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LEFT | Case-bearing Clothes Moth (*Tinea pellionella*) caterpillar extended from its silken case, into which it has incorporated some red fibers from the textile it's consuming. Woolens and other fabrics made of animal hair are targeted by some tineids.

items worldwide. Their casemaking caterpillars have the exceptional ability to digest keratin—the chemically resistant protein that makes up claws, fur, hair, hooves, nails, and horns of mammals. Clothes moth larvae are most problematic with stored fabrics, clothing, wall hangings, and tapestries that are not periodically washed.

CATERPILLARS AND MOTHS AS HUMAN FOOD

Caterpillars are highly nutritious—they are rich in protein, including all essential amino acids, unsaturated fatty acids, minerals, and vitamins. When dried, their protein proportion is comparable to that of raw beef and is far more sustainable environmentally, requiring less land, less water, and yielding minimal greenhouse emissions. Caterpillars, and less frequently moths, are important food sources for many indigenous peoples, especially in Asia, Africa, and Latin America. Large caterpillars, in particular those of giant silk moths (Saturniidae) that reach high local population levels, are frequently a target. Most famously, the Mopane Worm (*Gonimbrasia belina*) is eaten across southern Africa, either dried or cooked in prepared dishes. In Veracruz, Mexico, the *Arsenura* caterpillar, another giant silk moth, is targeted for human consumption. Australian tribes consume caterpillars, especially large-bodied, wood-boring cossids and hepialids. Among the most common is the Witchetty Grub (*Endoxyla leucomochla*), a cossid that bores in the stem and upper roots of various *Acacia*.

Indigenous groups in Mexico collect the Maguey Worm (*Comadia redtenbacheri*), a cossid that bores into agave leaves and roots. Single plants may yield hundreds of caterpillars. The larvae, known as *chilocuiles*, *chinicuiles*, or *tecoles* in Mexico, get increasingly red as they mature—prepupae are bright red. As such, the caterpillar also has become widely known as the red Maguey Worm and *gusano rojo*. Notably, Maguey Worm is the caterpillar most commonly found swirling at the bottom of some mezcal bottles.

The boiled pupae of silk worms, a by-product of sericulture, are an enormous nutritional resource. China alone produces more than 100,000 tons of Domesticated Silk Moth pupae annually. While the pupae are canned and sold as human food in Asia, more commonly they are dried and used as an additive in human foods or processed into animal feeds, especially for chickens.

In Bhutan and Tibet, the caterpillars of several species of *Pharmacis* and *Thitarodes* (Hepialidae) are highly valued as an aphrodisiac, a remedy for cancer and a sweep of other ailments, and a prophylactic for still other maladies, but only after the larvae have been attacked and mummified by a fungus (*Ophiocordyceps sinensis*)! As far as I am aware, there is scant evidence that the fungus zombies cure any ills, beyond what an alternative placebo would treat. The dried caterpillar–fungus cadavers are worth twice their weight in gold. Well-preserved specimens may sell for $140,000 a kilo. In Bhutan

LEFT | Large caterpillars such as this African saturniid are commonly roasted and sold in Asian, African, and Latin American markets.

BELOW | In Central and South America, caterpillars such as the Maguey Worm (*Comadia redtenbacheri*) serve as a protein supplement.

LEFT | Roasted mopane caterpillars (*Gonimbrasia belina*) for sale in a market. Late instars of this large silk moth are an important source of protein for many peoples across southwestern Africa.

LEFT | Ghost moth (Hepialidae) "fungus caterpillars" for sale on a Chinese market. The mycelia-ridden caterpillars are ground up and used as traditional folk medicine to treat various maladies and as an aphrodisiac.

the harvesting and sale of the mummies is a significant source of income for many rural families, with school activities sometimes scheduled around the annual appearance of the fungal fruiting bodies.

Adult moths are much less often consumed, with one important exception: Australia's Bogong Moth (*Agrotis infusa*), which gregariously aestivates in caves and scree high in the mountains of southeastern Australia. Each summer billions of the adults would migrate to the caves and other sheltered sites to await fall rains and the greening of the larval feeding sites. For centuries, Aboriginal tribes would come to the Bogong's montane aggregations to feast on the moths for weeks at a time. Changes in land use, agricultural intensification, and a severe drought in 2017 so diminished the moth's numbers that today many of the caves are empty, and the species is now regarded as endangered (see also page 55).

MOTHS AND PLANTS

Insects and plants have been evolving together for at least 400 million years. The fates of the two groups are inextricably intertwined and have spawned countless interactions over geological time. The three most archaic moth lineages, the Micropterigidae, Agathiphagidae, and Heterobathmiidae, have retained host associations similar to those believed to have existed at the time of their origin. In fact, there is much reason to believe many modern-day host associations are reflective of those of their ancient ancestors.

The vast majority of today's estimated 300,000 plus species of Lepidoptera feed on angiosperms (flowering plants). Angiosperms started diversifying as early as the Jurassic, or even before, at a time when cone-bearing plants (gymnosperms), ferns, club mosses, liverworts, and mosses were the ecologically dominant plants across Earth's terrestrial ecosystems. However, that all changed some 125 mya when angiosperms radiated and catapulted themselves (with the help of insects as pollinators) into ecological dominance across the planet. Moth–plant associations span the gamut from highly mutualistic and codependent to highly antagonistic, with caterpillars sometimes fully consuming their host plant, or in the case of shrubs and trees, defoliating, and not infrequently killing their hosts.

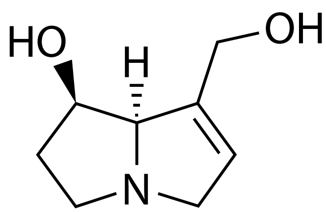
SECONDARY PLANT COMPOUNDS

Plants defend themselves from herbivores and other enemies using a battery of physical defenses that include spines, hooks, dense hairs, and

ABOVE RIGHT | A fairy moth (Adelidae) visiting a flower. The effectiveness of adelids and most other archaic moths as pollinators is in much need of study. Their cousins, the Prodoxidae, are renowned for their pollination services, upon which yuccas are entirely dependent.

RIGHT | A *Syssphinx raspa* caterpillar. While eating different plants across their range, local populations of many moths specialize on just one species at a given place—here, prairie acacia in southeast Arizona.

STRUCTURE OF RETRONECINE



ABOVE | Retronecine, a common pyrrolizidine alkaloid (PA), is a powerful secondary plant compound, toxic to liver tissues.

hardened tissues as well as a galaxy of chemical defenses, or secondary plant compounds (primary compounds are those needed for photosynthesis, respiration, and other basic metabolic functions). Secondary plant compounds known to deter herbivory by caterpillars include alkaloids, nonprotein amino acids, cyanide-producing compounds, cardenolides, glycosides, phenolics, terpenes, salts, silica, several classes of sulfur-containing compounds, and still others.

Any moth lineage that evolves the capacity to avoid, detoxify, tolerate, or sequester the secondary metabolites of a diverse, ecologically abundant plant lineage has much to gain evolutionarily. Should the moth lineage radiate in turn, it poses increasing selective pressure on the plant group. And as the herbivory pressures increase on a plant lineage, there would be increasing fitness benefits to any member of the plant lineage to evolve some *new* secondary compound or other means of self-protection. Upon doing so, the plant taxon, now freed of much herbivory, would be poised to radiate in turn.

