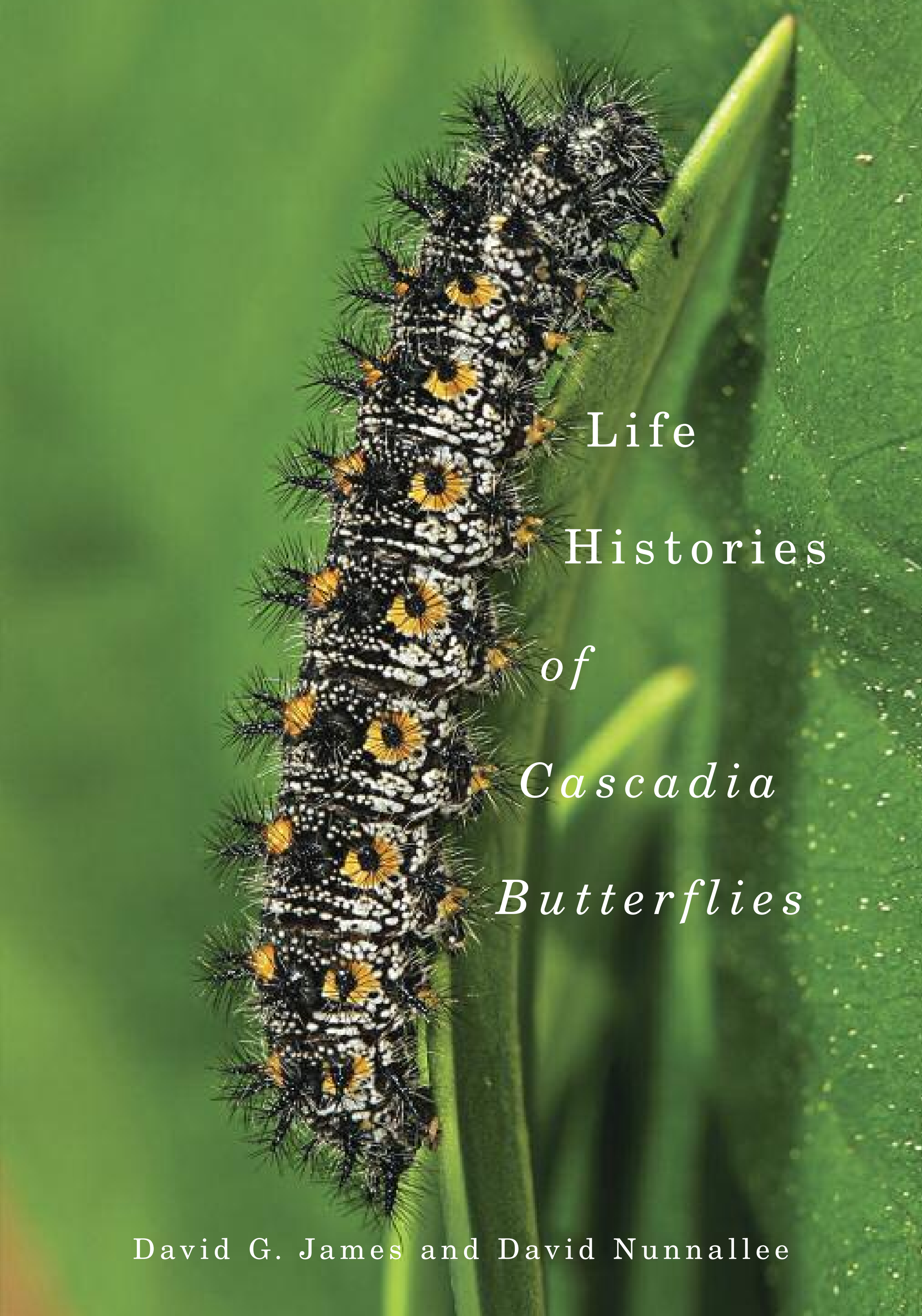
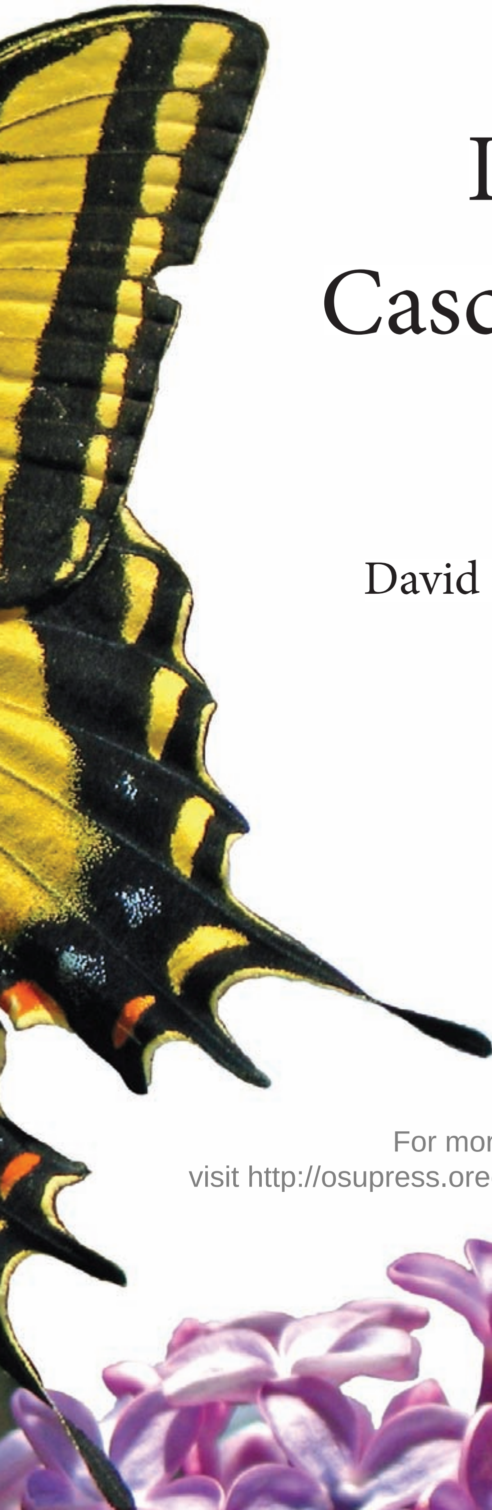


