

# Biology of larvae and adults of *Erynnis propertius* at the northern edge of its range

Kirsten M. Prior, Jason D.K. Dzurisin, Shannon L. Pelini,  
Jessica J. Hellmann<sup>1</sup>

Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556,  
United States of America

**Abstract**—We describe aspects of the life history of *Erynnis propertius* (Scudder and Burgess) (Lepidoptera: Hesperiiidae) by examining several populations over multiple years. We focused on peripheral populations of this species because they are isolated, are threatened by habitat loss, and may play an important role in driving poleward range expansion under increasing regional temperature. Our findings show that the annual larval growth rate does not vary directly with temperature, adult flight phenology and the timing of key resources respond to average daytime temperatures in spring, and population-density patterns among sites are robust over years across a broad region near the species' northern range limit. In addition, we provide descriptions of all larval instars for this species. This fundamental information about the biology, timing, and abundance of this species will facilitate further experimental study and improved assessment of its conservation status.

**Résumé**—Nous décrivons des aspects du cycle biologique d'*Erynnis propertius* (Scudder et Burgess) (Lepidoptera : Hesperiiidae) d'après l'étude de diverses populations pendant plusieurs années. Nous nous sommes intéressés aux populations périphériques de l'espèce parce que celles-ci sont isolées et menacées de perdre leur habitat et qu'elles peuvent jouer un rôle important dans l'expansion de l'aire de répartition vers les pôles à cause de l'accroissement de la température régionale. Le taux de croissance annuel des larves ne varie pas directement en fonction de la température; la phénologie de vol des adultes et l'apparition des ressources essentielles réagissent aux températures moyennes de jour du printemps; les patrons de densité de population dans les différents sites sont stables au cours des années dans une large région adjacente à la limite nordique de l'aire de répartition de l'espèce. De plus, nous présentons des descriptions de tous les stades larvaires de l'espèce. Cette information de base sur la biologie, la phénologie et l'abondance de l'espèce permettra de faire des études expérimentales dans le futur et de mieux évaluer son statut de conservation.

[Traduit par la Rédaction]

## Introduction

Butterflies (Lepidoptera) are widely recognized as important flagship species in conservation biology and serve as ideal models in the study of population dynamics, behavioral ecology, and evolutionary biology (Boggs *et al.* 2003). We discuss aspects of the life history of a specialist butterfly, *Erynnis propertius* (Scudder and Burgess) (Hesperiiidae), that is threatened by habitat loss and may be a useful indicator of a threatened ecosystem. We focus on the northern edge of its range, where populations are

fragmented naturally and artificially. This fragmentation provides an opportunity to study multiple distinct populations. Furthermore, it is important to characterize the populations of species at their northern range margin, given the potential for poleward range expansions as a result of climate change (Parmesan *et al.* 1999; Hellmann *et al.* 2008; Zakharov and Hellmann 2008).

*Erynnis propertius* is an oak-feeding specialist that occurs from southern Vancouver Island, British Columbia (BC), Canada, to Baja California,

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<sup>1</sup>Corresponding author (e-mail: hellmann.3@nd.edu).  
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**Table 1.** Description of the six study sites on Vancouver Island and Hornby Island, British Columbia.

Site No.	Latitude and longitude	Patch size (ha)	Distance to adjacent site (km)	Habitat type
1	48°25'N, -123°20'W	5.1	14.9 (S2)	Woodland / rocky outcrop
2	48°27'N, -123°28'W	16.1	38.7 (S3)	Rocky outcrop
3	48°47'N, -123°38'W	7.6	2.1 (S4)	Rocky outcrop
4	48°48'N, -123°37'W	6.8	64.1 (S5)	Woodland
5	49°27'N, -124°16'W	29.2	43.4 (S6)	Rocky outcrop
6	49°31'N, -124°36'W	2.3		Woodland

Mexico. The larvae feed on a variety of oak species in the southern portion of their range (Scott 1986; Pavlik *et al.* 1993; Opler 1999), but feed exclusively on Garry oak, *Quercus garryana* Dougl. *ex* Hook. (Fagaceae), in the northern third of their range. Both *Q. garryana* and *E. propertius* reach their northern range limit on southeastern Vancouver Island and the adjacent Gulf Islands, BC (Scott 1986; Layberry *et al.* 1998; Opler 1999; Guppy and Shepard 2001). *Erynnis propertius* is currently listed on BC's Blue list ("vulnerable") and is a candidate for federal listing under the Species at Risk Act in Canada (British Columbia Conservation Data Centre 2008; Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2008).

