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EXPOSED

Other caterpillars take the opposite approach to concealment, resting openly with gaudy and striking coloration so predators cannot miss them. However, the colors—usually contrasting hues such as black and white or black and yellow—are a warning that says, "Eat me, and you'll regret it!" These caterpillars contain toxins (usually sequestered from their host plant) that will cause vertebrate predators to fall ill and even die. The most famous example of this is the Monarch (*Danaus plexippus*), whose black-, yellow-, and white-banded caterpillar incorporates cardiac glycoside toxins from milkweed to defend itself, primarily from birds. So successful is this strategy that caterpillars of other non-toxic species will mimic the Monarch caterpillar's coloring to gain some protection against "once bitten" predators.

↖ The aposematic black, white, and yellow caterpillar of the Indra Swallowtail (*Papilio indra*). These striking caterpillars advertise their distastefulness to educated birds who avoid taking them as food.

↑ Early-instar caterpillars of some species, such as these California Tortoiseshell caterpillars (*Nymphalis californica*), aggregate for protection.

↗ Caterpillars of the Pale Imperial Hairstreak (*Jalmenus eubulus*) and its relatives provide essential nutrients to Meat ants (*Iridomyrmex* spp.) through various glands. In return, the ants protect the butterflies from predators and parasites throughout their immature stages.

Aggregation or gregariousness is another caterpillar behavioral tactic that reduces the odds of any single individual being attacked. This is often used by early-instar caterpillars before being superseded by other defense tactics as they mature. Communal caterpillars may also build silken webs, supports, and platforms to help keep the community together and dissuade natural enemies.

THE BENEFITS OF MUTUALISM

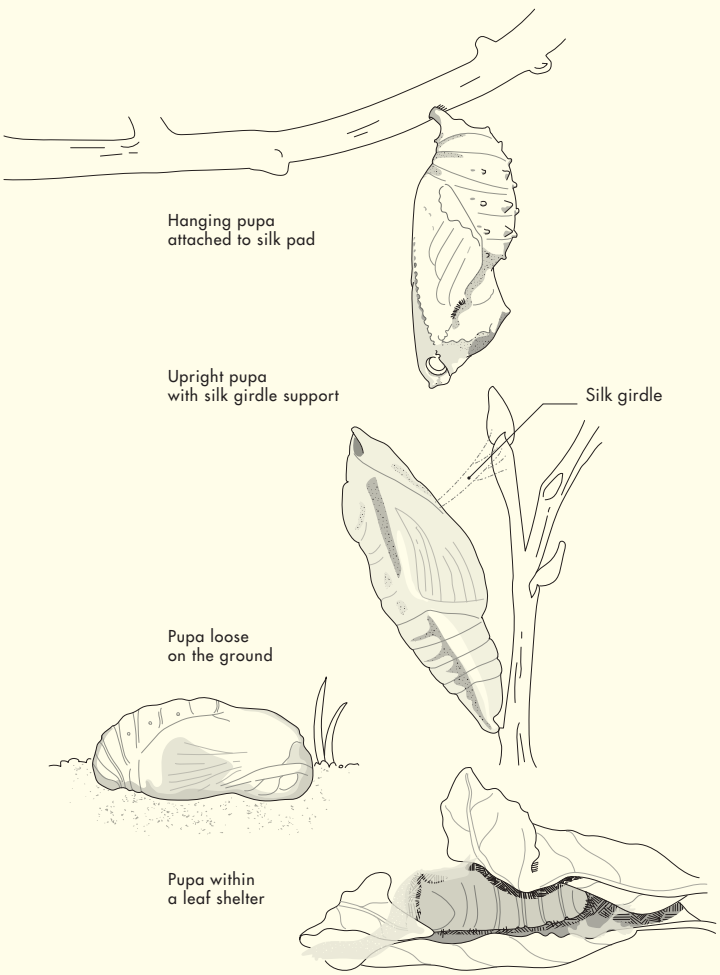
Some caterpillars, and particularly blues, coppers, and hairstreaks (Lycaenidae), have developed a defense strategy based on recruiting ant bodyguards to repel threats from predators and parasitoids.

Ants may be a significant predator of some butterfly caterpillars, but not the lycaenids, which have small glands that, when stimulated, excrete a sugar-rich "honeydew" that ants love. In a clear example of mutualism, the ants are provided with a nutritious food supply and the caterpillars receive protection from ants crawling over and around them, effectively preventing attacks from parasitic wasps, predatory bugs, spiders, and many other natural enemies.

Pupae: crucibles of transformation

The pupa, also known as a chrysalis, is the transformative stage between the hungry caterpillar and adult butterfly. The egg and the pupa are the only life stages of a butterfly that are immobile, although some pupae can flex if disturbed.

FORMS OF PUPAE



PUPA MODES

Butterfly pupae develop in one of four basic modes: loose, or sometimes in a sparsely spun cocoon on the ground; within a leaf shelter; hanging by the terminal end that is attached to a silk pad; or attached upright with a supporting silk girdle.

Skipper butterflies (Hesperiidae), including the European Skipperling (*Thymelicus lineola*; see pages 56–57), commonly form pupae in tied leaf or grass shelters, while hanging pupae are characteristic of brushfoot butterflies such as the Red Admiral (*Vanessa atalanta*; see pages 58–59). Girdled pupae are most often found in species in the families Papilionidae, Pieridae, and Lycaenidae. Forming a pupa that is either loose or lightly cocooned on the ground is rare in butterflies, although it is common in moths. Parnassian butterflies (members of the swallowtail family, Papilionidae), including the Mountain Parnassian (*Parnassius smintheus*; see pages 98–99) in western North America, eclose from pupae formed within a sparsely spun cocoon on the ground, as do a few species in the brushfoot family (Nymphalidae).