Life Histories of *Cascadia Butterflies*

David G. James and David Nunnallee



Life Histories of Cascadia Butterflies

David G. James and David Nunnallee

Oregon State University Press
Corvallis

The paper in this book meets the guidelines for permanence and durability of the Committee on Production Guidelines for Book Longevity of the Council on Library Resources and the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48-1984.

Library of Congress Cataloging-in-Publication Data

James, David G.
Life histories of Cascadia butterflies / David G. James, David Nunnallee ; foreword by Robert Michael Pyle.
p. cm.
Includes bibliographical references and index.
ISBN 978-0-87071-626-3 (alk. paper) -- ISBN 978-0-87071-648-5 (ebook)
1. Butterflies--Washington (State) 2. Butterflies--Northwest, Pacific. 3. Butterflies--Washington (State)--Pictorial works. 4. Butterflies--Northwest, Pacific--Pictorial works. I. Nunnallee, D. II. Pyle, Robert Michael. III. Title.
QL551.W2J36 2011
595.78'909795--dc23
2011020404

Oregon State University Press
121 The Valley Library
Corvallis, OR 97331-4501
541-737-3166 • fax 541-737-3170
http://oregonstate.edu/dept/press

Dedication

To my father, Alan James, and mother, Doreen James, for supporting and encouraging my interest in butterflies as an 8-year-old, which led to a lifelong passion for insects and their biology. Also to my entomologist wife, Tanya, and our gorgeous daughters, Jasmine Vanessa and Rhiannon Vanessa, for making this endeavor a truly enjoyable and family affair!

—David G. James

To my wife, Jo, for her unwavering support, companionship, and assistance, both in the field and at home.

—Dave Nunnallee

Table of Contents

Introduction

This book is the fulfillment of the authors' long-time dream to document all the life stages of all the butterflies of a significant geographic region, that of Cascadia. For David James the dream of comprehensively documenting butterfly life histories extends back to the 1960s in England, when he first began rearing butterflies—at the age of 8!

We define Cascadia for the purposes of this book as Washington State and the adjacent areas of northern Oregon, southern British Columbia, and the Idaho panhandle. Our coverage is virtually complete for Washington and nearly complete for these adjacent areas.

Area of coverage.

This work is the result of approximately twenty years of combined effort by the two authors to produce the information and photographs for this book. Initially both authors began this project independently, working separately and unbeknownst to each other for several years. The authors met early in 2005 and, recognizing that they had very similar goals, pooled their resources and efforts and have been working together ever since. David James is an associate professor in the Department of Entomology at Washington State University, Prosser, located in the Yakima Valley of eastern Washington. David Nunnallee is an engineer by occupation and a naturalist by avocation who resides in western Washington State near Seattle.