Such a situation would represent but two bouts in an ancient arms race that has been ongoing between insects and their host plants for millions of years dating back to at least the Permian Era—an ongoing coevolutionary battle that may account for much of the planet's species diversity.

Pyrrolizidine alkaloids (PAs), common to many borages (Boraginaceae), composites (Asteraceae), legumes (Fabaceae), and orchids (Orchidaceae), underlie much of the evolutionary successes of several groups of moths, and in particular the tiger moths (Erebidae: Arctiinae). PAs are potent liver toxins and mutagens when consumed by vertebrates. Tiger moth caterpillars that sequester PAs as caterpillars render themselves unpalatable to lizards, birds, and bats, and warn of their toxicity with yellow, orange, white, and black colors, in both the larval and adult stages, and in some cases, even the egg and pupal stages.

LARVAL DIETS AND HOST-PLANT SPECIALIZATION

Perhaps 98 percent of all Lepidoptera are herbivorous, with some 85 percent of these being host-plant specialists as caterpillars that eat just one or a few related plant species. The remaining taxa are either oligophagous, feeding on plants in just two to three plant families, or polyphagous, feeding on plants in four or more families. The ecological and evolutionary advantages and disadvantages of these strategies are active areas of inquiry among ecologists. Surely part of the explanation is that specialists become adept at detoxifying or otherwise processing the potpourri of secondary plant compounds that plants manufacture to protect themselves from herbivores and other enemies.

There is another eco-evolutionary advantage to host-plant specialization, in that, over time, the caterpillar of a specialist species can be shaped by natural selection to resemble its host plant—in color, shape, texture, reflectance—and adopt appropriate behaviors, to lower its apparency to visual predators such as lizards, monkeys, and

especially birds. This argument becomes more compelling when considering the fate of host-plant generalists, which are on different plants from generation to generation (and even day to day), and as a consequence are not well matched to any single plant.

The diversity of moth species hosted by a plant is largely a function of the host plant's geographic range, architectural complexity, and range-wide abundance; other determinants include the plant's apparency, physical and chemical properties, and degree of taxonomic isolation (for example, the number of congeners or family members growing nearby).

In addition to plants, there are moth caterpillars that feed on fallen leaves and flowers, fungi, lichens, and algae. Tineidae are unique among lepidopterans in that they can digest keratin, which allows their caterpillars to mature on diets of antlers and horns, feathers, fur (including wool), owl pellets, and turtle shell.

ABOVE LEFT | A male approaching a female Bella Moth (*Utetheisa ornatrix*). Males transfer PAs to their female partners during mating.

ABOVE | A Bella Moth larva sequesters PAs from its host plant. All four life stages of Bella Moths may be protected by PAs.

PLANT-FEEDING GUILDS

While most caterpillars feed on leaves, essentially all plant tissues are consumed by Lepidoptera. Many lineages, including Noctuidae, Geometridae, Pyralidae and Crambidae, Plutellidae,

ABOVE | Not all caterpillars eat green plants. Footmen or lithosiines radiated on lichens. The long setae on this *Eudesmia arida* caterpillar keep many of its smaller enemies at bay.

LEFT | A few small lineages of owlet moths feed principally on fungal hyphae. So far as known, all members of *Metalectra* are dietary specialists on fungi (and can be raised on store-bought mushrooms). This example is *Metalectra diabolica*.

Coleophoridae, Adelidae, and Agathiphagidae, among others, target fruits and seeds. Borers in nonwoody stems include many Noctuidae, Tortricidae, and Momphidae. These may feed on the entirety of the stem, while others specialize on certain tissues such as the meristems, pith, epidermis, or the outer photosynthetic tissues. Most gall-forming Lepidoptera are stem gallers.

Root feeding is surely more widespread than appreciated. Borers that enter above or just below the soil and tunnel into the roots include Hepialidae, Noctuidae (especially noctuines), and Sesiidae. Lepidoptera that can burrow through sand and friable soils—such as Hepialidae, Noctuinae, and Crambidae—will feed externally on roots.

Leaf-mining has been reported in some 20 families of Lepidoptera, and is especially common among archaic families and smaller microlepidopterans. Given that the leaf is also the caterpillar's environment, the host ranges of leafminers tend to be more specialized. Species-rich families include the Bucculatricidae, Gracillariidae, Nepticulidae, and Tischeriidae.

POLLINATION

Moths are among the most important insect pollinators, second only to bees. But just how important moths are to flowers remains one of the more poorly documented aspects of their biology because so much of their activity occurs after nightfall. Moth-pollinated flowers tend to be white, fragrant, and make their nectar available at night. Many members of the evening primrose (Onagraceae) and four o'clock (Nyctaginaceae) families do not even open their flowers until late afternoon or dusk.

Nearly all "moth flowers" produce sweet scents. Indeed, some of the flowers with the most pleasant fragrances are moth pollinated. The wonderful aromas of carnations, gardenias, honeysuckle, lilacs, narcissus, and the queen of all, jasmine, are volatiles, manufactured by plants to encourage pollen transfer by moths. Common floral scents include benzaldehyde, lilac aldehydes, linalool, methyl benzoate, and phenylacetaldehyde.

BELOW | Fruits and seeds like corn are targeted by many moth caterpillars, here a Western Bean Cutworm (*Richia albicosta*).

BOTTOM | Serpentine mines of *Phyllocnistis populiella* on aspen. The mature larva, visible on the lower left leaf, is beginning to spin its pupal crypt—a minute pinched fold fashioned along the leaf edge.

ABOVE | *Hemaris* are small day-flying sphingids that are often mistaken for bumblebees or hummingbirds. About 20 or so species are widely distributed across the northern hemisphere.

NURSERY POLLINATION

Of special note are nursery pollination systems wherein a moth species is both a dedicated pollinator and consumer of the host plant's seeds and fruits. Upon transferal of pollen to an appropriate flower, the female then lays her egg(s) in or on the flower—her offspring will mature on the developing seeds and associated tissues. The most renowned example of a nursery pollination system occurs in yuccas and yucca moths—the two lineages are engaged in an obligatory mutualism where the survival of each is interdependent and absolute. A more globally widespread and understudied nursery pollination system is that of *Silene* (family Caryophyllaceae) and the coronet moths (*Hadena*; Noctuidae) that see to the pollination of the world's 900 species of the genus.

Sphinx moths are recognized as important pollinators, especially in arid regions and the tropics. They are strong fliers, have the longest tongues of any insects, and at least some are thought to follow traplines—that is, they can remember the locations of widely scattered and sometimes distant nectar sources—an attribute that can be especially important in the tropics where many trees grow in low densities, often well removed from one another. Moreover, sphingids have acute color vision—the most sensitive known across the animal kingdom—enabling them to detect colors under extremely low light conditions and ensuring that they will be able to navigate to flowers even on new moons and under closed forest canopies.

