Immature Stages of Argynnis mormonia artonis (Lepidoptera: Nymphalidae) Compared to Argynnis mormonia erinna and Argynnis mormonia washingtonia in the Pacific Northwest, with Evidence for High Elevation-Mediated Melanism

Author: James, David G.

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IMMATURE STAGES OF *ARGYNNIS MORMONIA ARTONIS* (LEPIDOPTERA: NYMPHALIDAE) COMPARED TO *ARGYNNIS MORMONIA ERINNA* AND *ARGYNNIS MORMONIA WASHINGTONIA* IN THE PACIFIC NORTHWEST, WITH EVIDENCE FOR HIGH ELEVATION-MEDIATED MELANISM

David G. James

Department of Entomology, Washington State University, Irrigated Agriculture Research and Extension Center, Prosser, Washington 99350; email: david_james@wsu.edu

ABSTRACT. *Argynnis mormonia artonis* from Steens Mountain (2207 m) in southeast Oregon was reared and the immature stages illustrated and compared to those of two other *mormonia* subspecies resident in the Pacific Northwest, *A. m. erinna* and *A. m. washingtonia.* Gravid females oviposited readily in captivity on desiccating Common Dog Violet (*Viola riviniana*) and Western Bistort (*Polygonum bistortoides*) leaves and twigs. Larvae were reared on *V. riviniana* and after overwintering developed from first instar to pupa in 51–59 days at 24–27 ºC. Eggs, pupae and early instars (first-early fourth) of *A. m. artonis* are similar to those of *A. m. erinna* and *A. m. washingtonia*, but the fifth and sixth instars differ by being concolorously black instead of gray, brown or black with white markings. Late instars of *A. m. erinna* from a high elevation site (Mt Howard, northeast Oregon, 2445 m) were similarly dark colored. These and other observations indicate that larval populations of *A. mormonia* and perhaps other *Argynnis* spp. are polymorphic with a greater incidence of melanic late instars occurring in high-elevation populations.

Additional key words: development, coloration, Mormon fritillary, larvae, host plants

Argynnis mormonia (Boisduval) (Mormon Fritillary) ranges from Alaska south to Arizona and east to Manitoba, South Dakota, Utah and Colorado occupying mid-high elevation habitats. Pelham (2008) lists nine subspecies, three of which (*washingtonia*, *erinna*, *artonis*) occur in the Pacific Northwest. *Argynnis mormonia washingtonia* (Barnes & McDunnough) and *Argynnis mormonia erinna* (W. H. Edwards) are relatively widespread in the Pacific Northwest but *A. m. artonis* (W. H. Edwards) occurs only in southeast Oregon. Warren (2005) recorded *A. m. artonis* from Harney County, primarily in the Trout Creek Mountains and on Steens Mountain. Elsewhere, *A. m. artonis* is found in northern Nevada, Colorado and Montana (Scott 1986, Pelham 2008). James and Nunnallee (2011) described and illustrated the immature stages of *A. m. washingtonia* and *A. m. erinna* from the Pacific Northwest but did not feature *A. m. artonis*. I also present additional images and information on *A. m. erinna* and *A. m. washingtonia* from additional rearing studies.

Materials and Methods

Argynnis mormonia artonis was reared from gravid females obtained from a population near the summit of Steens Mountain (2207 m), Harney County in southeast Oregon. Nine females were obtained on August 9, 2009 and 16 females on August 18, 2010 and confined a few days later in plastic boxes (32 × 20 × 9 cm) with desiccating leaves of *Viola riviniana* Rchb. (Common Dog Violet). In 2009, 5 of the 9 females were confined with *Polygonum bistortoides* Pursh (Western Bistort). *Argynnis mormonia erinna* was reared from gravid females obtained from near the summit of Mt Howard (2445 m), (Wallowa County) in the Wallowa Mountains of northeast Oregon. Two females were obtained on August 20 2010 and confined with desiccating *V. riviniana* leaves in a plastic box (32 × 20 × 9 cm) on August 22. *Argynnis mormonia washingtonia* was reared from gravid females obtained from near Bear Creek Mountain (1871 m), Yakima County, in the Cascade Mountains of central Washington. Three females were obtained on August 26, 2010 and confined with desiccating *V. riviniana* leaves in a plastic box (32 × 20 × 9 cm) on August 27. Newly hatched larvae of all species were held in the plastic boxes at 20–26 ºC, natural daylength for ~ 1 month before overwintering at 4–5 ºC and 80–90 % relative humidity in darkness. Larvae were removed from overwintering after 107 (*artonis* 2009), 130 (*artonis* 2010) or 138 (*erinna*, *washingtonia*) days and held at 24–26 ºC in 2009 and 27 ºC in 2010. The 2009 *A. m. artonis* larvae were held under continuous illumination while the 2010 larvae and those of *A. m. washingtonia* and *A. m. erinna* were held under naturally increasing photophases from April 22. All early instars were reared on plastic arenas (15 × 9 cm) placed on saturated cotton wool in a plastic box. Each species cohort consisted of 40–50 first instars resulting in 5–10 adults. Leaves of *V. riviniana* with cut stems in the saturated cotton wool were provided for food and shelter. Later instars were reared in plastic cylinders (12 × 13 cm) with a gauze lid. Cut stems and leaves of *V. riviniana* in a small jar were provided for food and shelter with 6–8 larvae/cylinder. Observations were made on larval feeding, molting and pupating.