Life Histories of Cascadia Butterflies is a book about the immature stages—the eggs, larvae, and pupae—of the butterflies of the Pacific Northwest. The vast majority of the photographs and information were obtained by diligent and, usually, multiple rearings of individual species. This book is unique in the Americas in describing and illustrating with high-quality photographs all the immature stages of virtually all the butterfly species within a substantial geographic area. While there are other American publications that deal with butterfly larvae, there is no other publication in the New World, or to our knowledge in the Western world, with such a complete scope. Other publications either have complete life histories for a few butterfly species, or cover only the final instar (stage) of caterpillars for a wider selection of species; however, because many butterfly larvae change radically during their development, an illustration of only the final stage is often inadequate for identification or comparative studies.

Several converging factors underscore the need for a book of this kind. First, there has been a great surge of public interest in butterflies over the past decade or so. As members of the birding community have expanded their interests in recent years to butterflies, native plants, and dragonflies, they continue to search for interesting new pursuits, not to replace their natural history interests but to expand them. The study of butterfly larvae is a "natural" for this audience. Now that many people are becoming comfortable with identification of adult butterflies, they are ready to move on to immature stages. They want to be able to identify caterpillars they find, to locate larvae to rear with their children, or simply to expand their knowledge of the natural world. In addition, growing numbers of gardeners and horticulturists want not only to attract butterflies but also to provide a complete life history habitat for them and to be able to identify the larvae they find in their gardens.

Youngsters are our future. Rhiannon James enjoys her "butterfly nose."

There is also a great deal of interest in the immature stages of butterflies within the scientific community as a taxonomic tool for clarifying species relationships, for comparison of geographically separated populations, and as indicators of habitat degradation and climate change. Larvae are currently recognized, perhaps even more now than in earlier decades, for their value in differentiating butterfly species. In this book we hope that the considerable new information we present will help solve longtime problems in butterfly taxonomy and species identification. Professional and amateur entomologists are increasingly interested in the biology and ecology of butterflies because they provide excellent subjects for laboratory and field research.

Butterflies are dependent on their environment, most particularly on plants, and as human encroachment compromises their environments, many butterfly species are struggling to survive. As a result, in Cascadia several butterfly species have been listed as endangered within the past few years, and still others have been placed on candidate species lists. Such listings typically require recovery plans that in turn may include captive rearing programs. State agencies, zoos, universities, and conservation organizations are currently cooperating to rear some of the listed species for reintroduction to the wild. We cannot protect what we do not understand. We hope this book will increase our understanding of butterfly life histories and that this will lead to more effective preservation programs.

People have been fascinated with adult butterflies for centuries; however, the adults of many butterfly species live for only a week or so, with 98 percent of their life history hidden or unknown in immature stages, so a full understanding of the factors controlling populations must necessarily include the study of immature stages. Resources for understanding life histories are scattered and fragmentary. We hope that our comprehensive approach to showing all the life stages in our complete butterfly fauna will provide a reference point for others, to assist in regional and perhaps even international comparisons with similar faunas elsewhere.

We present a considerable body of new biological and ecological information on butterfly life histories, much of it gleaned from our multiple rearings of individual species. Data on egg laying, rates of development, instar number, feeding behavior, shelters, host-plant acceptance, defense strategies, natural enemies, and pupation are presented for the first time for many species. These data are combined with previously known but difficult to locate information, to provide a succinct overview of the biology and ecology of the immature stages of each species. For most species we highlight aspects of life history that need further research and include pertinent references to previously published research.

Prior to the species accounts we present overviews of fundamental themes relevant to immature stages of butterflies, like defense, natural enemies, dormancy, and habitats. We also include chapters on rearing, photography, and field techniques.

We hope that scientists and butterfly enthusiasts alike will be stimulated to conduct additional research and investigation of our fascinating butterfly fauna, or at least to record and share their observations, not only to satisfy individual curiosity and learn more about our natural history but also to help fill the many large gaps in our knowledge.