Madagascar's Comet Orchid (*Angraecum sesquipedale*) has a spectacular white, fragrant flower with an enormous nectar spur that often exceeds 10 in (25 cm) in length. As its name implies, the spur is a floral extension where a flower produces, and more to the point, caches its nectar reward. Charles Darwin, upon examining a bloom of the Comet Orchid, predicted that there must be a moth with a tongue long enough to reach to the bottom of the orchid's spur. It was not until 21 years after his death, that the moth *Xanthopan praedicta* was discovered—a moth known today as Wallace's Sphinx Moth—whose lingual siphon may exceed 11 in (28 cm) in length.

MOTH BEHAVIOR AND ECOLOGY

Just a few areas of the extraordinary palette of behaviors and ecological interactions of moths can be shared here. Because so much of what a moth is and does happens at night, suffice it to say, much more remains to be written. To some degree, the same is true for their caterpillars.

COURTSHIP AND MATING

Much regarding the reproductive behavior of moths appears elsewhere in these introductory pages and in the taxon profiles that follow, in large measure because moths, the ultimate stage of these insects, have a principal mission: to propagate. Those moths with a short adult lifespan are especially singularly minded: upon eclosion the female must find a mate, court, pair, and then get to the business of dispersal and oviposition. For males, only the first three of these activities will occupy their psyche. The major exceptions to the above are those species that enter a reproductive diapause before mating—a behavior common among those moths that hibernate or aestivate as adults.

In nearly all moths, the females produce the principal sex pheromone—that is, the scent to which males will orient and compete for mating opportunities. In most species, the primary sex pheromone is released by females from specialized abdominal glands soon after she has eclosed, typically immediately after her wings have fully expanded and before she has taken her first flight. In exceptional cases, such as ghost moths, this signaling system may be reversed.

Moths couple end-to-end. In Saturniidae, the male and female frequently remain in copula until nightfall of the next day. In Ditrysia, which account for about 98 percent of extant moth diversity, females have a separate reproductive opening solely for copulation. Further anterior in the female's abdomen, Monotrysia and Ditrysia have a sack-like enlargement, the bursa copulatrix that receives the male spermatophore, and less commonly multiple spermatophores. From the bursa the sperm must swim through a narrow duct, past the common oviduct, and make their way into a special gland, the spermatheca, where they await the passing of unfertilized eggs.

The male spermatophore and the bursa that can house it may well represent key innovations for moths. Spermatophores, depending on the taxon, routinely contain proteins, lipids and

LEFT | Fall-generation adults of Herald Moth (*Scoliopteryx libatrix*) (Erebidae) enter a reproductive diapause, seek out caves in which to overwinter, then mate and lay their eggs in the spring. An aggregation pheromone may be involved as the hibernating moths are often found clustered.

LEFT | A recently emerged Buck Moth (*Hemileuca maia*) "calling"; that is, emitting the female sex pheromone from a gland near the terminus of her abdomen.

sterols, carbohydrates, minerals, vitamins, and defensive chemicals, in addition to sperm, that will contribute to the fitness of both the female and the couple's offspring. Stated differently, the bursa allows the male to make massive energetic and defensive contributions to his partner and offspring that have played important roles in the diversification and ecological successes of Lepidoptera.

The extended duration of mating likely relates to the time necessary for the male to transfer his spermatophore to the female. In some species the male will lose considerable mass over the course of a single mating. There is some evidence that virgin males make preferred partners for females, and that, once-mated, males may have long refractory periods before they are able to constitute a second spermatophore, and even then, it may be of lesser value.

TERMINALIA AND SEXUAL CONFLICT

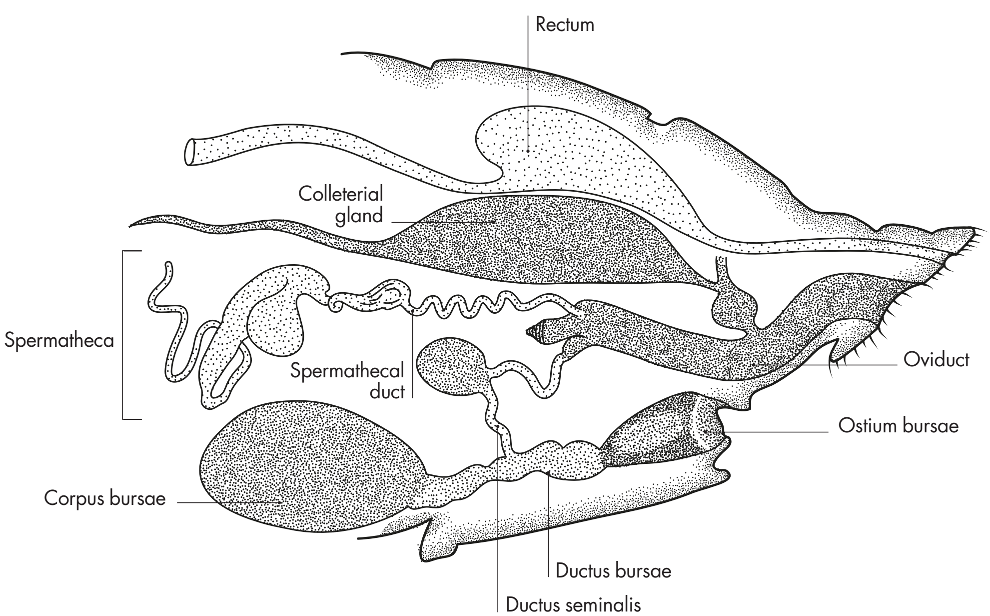
The male and female terminalia of moths tend to be quite complex morphologically, with the two fitting together like a lock and key. The male genitalia are particularly elaborate. Whether this complexity is due to sexual selection and the ancient battles of the sexes fighting to control paternity, or the need to prevent mating mistakes with closely related species, is a fascinating subject. But for whichever reason, the genitalia and associated secondary sexual structures are among the most rapidly evolving anatomical features of moths. As such, they are important for making species-level identifications by moth taxonomists, collectors, extension entomologists, and others.

In moths, as in many other animals, there is ongoing conflict between the sexes, with each having evolved multiple measures to control facets of reproductive interactions. At the point of courtship, the female has much control in that she determines when to call, when to proceed past courtship to accept a male partner, and when to expose her abdomen to her suitor. A female disinterested in a pursuant male can stop calling, fly off, or raise her abdomen to make it unavailable. Additional controls are built into the female's anatomy. In some moths, the ductus bursae is corkscrewed, which can prevent entry of the aedeagus of a closely related species that has not "coevolved" to meet the biomechanical demands required by the female's anatomy. Sperm precedence plays an important role. After mating, sperm are stored in the spermatheca, atop the female oviduct, where they await the passage of unfertilized eggs out of the common oviduct. The sperm near the entry duct are most likely to fertilize a given egg. Thus, a female that accepts a pairing with a second male will, in so doing, favor parentage by her most recent suitor.

In their attempts to control paternity, males have evolved numerous strategies to discourage subsequent pairings. The male spermatophore,

BELOW | Lateral view of a ditrysian moth abdomen. Note the separate openings for egg deposition (terminus of oviduct) and mating (ostium bursae).

