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OBSERVATIONS ON THE SEASONAL BIOLOGY AND APPARENT MIGRATION OF *ARGYNNIS* (*SPEYERIA*) *CORONIS* (NYMPHALIDAE) IN CENTRAL WASHINGTON

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Abstract. Opportunistic observations on the seasonal biology of *Argynnis coronis* in central Washington obtained over 40 years, suggest that the ecology of this species is characterized by well defined seasonal population movements between low and high elevations. Unfed first instar larvae diapause and overwinter in lithosol shrub-steppe areas immediately east of the Cascade Mountains feeding and developing on sagebrush violets (*Viola trinervata*) during March-May. Males eclose 7-14 days before females in mid-late May. After mating, females delay egg development and migrate 50–100 km westward reaching high elevations in the Cascades by late June-early July. Most males die in the shrub-steppe but a few migrate with the females. Female-dominated populations oversummer at 2,000-2,500m and are active feeding on flowers but remain non-reproductive. Ovaries develop in early August and females begin an eastward downslope movement returning to shrub-steppe areas by early September. Oviposition on soil, stones, rocks and ground level woody plants where violets grow in spring, occurs during September and early October.

Additional key words: overwintering, migration, reproductive diapause, oversummering, oviposition, shrub-steppe, Cascades

Argynnis (*Speyeria*) *coronis* (Behr) ranges throughout much of the western US from Washington and South Dakota to Colorado, Arizona and southern California (Scott 1986). In Washington and Oregon it occurs primarily along the Cascade Mountains and eastern foothills but also east of the Cascades in Oregon (Dornfield 1980; Hinchliff 1994, 1996; Pyle 2002; Warren 2005). A single generation flies from May to October in favored habitats, which include canyons, hillsides, shrub-steppe, forest margins and mountain meadows from 300–2500m (Dunford 2009). The ecology of this species is of great interest with altitudinal migration, adult reproductive summer diapause and hibernal larval diapause, apparent components of the annual life history in Washington and Oregon (Pyle 2002; James & Nunnallee 2011). Opportunistic observations on the biology of *A. coronis* obtained over 40 years in central Washington are summarized and presented here.

RESULTS

Overwintering and spring larval development. In common with all *Argynnis* spp., *A. coronis* overwinters as an inactive unfed first instar larva hidden in detritus, soil or under rocks on the ground (Fig.1). (Pyle 2002; James & Nunnallee 2011). In central Washington (Figs. 2 and 3), overwintering appears to occur in the eastern foothills of the Cascades, primarily in the shrub-steppe zone where the primary larval host plant, *Viola trinervata* (T.J Howell) T.J Howell ex Gray (Sagebrush Violet), occurs (Fig. 4). It is possible that some individuals overwinter at slightly higher elevations associated with other violet species (e.g. *V. nuttalli* Pursh.). Overwintering larvae diapause and do not readily respond to normally favorable stimuli (e.g. warmth and host plants), for ~ 3 months after hatching (James 2008). In the laboratory, larvae exposed to cold conditions (5 ºC) and darkness for 80 days broke diapause and commenced development reaching adulthood after 54 days at 25 ºC (James 2008). Larvae of *Argynnis* spp. are notoriously difficult to find, especially early instars, thus it is unclear when larvae of *A. coronis* begin feeding. Third instar larvae were discovered under rocks in the vicinity of V. *trinervata* (Schnebly Coulee, north ridge, Kittitas County (46.95 º N, 120.09 º

FIG. 1. Overwintering unfed first instar larva of *Argynnis coronis*.

W, 625m) on 26 April 1971 and 16 April 1988. They were also found in Ryegrass Coulee, Kittitas County (46.93 º N, 120.06º W, 457m) on 30 April 1973 and at the south fork of Ahtanum Creek, Yakima County (46.51º N, 120.91º W, 762m) on 10 April 1969). A developmental duration of ~8 weeks at 25 ºC (James 2008), suggests that adults eclosing in May likely commence larval development in late February or early March. Ambient maximum temperatures during March–April in eastern Washington shrub-steppe average 13–18 ºC (Yakima) indicating that heliothermic warming in the exposed habitat must play a major role in the rapid development of *A. coronis* larvae.