*Erynnis propertius* is a dominant member of a rich and diverse butterfly community associated with western Nearctic oak-grassland ecosystems. These ecosystems are fragmented in BC, where they are restricted to warm and dry microclimates (Erickson 1996). Changes in land use have caused significant loss of these ecosystems; less than 10% of original habitat in BC remains (Lea 2006). Much of the remaining habitat is degraded by encroachment of invasive species and increases in numbers of native shrubs and trees as a result of fire suppression (Fuchs 2001; MacDougall *et al.* 2004). Owing to its association with *Q. garryana* (larval food source) and flowering plants (adult nectar source), *E. propertius* may be a useful indicator of habitat quality for Garry oak ecosystems, a habitat of considerable conservation interest in BC and the Pacific Northwest of the United States of America (Brown and Freitas 2000; Fleishman and Murphy 2009).

*Erynnis propertius* is the largest skipper in coastal western North America (Guppy and Shepard 2001), yet few details are known about its life history. However, some details of adult flight times (Scott 1986; Guppy and Shepard

2001) and larval development (Hardy 1958) have been described.

The main objective of this study was to provide a more complete portrait of the life history of *E. propertius* by examining it over space and time. To achieve this goal we used a population-level approach, measuring individuals in six locations on Vancouver Island and Hornby Island, BC, over 5 years. We provide a quantitative description of the larval instars of *E. propertius*, compare larval growth rates, adult flight times, and population densities among sites and years, and relate these values to habitat and temperature variables.

## Materials and methods

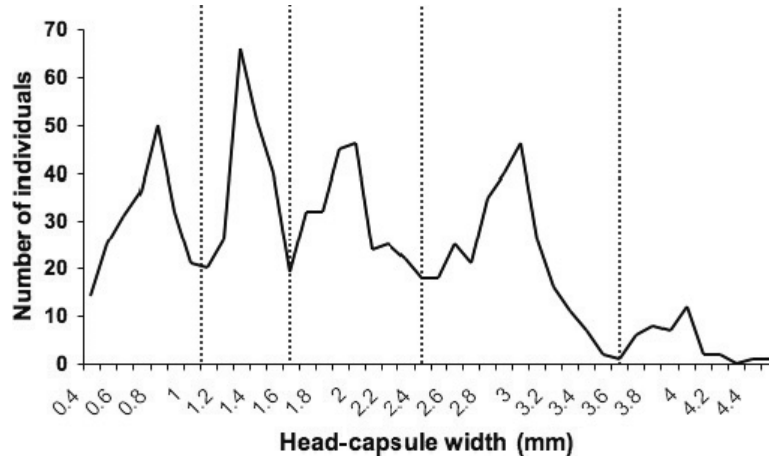
### Study sites

Six sites near the boundary of the oak-grassland ecosystem on Vancouver Island and Hornby Island were selected for study (Table 1). Sites were selected qualitatively based on the lack of invasive shrubs, presence of native nectar sources, and presence of host plants. All sites are within 150 km of the species' northern range limit and are separated by 2.08–64.11 km. Although we do not know how far *E. propertius* individuals disperse, their close association with patchily distributed host plants likely limits their ability to move among these sites. We assume, therefore, that our study sites, with the possible exception of S3 and S4 (Table 1), represent distinct populations.

### Description of immature stages: egg, larva, and pupa

In each year of our study, females were caught in the field from the end of April to the middle of May at all study sites. Enclosures (30.45 cm<sup>2</sup>) covered with green polyester netting (mesh size 9 × 8/cm) were used to house five or six females each. Females were fed twice a day with diluted honey-water. Freshly cut *Q. garryana* branches were placed in water

**Fig. 1.** Frequency distribution of head-capsule widths for *Erynnis propertius* larvae from the second instar onward at six sites on Vancouver Island and Hornby Island, British Columbia, pooled across all sites and years (2003–2006). The dotted lines denote different instars, delineated as the peak between low points in the distribution.



in each enclosure and replaced every other day. Host plants were placed with their leaves touching the top and corners of the cages, where the captive females spent most of their time.

Enclosures were kept outside in a sunny area in 2003 and in subsequent years in greenhouse conditions, where fluorescent lighting was used to mimic daylight on a 14L:10D cycle and incandescent lights were used on cool days to keep the temperature close to 30 °C. We obtained the greatest egg yield on sunny days when the greenhouses were humid and the females were exposed to natural as well as fluorescent light. Eggs laid by captive females were collected every other day.

Collected eggs were put on leaves of potted *Q. garryana* plants that were covered with fine Dacron chiffon mesh (39/cm) in the greenhouse or placed in field enclosures (described below). We measured body length, body width, and head-capsule width (HCW) of 47 first-instar larvae that were reared on potted plants under greenhouse conditions in 2008. Other instars were measured in field enclosures, and larval growth rates were calculated in 2004–2006. In addition, during the winter of 2005, 11 first-instar larvae were reared to adulthood in a greenhouse set to Vancouver Island conditions (*i.e.*, temperature and light regimes were changed every 2 weeks using averages calculated over the previous 5 years).