The Life History of a Butterfly

In this, the twenty-first century, the life history of a butterfly features in the curricula of most preschool and nearly all elementary school students. Today's children often know more about the fantastic metamorphosis through which butterflies pass than their parents do. Today, many 5-year-olds experience firsthand in the classroom the thrill and excitement of rearing their own "pet" caterpillar, thanks to companies providing butterfly livestock. Rearing companies in North America supply and ship eggs and caterpillars of Painted Lady butterflies along with artificial diet, so that nearly every schoolchild has the chance to see for him or herself the miracle that is the basis of this book. Observing butterfly development from egg to caterpillar to chrysalis is a tremendous life experience as well as learning experience for children, one they can carry with them the rest of their lives. It is hoped that it will also stimulate some of them to learn more about the butterflies in their area and to look at other life cycles.

Life Histories of Cascadia Butterflies documents individual life histories, each one unique in major or minor details of biology and ecology; however, all these life histories have the same underlying physiology of metamorphosis. All butterflies court, mate, and lay eggs that hatch into caterpillars (larvae). Larvae feed and grow, molting a number of times before becoming chrysalids (pupae) within which the adult butterflies develop and from which they ultimately emerge.

Freshly eclosed butterflies are in mint condition and, depending on temperature and sunshine, may take their first flights within an hour or so. All newly eclosed butterflies expel a red or orange fluid known as meconium, an accumulated waste product from the pupal stage. Nutrients are carried over from the pupal stage, and most newly eclosed butterflies do not need to seek nectar for at least a few hours and maybe a day or so, depending on activity. In most species, males develop faster and eclose before females (a phenomenon known as protandry), sometimes by up to a week or ten days. Consequently, when females eclose, males usually find them immediately and mating quickly follows. This means that for the majority of species, any female caught has usually been mated and will lay fertile eggs; there are exceptions, however, particularly during early spring, when cooler conditions may limit butterfly activity and females may remain unmated for a longer period. In some species, females eclose with mature eggs in their ovaries, but in others a period of feeding and maturation is needed before eggs are laid (e.g., most nymphalids). Butterflies that enter diapause as adults (e.g., Mourning Cloak, anglewings) may not develop their ovaries for 2–10 months, depending on the species.

Euphyes vestris (Dun Skipper) mature eggs with larval heads visible inside.

Euphilotes **sp. ovipositing on** ***Eriogonum heracleoides.***

Butterflies lay or oviposit eggs on healthy host plants chosen by the female. In some cases, eggs are laid on nonplant substrates (ground, rocks, etc.) near host plants or on senesced or dead hosts (e.g., fritillaries). In these cases, the eggs don't usually hatch until host plants reappear. Females can be extremely "choosy" when selecting oviposition sites and use visual and chemical cues to make their "decisions." Visual and/or long-distance olfactory stimuli guide females to the correct host plants, which are then chemically tested by drumming forelegs on leaves, stems, or flowers. Females are rarely satisfied with the first plant part they test and visit a number before bending their abdomen and laying an egg. Eggs are laid singly or in masses on upper or lower surfaces of leaves, on buds or flowers, or encircling twigs.

Butterfly eggs are all small but vary from the miniscule (0.4 × 0.2 mm, Pygmy Blue) to the robust (2.0 × 1.0 mm, Two-tailed Swallowtail). Species that lay eggs in batches may glue up to 300 together, covering an area of 3.0 × 1.0 cm. Small and cryptically colored, butterfly eggs are rarely found by casual observers. They develop rapidly, usually hatching within 2–10 days according to temperature. The neonate larva emerges from the egg by cutting an exit hole in the shell with its mandibles. In some species a circular "lid" is opened from the top of the egg, in others a hole is made in the wall. Neonates of some species consume the entire eggshell on the way out while others leave the empty eggshell with a telltale exit hole.

The first-instar larva immediately sets about feeding and protecting itself. It may move to a more protected location on the plant, cover itself with some strands of silk, or in the case of gregarious larvae join with its siblings in creating an extensive silk-web nest. First instars usually feed rapidly, with the larva often doubling in size from 1–2 mm at hatch to 2–4 mm within a few days. Once the larval "skin" (integument) tightens and appears stretched, the larva is nearing the first molt or ecdysis. Premolt larvae are also characterized by a swelling at the head end caused by development of the larger inelastic head capsule of the next instar. Premolt larvae spin a small pad of silk on which they attach their claspers and remain motionless for 12–48 hours. Larvae awaiting ecdysis are vulnerable to predation; thus they often select protected or hidden sites. Molting begins at the head end, with the integument splitting and moving backward along the body as the larva moves forward slightly. In most species the larva consumes the old integument except for the sclerotized head capsule. Molting takes little more than a few minutes to complete, and the new instar soon resumes feeding, seemingly making up for lost time. Newly molted larvae often show temporary coloration

The 2mm armored egg of ***Adelpha californica*** **(California Sister) dwarfs the finely textured 0.4mm egg of** ***Brephidium exilis*** **(Western Pygmy Blue).**

that disappears within 2–12 hours. Larvae may molt 3–5 times, developing through 4, 5, or 6 instars, depending on species and sometimes generation. In species that may have larval development interrupted multiple times by diapause, 7–9 instars may occur; however, most species have 5 instars with an approximate doubling of length in each successive instar. In this book we present new information for a number of species on the number of instars completed, but this is an area needing more research.