Estimates of the length of larvae at the beginning and end of each instar are given. Individuals showed little variation (± 1 mm) in these lengths. High resolution images were taken of eggs, all instars and pupae using a Canon digital SLR camera (EOS 1DS Mark II) mounted on a tripod. A Canon MP-E 65mm 1X–5X macro lens was used together with a Macro Twin Lite MT – 24 EX flash lighting system.

RESULTS

Immature stages. The egg of *A. m. artonis* (Fig. 1) is very similar to those of *A. m. erinna* and *A. m. washingtonia* (James and Nunnallee 2011). It is broad-based, measuring 0.8–0.9 mm at its base, conical and creamy white when first laid becoming orange-brown with indistinct red spots prior to hatching. There are 22–26 vertical ribs merging to ~ 12 at the top.

Larval instars of *A. m. artonis*, *A. m. erinna* and *A. m. washingtonia* reared in this study are shown in Fig. 2. The first instar of *A. m. artonis* measures 1.25–1.5 mm after hatching and is very similar to the other subspecies, medium-dark brown becoming lighter with maturity with a shiny black head and 8 prominent black bullae across each segment. Each bulla carries a long dark seta sometimes with a droplet at the tip (see James and Nunnallee 2011). The prothoracic shield is sclerotized and black as is the anal plate. At maturity the first instar measures 3 mm. The second instar of *A. m. artonis* is black with a wide pale stripe dorsally and a shiny black head. Six prominent black spines traverse each segment each bearing ~ 10 setae. Laterally, the spines have pale bases which become orange during the instar. Prior to molting the second instar is flecked with white laterally. The second instar develops from 3 to 6 mm in length and is very similar to those of *A. m. erinna* and *A. m. washingtonia* (Fig. 2). The third instar of *A. m. artonis* is also very similar to the other two subspecies and grows from 6 to 9 mm. It is predominantly black with a pale dorsal stripe bisected by a dark line. The bases of all spines are orange and lateral white flecking is prominent. The black spines each bear 14–16 setae. Initially, the fourth instar of *A. m. artonis* is similar to the third instar but most individuals darken during the instar with the orange bases of spines contracting and white flecking diminishing. This differs from fourth instar *A. m. erinna* and *A. m. washingtonia* which are grayer with increased white markings (Fig. 2 and James and Nunnallee 2011). Some fourth instar *A. m. artonis* have distinct brown markings on the head dorsolaterally, similar to the other subspecies, but other individuals retain a completely black head. Fourth instar *A. m. artonis* develop from 9 to 15 mm in length. The fifth instar of *A. m. artonis* (growing from 15 to 20 mm) is dark but laterally there are whitish-orange vermiform markings and the orange bases of spines are more prominent. The dorsal white band bisected by a dark line is prominent against the dark ground color. The fifth instar of *A. m. washingtonia* is distinctly lighter than *A. m. artonis* due to increased areas of white flecking (Fig. 2 and James and Nunnallee 2011). Fifth instars of *A. m. erinna* reared in this study were almost as dark as *A. m. artonis*, unlike *A. m. erinna* reared and described by James and Nunnallee (2011) which had 'extensive white