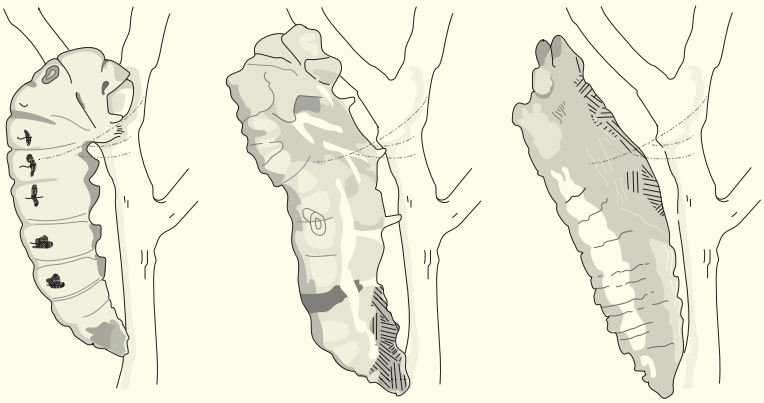
TRANSFORMATION

Once a pre-pupal caterpillar has selected its pupation site, it shrinks a little and waits motionless for a day or so for the final molt.

Caterpillars that form hanging pupae adopt a characteristic "J" shape. After 24–48 hours, the caterpillar's skin splits behind the head, revealing the soft pupal case that has formed beneath. With much wriggling, the caterpillar skin moves down the body, revealing more of the soft new pupa. Once the shed skin reaches the last segment, the tip (also known as a cremaster) probes and seeks the silk pad spun by the pre-pupal caterpillar. With hanging pupae, this is a critical phase; if the cremaster fails to make contact with the silk pad, the soft and vulnerable pupa will fall to certain death. After attachment, more wriggling occurs, which results in the shed skin falling away. After a few minutes the pupa stops moving, hardens, and becomes the color that protects it until the adult stage.

J-shaped pre-pupal caterpillar

A typical pre-pupal caterpillar before transforming into the pupa or chrysalis.



The pre-pupal stage of a caterpillar awaiting its final molt.

The skin moves down the caterpillar's body as it molts.

The caterpillar's skin is fully molted, leaving a soft pupa prior to it hardening.

Ecdysis: from pre-pupal caterpillar to pupa

The process of a caterpillar shedding its skin for the final time and transforming into a pupa is called ecdysis. This swallowtail caterpillar is shown in pre-pupal, mid-ecdysis, and new pupal stages.

HIDDEN FROM VIEW

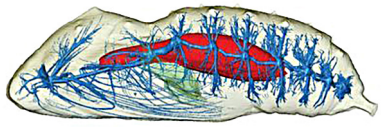
Being immobile and unable to defend itself, the pupa must remain hidden in a protected location away from foraging predators and parasitoids. This is invariably the case for most butterflies, the pupa being the least-seen stage in its life cycle. In its last day or two, the full-grown caterpillar has the crucial task of finding a suitable location for its transformation into a pupa. Most caterpillars at this point become duller in color and begin to wander in search of the perfect place to pupate. Some, such as the Red Admiral, will pupate on their host plant but will bind together some leaves with silk to create a "tent" to cover and hide the pupa. For a wandering caterpillar, the perfect location may be a twig within a bush, a blade of grass within a meadow, or simply on the ground. It may travel up to 330 ft (100 m) from its host plant in search of such a spot.

In addition, pupae are cryptically colored and shaped. For example, the pupae of orange-tip (*Anthocharis* spp.) butterflies are colored to match their background and are shaped like a large thorn. The pupae of butterflies defended by toxins, on the other hand, are often showy to advertise their distastefulness. The pupae of crow butterflies (*Euploea* spp.), for example, look like molten metal. Undoubtedly, some pupae still fall prey to foraging birds and small mammals, and parasitic wasps can locate them by smell. For most species, however, if a caterpillar is able to transform into a pupa and manages to escape from parasitoids, there is a good chance it will produce a butterfly.

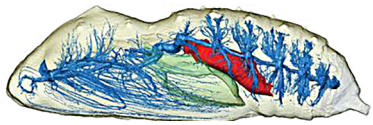
THE MAGIC WITHIN

The pupa is the least-studied stage of butterfly life, yet it is the most transformative. We still do not know exactly what happens during this process, but modern imaging techniques are allowing glimpses. Micro X-ray computed tomography scans now allow us to see some of the development that happens within a pupa. For pupae that develop during the spring or summer, this remarkable transformation takes just a week or two. For many species—including orange-tips (Pieridae), swallowtails (Papilionidae), and hairstreaks (Lycaenidae)—the pupa is the overwintering stage, so it can remain dormant for months or, in some cases, two or three years.

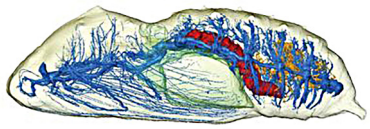
LATERAL VIEW DAY 1



LATERAL VIEW DAY 7



LATERAL VIEW DAY 13



↑ Development within the pupa of a Painted Lady (*Vanessa cardui*) butterfly over 13 days as shown by high-resolution X-ray computed tomography scans. Red shows the forming gut and blue shows the tracheal (breathing) system. The Malpighian tubules, which function like a kidney, are shown in orange.