FEMALE REPRODUCTIVE ANATOMY



LEFT | In some hepialids the mate-signaling system is reversed: virgin females must fly upwind, tracking a sex pheromone, to locate a calling male. Here, *Phymatopus hectoides* is releasing his pheromone from hundreds of androconia borne on the hind tibiae. (During the day the tibiae and androconia are tucked into deep pockets on the sides of his abdomen.)

transferred to the bursa copulatrix during mating, can be so large in some taxa that the female is incapable of accepting another mate. In other taxa, the female can pair again, but only after she has digested the first spermatophore, which can take days. Males of some moths leave pheromones behind that render a female less attractive, at least through some refractory period. Bordering on the sinister, a number of moths have sharp, deciduous spines on their aedeagus that are left behind in the female genital tract after mating to thwart mating attempts by subsequent males.

PHEROMONES

Moths produce many different sex pheromones, with those of the females being chemically dissimilar to those produced by males. Female sex pheromones tend to be straight-chain, 8- to 20-carbon aliphatic compounds, with one or two double bonds and a chemically active moiety (acid, alcohol, aldehyde, ketone). As a rule, female sex pheromones are odorless to humans.

Because female sex pheromones are rather chemically simple in their diversity, there can be cross-reactivity among both closely and distantly related species. In most cases, and especially when two or more congeners are sympatric (that is, active at the same locale), the exact blend of constituent molecules in the sex pheromone cocktail will differ. Species-specific signaling can also be attained by having pheromone blends with differing chiralities. Cross-reactivity and mating mistakes also can be prevented by related species calling at different times of night, being active during different seasons, or by occupying separate habitats or regions.

Males may also employ pheromones that are important for female acceptance in some lineages. Most male pheromones are released from specialized scales called androconia that are deployed only in the vicinity of the calling female, as part of a pre-mating courtship. The androconia responsible for pheromone release tend to have an elaborate ultrastructure, which provides an exaggerated surface area for rapid volatilization of the pheromonal compounds. Male scent scales and brushes are most commonly found in association with the genital capsule, adjacent abdominal segments, or on the wings, but also occur on the legs (especially the hindlegs, which are those most proximate to the genitalia); less commonly, they occur on antennae and labial palpi.

Androconia can be single specialized scales or, more commonly, scale clusters that form brushes, "hairpencils," scent patches, or, in special cases, incorporated into elaborate courtship organs. A storied example is that of the abdominal courtship brush present in many Noctuidae. The organ, secreted in a pleural fold of the abdomen until needed, consists of two levers, an elaborate distal androconial brush, composed of dozens of golden, pheromone-laden setae, and a pheromone-producing gland. Immediately prior to coupling, the brush is pulled from the pocket and the androconia splayed.

MIGRATION

Moths include several of the most notable and economically consequential insect migrants. A significant fraction of the world's most destructive crop pests migrate on storm fronts, sometimes in hordes so massive that they show up on weather-tracking radar. A widespread migratory scenario among moths is to move out of tropical and semitropical areas into temperate regions to exploit the abundant, nutrient-rich vegetation that becomes available each spring. In tropical regions, analogous mass movements take place between wet and dry forests that are synced up with rains and allow the moths to take advantage of the availability of new growth.

Because these movements occur at night, the migrations of moths are less familiar and less studied than those of butterflies. There is also increasing evidence that many, if not most, moths migrate at heights of 1,000 ft (300 m) or more—

BELOW | Urania Swallowtail Moths (*Urania fulgens*) puddling during mass migration to a forest with new growth of *Omphalea*, its larval host.

ABOVE | Grizzly Bear flipping rocks in search of aggregations of aestivating Army Cutworm (*Euxoa auxiliaris*), which make up an important part of the summer diet of Grizzlies in the Rockies of North America.

moving on aerial conveyor belts that can propel their movements at speeds often exceeding 60 mph (100 kmh). At these velocities, moths, and especially the microlepidopterans, are essentially aerial plankton that are simply taking advantage of atmospheric currents that will carry them great distances over a single night.

Sunset moths (family Uraniidae) make spectacular migrations. These swallowtail-sized, day-flying moths—dazzling in their beauty of intermixed metallic green and orange scales—are renowned for their mass movements from jungles of older foliage to sites in which their host plants are producing new leaves. While most of the migration occurs above the canopy, and might be entirely missed by the casual naturalist, both sexes become visible at ground level when they descend to gather water and salts at mud.

Two related noctuids warrant special mention: the Army Cutworm (*Euxoa auxiliaris*) and the Bogong Moth. The Army Cutworm is an abundant species that inhabits the high prairies, grasslands, and steppes flanking the Rocky Mountains of the United States and Canada. Its larvae mature on the lush grasses and forbs of spring (including alfalfa and row crops). The adults eclose weeks later by the millions, and begin their annual migration into the mountains, where they gather in huge numbers in talus slopes and aestivate over the dry summer months, when their grassland habitats have browned and become hostile. Millions if not billions remain in a state of reproductive diapause, sequestered under rocks in the high scree. In Yellowstone National Park, and no doubt elsewhere, many insectivorous mammals dine on the aggregations through the summer months. Most famous among these are grizzly bears. A single bear may eat 20,000–30,000 moths a day—as much as one-third of the calories required for an entire year may derive from the consumption of the moths. With the return of rains in the autumn, the survivors emerge from their aestivation sites and begin the reverse migration to the greening grasslands where they will lay their eggs and start the cycle anew.

Australia boasts an even more exceptional migrant, the Bogong Moth. Its biology mirrors that described above of the Army Cutworm, being a grass and forb feeder whose caterpillars mature in spring in low-elevation grasslands. Until recently its numbers were estimated to be in the billions, and it ranked among the world's more abundant animals. Dozens of mammals and indigenous nations fed on the aggregations of aestivating moths that gathered in caves across southeastern Australia (see also page 42). During the spring migration the moths were so numerous as to slow trains and shut down many public events. The fortunes of the Bogong took an abrupt turn in 2017 when a severe, three-year drought struck eastern Australia. Moth numbers suffered mightily, many caves have since gone unoccupied, and the Bogong is no longer seen in abundance over much of its range. So grave has been the decline that the moth was listed in 2021 as an endangered species by the International Union for Conservation of Nature (IUCN).

The fraction of moths that migrate is poorly known, as virtually all the flight activity happens under cover of darkness, and much is far above the ground where the phenomenon is intractable to

LEFT | The mass migrations of the Bogong Moth (*Agrotis infusa*) were legendary—dense enough to close down schools and church services and disrupt travel.

study. As a general rule of thumb, migration is the norm in dry, seasonal habitats, deserts, and other arid lands, where water is scarce and vegetation becomes unsuitable for caterpillar development over long periods, and especially in regions where the rainfall pattern is sporadic. It is also common from tropical and subtropical regions that do not experience freezes, into temperate and boreal areas, in spring and summer.

DIURNALITY IN MOTHS

While many of the most archaic moth lineages are brightly colored day-active animals, the vast majority of moths are nocturnal. The five largest families of Lepidoptera, in order of decreasing richness (Erebidae, Geometridae, Noctuidae, Tortricidae, and Crambidae), are essentially nocturnal. Yet, each of these families has spawned multiple lineages that are day-active, but virtually all are small groups and of little ecological consequence. I suspect if we knew the phylogeny of moths in detail, we would learn of more than 200 instances where a nocturnal moth group gave rise to a new diurnal species or lineage, but only one of these has met with great success—we call these butterflies. Three moth families with a preponderance of diurnal species include the Castniidae, Sesiidae, and Zygaenidae.