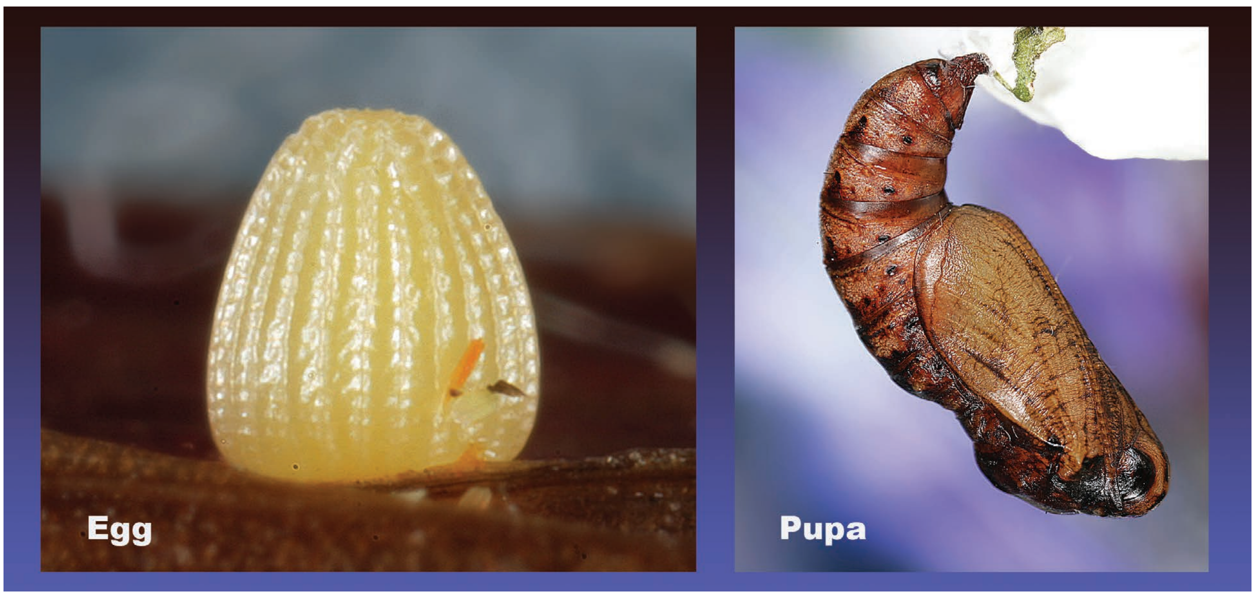

FIG. 1. Egg and pupa of *Argynnis mormonia artonis* from Steens Mountain, Oregon.