← Pupae of grass-feeding caterpillars like those of the Common Wood Nymph (*Cercyonis pegala*) in North America are beautifully camouflaged in a sea of grass.

A BUTTERFLY IS BORN

A few days before an adult butterfly emerges, or ecloses, the pupa darkens. On the day before, the pupal shell becomes transparent, showing the patterns and color of the butterfly's wings. At this stage, eclosion is just hours away. Most butterfly pupae eclose soon after sunrise to optimize successful emergence, post-eclosion drying of wings, and inaugural flight.

Eclosion begins with the butterfly pushing with its legs against the pupal shell. Once the legs are free, the butterfly uses them to grab hold of the shell and pull the rest of itself out. The newly eclosed butterfly then hangs from the shell or nearby support as its initially tiny, crumpled wings slowly increase in size as hemolymph, or insect blood, is pumped through their veins. This is a vulnerable time for a butterfly, as it is unable to fly away from predators and its wings are easily damaged. All being well, the wings will reach their full size within 15 minutes, although full hardening may take a few to several hours depending on temperature. Caterpillars of the Moth Butterfly (*Liphyra brassolis*; see pages 94–95) pupate and eclose inside weaver ant nests and must flee quickly to avoid being eaten. Their crumpled wings remain soft for hours to allow them time to escape and find a safe place to hang their wings to dry.

A METAPHOR FOR CHANGE

The pupa arguably hosts the most incredible "magic trick" in the natural world. The transformation from non-flying, wormlike, hungry caterpillar to colorful, flying adult butterfly is truly one of nature's marvels that will never fail to amaze and make people think. Indeed, this metamorphosis has long been used by people as a metaphor for change, specifically how study of butterflies has been introduced to at least one prison: by rearing Monarch butterflies, inmates were able to recognize and visualize the transformation they could make in themselves. The humble pupa is a powerful symbol for change.

← Just a few hours from eclosion, this pupa of a Satyr Comma (*Polygonia satyrus*) shows the wing colors of the adult butterfly through the transparent pupa shell.

Adult butterflies: beating the odds

The adult butterflies flying around your backyard are success stories, having beaten the overwhelming odds against their survival. They are among the few survivors in a population that have avoided death, the threat of which is omnipresent throughout their immature lives.

SURVIVAL OF THE FITTEST AND LUCKIEST

Newly eclosed butterflies have escaped predation, parasitism, disease, and death from unfavorable environmental conditions, including excessive heat, drought, cold, storms, and food shortages. Few butterfly eggs survive to become adult butterflies: in most species the figure stands at less than 10 percent, although often it is much lower than that. The life history of butterflies is truly a story of survival of the fittest and perhaps also the luckiest.

HARBINGERS OF SPRING

After the gloom and cold of winter in temperate regions, nothing lifts the human spirit as much as seeing a butterfly flitting among the first flowers of the year. Usually, the first butterfly to appear will be a species that has hibernated and been awoken by the first warm day of early spring. Many people are stunned to know that an adult butterfly (also called an imago) can overwinter, withstanding often severe cold periods, to emerge at the first hint of spring. In Europe and North America, early-spring butterflies include nymphalids and brushfoots such as a tortoiseshell or Red Admiral (*Vanessa atalanta*).

A little later, the true harbinger of spring on these continents appears: the orange-tips (*Anthocharis* spp.), which spend winter as a pupa. Orange-tips are often seen sailing down pathways and wooded lanes, checking out crucifers for nectar and egg-laying. In many parts of the world the first spring butterfly will be the slightly pestiferous Small Cabbage White (*Pieris rapae*), which also overwinter as a pupa. Even cabbage growers may feel joy at seeing the year's first white butterfly!

↑ The Red Admiral is a welcome sight in spring in Europe and North America, having overwintered or migrated from more southerly climes.

← A Monarch butterfly eclosing from its pupa. With its wings soft and crumpled, this is a very vulnerable time in the life of a butterfly. After a few hours, the wings are firm and straightened and it is ready for the maiden flight.

ANTHOCHARIS JULIA

Julia Orange-tip

Harbinger of spring

SCIENTIFIC NAME	*Anthocharis julia* (W.H. Edwards, 1872)
FAMILY	Pieridae
NOTABLE FEATURES	Orange tips to the forewings
WINGSPAN	1–1½ in (25–38 mm)
HABITAT	Open habitat, particularly lanes, roadsides, meadows, glades, and canyons

The Julia Orange-tip is a true harbinger of spring in western North America. Other orange-tip species are also early spring fliers in other parts of the world. Orange-tip butterflies are unmistakable, with orange corner patches on the forewings.

Orange-tips resonate with people because of their simple yet striking beauty and their welcome early-spring appearance after a long winter. The lower surfaces of the wings are also beautiful, with green marbling and yellow veins. The single annual generation flies for just two or three weeks and spends most of the year as a dormant pupa. The Julia Orange-tip is an avid flower visitor, seeking nectar from spring-flowering plants such as mustards, fiddlenecks, and phlox.