For larval monitoring in the field, 7–21 eggs were placed directly on *Q. garryana* branches in each enclosure. Enclosures consisted of round

wire frame cages (41 cm diameter × 60 cm length) covered with fine Dacron chiffon mesh to prevent the escape of caterpillars and the entry of predators and competitors. Within a site, enclosures were placed in close proximity to each other, at similar heights and exposures, to reduce microclimatic variation.

In 2008 we calculated the average HCW from the cohort of first-instar larvae. To describe instars from larvae measured in the field (2003–2006), we plotted the frequency of HCW values in a cumulative data set from the second larval instar onward. The HCW ranges for each instar were delineated by marking the low points between peaks in a frequency plot of HCW values (Fig. 1) and a weighted average HCW was calculated for each instar (Table 2) (*e.g.*, Dyar 1890; Leibe *et al.* 1980; Hamon *et al.* 1984). We performed least-squares regression on  $\ln(\text{HCW})$  and the instar number (1–6) to see whether *E. propertius* grows according to Dyar's rule, as many other arthropods do (*e.g.*, de Groot 1998; Verdinelli and Sanna-Passino 2003).

The growth rate of field-reared larvae was measured by plotting larval volume ( $\pi(\text{length})(\text{width}/2)^2$ ) against instar. An exponential curve was then fitted to these data using least squares and the growth rate for the larvae in each enclosure was estimated as the exponent of the best fit model. Growth rates in 2004 were log-transformed. Mean larval growth rates were compared among sites in 2004 and 2005 separately using ANOVA and Tukey's post-hoc

**Table 2.** Description of *Erynnis propertius* instars, including head-capsule widths (from Fig. 1), body lengths of caterpillars in each instar, and the dates on which these instars were first observed in the field.

Instar	Head-capsule width (mm)			Body length (mm)*	Date first observed
	Range	Mean	<i>n</i>		
1	0.3–1.0	0.61	47	3.34 (0.44)	—
2	0.4–1.1	0.87	168	4.95 (1.07)	19 May
3	1.2–1.6	1.43	203	7.35 (1.51)	20 May
4	1.7–2.5	2.07	263	10.54 (2.21)	1 June
5	2.6–3.6	3.01	247	15.04 (3.01)	7 June
6	3.7–4.6	4.03	40	19.36 (1.12)	1 July

\*Values are given as the mean, with the standard deviation in parentheses.

test. Growth data were pooled over all sites to test for differences between years, and comparisons were made between 2004, 2005, and 2006 using ANOVA and Tukey's post-hoc test.

#### Description of the adult stage: flight season and population density

Adult butterflies were surveyed by observing the number of individuals within 5 m of transect lines placed at least 40 m apart at each study site (Pollard 1991; Pollard and Yates 1993). Adult butterflies were observed flying, resting, and nectaring. Surveys of adults were repeated approximately six or seven times per site in 2003–2007. Transect length was standardized to site area so that approximately 20% (19%–26%) of each site was observed during each survey. Surveys were performed between 1000 and 1600 on warm, mostly sunny days. Visibility within a site (*i.e.*, the ability of a surveyor to see adults within a 5 m radius) was roughly consistent across sites. Double-counting of individuals was possible but was likely minimized by transect spacing, the relatively sedentary flight of this species (K.M. Prior, personal observation), and intervals lasting several days (7–10) between surveys. Peak flight dates (*i.e.*, the period of highest population density) were calculated as the weighted average of butterfly observations across the season.

We calculated population density at each site by estimating the area under the individuals observed *versus* flight date curve using a method of trapezoidal summation divided by patch size (ha) (Rothery and Roy 2001; Hellmann *et al.* 2008). Because of an early start to the growing season in 2004 (see Results), we missed approximately the first 8 days of adult flight.

Because the first part of this curve is missing, the estimated peak flight dates in that year are probably pushed forward in time. Densities were square-root-transformed to normalize the data.

