to the montane zone, but how isolated it actually is is quite unknown. Nor is there any information bearing on how long *occidentalis* has been there—whether it is a Pleistocene relict or a recent colonization. There are much more isolated, certainly relict *occidentalis* populations in other localities east of the Front Range—the Black Hills of South Dakota and perhaps the Pine Ridge of northwestern Nebraska—which deserve study in this regard.

**Acknowledgments**

Of the collectors who provided vital information and who have been credited in the text, special thanks are due Mr. William Patterson and Dr. Ray Stanford, without whose help these experiments would have been impossible. Mr. Mark Kauzer assisted in field work and Mrs. Adrienne R. Shapiro in rearing. This research is part of a larger study of colonizing ability and the evolution of seasonality in *Pieris* funded by the Committee on Research, UCD, under grant D-804.

**Literature Cited**