Adults: Eclosion, courtship and mating. Adults eclose from early May to late June, depending on temperatures experienced during March–May. Males appear 7–14 days before females, similar to that reported for Californian populations of *A. coronis* (Sims 1984). In a seasonal survey at Schnebly Coulee, Kittitas County in 2004, males were first observed on 6 June nectaring heavily on *Salvia dorrii* (Kellogg) Abrams (Purple Sage). Females were first observed on 19 June. On 3 July, no adults were seen at this location. During 2005–2010, first adults were seen annually between 17 May and 26 May in the Yakima-Naches district of central Washington. In 2007, adults began eclosing around 26 May and on 3 June ~50 males were seen on the slopes of Umtanum Canyon, Kittitas County, 27 km N of Yakima (46.85º N, 120.48º W, 508 m) nectaring and searching for females. In 2010 adults began eclosing around 20 May continuing for ~4 weeks. On 3 June ~25 newly eclosed adults were seen near Cowiche Mt, 19 km west of Yakima, Yakima County (46.65º N, 120.75º W, 620 m) during 1 hour. Most were males engaged in rapid, low, searching flight (hazy sunshine, 17–21 ºC), seeking females. A number of individuals (3–4) were resting on small shrubs with unhardened wings. Newly eclosed individuals resting on the ground or on small