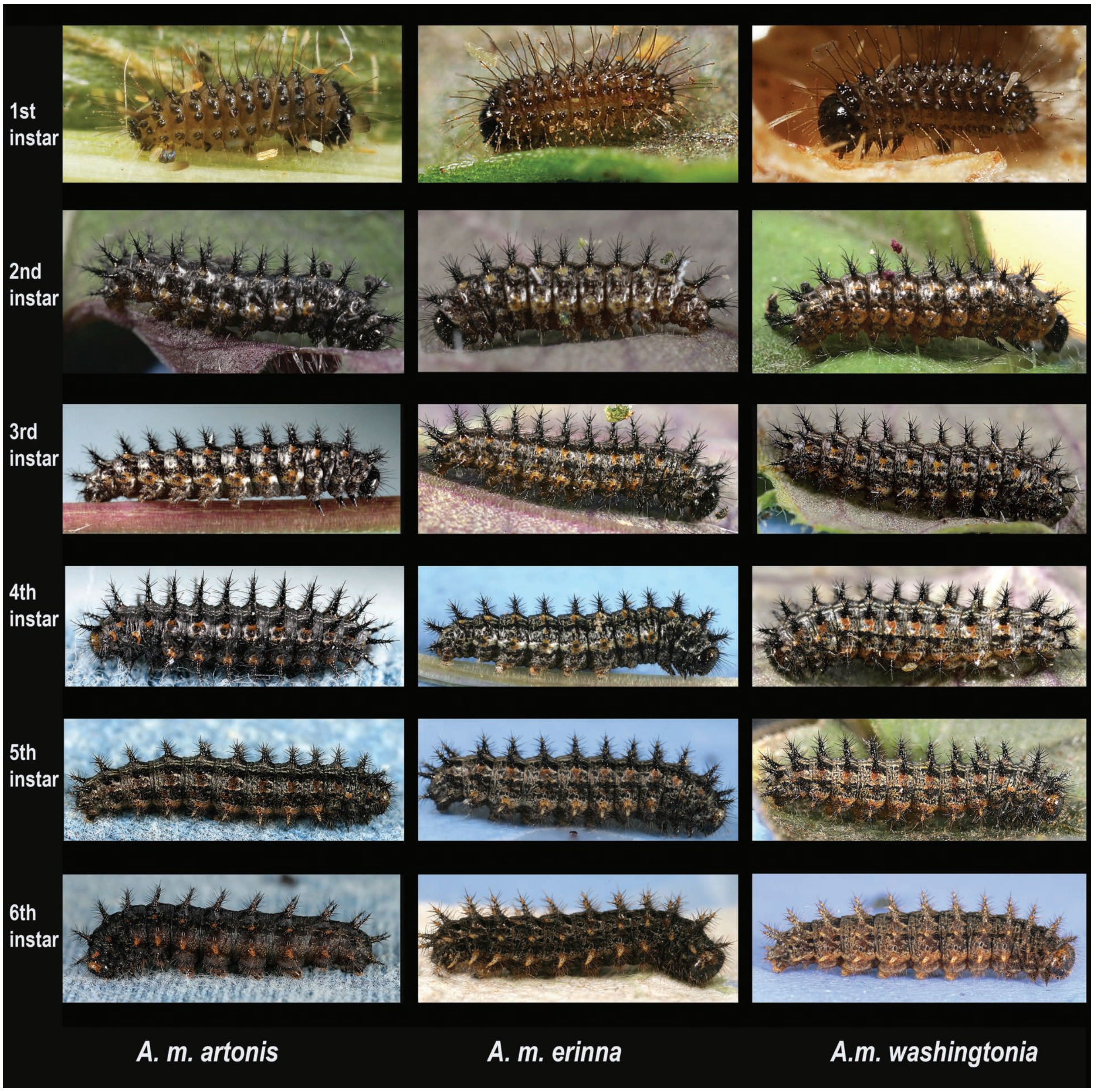

FIG. 2. First to sixth instars of *Argynnis mormonia artonis*, *A. m. erinna* and *A. m. washingtonia* from Steens Mountain (OR), Mt Howard (OR) and Bear Creek Mountain (WA), respectively.

vermiform' markings, similar to fifth instar *A. m. washingtonia*. Most individuals of *A. m. artonis* and *A. m. erinna* in early sixth instar were shiny jet black with whitish to orange spines, contrasting with the brownish-gray final instar of *A. m. washingtonia* (Figs. 2 and 3). Sixth instar *A. m. erinna* in this study were substantially darker than in the reared individuals of this subspecies described in James and Nunnallee (2011). In the current study the dorsal pale stripe prominent in sixth instar *A. m. washingtonia*, was much reduced or absent in sixth instar *A. m. erinna* and *A. m. artonis*. Some individuals of *A. m. artonis* and *A. m. erinna* had fine brown speckling overlying the black ground color creating a more mottled black appearance but these larvae are still substantially darker than sixth instars of *A. m. washingtonia*. The heads of sixth instars of all three subspecies are black with orange-brown markings dorsolaterally that vary in extent (Fig. 4). A summary of phenotypic differences in late instars of *A. m. artonis*, *A. m. erinna* and *A. m. washingtonia* is provided in Table 1. Sixth instars of *A. m. artonis* grow from 20 to 32 mm in length, comparable to the other two subspecies.