#### Site descriptions: vegetation, phenology of resources, and temperature

Vegetation at each site was described in 2003–2005 using 1 m<sup>2</sup> quadrats 20 m apart along evenly spaced transects. The total area surveyed was standardized by site size so that each hectare was represented by approximately 20 (range 18–24) sampling quadrats. In each quadrat we surveyed percent cover of forbs, grasses, shrubs, and bare ground. Cover was assessed as <25%, 25%–50%, 50%–75%, or >75%, and the midpoint of each range was used in analyses. We also counted the individual plants of species of *Camassia* Lindl. (Liliaceae) in 2003–2005 and *Vicia* L. (Fabaceae) in 2004–2005; both genera are prominent nectar sources for *E. propertius* (Table 3). To estimate plant species abundance, we assigned each quadrat to the lower end of a base-3 categorical interval (*e.g.*, 1, 4, 11, 31, ...) and estimated the abundance of *Q. garryana* by calculating the percentage of quadrats containing oak cover. Cover types and plant species abundance were relatively constant over the 3-year study period; therefore, we used an average value over all of the years. Mean rank scores were calculated because of the non-normality of the data, and a Kruskal–Wallis test and  $\chi^2$  approximation was used to test for differences in the vegetation variables among sites. One exception was the use of ANOVA to test for differences in *Q. garryana* cover among sites. Where there were differences, sites were ranked according to

**Table 3.** Observed nectar sources for adult *Erynnis propertius* on Vancouver Island and Hornby Island, British Columbia.

Scientific name	Common name	Peak flowering date*	Flower count
<i>Camassia</i> Lindl. (Liliaceae)	Camas <sup>†</sup>	5 May (124)	4854
<i>Cerastium arvense</i> L. (Caryophyllaceae)	Field chickweed <sup>†</sup>	8 May (127)	1294
<i>Plectritis congesta</i> (Lindl.) DC. (Valerianaceae)	Shortspur seablush <sup>†</sup>	10 May (129)	7281
<i>Vicia</i> L. (Fabaceae)	Vetch <sup>‡</sup>	27 May (146)	2324
<i>Zigadenus venenosus</i> S. Watson (Liliaceae)	Meadow deathcamas <sup>‡</sup>	30 May (149)	274
<i>Delphinium menziesii</i> DC. (Ranunculaceae)	Menzies' larkspur <sup>‡</sup>	1 June (151)	574
<i>Allium cernuum</i> Roth (Liliaceae)	Nodding onion	7 June (157)	31
<i>Allium acuminatum</i> Hook. (Liliaceae)	Tapertip onion <sup>§</sup>	17 June (167)	1052
<i>Lychnis coronaria</i> (L.) Desr. (Caryophyllaceae)	Rose campion	17 June (167)	39
<i>Triteleia hyacinthina</i> (Lindl.) Greene (Liliaceae)	White brodiaea <sup>§</sup>	21 June (171)	544
<i>Brodiaea coronaria</i> (Salisb.) Engl. (Liliaceae)	Crown brodiaea <sup>§</sup>	22 June (172)	244
<i>Symphoricarpos albus</i> (L.) S.F. Blake (Caprifoliaceae)	Common snowberry	26 June (176)	179

**Note:** Symbols denote those species that were the most abundant during three different portions of the flight season.

\*Estimated as the weighted average Julian date (in parentheses) of flower counts pooled over sites.

<sup>†</sup>Early season: 5 May – 10 May.

<sup>‡</sup>Midseason: 27 May – 7 June.

<sup>§</sup>Late season: 17 June – 22 June.

**Table 4.** Variation in all vegetation variables observed among sites on Vancouver Island and Hornby Island, British Columbia (df = 6,  $P < 0.001$ ).

	1	2	3	4	5	6
<i>Camassia</i> spp.	S6 (1420)	S5 (1470)	S1 (1478)	S4 (1928)	S2 (2078)	S3 (2653)
<i>Vicia</i> spp.	S2 (1036)	S5 (1238)	S3 (1376)	S6 (1412)	S1 (1429)	S4 (1725)
Forbs	S5 (1509)	S2 (1570)	S1 (1787)	S6 (2203)	S4 (2305)	S3 (2577)
Shrubs	S5 (1523)	S6 (1655)	S1 (1786)	S4 (2029)	S3 (2124)	S2 (2127)
Grass	S2 (1491)	S1 (1515)	S3 (1809)	S5 (1813)	S4 (2230)	S6 (2556)
Bare ground	S4 (823)	S6 (959)	S3 (1207)	S5 (2090)	S1 (2108)	S2 (2146)

**Note:** Sites are ranked from lowest (1) to highest (6) for each vegetation type; values in parentheses are mean rank scores. No variation in density of *Quercus garryana* was found among sites ( $F_6 = 3.65$ ,  $P = 0.060$ ), therefore sites are not ranked for this vegetation variable.

highest mean rank score (Table 4). We also regressed butterfly density in each year on mean rank score for all vegetation variables.

To assess the phenology of nectar-plant resources, we repeatedly measured them at each site during the butterfly season. On each butterfly-recording day in 2005–2007, we counted the flowers in a 1 m<sup>2</sup> quadrat at the end of 30 m intervals of each butterfly transect (Table 3). Peak flowering dates for each site in each year were calculated similarly to peak flight dates, using a weighted average. In addition, peak flowering dates for each plant species were calculated from counts pooled over all sites and years (Table 3) to reveal seasonal differences in timing of flowering among species.