Females lay their eggs singly—usually only one per mustard plant unless plants are scarce, when overcrowding can occur. The eggs are slender, initially white and then turning bright orange-red, and are laid on all parts of the plant. The highly cryptic green caterpillars preferentially feed on buds and flowers before consuming leaves and stems. Blending in with the exact tones of mustard greens helps caterpillars evade detection by predators, although some fall prey to parasitoid wasps and disease.

HEDGING THEIR BETS

In marginal arid environments, some individual Julia Orange-tips may hedge their bets by taking an extended rest as pupae. The pupae are green when formed and the host plant is still green, but turn brown when the plant and those nearby plants wither. While most pupae produce butterflies the following spring, some remain dormant for two or more years. This is thought to spread the risk of butterflies eclosing into unfavorable conditions for survival and reproduction, as can occur when a dry spring causes predominantly drought-stressed or limited numbers of host plants.

→ The Julia Orange-tip is an unmistakable spring butterfly with its namesake orange-tipped forewings contrasting gorgeously with the white hind wings and black body.

SAROTA GYAS

Gyas Jewelmark

A brilliant butterfly with an unusual diet

SCIENTIFIC NAME	*Sarota gyas* (Cramer, 1775)
FAMILY	Riodinidae
NOTABLE FEATURES	Blue stripes appear metallic; legs and wing margins covered with long, hair-like scales
WINGSPAN	½ in (10–10.5 mm)
HABITAT	Rainforests from sea level to 800m

The Gyas Jewelmark and its relatives are strikingly colored with bold orange and yellow wings punctuated by shiny blue stripes. The caterpillars' unusual habits are even more interesting.

Unlike some other tropical metalmarks, the caterpillars of the Gyas Jewelmark do not live with ants. In fact, they are covered with long hairs called setae that are directed at an ant or other predatory insects in defense. Upon contact with the hairs, the ants retreat and groom themselves in an apparent attempt to remove small, broken fragments of the minutely barbed setae. The adult butterflies are usually active in the morning, encountered along streams and forest edges perched on leaves. Males stake out a territory and guard it against intruding males, and challenges to their domain by rival males will be contested in a fast-paced, spiraling aerial dog-fight. Those that are successful have a chance of mating with females, which fly along inspecting the males and their territories.

LIVER(WORTS) FOR DINNER

The Gyas Jewelmark caterpillars have an unusual diet. Instead of feeding on vascular plants, as most butterflies do, they feed on liverworts in the family Lejeuneaceae. These ancient plants are related to mosses and grow as epiphylls—tiny plants that live on the leaves of the trees in rainforests. Given the choice between fresh, tender leaves and old leaves encrusted with epiphylls, the caterpillars will always eat the epiphylls, leaving the new foliage untouched. Adults have a more typical diet of floral nectar, often from species of *Alibertia* or *Croton*. They have also been observed feeding on the extrafloral nectaries of some plants. These are small nectar-producing glands found on plant leaves; the nectar is often consumed by ants that guard the plant, protecting it from herbivores.

→ The bedazzled wings of a male Gyas Jewelmark, fringed with hair-like scales, glisten as he rests on the underside of a leaf.

PAPILIO MULTICAUDATA

Two-tailed Tiger Swallowtail

Successful in suburbia

SCIENTIFIC NAME	*Papilio multicaudata* (W.F. Kirby, 1884)
FAMILY	Papilionidae
NOTABLE FEATURES	Large, with yellow and black "tiger" stripes
WINGSPAN	5 in (130 mm)
HABITAT	Canyons, gardens, parks, shrublands, and watercourses

The Two-tailed Tiger Swallowtail is one of the most common large butterflies in North America. In fact, it is the largest butterfly in western North America, with a wingspan of 5 in (130 mm). It can be found in most habitats from sea level to the mountains.

The large size and striking yellow and black stripes of the Two-tailed Tiger Swallowtail catch the attention of even casual observers, especially since the species is common in urban parks and gardens. The single brood flies from late April to August, sometimes joined by a partial second brood late in the summer.

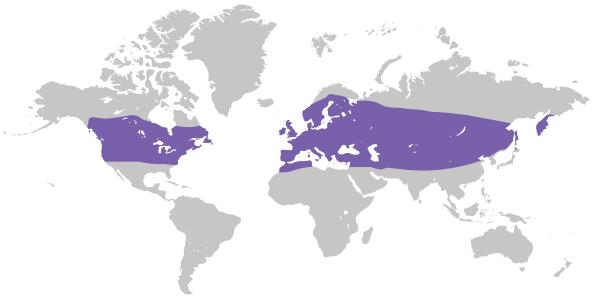
Male Two-tailed Tigers range widely as they seek females, patrolling up and down corridors such as canyons and creek beds. Females spend most of their time in proximity of their host plants or visiting flowers. Two-tailed Tiger Swallowtails use species of *Prunus* (including cherries and plums), ashes, and serviceberries as host plants, many of which are grown as garden ornamentals, helping to explain the success and abundance of this species in urban and suburban areas. Both sexes visit a wide variety of ornamental and native flowers, and males commonly visit mud puddles to gain moisture and minerals, often with other swallowtails.

After mating, the female flies from tree to tree, being very choosy in her search for an oviposition site, before laying a single round green egg on the upper surface of a leaf. She then flies to a different plant—often a considerable distance away—to search for the next oviposition site. Two-tailed Tiger Swallowtails are often on the wing, which is another reason they tend to get noticed.