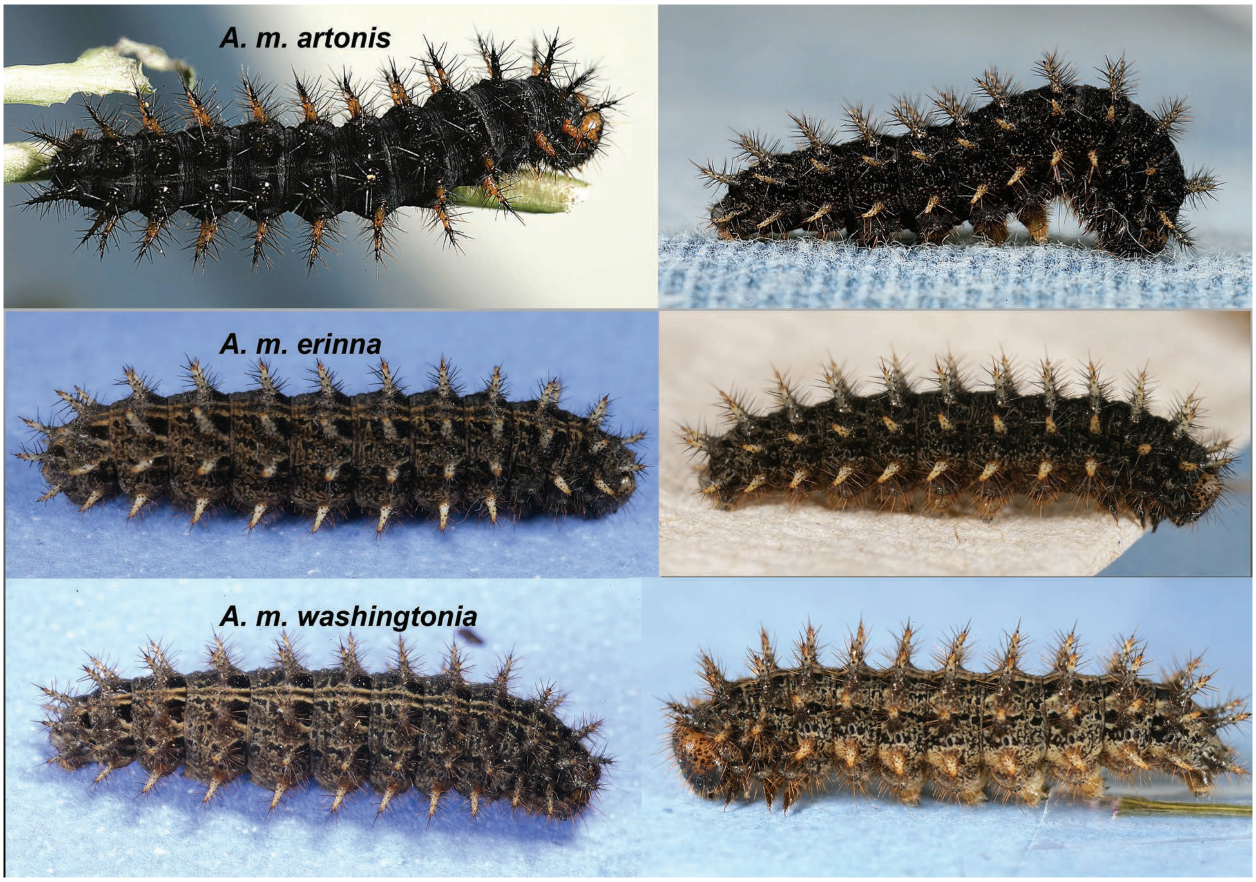

FIG. 3. Dorsal (left) and lateral (right) views of sixth instar *Argynnis mormonia artonis* (Steens Mountain, OR), *A. m. erinna* (Mount Howard, OR) and *A. m. washingtonia* (Bear Creek Mountain, WA).