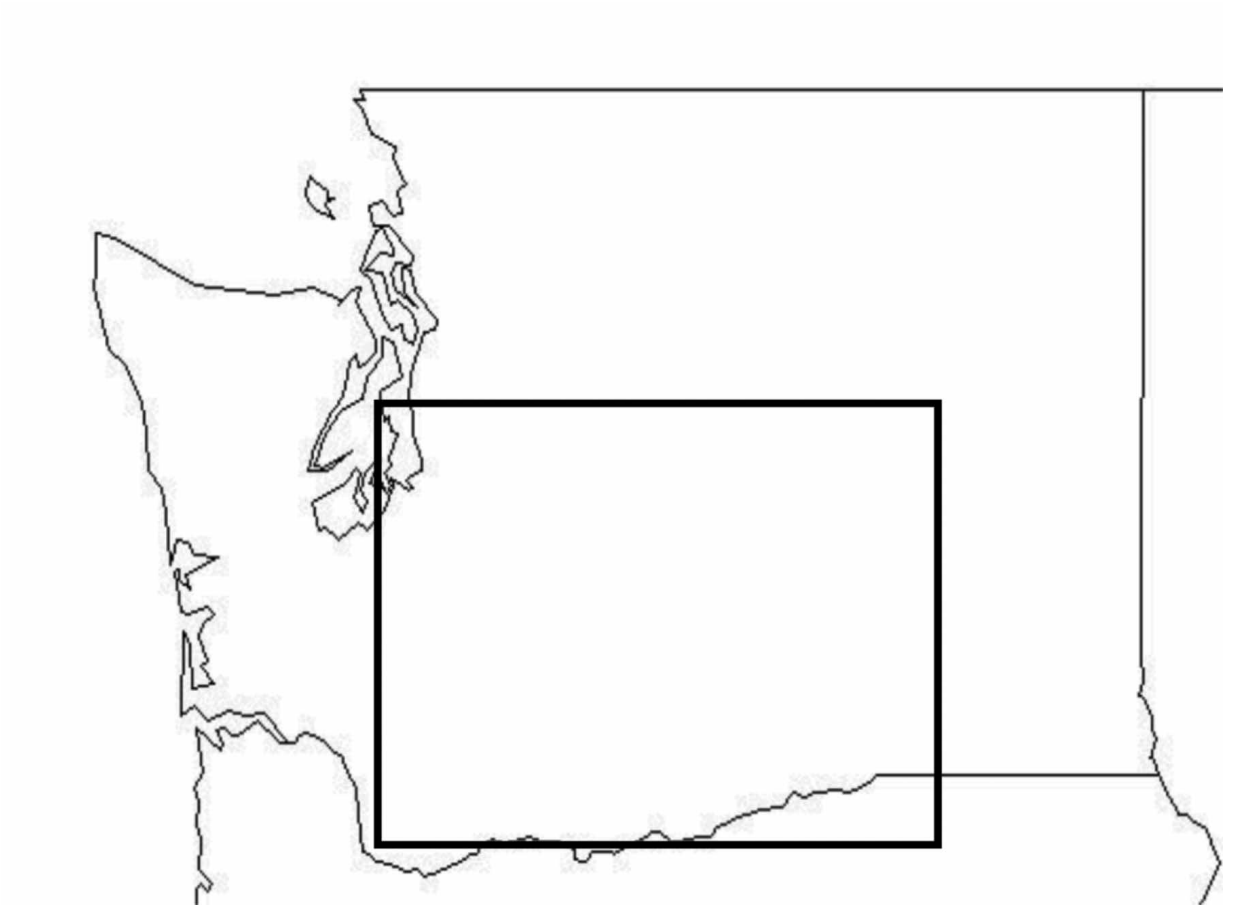

FIG. 2. Approximate area of Washington State in which observations on *Argynnis coronis* were made 1969–2010.