Moths that inhabit cold environments—high latitudes and alpine ecosystems—are often diurnal, presumably because daytime temperatures are more favorable and vertebrate predation pressures are lowered. In alpine communities and above 60° north or south latitude, a great many moths are diurnal perforce. Several traits are associated with this transition.

LEFT | Diurnal moths often have comparatively large compound eyes, and none more so than those of fairy moths, where the eyes sometimes fuse over the top of the head.

ABOVE | Aposematically colored moths typically are rendered in bright red, orange, and yellow, often paired with black or white markings, to warn of their unpalatability.

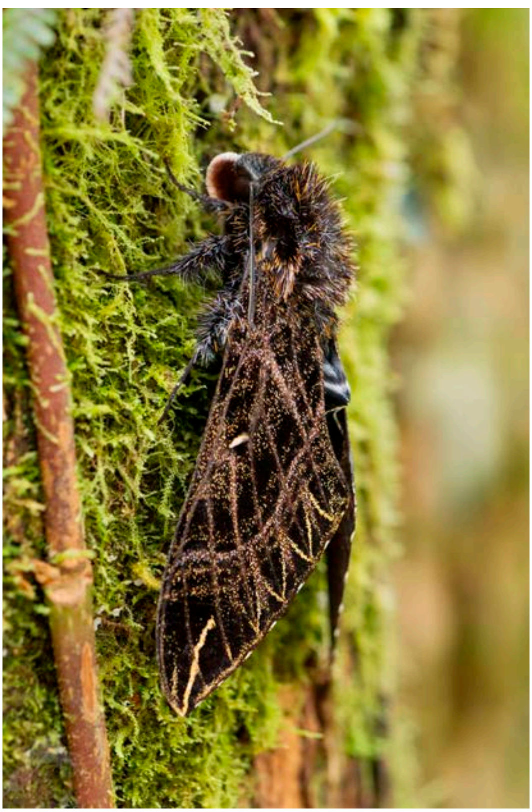
With the exception of butterflies, most diurnal moth lineages are smallish, so small that they are commonly ignored by birds and other visual predators. Nocturnal species tend to be green, brown, gray, or rendered in earth tones that can go unnoticed during the day when they are perched. By contrast, diurnal moths are often white, brightly colored, or otherwise more conspicuously rendered than their nocturnally active sister taxon. Diurnal moths that are palatable tend to be fast fliers, making them challenging quarry.

A large fraction of diurnal moths includes those that are chemically protected and unpalatable to birds. As such, they can operate in daylight with some level of impunity—these tend to be aposematic (brightly colored), slow-flying, and often hardy in constitution, that is, potentially capable of surviving a predator attack. Such species often anchor the abundant mimicry systems (see page 62) found across the order.

Because visual cues replace the primacy of odor communication in day-flying moths, the antennae are often smaller than those of closely related nocturnal species. In many moths the compound eyes of day-active species may be larger, and especially so in male diurnal adelids, with enormous compound eyes, that may join over the top of the head. But in still other lineages the eyes of diurnal moths are conspicuously smaller than those of their closely related nocturnal cousins.

DISTRIBUTION AND HABITAT

Moth diversity increases with proximity to the equator, although there are important lineages that



LEFT | *Euryglottis aper*, a large tropical hawk moth of western South America. Note its large, coiled tongue, which extends for many inches when it's actively nectaring (pollinating).

ABOVE | *Automeris* is a large New World genus with more than 70 species. The prominent eyespots are concealed at rest. Upon disturbance, the forewings are thrown forward to startle its attacker. Shown here is *Automeris amanda*.

become more speciose at higher latitudes (before dropping off at still higher latitudes). It is possible that as much as 80 percent of all moth diversity is endemic to tropical ecosystems, with diversity peaking in the neotropics. Nowhere is as rich as the foothills of the Andes, with the equatorial regions of Colombia, Ecuador, and Peru boasting the highest planetary diversity of moths.

Moths occupy virtually all terrestrial communities; if there are plants, there are likely to be moths. A few lineages are fully aquatic in freshwater—with the acentropine crambids being the most diverse and ecologically successful. Acentropine caterpillars feed on algae as well as aquatic plants. As would be expected, moth richness increases with plant diversity: scrublands have more diversity than grasslands and woodlands support more species than shrublands. Likewise, moth diversity increases with the architectural complexity of their hosts: trees support more species than shrubs, which support more diversity than forbs. In temperate regions, it is likely that the 10 most abundant tree genera support more than half of all the species of moths in a given community. Across the northern hemisphere, but especially in North America, oaks are the clear frontrunner: more than 1,000 species of moths are known to feed on oaks in America north of Mexico—a number that will increase as life histories of many western moths still await discovery.

NATURAL ENEMIES

Moths and their caterpillars are eaten by legions of other animals both small (for example, ants) and a sweep of larger animals: fish, amphibians, reptiles, birds, and mammals. Many birds are reliant on caterpillars, timing their migrations

ABOVE LEFT | *Eupackardia calleta* caterpillar. The larvae are disruptively colored as well as boldly marked. Upon disturbance, they will secrete a fluid rich in biogenic compounds from their scoli, which repels ants and other enemies. Note the very small clear droplets on segments A3, A7, and A8.

LEFT | Wasp moths have radiated across the planet's tropics. More than 3,000 species have been described. This Neotropical *Cosmosoma* is best regarded as a Müllerian mimic of wasps, as it is unpalatable as well, protected by the pyrrolizidine alkaloids consumed during its larval stage.

ABOVE | (*Left*) A swarm of aquatic moths. (*Right*) An early instar aggregation of Buff-tip moths (*Phalera bucephala*) on an oak leaf.

and breeding to annual peaks of caterpillar abundances in late spring, with both clutch size and fledging success often tied to caterpillar availability. One study found that it took 6,000–9,000 caterpillars to rear one clutch of Black-capped Chickadees. Lizards and snakes are also avid caterpillar hunters.

Caterpillar- and pupa-feeding mammals include bats, mice, voles, shrews, chipmunks, squirrels, raccoons, skunks, foxes, and bears. In tropical regions, monkeys are important predators of caterpillars. Many indigenous peoples also eat caterpillars (see pages 41 and 42).

Adult losses to vertebrates pale in comparison to those suffered by the eggs, caterpillars, and pupae. However, bats harvest enormous quantities of moths. The Mexican Free-tailed Bat colony of perhaps 1.5 million adults that roosts under the Congress Avenue Bridge in Austin, Texas, is estimated to consume over 20,000 lb (9,000 kg) of insects most nights when pups are nursing—much of that harvest is moths. Nighthawks and related caprimulgid birds are also moth specialists.