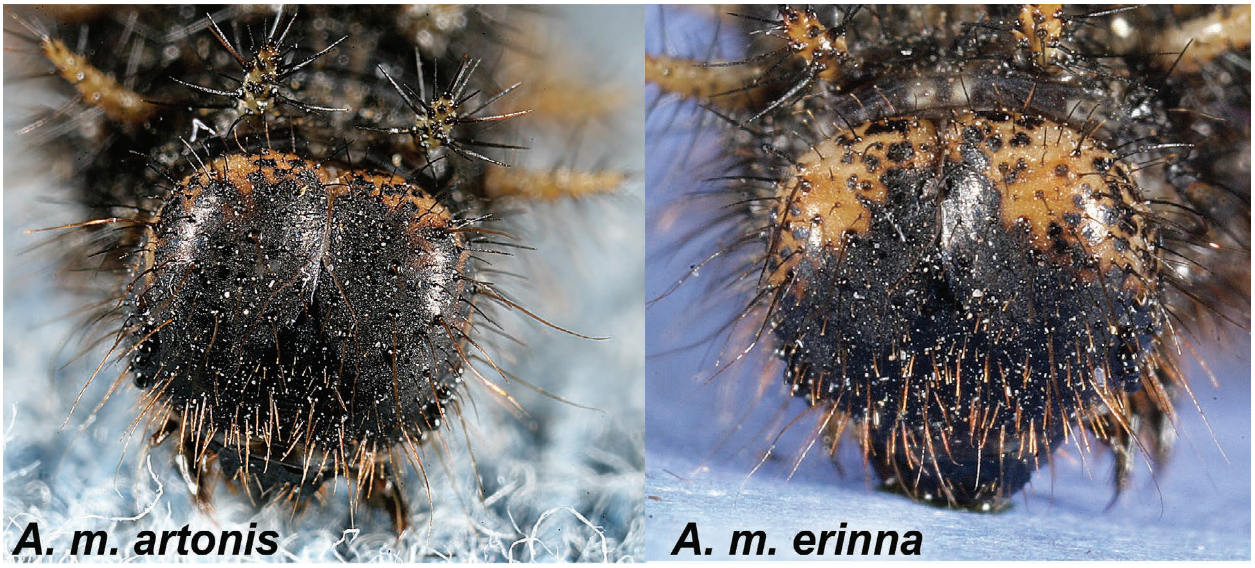

FIG. 4. Head capsules of sixth instar *Argynnis mormonia artonis* (Steens Mountain, OR) and *A. m. erinna* (Mount Howard, OR).

The pupa of *A. m. artonis* is light-medium brown with variable dark markings and measures 17–18 mm in length (Fig. 1), very similar to the pupae of *A. m. erinna* and *A. m. washingtonia* (James and Nunnallee 2011).

Biology of immature stages. Accounts of the biology of *A. m. erinna* and *A. m. washingtonia* immature stages are presented in James and Nunnallee (2011). The biology of immature stages of *A. m. artonis* is likely to be similar. The host plant used by *A. m. artonis* at Steens Mountain is uncertain, although *Viola purpurea* Kellogg (Goosefoot Violet) appears to be the only violet occurring at the upper elevations where *A. m. artonis* is found. However, this violet or any other violet species do not appear to be present in many of the locations where *A. m. artonis* is abundant. Western Bistort (*P. bistortoides*) is abundant in all of the locations where *A. m. artonis* flies and gravid females readily oviposited on this plant in captivity, suggesting it should be investigated as a potential host plant.

First instars of *A. m. artonis* overwintered well with a low mortality rate (<5 %). Feeding commenced after 3–7 days at 24–27 ºC. All instars readily accepted *V. riviniana* as a host plant but first instars rejected *Viola odorata* L. (Sweet Violet) and *Vaccinium* sp. (Blueberry). First instars fed well on Pansy (*Viola tricolor* L.) but this was discontinued as a host after this instar. Development from commencement of feeding to pupation took 59–65 days at 24–26 ºC (2009) and 51–55 days at 27 ºC (2010) (53–55 and 55–58 days respectively, for *A. m. washingtonia* and *A. m. erinna* at 27 ºC). Six to eight days were spent in each of the first four instars with 20–30 days spent in the final two instars. Pupation occurred near the bottom of containers usually under a leaf in a shelter constructed with sparse strands of silk. Pupae were held at 18–21 ºC and adult individuals eclosed after approximately 4 weeks.

Discussion

The early immature stages (egg–early fourth instar) of *A. m. artonis* from Steens Mountain in southeast Oregon are similar to those of *A. m. erinna* and *A. m. washingtonia*, but late instars (fifth, sixth) are substantially darker than those of *A. m. washingtonia* and previously described populations of *A. m. erinna* (James and Nunnallee 2011). Late instars of *A. m. erinna* reared in this study from Mt Howard in northeast Oregon were as dark as those of *A. m. artonis*. The final instars of *A. m. artonis* from Steens Mountain and *A. m. erinna* from Mt Howard are almost concolorously black and very similar to the late instars of *Argynnis hydaspe* (Boisduval) and *Argynnis hesperis* (W. H. Edwards) (James and Nunnallee 2011). The *A. m. artonis* and *A. m. erinna* larvae reared in this study originated from populations that occur above 2200m, significantly higher than the *A. m. washingtonia* population (1877 m) reared in this study. The *A. m. washingtonia* larvae described by James and Nunnallee also originated from approximately 1800 m and their *A. erinna* larvae came from a population at 990 m. The only other published images available of final instar *A. m. mormonia* (Guppy and Shepard 2001; *opis*, Miller and Hammond 2007, *erinna*, no elevation data) show lighter-colored larvae similar to those in James and Nunnallee (2011). It seems likely that the darker color of high elevation final instars of *A. m. artonis* and *A. m. erinna* may be due to increased melanism developed as an adaptation to enhance body temperatures and development under cool conditions. Increased melanism at high elevations is a predominant adaptation in insects generally and Lepidoptera in particular (Hodkinson 2005). Caterpillars of a number of butterfly and moth species have been shown to be more melanic under cooler conditions and better able to attain optimal body temperatures for development than their