FAMILIAR CATERPILLARS

Two-tailed Tiger caterpillars are large and green, with false eyespots near the head that the caterpillar enlarges by stretching when threatened. A threatened caterpillar will also produce a malodorous Y-shaped fleshy organ, known as an osmeterium, from behind its head to repulse the threat. Fully fed caterpillars turn dark brown and wander extensively to find a pupation site, often attracting the attention of children. Pupae are formed on upright surfaces, including walls and tree trunks, and blend in with the background. Adult butterflies emerge the following spring.

→ The Two-tailed Tiger Swallowtail, with its five-inch wingspan and contrasting black and yellow "tiger" stripes, attracts a lot of attention as it flies and glides through suburban gardens in the towns and cities of western North America.



THYMELICUS LINEOLA

European Skipperling

A successful colonizer

SCIENTIFIC NAME	*Thymelicus lineola* (Ochsenheimer, 1808)
FAMILY	Hesperiidae
NOTABLE FEATURES	Small, fast, unmarked skipper
WINGSPAN	¾–1 in (20–25 mm)
HABITAT	Hayfields, meadows, pasture, and waste ground

The European Skipperling, also known as the Essex Skipper in the UK, is one of two introduced butterflies that now occur widely in North America, the other being the Small Cabbage White (*Pieris rapae*). It is a small, fast-flying butterfly found in grassy areas.

Females produce pale yellow eggs that are uniquely shaped, pill-like, and laid in strings on grass. They oviposit on many different kinds of grasses, although they prefer tall species; in Europe, cocksfoot grass (*Dactylis glomerata*) is a favorite. Unlike the eggs of most other skippers, European Skipperling eggs overwinter and hatch in spring. Curiously, the dormant embryonic caterpillar can be seen through the overwintering eggshell. The caterpillars are green and construct nests on their grass host plants. They pull a single blade of grass into a neat tube and then pin it together with tidy silk cross-ties. The caterpillars remain hidden to the world within these tubes by day and emerge at night to feed. Pupation also occurs within the tubes.

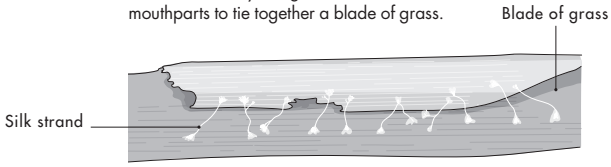
A SUCCESSFUL COLONIST

Introduced to Ontario, Canada, in 1910, this species is now common in the eastern USA and some parts of the Pacific Northwest. Sometimes hyperabundant and outnumbering all other butterflies, the European Skipperling is still expanding its range in North America. Ironically, perhaps, it is declining in abundance in the UK. It also occurs widely through Europe, Asia, and northern Africa. The species is common in agricultural fields, where it can occasionally be a pest of timothy grass (*Phleum pratense*). As dusk approaches, European Skipperlings move to sheltered sunlit areas of tall grasses, where they sometimes roost in the hundreds, often with multiple individuals sharing a single grass head.

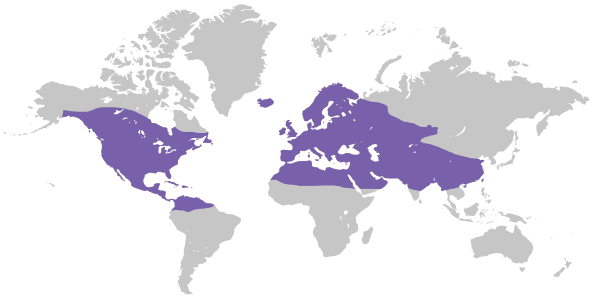
European Skipperlings are exceptional colonists. Their spread is facilitated by their habit of feeding on widespread, common host plant grasses and their high mobility, with populations advancing up to 19 miles (30 km) annually in the USA. Another way in which populations of this butterfly spread is as dormant overwintering eggs on grasses dried for hay that are then transported long distances.

Caterpillar nest

Caterpillars of European Skipperlings construct nests by using silk from their mouthparts to tie together a blade of grass.



→ The European Skipperling is a European export to North America where it can now be found in meadows and pastures in the northern USA and southern Canada.



VANESSA ATALANTA

Red Admiral

Also known as Red Admirable

SCIENTIFIC NAME	*Vanessa atalanta* (Linnaeus, 1758)
FAMILY	Nymphalidae
NOTABLE FEATURES	Coal-black with scarlet bands
WINGSPAN	2–2½ in (50–65 mm)
HABITAT	Open habitat including parks, gardens, grassland, woodlands, and mountains

The Red Admiral is also known as the Red Admirable, which is perhaps a more fitting name since the admiral butterflies belong to the genus *Limenitis*, and the species *V. atalanta* is in the genus *Vanessa*. This charismatic and striking butterfly is, indeed, one to be admired.

The caterpillar of the Red Admiral leads a solitary and hidden life within a drooping leaf tent that it constructs on a stinging nettle (*Urtica dioica*) host plant. Feeding occurs within or outside the shelter at any time of night or day. Red Admiral caterpillars rarely wander from the host plant to pupate, and the pre-pupal caterpillars will sometimes make a leaf umbrella to shelter the pupa. In the UK, the species also uses hop (*Humulus lupulus*) as a host plant, although this is not the case in the western USA, where hop plants are often ignored. Females lay their ribbed green eggs singly, usually on the lower surfaces of nettle leaves. Caterpillars take about three weeks to develop and pupate.