Butterfly larvae come in all shapes, colors, and sizes, as amply illustrated in our accounts; however, they all have the same purpose of consuming plant material to enable development and maturation while avoiding being eaten themselves. Larval development can be rapid in some species, taking as little as 10 days from oviposition to pupation (Western White), while larvae of other species may take 3–6 months (e.g., Mormon Metalmark). Developmental duration is strongly influenced by the timing of optimal periods for adult survival and reproduction.

***Pyrgus centaureae* (Grizzled Skipper) egg hatching. Larva has chewed hole in eggshell and is emerging.**

Final instars consume 60–80% of the total plant mass eaten by larvae during development; consequently, final instars show the greatest increases in length and girth. The largest butterfly caterpillar in Cascadia is the final instar of the Two-tailed Swallowtail, which may reach a length of 60 mm. Contrast this with the final instar of Cascadia's smallest species, the Pygmy Blue, which reaches only 11 mm at maturity.

When nearing maturity, full-fed larvae often change color slightly or dramatically, and some enter a wandering phase. The "wanderers" seek sites away from the host plant for pupation. Species that pupate on the host plant (e.g., many lycaenids) do not wander. Examples of wanderers are common among the brushfoots and swallowtails, which may travel many meters from the host plant before choosing a site for pupation.

Pupation describes the change from active eating machine (larva) to the immobile, nonfeeding preparatory stage (pupa) that will ultimately yield the adult butterfly. Pupae are formed in one of four basic modes: loose on the ground, within a "cocoon" or shelter, hanging by the terminal end (cremaster) attached to a silk pad, or attached upright by cremaster with a supporting silk girdle. Loose pupae are common in moths but rare in butterflies, confined to a few satyrs (e.g., *Oeneis* spp.). Skippers commonly form pupae within tied-leaf or grass shelters, while some fritillary and satyr species construct less robust leaf shelters. Hanging pupae are characteristic of brushfoots and satyrs, while girdled pupae are found in swallowtails, whites, sulphurs, and lycaenids. When a pupation site is selected, the prepupal larva shrinks a little and waits motionless for the final molt to occur. Larvae that form hanging pupae adopt a characteristic J shape. After 12–48 hours, the larval skin splits behind the head, revealing not another caterpillar integument, but a fleshy, soft integument, usually green, yellow, or orange. With much

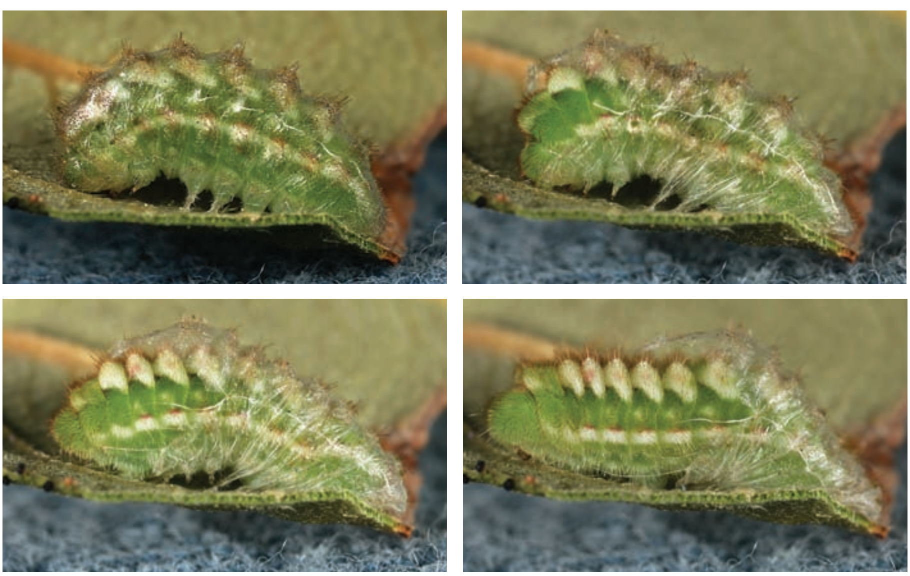
***Atalopedes campestris* (Sachem) L4 just prior to molt. Note expanded thorax; head is already withdrawn from old head capsule.**