Invertebrate predators account for most caterpillar predation. Foremost among these may be ants—especially in tropical and semitropical regions, where ants may exceed the mass of the resident vertebrates. For example, more than 400 species of ants have been recorded from La Selva Biological Station in Costa Rica—most of these eat caterpillars. Then come spiders. Lynx and other foliage-gleaning spiders are important enemies of caterpillars. Large orb-weavers build efficient moth-trapping webs and even have adhesives that appear to be specialized for the capture of moths. A few spiders use analogs of a moth's mating pheromone to attract males that are in search of calling females. Bolas spiders spin a silk line, with a sticky terminal droplet laden with an attractant, which they wield about with a leg, to ensnare incoming males. A few species of large, orb-weaving spiders of genus *Argiope* produce volatiles that attract mate-seeking, day-flying saturniids into their webs.

Yellow jackets and paper wasps are especially fond of caterpillars and spend much of their

LEFT | A mongoose carts off a saturniid caterpillar. Diurnal mammals and birds that hunt caterpillars and other insects by day have shaped everything a caterpillar is about: its form, its color, how it feeds, when it feeds, and more.

BELOW LEFT | Spiders take a major toll on caterpillars, especially through early instars when the larvae are small. Later, they thin the ranks further, trapping moths in their webs.

foraging time hunting them. To these, we can add the legions of earwigs, assassin bugs, stink bugs, lacewing larvae, lady beetles, and other lineages of wasps. Some sphecid wasps provision their nests with caterpillars that they have paralyzed (but not killed, as these would soon rot). Entombed within the wasp's underground nest, the hapless caterpillar is then slowly eaten alive by the larva of the wasp. Caterpillars that feed on forest-floor plants, or descend to the ground to pupate, fall prey to still other enemies. Wolf and more than a dozen other families of spiders and ants likely get the lion's share, but centipedes and ground-dwelling beetles also pose a threat. Much of the text above addresses predators and parasitoids that attack middle and late instars. However, in many species, the greatest mortality rates occur in the egg and in the early instars, where the ranks are thinned by predatory mites, minute wasps, lacewing larvae, lady beetles, and other foliage-gleaning predators.

With the exception of mites, punkies (minute flies), and a few minute parasitic wasps, neither moths nor their caterpillars have any true parasites—that is, small animals that feed on them and then move off without killing the host. However, the early stages of moths are targeted by a seemingly endless number of flies or wasps that attack the eggs, caterpillars, and pupae. There is growing molecular evidence that there may be more than 20,000 species of parasitoid flies (nearly all Tachinidae) and more than 400,000 species of parasitoid wasps with most of these targeting the early stages of moths. At least three families of minute wasps, but especially trichogrammatids, attack insect eggs. Most parasitoid wasps and flies specialize on the larvae and pupae of Lepidoptera, with tachinid flies, and braconid, chalcidoid, and ichneumonid wasps being most prevalent.

The vast majority of insect parasitoids feed internally. Parasitized larvae suffer rather gruesome deaths. Typically, the larval stage of the fly or wasp feeds initially on nonlethal tissues, and then, in a final pulse of growth, consumes much of the caterpillar. In most, the host caterpillar is killed at the time the parasitoid matures and exits the vanquished cadaver. In some, the caterpillar, while mortally compromised, is fated to stand guard over the cocoon(s) of the wasps that attacked it, until the new generation of wasps hatch and fly off. A few groups of ichneumonid wasps are specialized on moth pupae. These can be observed hunting for cocoons and pupal cells on forest floors. Caterpillars and pupae in moist environments—marshlands, mesic forest, and along riparian corridors—also fall victim to both nematodes and horsehair worms.

The same types of pathogens that infect most animals also attack moths and caterpillars: viruses, bacteria, protozoans, and fungi. The fungus *Cordyceps*, an enormously successful genus with perhaps 600 species worldwide, attacks many Lepidoptera, especially those that live in soil as larvae. *Beauvaria* fungi, too, are a common enemy of caterpillars, especially those that live in the soil or other moist environments.

Many of these disease agents have been used in biological control programs to control pest species, in part because pathogens tend to be very specific

ABOVE LEFT | More than 8,500 tachinid flies have been described, with thousands more awaiting recognition—most of these parasitize caterpillars. *Compsilura cocinnata* (shown here) was introduced into North America as a biological control agent to attack the Spongy Moth (*Lymantria dispar*).

LEFT | Tiger moth caterpillar attacked by a microgastrine braconid wasp. More than 30 of the wasp cocoons are visible here—and all have hatched (note the open or missing opercula).

ABOVE LEFT | Zombie caterpillar. Having fed inside the noctuid, a microgastrine wasp larva exited and spun its cocoon under the caterpillar, which, still alive, serves to protect the wasp from predators.

ABOVE RIGHT | Pupa of a hepialid attacked by a *Cordyceps*. The fungus releases spores to infect the next generation of caterpillars.

and are only capable of infecting a small group of species. Extended periods of cool, wet weather, especially through spring months, favorable to pathogens, are associated with taxonomically widespread population downturns in many Lepidoptera. The fungus *Entomophaga maimaiga* has been spectacularly successful in bringing down outbreaks of the Spongy Moth (*Lymantria dispar*). The bacterium *Bacillus thuringiensis* is used worldwide in gardens, croplands, and forests to control pestiferous caterpillars. In general, viruses have highly specific host ranges, but are expensive to produce, and as such are only rarely employed as biological control agents. However, entomopathogenic viruses have great potential to be used in genetic engineering—for example, when their toxin-producing genes are inserted into a plant genome.

APOSEMATISM AND MIMICRY

While the vast majority of moths are cryptic in coloration, rendered in camouflaging greens, grays, and earth tones that blend in with foliage, bark, or soil by day, moths that are chemically protected and unpalatable are commonly aposematic. That is, they advertise their presence with bold wing and body colors: yellows, oranges, and reds that are accentuated with additional white and black markings. Bright white colorations, which are conspicuous both day and night, are another way distasteful moths commonly advertise their chemical protection.

The chemical ecology of such moths is worthy of its own book. The toxins and defensive chemicals that ward off would-be predators—iridoid glycosides, cyanogenic glucosides, cardiac glycosides, and a sweep of alkaloids—consumed by the caterpillar, sequestered and concentrated, can be passed through the pupal stage and on to the adult. Few moths manufacture their own defensive compounds: these are usually simple acids, aldehydes, and ketones. Smoky moths (Zygaenidae) and related families are famous for their ability to manufacture cyanide or compounds that yield cyanide when either the caterpillar or adult is under attack.

Typically, the defensive chemicals occur in high concentration throughout the body but may also be incorporated into wing and body tissues. A special case is that of *Hylesia metabus* of northern South America. The hairlike deciduous scales of the female's abdomen are highly irritating to human eyes and skin, and can be so problematic during periods when the adults are common that villagers will turn off their lights in order to protect themselves and their homes. A few lineages exude toxin-laden hemolymph ("blood") when under attack that can, in some cases, terminate the attack and allow the moth to escape.

Mimicry, arguably one of the most compelling cases of evolution and the uncanny powers of natural selection, was unknown to Darwin at the time he wrote *On the Origin of Species*. Instead, English naturalist Henry Walter Bates discovered mimicry while studying butterflies in South America. Given that butterflies are little more than day-flying moths, it should come as no surprise that many moths are mimetic, especially among the day-flying species, where color and patterning are crucial for survival. Moths may be

ABOVE LEFT | Unpalatable caterpillars (here, *Didugua argentilinea*) warn of their unpalatability with bright colors, patterns, and conspicuous behaviors; for example, they are much more likely to eat during daylight hours.