PUGNACIOUS AND TERRITORIAL

With solid red, scarlet, or orange bands on a coal-black background, this butterfly is exceptionally striking. It is also very tough, able to live many weeks and even sometimes months as an adult. It may overwinter as an adult or migrate south.

The Red Admiral is widespread, occurring in North America, Europe, and Asia in a wide range of habitats, including gardens, parks, forests, meadows, orchards, and mountains. It is a strong flier and a lover of flowers, particularly butterfly bushes (*Buddleja*) in home gardens.

The male Red Admiral is pugnacious and territorial, perching on hilltops, bushes, or the ground, particularly late in the afternoon, from where it flies out to intercept intruders. Adults visit many kinds of flowers, and both sexes are also partial to feeding on rotting fruit, flows of tree sap, dung, and carrion. Feeding on fallen fruit is common in the fall, and may help the butterflies survive the winter or fuel migration. Red Admirals usually migrate northward in spring and south during fall, although some successful overwintering occurs in the UK and northwest North America, particularly in mild winters.

→ The Red Admiral has fabulous contrasting coal-black and scarlet-orange patterning. Alderman is yet another traditional English name for this butterfly, referring to the red and black clothes worn by aldermen in the past.

BUTTERFLY BEHAVIOR

The flight of the butterfly

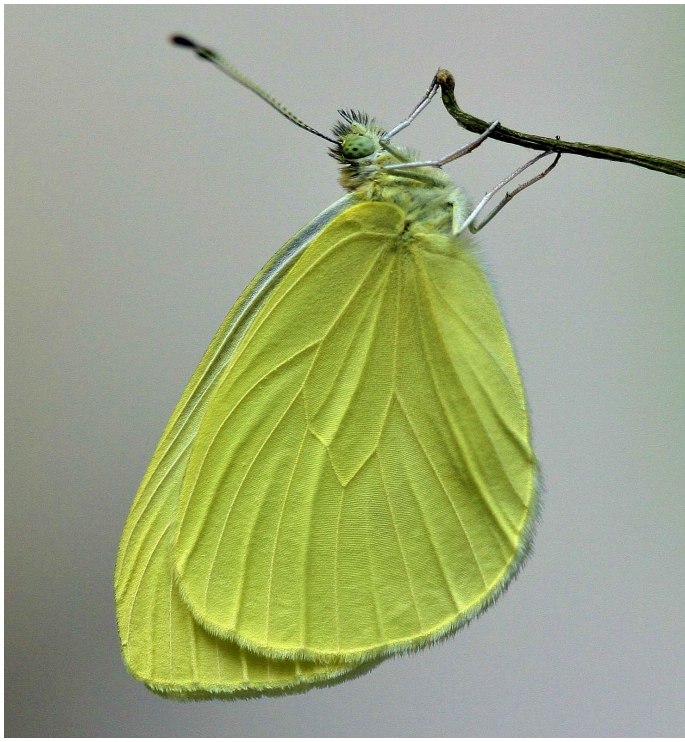
The flight of butterflies is a wondrous and amazing thing, about which scientists still have much to learn. Butterflies are able to fly just hours after emerging from their pupa, as soon as their wings have dried. Unlike birds, their parents do not teach them this skill and they must rely on instinct alone.

BUTTERFLY WINGS ADJUST BODY TEMPERATURE

Being cold-blooded, butterflies can fly only when the temperature is above a certain threshold, usually around 57°F (14°C). Nerve cells in a butterfly's wings can detect light and heat. They use the sun to regulate their body temperature, which is one reason they bask in its rays. In temperate areas butterflies bask to raise their temperature, while in the tropics where they can overheat, their wings can radiate heat to cool them off. Overheated butterflies can also seek shade and rest.

Basking enables butterflies in temperate regions to substantially raise their body temperature above ambient conditions, so they can fly when shade temperatures are cool as long as the sun is shining. Some species can warm up faster by shivering, which generates internal heat.

Temperate butterflies have also evolved other means of warming themselves up, including having dark, hairy bodies. The dark color absorbs heat, which is then trapped by the hairs. With their large surface area, the wings warm up relatively quickly and transfer heat to the body through the circulation of hemolymph.



← A Redspot Sawtooth (*Prioneris philonome*) takes flight on the Indonesian island of Sumatra.

↗ A Margined White (*Pieris marginalis*) dries its wings soon after eclosion in readiness for the first flight.

→ The dark, hairy body of the Blue Copper (*Tharsalea heteronea*) enhances the warming obtained by reflectance basking in sunshine.

Butterflies bask in different ways. Dorsal baskers, such as some Nymphalidae—including tortoiseshells, the Peacock (*Aglais io*), and sailers (*Neptis* spp.)—bask on flat ground with their wings open, often on a warm path. This traps warm air beneath the wings and body. Lateral baskers, such as many browns (Nymphalidae) and jezebels (*Delias* spp.), bask with their wings shut, but lean slightly to expose the undersides to the sun. Reflectance baskers, such as some whites (Pieridae), hold their wings at an angle to reflect the sun's warmth to the body.

In the middle of summer, butterflies may have the opposite problem: that of overheating. Once shade temperatures exceed 86–95°F (30–35°C), many butterflies seek shade, stop flying, and close their wings.

↑ The West Coast Lady (*Vanessa annabella*) is a dorsal basker, fond of basking with wings outspread on bare, warm ground, catching the sun's rays and trapping the warmth from the ground.

↗ The Western Green Hairstreak (*Callophrys dumetorum*) is a lateral basker, absorbing warmth through the undersides of its wings.