Argynnis egleis **(Great Basin Fritillary) hanging in a J prior to pupation.**

wriggling, the larval "skin" moves down the body, revealing increasingly more of the soft new pupa. Once the shed skin reaches the terminal segment, the pupal cremaster probes and seeks the silk pad spun earlier by the prepupal larva. With hanging pupae this is a critical phase; if the cremaster fails to make contact with the silk pad to which it attaches with tiny hooks, the soft pupa will fall, likely to its death. After attachment, more wriggling usually results in the shed skin dropping away from the pupa, and eventually the pupa stops moving. During the next 24 hours, the pupa hardens and assumes the coloration that allows it to blend in with the environment. In a number of species, final coloration of the pupa is dependent on the immediate environment. For example, within a single species (e.g., swallowtails, whites), pupae formed on plants tend to be greener than those formed on sticks and boulders, which are usually gray-brown.

Forms and coloration of pupae are as diverse as larvae, but unlike larvae, pupae never draw attention to themselves. A wildly colored caterpillar can thrash around and be very aggressive to potential predators, but a strikingly colored pupa would simply attract attention and end up as a snack. Even Monarch pupae that contain toxins do not advertise this fact and are colored to blend in. "Blending in" is the pupal theme, with virtually all pupae demonstrating some form of camouflage and crypsis. Consequently, pupae are usually hard to find; however, if a pupa is found and disturbed, it may respond by wriggling, presumably in an attempt to startle and dissuade consumption. The pupa of the Great Spangled Fritillary is a great "wriggler," which may dissuade small rodents on the forest floor from snacking on it.

Celestrina echo echo **(Echo Blue) molting from L3 to L4.**



Papilio multicaudata **(Two-tailed Swallowtail) pupation series: Mature larva shedding skin to reveal pupa.**

The pupa hosts the greatest magic trick in the natural world: construction of a butterfly from caterpillar soup. Some recognizable parts of a butterfly are present within a caterpillar (e.g., reproductive organs), but the genesis of most parts and assimilation take place within the pupal shell. Not only is this metamorphosis wondrous, it can also be rapid, with the transformation sometimes taking as little as 5–7 days to complete (e.g., Milbert's Tortoiseshell). In contrast, the pupae of some species oversummer and overwinter in diapause, sometimes for 2–3 years (e.g., some whites and swallowtails). A few days before a butterfly ecloses, the pupa darkens, betraying the advanced stage of development. During the final day, wing patterns and color show through the wing cases, and all parts of the body become apparent through a shell that becomes increasingly transparent. This is known as the pharate pupa stage, with eclosion just hours away.

Adult eclosion from the pupa is synchronized in many species to occur early in the morning, often soon after dawn, presumably to enable the best opportunities for successful eclosion, post-eclosion "drying" of wings, and inaugural flight. Eclosion begins with the butterfly pushing with its feet against the shell covering the legs, antennae, and proboscis. Once the legs are free, they grab hold of the shell, pulling out the rest of the body (substantially aided by gravity in hanging pupa species), until the entire butterfly is fully extricated. Hanging and girdled pupae species usually hang from the pupal shell or a nearby support, whereas butterflies eclosing from pupae on or near the ground wander for a short while to find an appropriate support site. Once a site has been chosen, the butterfly begins pumping hemolymph through the wing veins and sets about zipping together the two parts of the coiled proboscis to form a tube for sipping nectar. This vulnerable period passes quickly, with most species "pumping" wings to full size within 5–15 minutes; however, the wings remain limp and flaccid for another hour or so (depending on temperature), and the butterfly is unable to fly during this time. If a butterfly ecloses around 6 AM on a warm summer's morning, it will be capable of flight by breakfast time, ready to begin the cycle all over again.

Polygonia satyrus **(Satyr Comma) pharate pupa, adult wings visible inside.**

The life cycle of a butterfly may occupy as few as 28 days in summer or a whole year (or more), but the basics remain the same. The details differ in extraordinary ways, and this book offers an introduction to the lesser known parts of a butterfly's life. We have uncovered many details and secrets of the immature lives of Cascadia butterflies, but many more remain to be discovered.