LEFT | Tiger moths may represent the largest radiation of mostly aposematic animals on the planet, with more than 11,000 described species.

either Batesian (where palatable species mimic a toxic model) or Müllerian (where unpalatable species come to resemble one another). Among these are hundreds of bee and wasp mimics, which have clear wings, devoid of scales, that resemble bumblebees or wasps in flight. The likeness of some clearwing moths (Sesiidae) and wasp moths (ctenuchine Erebidae) to their models is so close that all but the best-informed insect aficionados are likely to be fooled. Add to these a scattered smorgasbord of small, day-flying cossids, saturniids, sphingids, lasiocampids, a smattering of zygaenoids, and still others.

LEFT | The deciduous body hairs and scales of *Hylesia metabus*, a diminutive saturniid endemic to northern South America, cause particularly aggravating cases of region-wide dermatitis when they are on the wing.

BELOW | This ostentatious pericopine tiger moth (*Composia credula*) is protected by high titers of pyrrolizidine alkaloids (PAs) that are sequestered by its caterpillar.

OBSERVATION

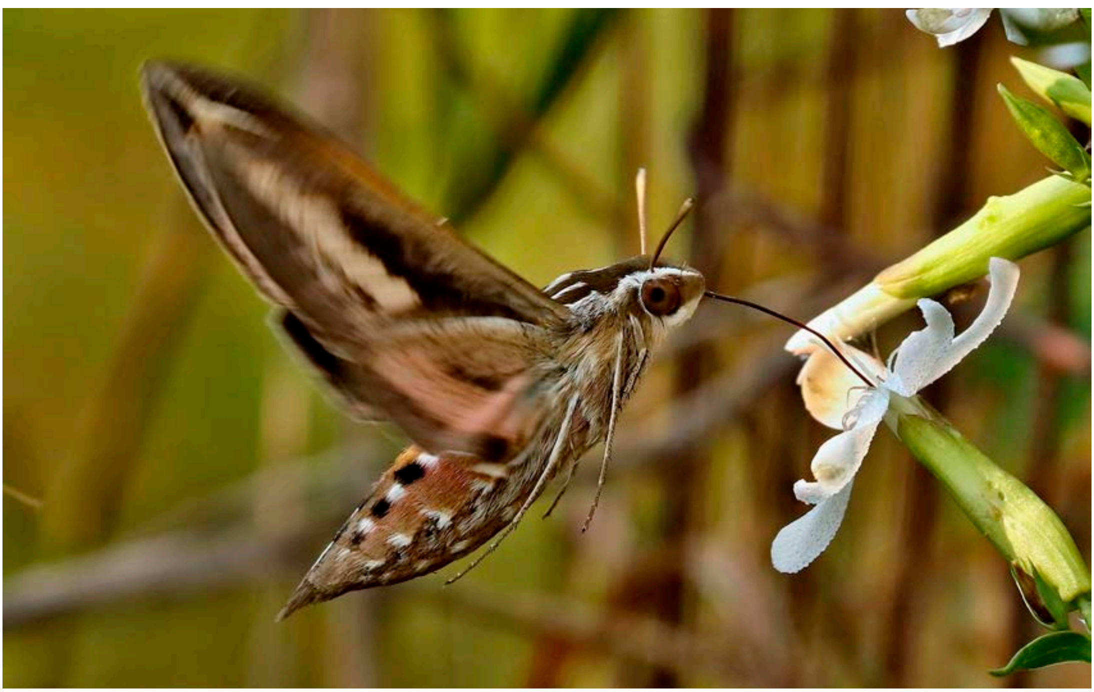
Moths are among the easiest insects to observe as the vast majority come to lights at night, especially light sources rich in UV wavelengths. Partly for this reason, moth watching and especially moth photography are rapidly gaining in popularity among naturalists and community scientists around the world. Dozens of social media groups now anchor to moth watching and photography.

WHERE TO FIND MOTHS

The first rule of thumb is to search for moths at sites with high plant diversity. While woodlands and forests generally have the greatest species diversity, ecotones where early successional habitats intermingle about forested communities will be the most productive. Over the course of time, seek out different plant community types. Where water is limited, explore canyons and sites with water at or near the soil surface. Diversity drops off quickly with human activity: target sites away from yards, artificial lighting, and areas of abundant exotic plant growth, when circumstances allow.

Expect substantial species turnover during the year, with richness peaking for adults in late spring in temperate areas, and at the start of the wet season in ecosystems with a pronounced dry season. In extremely wet forests, species richness may peak in the dry season. For caterpillar hunting, shoot for three weeks after the peak for

BELOW | The White-lined Sphinx (*Hyles lineata*) is one of the most important pollinators across the deserts and drylands of North America.



LEFT | Meadows rich in floral resources are a great place to search for moths by day and night. Dusk is a special time that can be particularly rewarding.

LEFT | The Madagascan Moon Moth (*Argema mittrei*), regarded by many to be among nature's most beautiful and extraordinary animals. Tail lengths vary considerably—this individual is especially well endowed.

adults. Different species fly at different times of the year—many fly only in spring, others in summer, some lineages eclose in the fall with a subset of these persisting through the winter as adults—these may be seen on warm winter nights feeding on sap flows. This latter set tends to go into reproductive diapause until late winter and early spring, when mating occurs.

Different species have their peak flight at different times of the night or day. Dusk is a wonderful time to hunt for moths as many species are on the wing shortly after sundown when there is ample light to see without employing a headlamp. This is a prime time to look for many ghost moths (Hepialidae), plume moths (Pterophoridae), and other microlepidopterans.

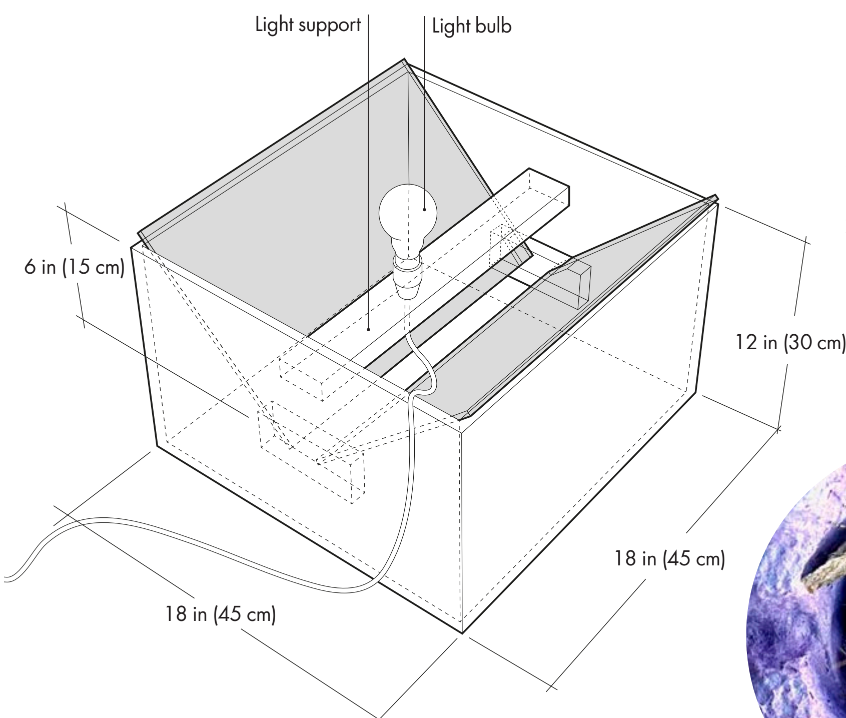
Many giant silk moths (Saturniidae) fly principally after midnight. The twilight period before dawn is supposed to be especially good for grass-miner moths (Elachistidae), but is relatively quiet, with most moths making beelines for safe resting sites to pass the day.