↗↗ Most blues (Lycaenidae) are reflectance baskers, directing the sun's rays and warmth to the body.

STRONG WINGS

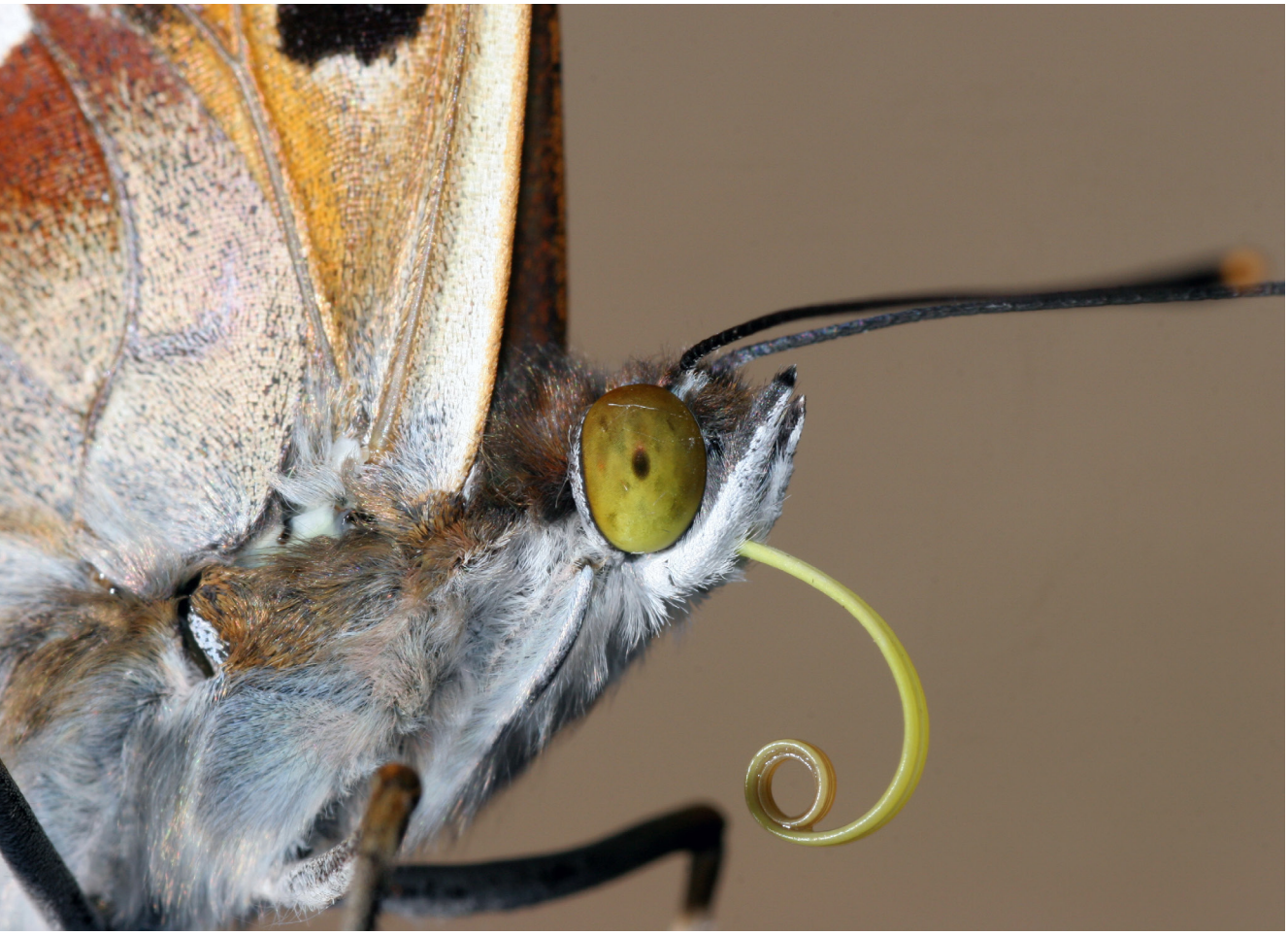
Being able to fly gives butterflies a great advantage over wingless insects. In a second, they can be up and away from danger or on their way to finding nectar. Most people think that butterfly wings are extremely fragile, but the truth is that they are stronger and more resilient than one would expect—they have to be, to endure the physical stresses of flight, which may include journeys of hundreds of miles in migratory species. Today, with the aid of slow-motion cameras, scientists better understand the physics of butterfly flight.

Although a butterfly's wings appear rigid, in reality they are quite flexible. In flight, a butterfly rolls and twists its wings to create lift, thrust, and exceptional maneuverability. Although all butterflies share the same basic wing design and the physics of flight are universal, those from different families show a surprising range of flight patterns.

Small-winged skippers have fast, short, darting flights. Large brushfoot and swallowtail butterflies can fly rapidly by flapping their broad wings and soaring. Brown butterflies such as Ringlets (*Aphantopus hyperantus*) and Meadow Browns (*Maniola jurtina*) have a jerky type of undulating flight, usually fairly low to the ground and often within tall grass. Some butterflies use gliding as a major component of their flight. The sailers (*Neptis* spp.) glide above the vegetation with their wings open flat, rarely closing them to flap. On the other hand, many Satyrinae butterflies, including the genus *Ypthima*, somehow manage to fly with their wings closed above their heads most of the time.