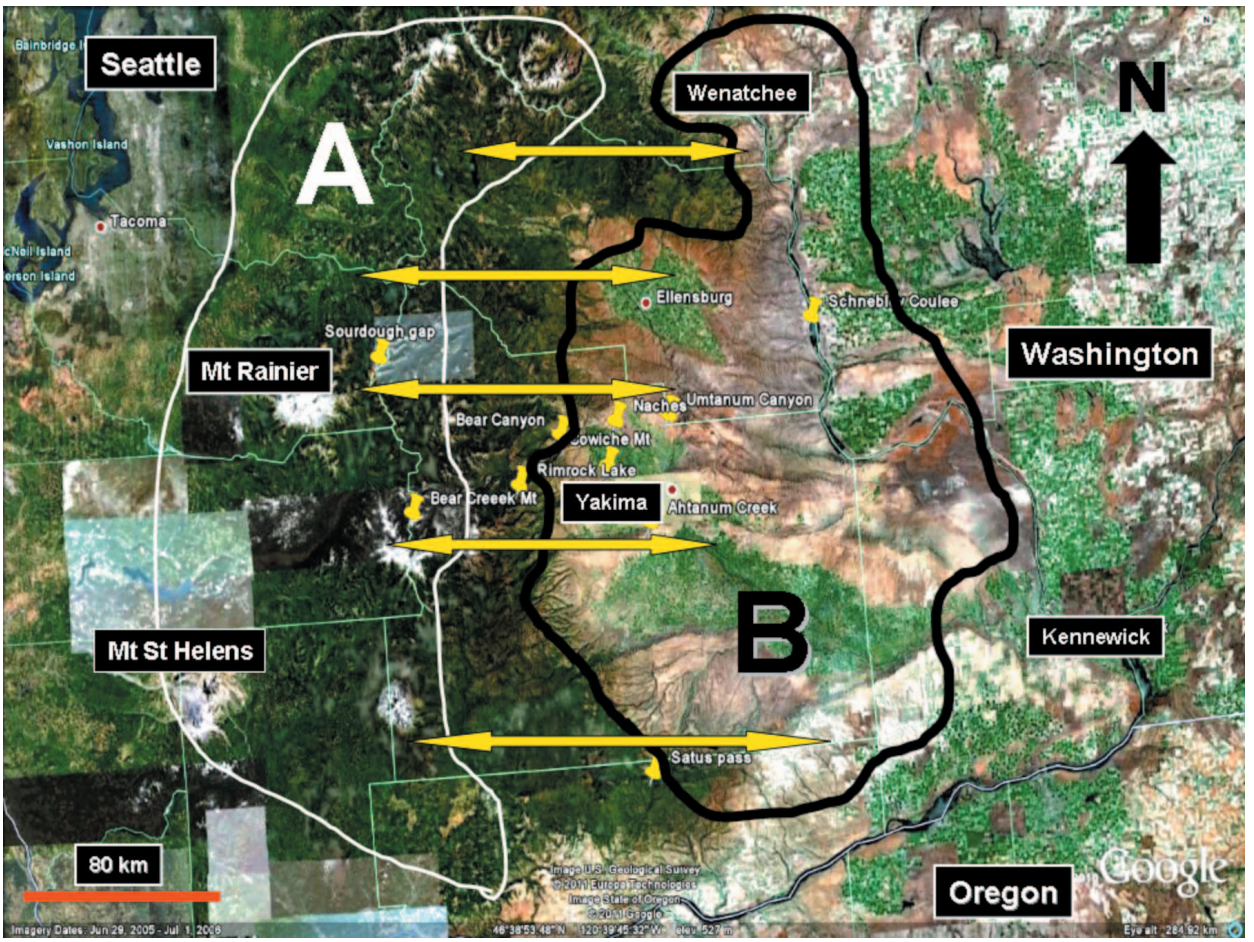

FIG. 3. Approximate summer (**A**- Cascade Mountains) and fall-spring (**B**-shrub-steppe) ranges of *Argynnis coronis* in central Washington. Putative late spring (west) and early fall (east) migration indicated by arrows.

FIG. 4. Larval host of *Argynnis coronis*, Sagebrush Violet (*Viola trinervata*), in spring.

FIG. 5. Copulating pair of *Argynnis coronis* in June.

FIG. 6. Male *Argynnis coronis* imbibing from damp mud in June.

FIG. 7. Desiccated Sagebrush Violet (*Viola trinervata*) at Cowiche Mountain in October.

shrubs showed a 'startle response' when disturbed, rapidly opening and shutting wings with no flight. Two copulating pairs were seen with females carrying males (Fig. 5). Nectaring occurred primarily on two buckwheat species, *Eriogonum heracleoides* Nutt. (Parsley Buckwheat) and *Eriogonum compositum* Dougl. ex Benth (Northern Buckwheat). Males were also seen during June imbibing from damp mud in groups of up to a dozen (Fig. 6). Eclosion was still occurring at this site on 17 June with fresh females clinging to low shrubs and conspicuous mate-searching by males. Four hours of observation on 1 July resulted in ~40 males seen searching for females which appeared to be absent. Most individuals showed significant wing wear on this date. By mid June all Viola host plants have withered and desiccated, remaining dormant until the following March.

Adults: Westerly upslope migration by females. Once mated, females appear to undertake an upslope, westerly migration, which ultimately takes them to the highest peaks of the Cascade Mountains (Fig. 3). On 4 June 2009, an estimated 150 *A. coronis* females were seen flying rapidly westward in a number of meadows and along roads and trails near Rimrock Lake, 53 km west of Yakima, Yakima County (46.62º N, 121.18º, 1134 m) during 4 hours (10:00–14:00h, sunshine, 25–27 ºC). During 13:00–14:00h, females passed through a meadow at a rate of 2–3 per minute. Flight was purposeful and mostly uninterrupted by nectaring. Limited nectaring was observed mid morning on dandelion and Ceanothus. Captured females (35) had plump abdomens and all continued westward flight after release. No males were seen. On 17 June 2010, 32 females were seen flying westward at Cowiche Mt in partial sunshine and temperatures of 18–21 ºC during two hours.