We calculated the time of flushing of *Q. garryana* as the average of dates when leaves

were observed to be between 1 and 50 mm in length (approximately the first half of leaf growth) on four reference trees at each site in each year.

Temperature at each study site was recorded using HOBO temperature and humidity data loggers (Onset Computer Corporation, Bourne, Massachusetts, and Davis Instruments Corporation, Hayward, California, respectively). Loggers were placed in locations that were not shaded at any point in the day and on a south-facing slope if available. This was done so that microclimatic differences within sites did not confound site differences. The average daytime temperature (1000–1600) between April and July was calculated using the logged data. The average temperature in spring and summer was calculated as the average daytime temperature from 19 April to 24 May (Julian dates 110–145) and from



25 May until 28 June (Julian dates 146–180), respectively. Least-squares regressions were performed between spring temperatures and peak flight dates, *Q. garryana* flushing dates, and peak flowering dates to look for relationships between temperature and butterfly and resource phenology.

## Results

### Description of immature stages: egg, larva, and pupa

Eggs are laid singly on *Q. garryana* leaves and, under ambient outdoor rearing conditions, were most commonly found on the top of the leaf adjacent to the midrib. Oviposition occurred from mid-April to late May under ambient outdoor conditions and from 24 April and 9 May under greenhouse conditions. Eggs are hemispherical, are approximately 0.75 mm in diameter, and have distinct vertical ridges. Coloration changes as the egg develops. Immediately after oviposition, the eggs are a muted green; within approximately 3–8 days, they turn bright green; and within 4–16 days (on average, 8 days after oviposition), they turn a burnt orange. Just before eclosion, an orange larva is visible through the egg's translucent green chorion.

First-instar caterpillars have a body length of  $3.34 \pm 0.44$  mm (mean  $\pm$  SD) and a mean HCW of 0.61 mm (Table 2). The frequency distributions of HCW values measured on second-instar and later larvae at all sites and in all study years produced a curve with five peaks (Fig. 1), suggesting that *E. propertius* larvae develop through six instars (Table 2). Mean HCW and body length for each instar are presented in Table 2. The larvae grow according to Dyar's rule: there is a linear relationship between a particular instar and  $\ln(\text{HCW})$  ( $y = 0.39x - 0.86$ ;  $r^2 = 0.99$ ,  $n = 6$ ,  $P < 0.001$ ).

First-instar caterpillars have an orange head and body. Between the second and fourth instar they have a black head and green body and the head capsule starts to show orange spots. During the fifth instar, the head capsule varies from dark to light brown with orange to brown markings. Sixth-instar caterpillars have a large (4.03 mm) flesh-colored head capsule. First-instar caterpillars are usually found on the underside of the leaf not far from their partially eaten egg case. Second-instar caterpillars are often found on a bed of webbing, and from then on caterpillars are found in shelters created by folding a leaf or

webbing two leaves together. Caterpillars remain in these shelters over the growing season and during the winter months. Overwintering caterpillars in their shelters can be found on the tree or in the leaf litter.

The 11 larvae observed through pupation and eclosion entered a quiescent state in early September. Two of these individuals pupated and eclosed in early September. The remaining larvae pupated the following March and eclosed in early to mid-April. The pupal exoskeleton is translucent, making the pupae appear white or cream-colored initially, and they turn brown as development proceeds.

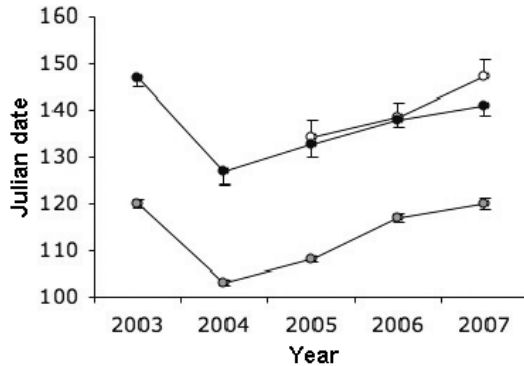
The average growth rate of caterpillars for all sites was 0.065 mm<sup>3</sup>/day (SD = 0.007 mm<sup>3</sup>/day;  $n = 43$ ) in 2004, 0.089 (SD = 0.024 mm<sup>3</sup>/day;  $n = 32$ ) in 2005, and 0.085 (SD = 0.020 mm<sup>3</sup>/day;  $n = 8$ ) in 2006. We found no variation in larval growth rate among sites in 2004 ( $F_{5,39} = 1.07$ ,  $P = 0.390$ ) or 2005 ( $F_{5,27} = 0.170$ ,  $P = 0.972$ ). Growth rates varied significantly among years over the 3 years of study, with the slowest growth occurring in 2004 ( $F_{2,80} = 20.80$ ,  $P < 0.001$ ). Growth rates in 2005 and 2006 were not statistically different ( $P > 0.050$ , Tukey's post-hoc test).