Table 1. Summary of phenotypic differences in late instars of *A. m. artonis, A. m. erinna* and *A. m. washingtonia* in populations from high (> 2000 m) or low (< 2000 m) elevations in Washington and Oregon.

	A. m. artonis (high elev.)	*A. m. erinna* (high elev.)	*A. m. erinna* (low elev.)	*A. m. washingtonia* (low elev.)
Fourth instar	Darkens late in instar	Gray with pale markings	Gray with pale markings	Gray with pale markings
Fifth instar	Dark	Dark	Gray with pale markings	Gray with pale markings
Sixth instar	Jet black. Dorsal stripe absent or much reduced	Jet black. Dorsal stripe absent or much reduced	Brownish-gray with prominent white dorsal stripe	Brownish-gray with prominent white dorsal stripe

less melanic counterparts (James 1986, Goulson 1994, Hazel 2002, Solensky and Larkin 2003, Davis et al. 2005, Nice and Fordyce 2006). Larval populations of all *A. mormonia* subspecies likely express color polymorphism with darker phenotypes rare at low-mid elevations becoming increasingly prevalent at higher elevations as the need for solar-mediated enhancement of development increases.

The final two instars of six northwestern *Argynnis* spp., including *A. mormonia*, generally occupy 30–50% of the larval developmental period (James 2008), thus the greatest need to accelerate development should occur during these instars. I suggest that increased melanism in late instars may not be confined to *A. mormonia* but may also occur in some other western North America *Argynnis* spp. that occupy a range of elevations. For example, *Argynnis hesperis* (Gunder) and *Argynnis atlantis* (W. H. Edwards) occur in mid-high elevation habitats in the Pacific Northwest and have larvae that appear to vary considerably in the amount of black coloration in late instars (Scott et al. 1998). The sixth instar of *A. atlantis* is shown with substantial areas of white markings in James and Nunnallee (2011) but sixth instars from Mt. Howard are entirely black (James in prep.). Color polymorphisms in *Argynnis* larvae clearly have the potential to confuse species identifications. Much of the described larval color variation in *A. hesperis, A. atlantis* (Scott et al. 1998) and *A. mormonia* (Dunford 2009) may simply be a consequence of different temperatures affecting different populations during development.

The commercially available violet used in this study, *V. riviniana*, is invariably mislabeled as *Viola labradorica* Schranck (Labrador Violet). Thus, recent publications reporting acceptability of *V. labradorica* to *Argynnis* larvae (James 2008, James and Nunnallee 2011 actually refer to *V. riviniana. Viola riviniana* is a suitable host for *A. m. artonis* as it is for *A. m. erinna, A. m. washingtonia, Argynnis egleis* (Gunder), *Argynnis hesperis dodgei* (Gunder) and *A. atlantis*. Its acceptance in other Pacific Northwest *Argynnis* spp. is limited to late instars (James 1986, James and Nunnallee 2011). The possibility of *A. m. artonis* using *P. bistortoides* as a natural host at Steens Mountain needs investigating. *Polygonum bistorta* L. is recorded as a larval host for the European Fritillary *Mesoacidalia aglaja* L. and a number of *Boloria* and *Clossiana* spp. also use various *Polygonum* spp. as larval hosts (Robinson et al. 2010). The larval development period of *A. m. artonis* of 51–59 days at 24–27 ºC was similar to that of *A. m. washingtonia* and *A. m. erinna* at 27 ºC (James and Nunnallee 2011). It was also comparable to the developmental rates of *Argynnis coronis simaetha* dos Passos and Grey, *Argynnis zerene picta* (McDunnough), *A. e. macdunnoughii* and *Argynnis cybele leto* (Behr) (James 2008).

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