Life Strategies

Despite their fragile appearance and sometimes ephemeral existence, butterflies are tough, seasoned survivors. Every delicate butterfly flitting over a flowery meadow is the survivor of millions of generations of resilient ancestors that endured, outsmarted, or avoided drought, disease, predators, parasitoids, competitors, storms, volcanoes, and even ice ages. Survival in the butterfly world requires adaptation, flexibility, and strategy, and Cascadia butterflies have become experts in all these endeavors.

***Aglais milberti* (Milbert's Tortoiseshell) eggs on Stinging Nettle.**

Host Plants: Butterflies are inextricably linked to plants, not only as nectar sources for adults but also for larval food. Most adult butterflies will use whatever nectar source is available, provided the timing is right and they are physically able to access the nectar (proboscis length vs. flower depth); however, larvae of every butterfly species have adapted to certain host plants, some depending entirely on a single kind of plant for survival. Many other butterflies have adapted to use several closely related plant species, and a few are able to utilize a very wide range of plants. A butterfly species that overwinters as an egg needs fresh succulent food as soon as it hatches, in most cases early in the spring, so only plants that grow early in the spring are candidates as hosts. Butterflies that overwinter as pupae will eclose to adults in spring, immediately needing nectar but not requiring a larval host until sometime later, when the plant selection may be different from that available to species overwintering as eggs. Life cycle timing, or phenology, is an important determinant in host-plant selection.

Why have some butterfly species adapted by depending on only one or a few plants while others use many? There is no doubt that the ability of plant generalists, such as the Painted Lady, Gray Hairstreak, and Variegated Fritillary, to use many kinds of host plants has rendered them highly successful, allowing them to colonize vast areas, worldwide in the case of the Painted Lady. Specialization on only one or a few plants can also be a highly successful strategy if those plants are widespread and common (e.g., the case of the Cabbage White). California Tortoiseshell larvae feed almost exclusively on *Ceanothus* spp., but they are highly successful as the plants are widespread and common

***Vanessa cardui* (Painted Lady) larva on Canada Thistle surrounded by sharp spines.**

over vast areas of the mountainous West. The Mountain Parnassian uses only stonecrops, greater fritillaries only violets, and Milbert's Tortoiseshells only Stinging Nettle, but these plants are widespread and the butterflies are very successful.

Niche exploitation occurs throughout the natural world, and Lepidoptera are no exception in a natural process of testing the boundaries and seeking a new advantage against competitors; however, it can also be a risky strategy, with some butterfly species becoming restricted to a single plant species that may be very limited in distribution and/or abundance. The Johnson's Hairstreak specializes on a species of *Arceuthobium* (dwarf mistletoe) that grows on mature hemlock trees, but with the human deforestation of old growth forests, this habitat has largely disappeared, and the Johnson's Hairstreak is now at risk. In Washington State the Golden Hairstreak feeds only on chinquapin, a broadleaf tree that barely reaches into this area, so this population is tentative and at the mercy of commercial logging operations, although it is secure farther south in Oregon.

***Euphilotes* on *Eriogonum thymoides*, L2, displaying its long extendable lycaenid neck useful for hollowing out host plants through a small entry hole.**

Some butterflies, such as *Euphydryas editha* (Edith's Checkerspot), have adapted to using two different host plants, one for young larvae in the summer (*Castilleja*), and a different host for the spring larvae (*Collinsia* or *Plantago*) after passing the winter half-grown. Such alternate hosts can be very different, although they are usually from the same or a closely related plant family. Chemical cues undoubtedly play a strong role in selection of alternate hosts; some unrelated or introduced plants may contain chemicals similar to the preferred host, thus inducing larvae to experiment.

The part of a plant preferred by larvae can be very important, and each species of butterfly tends to specialize on only one or a few parts. Some species feed only on leaf buds, others on young leaves, others on mature leaves. Other species require flower buds, flowers, seeds, or even stems. The different parts of a plant develop at different times, so this level of specialization restricts the time period when the larvae can grow. Buds, flowers, and seeds are more nutritious (generally containing 2–10 times more nitrogen) than leaves or stems, promoting faster growth but restricting larvae to a shorter growth period (leaves usually persist longer). Use of different plant parts allows multiple species to use the same host plant without direct competition, as does the staggered timing of the different parts, another niche-exploitation strategy. Food sources such as grasses and evergreen needles are low in nutrition but hugely abundant over vast areas, so larvae exploiting these resources grow slowly but have little competition.