Adults: Non-reproductive females oversummering at high elevations. *Argynnis coronis* adults are generally absent in shrub-steppe localities from about the end of June until September. No *A. coronis* adults were observed from 8 July–30 August 2005–2010 on multiple field excursions at Cowiche Mt, Bear Canyon, Umtanum Canyon and many other shrub-steppe locations near Yakima, Ellensburg and Wenatchee. In 2010 the last individuals (worn males) were seen at Cowiche Mt on 7 July. The majority of males appear to remain in sage-steppe until death, although a small number apparently follow females upslope. Males and females were present at Satus Pass, Klickitat County (45.92º N, 120.65º W, 987 m) on 13 June 2007, likely en route to higher elevations, but this location is only ~5 km from the nearest shrub-steppe habitat (500–600 m). Female-dominated populations of *A. coronis* occur at high elevations (2000–2500 m) in the Cascade Mountains during July–August, for example at Bear

FIG. 8. Female *Argynnis coronis* ovipositing on wood of *Artemisia rigida* on the ground at Cowiche Mountain on 12 October 2010.

Creek Mountain, Yakima County, 68 km west of Yakima, (46.53º N, 121.34º W, 2200 m) and Sourdough Gap, Pierce County, 85 km west north west of Yakima (46.90º W, 121.50º W, 2000 m). Males are rarely seen at these sites (e.g. five seen at Bear Creek Mt during 6 years of observation). High elevation summer populations are flight-active and individuals spend much time feeding from the flowers of alpine plants like phlox, buckwheats, asters and bistort. At Bear Creek Mt, females in July are found in lower meadows (~ 2000 m) but by early August they only occur on the highest ridges (~ 2200 m) usually the only sites where phlox and asters are still blooming. There is no evidence that females aestivate at these high elevations. Although no dissections have been made, it is clear that females at these high elevations are non-reproductive and likely contain undeveloped ovaries at least until August. Sims (1984) showed that females of Californian *A. coronis* are in reproductive diapause for a 3–5 week period in summer. Four females collected from Bear Creek Mt on 30 July 2005 oviposited after 7 days (James 2008). However, large numbers of eggs were not produced until the second half of August.

Adults: Easterly downslope migration. Easterly movement of females downslope begins in mid-late August. In the seasonal survey at Schnebly Coulee, Kittitas County in 2004, females were first observed on 15 August, nectaring on *Chrysothamnus* sp. In most years *A. coronis* is hard to find at Bear Creek Mt in the second half of August. On 31 August 2009 ~ 20 females showing uninterrupted strong easterly flight were seen on the access road (FR 1204) to Bear Creek Mt at ~ 1500–1800 m. On 31 August 2005 large numbers (25–30) of females reappeared in Bear Canyon, Yakima County, 32 km west north west of Yakima (46.70º N, 120.89º W, 644 m) after an absence of 2.5 months. On 11 September 1999, numerous females were observed nectaring on garden blooms in the city of Ellensburg, Kittitas County (47.01º N, 120.5º W, 486 m), on the floor of the Kittitas Valley. During 2007–2010 *A. coronis* females appeared in Yakima City during the last days of August or first days of September, becoming common visitors to gardens visiting Buddleia and asters during September.

Adults: Autumn reproductive populations in shrub-steppe. On 10 September 2007, ~50 females were seen on blooms of *Chrysothamnus nauseosus* (Gray Rabbitbrush) in Umtanum Canyon during 2 hours. On 29 September 2006 at the same location only 12 were seen plus one male. On 13 September 2010 an estimated 100 *A. coronis* females were seen nectaring on *C. nauseosus* in a canyon near Cowiche Mt (sunshine, 26 ºC, 13:00–14:00h). A further 20–30 were observed on adjacent hillsides and plateaus searching for oviposition sites. Similarly, on 27 September ~75 were seen nectaring and ~25 ovipositing (sunshine, 25 ºC, 13:30–15:00h). One very worn male was caught. On 29 September ~50 were seen nectaring and ovipositing. On 12 and 13 October, 6 and 9 females were seen respectively, ovipositing or searching for oviposition sites. On 18 and 21 October no females were seen ovipositing, but on each date 2 were seen nectaring on rabbitbrush. Late October females had thin bodies and faded, worn wings.