### Description of the adult stage: flight season and population density

Adult *E. propertius* were observed at the study sites between 4 April and 29 June during 2003–2007. On average, peak flight occurred on 17 May (SD = 9 days; range 1 May – 1 June). The first adult was observed flying (but was not recorded in surveys) on 30 April in 2003, 4 April in 2004, 17 April in 2005, 24 April in 2006, and 19 April in 2007. Peak flight occurred at roughly the same time at all sites in each year, though often earliest at S6 and S2 and latest at S3 and S4. On average, peak flight was earliest in 2004 (8 May), followed by 2005 (13 May), 2006 (16 May), 2007 (21 May), and 2003 (25 May) (Fig. 2).

Our population surveys indicate that *E. propertius* was generally the most abundant butterfly in the oak meadows that we studied during spring and early summer, except at S2, where *Celastrina argiolus* (L.) (Lepidoptera: Lycaenidae) was more common. Densities of *E. propertius* were highest at the most northerly sites (S5 and S6) and lowest at the most southerly sites (S1 and S2) in 4 out of the 5 years of study (Fig. 3).

**Fig. 2.** Peak flight dates for *Erynnis propertius* (●), flushing dates for Garry oak, *Quercus garryana* (○), and peak flowering dates (gray circles) at six sites on Vancouver Island and Hornby Island; values are given as the mean  $\pm$  SE over all sites. The flight date and oak flushing date are presented for all years (2003–2007) and peak flowering dates for 2005–2007.



#### Habitat descriptions: vegetation, phenology of resources, and temperature

Patch size ranged from 2.3 ha for S6 to 29.2 for S5 (Table 1). There was no relationship between patch size and *E. propertius* density ( $r^2 = 0.02$ ,  $n = 6$ ,  $P = 0.937$ ). Though there was no significant variation in the density of *Q. garryana* among sites ( $F_6 = 3.65$ ,  $P = 0.060$ ), there was significant variation in all other vegetation variables ( $df = 6$ ,  $P < 0.001$ ) (see results in Hellmann et al. 2008). S5 and S6 consistently had the highest density of *E. propertius* (Fig. 3), but they were ranked lowest in densities of important nectar resources (e.g., *Camassia* spp.) and never had the highest density of forbs or other important nectar resources such as *Vicia* spp. (Table 4). S5 and S6 had the lowest shrub cover and highest grass cover and S2 (the site with the lowest population density) had low grass cover and high shrub cover (Table 4). There was no relationship between *E. propertius* density and shrub cover in any of the years ( $n = 6$ ,  $P > 0.204$ ), but there was a significant positive relationship between *E. propertius* density and grass cover in 2004 ( $r^2 = 0.07$ ,  $n = 6$ ,  $P = 0.040$ ; also see Hellmann et al. 2008).

On average, mean *Q. garryana* flushing dates were earliest in 2004 (13 April), followed by 2005 (18 April), 2006 (27 April), 2003 (30 April), and 2007 (30 April) (Fig. 2). Mean leaf flush occurred 23 days (SD = 2 days) before peak flight.

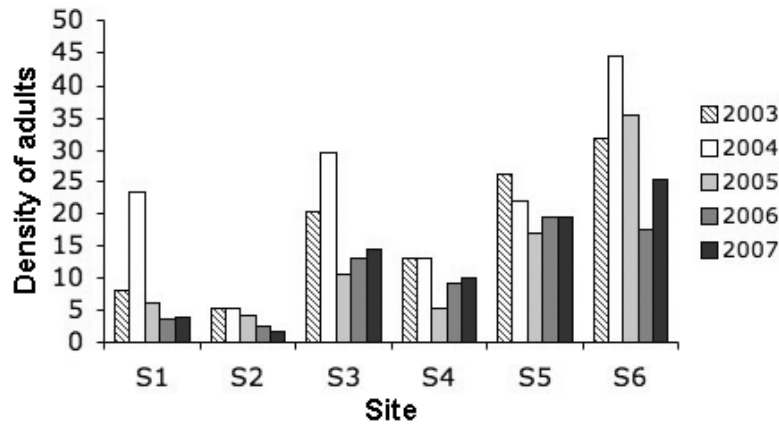
Peak flowering was earliest in 2005 (14 May) followed by 2006 (17 May) and 2007 (27 May) (Fig. 2). Peak flight dates were approximately the same as peak flowering dates for nectar sources, except in 2007, when peak flowering occurred 7 days after peak flight (Fig. 2). Different nectar-producing species flowered during different periods of the flight season. During the early part of the flight season, *Camassia* spp. (5 May) and *Plectritis congesta* (Lindl.) DC. (Valerianaceae) (10 May) produced the highest number of flowers. Later, *Vicia* spp. (27 May), *Delphinium menziesii* DC. (Ranunculaceae) (1 June), and *Zigadenus venenosus* S. Watson (Liliaceae) (30 May) were the most abundant nectar resources. *Allium acuminatum* Hook. (Liliaceae) (17 June), *Triteleia hyacinthina* (Lindl.) Greene (21 June), and *Brodiaea coronaria* (Salisb.) Engl. (22 June) (all Liliaceae) are important nectar resources at the end of the flight season (Table 3).