Voltinism and Phenology: The number of generations or broods developed over the course of one year is referred to as voltinism. The benefit of having multiple broods per year is that a species can expand its population with each brood, ultimately improving the chances of survival and success; however, late broods are often at risk of failure due to drought or early winter, so producing multiple broods may be a gamble. Voltinism is very much related to climate, and climate is related to latitude and/or elevation. A single species will often have more annual broods in its southerly range than in its northern (or higher elevation) range. Bivoltine (or "double-brooded") butterflies have two broods per year, and biennial species have one brood over two years. In Cascadia, most butterflies

Hesperia juba (Juba Skipper) L5 in a typical grass skipper nest.

are univoltine, with one brood per year; however 39 of about 150 Cascadia species may be bivoltine at least on occasion, and 5 are biennial, most of these flying only in even-numbered years. Voltinism is largely a response to the growing season of host plants. When the growing season is short, larvae are unable to develop in a single season and must continue to grow the following year, overwintering as immature stages during two winters. Biennialism is common in northern Canada; all of Cascadia's biennial butterflies are northern species, most of which marginally range into our area. Those that do range farther south (*Oeneis* spp. in California) typically become univoltine. Longer growing seasons in southerly areas produce good-quality host plants persisting well into late summer, providing an opportunity for more generations. Some butterfly species with flexible voltinism opportunistically develop a second brood when conditions are optimal, or "hedge their bets" with broods that are part univoltine and part bivoltine. This occurs in the Purplish Copper, with mid- to late-summer eggs either entering winter dormancy or hatching to produce a late summer–autumn adult generation.

Phenology refers to the timing of biological events in relation to climate and season. The phenology of butterfly life cycles in Cascadia is strongly influenced by temperature and photoperiod, with growth and development restricted to approximately nine months of the year in most species. Butterfly life cycles are adaptations to resource availability (e.g., host plant, warm temperatures). Consequently, different climatic regions and vegetation types within Cascadia produce different phenologies. For example, most plants in the arid shrub-steppe ecosystem of eastern Washington and Oregon characteristically have a brief but intense period of vegetative growth, flowering, and seed set during March–June. The phenologies of a number of butterfly species are driven by this ephemeral period of optimal environmental conditions. Development of these spring species from adults (produced by overwintering pupae) to next generation overwintering pupae typically takes as little as 4–6 weeks. Some spring species become dormant during summer in eastern Cascadia, when temperatures are excessively hot and host plants are dead or inedible, but produce a second generation of adults when temperatures ameliorate in late summer-autumn and host plants put out new growth. An example of this occurs with the Juba Skipper and some other skippers whose larvae feed and develop rapidly in mid- to late spring when host grasses are green. Once final instars are fully fed, they enter dormancy in silk-tied nests, not moving or feeding for 4–6 weeks during the heat of summer. During late August the larvae pupate, and adults eclose and lay eggs in September when grasses are showing at least some new growth. These skippers therefore avoid an unfavorable time of year by pausing development (James, 2009b).

Nectar and host plant–rich shrub-steppe habitat in Benton Co., Wa. during April, home to swallowtails and whites.

“The publication of James and Nunnallee, or ‘the Daves’ as we know them, is a matter for unreserved celebration, not only for lepidopterists and nature lovers of all stripes, but for anyone who cares about our butterflies’ lives, futures, conservation management, and the plants with which they have co-evolved.” ROBERT MICHAEL PYLE, author of *Mariposa Road: The First Butterfly Big Year*

Life Histories of Cascadia Butterflies presents, for the first time in North America, the life stages of the entire butterfly fauna of a geographic region. In exceptional and riveting detail, this authoritative field guide describes and illustrates the life histories of the butterflies of the Pacific Northwest.

Virtually all of the 158 butterfly species occurring in southern British Columbia, Washington, northern Idaho, and northern Oregon are included in the book. Color photographs of each stage of life—egg, every larval instar, pupa, adult—accompany information on the biology, ecology, and rearing of each species.

Life Histories of Cascadia Butterflies is an unparalleled resource on the natural history of immature stages of butterflies in the Pacific Northwest—and beyond, as many of Cascadia’s butterflies occur in other parts of North America as well as Europe and Asia. It provides interested citizens with a basic understanding of the region’s rich butterfly life and serves as an invaluable reference for scientists and lepidopterists.

Oregon State University Press

ISBN 978-0-87071-626-3

9 780870 716263

Cover photographs by David G. James and David Nunnallee
Cover images depict life stages of *Euphydryas colon*
Cover design by David Drummond