On 27 and 29 September and 12 October the oviposition behavior of a total of 25 ovipositing females was studied at Cowiche Mt. Females flew close (~0.3 m) to the ground alighting only in areas lacking in grass and comprised mostly of rocks, stones and bare earth. These areas supported densest concentrations of desiccated sagebrush violets (Fig. 7). Areas with abundant cheat grass (*Bromus tectorum* L.) were inspected by females but rejected for oviposition. Fire-affected areas (a wildfire on 18 July 2010 produced a mosaic of burned and unburned patches) appeared to be ignored by female *A. coronis*, which flew over them at heights > 2 m. Eggs were laid singly on rocks, soil and plant material including ground level trunks and stems of Stiff Sagebrush (*Artemisia rigida* (Nutt.) A. Gray) (Fig. 8). After an egg was laid the female either crawled or flew briefly 5–25 cm before ovipositing again. In most instances 2–3 eggs were laid in close proximity before the female flew to another location 5–30 m away. One female laid 8 eggs, each separated by 5–8 cm before flying to a new patch. Bouts of oviposition were occasionally interrupted by visits to flowers for nectar. Oviposition continues into early October in most years but is usually finished by mid month.

DISCUSSION

Collectively, the observations reported here indicate that the life history of *A. coronis* in central Washington is characterized by seasonal, well defined population movements between low and high elevations (Fig. 3). Early workers recognized the vagile nature of *A. coronis* populations (e.g. Hammond 1974, 1981; Sims 1984) but did not report the seasonal migration strategy we describe here.

Oviposition, overwintering and development of immature stages occurs in shrub-steppe areas east of the Cascades with adults (and eggs) escaping the summer drought and heat of this low elevation zone by migrating 50–100 km to spend the summer months in alpine environments (Fig. 3). Most of our evidence is circumstantial and confirmation of the strategy must await more detailed and experimental studies. For example, marking of significant numbers of newly-

eclosed spring adults is needed to confirm migration to alpine zones and back again.

While summer diapause and altitudinal migration appears to be a feature of *A. coronis* ecology in central Washington, studies are needed to determine whether this strategy also occurs in other parts of the species' range. In Oregon, populations in eastern basin lands and ranges of the south-east also appear to 'move about' although populations on the eastern slopes of the Cascades and in the Ochoco-Blue-Wallowa Mountains appear to be sedentary. The observations of Shapiro & Manolis (2007) suggest seasonal movements occur in the Sacramento valley of northern California where *A. coronis* 'disappears' during summer, females reappearing and laying eggs in September. Sims (1984) showed in laboratory studies that female *A. coronis* in California spend 3–5 weeks during summer in reproductive diapause but did not provide information on behavior during this period. Confirmation of reproductive status is needed for Washington female *A. coronis* during June–August as well as information on mechanisms and/or environmental cues responsible for induction and termination of dormancy. Is induction cued by increasing daylengths or is it genetically programmed? Sims (1984) showed that short daylengths (12 hrs) hastened diapause termination in Californian *A. coronis* females. Our observations in Washington indicate females commence oviposition when daylengths decline from 15 to 14.5 hrs (early August).

Female reproductive diapause was also described for Kansas populations of *Speyeria* (*Argynnis*) *idalia* (Kopper et al. 2001), which breeds at low elevations in native grasslands. In common with the shrub-steppe/*A. coronis* system, violet host plants in Kansas grasslands occur only in spring and female *A. idalia* have an extended non-reproductive life span during summer before laying eggs during autumn. Unlike *A. coronis*, *A. idalia* does not migrate out of the hot, dry grasslands during summer. Females, instead show reduced activity and avoidance of sunlight (Kopper et al. 2001), suggesting aestivation. Aestivation serves the same function as migration to a cooler zone by limiting exposure to high temperatures.