The average spring temperature was highest in 2004 (22.09 °C), followed by 2006 (19.22 °C), 2005 (19.17 °C), 2007 (18.34 °C), and 2003 (16.72 °C). There was little variation in summer temperature among years (range 23.74–25.11 °C). Average spring temperature had a positive relationship with mean flight date ( $r^2 = 0.88$ ,  $n = 5$ ,  $P = 0.018$ ) but not with flushing date ( $r^2 = 0.74$ ,  $n = 5$ ,  $P = 0.060$ ) or peak flowering date ( $r^2 = 0.86$ ,  $n = 3$ ,  $P = 0.245$ ). However, all these variables were highly correlated with each other ( $r^2 > 0.70$ ).

#### Discussion

Understanding the life history of a species is essential for further experimental study and aids in conservation efforts. In this study we identified six instars in *E. propertius*, based on HCW values for each instar. From a single field collection, Hardy (1958) reported four or five instars in this species but he did not know the instar stage of the larva at collection. We found a linear relationship between instar and HCW, so *E. propertius*, like many other Lepidoptera, grows according to Dyar's rule (e.g., Dyar 1890; Verdinelli and Sanna-Passino 2003; but see Goettel and Philogene 1979; Elmes et al. 2001). The number of instars can vary (Guppy 1969; Goettel and Philogene 1979) because the size of the larva, not the number of molts, determines when it enters the pupal stage (Guppy 1969; Nijhout 1975). However, in the current study we could not detect variability in instar

**Fig. 3.** Estimated densities of adult *Erynnis propertius* at six sites on Vancouver Island and Hornby Island during 2003–2007.



number because of our population-level approach.

*Erynnis propertius* has previously been described as univoltine in BC, with the possibility of multiple generations in the southern portion of its range (Scott 1986; Guppy and Shepard 2001; S.L. Pelini, personal observation). We found two individuals collected in BC that pupated and eclosed in the fall. This suggests that multivoltinism is possible near the limits of the species' range.

Growth rates of *E. propertius* larvae were similar throughout the study area but varied among years. The slowest growth occurred in 2004, a year with an unusually warm spring (2 °C warmer, on average, than in 2005, the next warmest year). Temperature, along with food availability (e.g., Guppy 1969; Zenner-Polania and Helgesen 1973) and parasitism (e.g., Nealis 1987), has been shown to affect growth rates of holometabolous insects, and an unknown set of these factors likely plays a role in interannual variation in the growth of *E. propertius* larvae.

Peak flight occurred in mid-May throughout the region, with *E. propertius* flying between early April and late June. This description of the flight season differs from that of Guppy and Shepard (2001), who reported *E. propertius* flying from April to July with peak flight in June. Peak flights occurred at approximately the same time among sites within years. However, peak flight dates varied among years. In the current study the largest difference in flight phenology among years occurred in 2004, the year with the highest spring temperatures. Adults emerged almost 2 weeks earlier in 2004 than in any other year and peak flight time was 5 days earlier.

There was no variation in average daily summer temperature among years, however, so summer temperatures do not appear to explain the variation in adult flight phenology. Other studies have shown that first flight dates and peak flight dates respond most strongly to spring temperatures. For example, early springs have been related to earlier flight dates in *Apis mellifera* (L.) (Hymenoptera: Apidae) and many butterfly species (e.g., Roy and Sparks 2000; Stefanescu *et al.* 2003; Gordo and Sanz 2005, 2006). Many of these studies, however, showed that early-spring temperatures (February–April) were an important cause of earlier emergence. However, we did not measure climate variables before the start of the flight season.