Adult feeding habits

Flying, seeking mates, and producing offspring are all high-energy activities, so butterflies must feed. A newly eclosed butterfly does have some stored nutrients, carried over from the caterpillar stage, but these are usually expended within a day or two.



A SIMPLE DIET

The diet of a butterfly is simple: sugar (with perhaps a dash of amino acids), water, and salts. Flowers provide all of these requirements, and virtually all butterflies can derive the nourishment they need from a wide range of different flowering plants.

Nectar is a sugar-rich liquid contained in nectaries within flowers. Butterflies access the nectar with their proboscis, a hollow tube they use to probe nectaries and absorb nectar. It used to be thought that the proboscis functioned like a straw, sucking up nectar, but recent research has shown that it acts more like a sponge, absorbing the fluid.

INTOXICATING SUGAR SOURCES

Being avid flower feeders, butterflies get most of their sugar requirements from flowers. However, some species find alternative sugar sources, including sap flows from trees and honeydew, a sweet, sap-like juice excreted by aphids, mealybugs, and scale insects. Caterpillars of *Allotinus* and *Miletus* eat aphids. Adults of these species do not visit flowers, but imbibe honeydew of aphids, which they ate when younger. In the western USA, California Tortoiseshells (*Nymphalis californica*) are often seen on non-flowering conifer trees in late summer, probing needles and branches for honeydew from the aphids that live there. Other brushfoots, including Red Admirals (*Vanessa atalanta*), can be found in the fall feeding on overripe fruits that have fallen to the ground. These sugars have often fermented, and butterflies that drink to excess can become intoxicated. Such butterflies apparently lose their inhibitions and do not fly away when approached or if danger threatens.

FATS FOR ENERGY AND A LONG LIFE

Most butterflies use the sugars they obtain from flowers directly to maintain life and function, particularly flight and maturation of reproductive organs. In late summer and early fall, some species—including the North American Monarch (*Danaus plexippus*)—convert nectar sugars to lipids (fat), which they then use to fuel their famous migrations across hundreds or thousands of miles to overwintering sites in California and Mexico. Monarchs also store lipids to enable them to survive through the winter months in relative dormancy. Other species that overwinter as adults within their habitats, such as Mourning Cloaks and anglewings (Nymphalidae), also convert sugars to lipids to aid their survival.

← The proboscis is a coiled, hollow tube that butterflies use to imbibe nectar and other nutrients. It absorbs like a sponge rather than as a suction device.

↗ A male brownie (*Miletus* sp.), uncurls its unusually short proboscis to feed on the honeydew of sap-sucking insects that are tended by *Dolichoderus* sp. ants.

PUDDLING PARTIES

Sometimes butterflies are seen gathered on damp soil or sand, seemingly so engrossed in feeding that you can get quite close to them. These gatherings are common wherever and whenever the weather is hot and dry. The most common participants in these so-called puddlings are swallowtails, whites, blues, and brushfoot butterflies.

Aside from obtaining moisture, puddling butterflies are also absorbing salts that they need for flight and metabolic functions. Salts are rare in flowers and are not accumulated by caterpillars. Curiously, nearly all puddling butterflies are males, but this is likely related to their need to provide salt and minerals to females as a nuptial gift at mating. Males with extra stored sodium are more attractive mates for females than those without the mineral, and have increased chances of offspring survival.

↑ Butterflies puddling in Brunei. Bornean Sawtooth (*Prioneris cornelia*), grass yellows (*Eurema* spp.), and Orange Gull (*Cepora iudith*) butterflies imbibe minerals from a damp area on the rainforest floor at Temburong National Park, Brunei.

→ Swallowtail butterflies like this Lime Swallowtail (*Papilio demoleus*) have long legs and a long proboscis, which allow them to exploit many different kinds of flowers.

FLOWER PREFERENCES

Different butterflies have different flower preferences. Some species clearly prefer flowers of a particular color, but many of the preferences are determined by flower structure and proboscis length. Butterflies with a relatively short proboscis can only gain nectar from flat, open flowers with shallow nectaries, such as daisies. Butterflies with a longer proboscis feed from tubular flowers with more deeply embedded nectaries, such as butterfly bush and thistles.

← A group of Great Blackveins (*Aporia agathon*) feed on dung in Nepal.

OTHER SOURCES OF MINERAL SALTS

Lepidopterists discovered long ago through personal experience that urine-moistened sand or soil is highly attractive to thirsty butterflies. Urine is a good source of sodium and "wild urine" is available from some online commercial sources as a butterfly attractant.

Another source of salt that butterflies will sometimes drink is human perspiration. Some butterflies will alight on a sweaty person and then probe their salty skin with their proboscis. Even sweaty clothes, boots, and hats worn on summer hikes can attract salt-seeking butterflies.

Some butterflies find salt in strange places. Crocodile tears may be insincere, but they are a good source of salt for some tropical butterflies, as are turtle tears. Another bizarre source of sodium that butterflies will take advantage of is blood—observers have reported that clothing soiled with fresh blood drawn by leeches has attracted feeding skipper and gossamer wing butterflies in India.

Salt and minerals can be obtained from another slightly off-putting source: animal dung. Clusters of butterflies feeding on animal dung are a common sight in tropical and subtropical areas, and in hot summers in more temperate areas. Another similarly dubious source of salts and minerals that butterflies sometimes use is carrion. Even insect carrion splattered over the front end of a car may attract feeding butterflies.

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