Females of a number of *Argynnis* species have been reported as mating only once (Shields 1967; Burns 1968; Kopper et al. 2001). Three freshly emerged *A. coronis* females examined by Sims (1984) each had a single spermatophore, so it is likely that single matings are characteristic of this species too. However, although rare, males were seen in alpine summer and autumn shrub-steppe populations so it is possible that some females may mate more than once. The importance and phenology of males in the annual life history of *A. coronis* needs further study.

The observations on oviposition indicate that female *A. coronis* are able to distinguish between areas that have violets and those that do not. Female avoidance of cheat grass covered areas corresponds to the relative scarcity of V. *trinervata* plants in grassy areas (James unpubl. obs.). The absence of oviposition in burned areas suggests that the cues guiding site selection by females (volatiles from senesced violets?) are absent in these areas. Our observations of *A. coronis* ovipositing on ground level parts of sagebrush are similar to those of Durden (1965) who found females of *Speyeria* (*Argynnis*) *callippe* Boisduval ovipositing on woody parts of sagebrush in Wyoming. Durden (1965) considered *Artemisia* as a possible host plant for *A. callippe* but it is more likely that sagebrush simply provided a convenient oviposition site near to violets as it does for female *A. coronis* in central Washington. Observations on oviposition by *A. coronis* have rarely been made by us or others and the extent of breeding grounds in central Washington is unclear. *Viola trinervata* occurs strictly in lithosol shrub-steppe habitats (sagebush flats, rocky hillsides) in a narrow band east of the Cascades. In similar habitats in Oregon V. *trinervata* is replaced by *V. beckwithii* Torr. And Gray (Great Basin Violet), a recorded host for *A. coronis* in Oregon (Warren 2005). The limited areas of lithosol shrub-steppe habitats present in Washington and Oregon may be critical to the survival of *A. coronis* and conservation of this species should feature in shrub-steppe management and conservation (Wooten 2002).

A prolonged female life span and associated reproductive dormancy appears to be characteristic of a number of species in the greater fritillary genus *Argynnis* in North America, primarily those occupying habitats with hot, dry summers. In contrast, species resident in higher elevation, cooler habitats like *A. mormonia* Boisduval and *A. egleis* Behr show no delay in female oviposition (Boggs 1987; James & Nunnallee 2011). *Argynnis coronis* is the only *Argynnis* species to date for which altitudinal migrations have been described, although *A. callippe* has been observed migrating downslope in late August and September in central Washington and may have a similar ecology. The ecological rationale for *A. coronis* delaying oviposition in shrub-steppe is likely tied to better survival of eggs and first instar larvae from September onwards than during July–August. Air temperatures in shrub-steppe areas of central Washington during summer routinely exceed 35–38 ºC with relative humidities often < 10% and little or no cloud cover resulting in day time ground temperatures in excess of 50 ºC. Kopper et al. (2001) suggested a similar rationale for the adoption of

aestivation and reproductive dormancy by females of *A. idalia* in Kansas.

Our observations suggest *A. coronis* populations in central Washington are highly adapted to exploiting an ephemerally favorable environment in spring then vacating it during the harsh conditions of summer. Escaping an unfavorable environment along with suppression of reproductive development is characteristic of the oogenesis-flight syndrome first postulated by Johnson (1969). In most butterfly examples of this syndrome, escape is from a cold environment (e.g. *Danaus plexippus* L.). The shrub-steppe habitat and the endemic violet species, *V. trinervata* are clearly critical to the ecology of *A. coronis* in central Washington. *Viola trinervata* is locally common but it is absent in many seemingly suitable shrub-steppe sites, particularly those with abundant cheat grass. Additionally, shrub-steppe is one of North America's most imperiled and neglected ecosystems (Noss & Peters 1995) with areas in Washington rapidly declining with the development of irrigated agriculture and urbanization (Wooten 2002). Efforts are required to expand and consolidate our understanding of the ecology of *A. coronis* and to highlight the vulnerability of this species to continued degradation of the shrub-steppe ecosystem.

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