Peak flight of *E. propertius* occurred approximately 23 days after leaf flush of *Q. garryana*. Although many oak-feeding Lepidoptera lay eggs on newly flushed leaves (Feeny 1970; Forkner *et al.* 2004; Murakami *et al.* 2005), *E. propertius* lays eggs when leaves are approximately half their full size. At this time, *Q. garryana* leaves have not developed a thick waxy layer (K.M. Prior, personal observation) and thus early-instar larvae probably avoid feeding on less palatable, older leaves. We did not record dates of egg-laying in the field or position of eggs on “wild” *Q. garryana* trees, but this information might show whether *E. propertius* prefers to lay eggs on leaves of different ages, sizes, or positions in the tree canopy, or if they prefer particular trees.

Dates of leaf flush and peak flight changed in tandem over the years and were earliest in the year with the warmest spring (2004) and latest in the year with the coolest spring (2003)



(Fig. 2). This suggests that host-plant resources and timing of butterfly flight are somewhat robust to climatic variation. However, we have only a 5-year data set, and a longer time series would include greater variation in temperatures and thus could be used to test the robustness of synchrony between this butterfly and its host plant.

Climate change has been shown to cause decoupling of host plant – insect synchrony in other systems (Visser and Holleman 2001; Hellmann 2002; van Asch *et al.* 2007; Pelini *et al.* 2009). Our observation of reduced larval growth in 2004 in the warmest year could reflect some potential for decoupling driven by climate. This inference has limitations, however, because we manipulated “egg-laying” times by putting eggs in enclosures and so they could be skewed relative to natural oviposition. In 2004, for example, oak leaf flush occurred approximately 10 days earlier than in 2003 and 2005. Therefore, early-instar larvae in our enclosures could have encountered leaves that were more phenologically advanced than they would have experienced when ovipositing naturally. Increases in levels of tannins and decreases in essential nutrients, including nitrogen, occur over the season in *Quercus* spp. (Feeny 1970; Forkner *et al.* 2004). Thus, in 2004, experimental larvae could have encountered leaves that were lower in nutritional quality, thereby incurring a decrease in their growth rate.

Peak flowering also occurred at approximately the same time as peak flight over the years. However, adult *E. propertius* were observed nectaring on a suite of native and non-native wildflowers that peak at different times during the flight season (Table 3). During peak flight (1 May – 1 June), *Camassia* flowers were common at most study sites. They were uncommon at S6 and S1 (Table 4), however, and *Vicia* spp. and *P. congesta* likely served as nectar sources at those sites. At S6, *Z. venenosus* was also abundant and likely an important nectar resource. After peak flight (June), the majority of forbs in the meadow have senesced. Many Liliaceae (*e.g.*, *Allium*, *Brodiaea*, and *Triteleia*) begin to flower and are important nectar resources for the last month of flight (Table 3).

There was a robust pattern of differences in *E. propertius* density among sites over the years. S6 and S5 had the highest population densities in 4 of the 5 years of sampling, and S2 had the lowest densities in all of the years. Interestingly, *E. propertius* density consistently

increased with decreasing distance to the edge of the range in all study years (Fig 3; Hellmann *et al.* 2008). However, no local habitat factors were correlated with *E. propertius* density except for an increasing positive relationship with percent grass cover in 1 out of the 5 years (Table 4; Hellmann *et al.* 2008).

*Erynnis propertius* is not found in all *Q. garryana* patches on Vancouver Island. We have observed that many patches of suitable size (*i.e.*, larger than S6), and with nectar resources that are surrounded by urban and residential areas, lack *E. propertius*. These observations suggest that sites could be vulnerable to extirpation, that a minimum set of factors is necessary to support a population, and (or) that human behavior in urban areas (*e.g.*, pesticide use) affects *E. propertius*. In addition, fragmentation and isolation of urban patches could prevent recolonization.

Maintaining healthy populations of *E. propertius* is an important conservation goal, especially with increasing development and urbanization in and around Garry oak ecosystems. Our data do not suggest a relationship between *E. propertius* and host-plant density, but all our sites were chosen for their high abundance of *Q. garryana*. Thus, host-plant abundance still could be limiting elsewhere in the region. It is possible that host-plant quality (*i.e.*, levels of nutrients and secondary compounds) affects *E. propertius* density; this would be an interesting avenue to explore. The amount of neither forbs nor their competitors (*i.e.*, grasses and shrubs) was related to butterfly density (except in 2004), but we have found that different nectar resources peak during different portions of this species' flight period. This suggests that a suite of wildflowers could be important in providing nectar over the season (Table 3).

Finally, temperatures are projected to increase in the region occupied by *Q. garryana* meadows and *E. propertius* (Mote 2003; Hamann and Wang 2006). Because flight phenology and timing of key resources seem to be coupled, and population densities at most sites varied little over years, these populations could be robust to changes in climate. High population densities of this species at its most northerly sites also could facilitate range shifts. However, northward migration of *E. propertius* will be limited by the lack of *Q. garryana* outside its current range.

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