LIGHTING FOR MOTHS

While moths will come to any bright green, blue, or UV-rich light, UV wavelengths are the most attractive, and a must for the serious moth photographer or collector. You can enhance a light's effectiveness by placing the bulb proximate to a white sheet that reflects much of the light out into a habitat that is the target of a night's sampling efforts. Within a night or two, stationary lights become feeding stations for bats by night and birds by morning. Shut your lights down as much as an hour before dawn and shake the sheets to give the moths time to settle elsewhere, especially if you are running a light at the same location night after night.

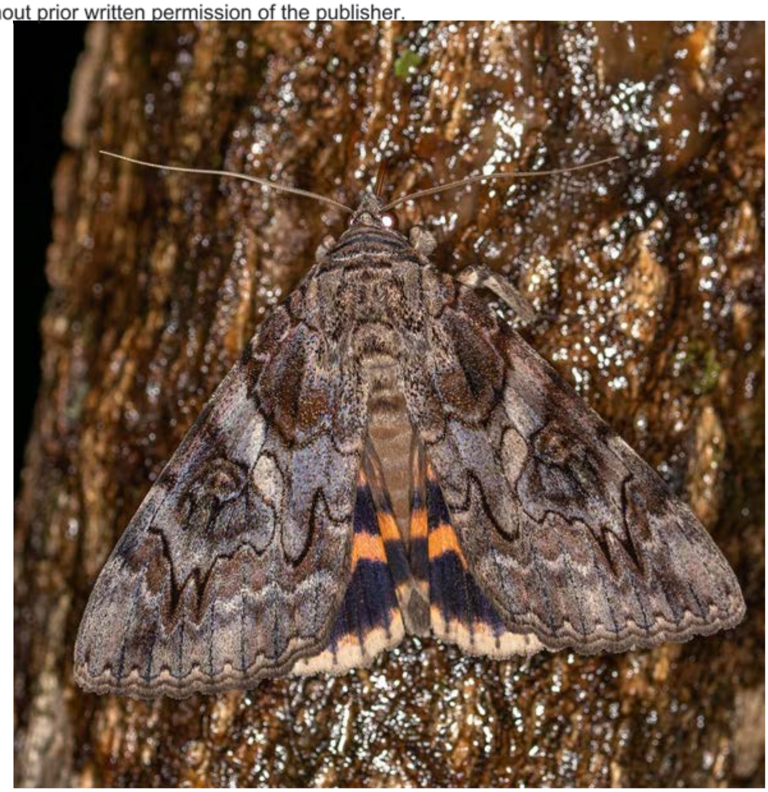
Many light trap variations are available for use with or without killing agents. Live trapping is highly encouraged where the moth fauna is known, imperiled species are present, where images of live moths are desired, and when seeking to capture a gravid female for breeding purposes. One live-trapping method that is both inexpensive and effective is to place the light among or directly over an assortment of 10 to 20 egg carton tops or bottoms that provide numerous

SKINNER (LIVE) LIGHT TRAP



LEFT | Skinner and Robinson traps are designed to trap moths alive so that the moths can be easily tallied and released the next morning. The bottoms are often covered with egg carton halves (inset) to provide hiding places in which the adults can settle.

RIGHT | Sugary baits that have begun to ferment are highly attractive to many moths and are a reliable means to see some moths that are only weakly attracted to light; migratory erebids sometimes gather in huge numbers; nearly all noctuine winter moths are bait-feeders; virtually all *Catocala* (shown here) are drawn to fermenting baits.



dark places in which moths can take shelter. Place the set of egg cartons in a wide-mesh laundry bag or the equivalent (see page 70). Live traps should be serviced in the morning, before the traps are exposed to direct sunlight, with all but the needed species released.

Scientists use kill traps when they have minimal opportunities to visit a site over the course of a year—for example, when sampling in remote locations, when moving between sites on consecutive days, when a site is due for development or about to be lost to agriculture, for scientific purposes, and other reasons. Their use should be judicious and efforts made to ensure maximal use of the collected insects. The Lepidopterists' Society has a "Statement on Collecting Lepidoptera" that should be followed by professionals, students, wildlife biologists, environmental consultants, and others.

BAITING

Males and females of many moths take nourishment from the sugary solutions provided by flowers, broken tree limbs, oozing plant wounds, fruits (including those that are overripe or even rotting), as well as accumulations of honeydew excreted by aphids and other homopterans. Tree wounds are especially attractive to many moths—any moist bark patch that has an abundance of flies, wasps, and especially butterflies during the day is sure to be a flurry of moth activity by night. These same moths can be drawn to sugary baits that are fermenting, with those that smell strongly of alcohol performing best.

Bait concoctions vary from simple to complex, and even bizarre. Simply "paint" it onto a tree trunk, at about chest level, or place it in a bowl elevated above the ground. In treeless landscapes,

ABOVE | Moths make wonderful subjects for backyard and local-area surveys and offer a gateway to the study (and protection) of nature.

the bait can be poured over sponges placed on inverted lids or some other solid substrate.

Like mammals, moths sometimes become intoxicated—species that are wary and unapproachable under normal conditions can be so intoxicated that you can pick them up by hand and photograph them. Conversely, underwing moths (Erebidae: *Catocala*), the principal quarry of many moth baiters, typically remain wary and will flee as soon as a strong light is shown on their position. Approach baiting stations quietly and avoid shining bright lights directly on the feeding moths. The red wavelengths of some headlamps are less alarming, but you still want to avoid shining the light directly on the moth. Many moths have ears—a stealthy approach without conversation is best.

Sugary baits work well in the fall and winter for myriad erebids, noctuids, and some lineages of tortricids and oecophorids. The method works best where sugary resources such as overripe and rotting fruits are commonly available to the local moth fauna; conversely, baits are seldom effective in desert and dryland habitats that lack naturally occurring sugary analogs to moth baits. Expect the yields to differ greatly and inexplicably among nights, depending on the bait, humidity, recent rains, cloud cover, and ambient weather conditions. Baiting can be especially productive over droughty periods, when natural alternatives have been scarce.

Finding and photographing diurnal moths is more challenging, and in many ways more rewarding, as you often have to know more about

LEFT | One of the easiest means to live-trap moths is to place a UV light source and egg cartons into an open-mesh laundry bag. Moths attracted to the light will settle into cartons where they are protected from birds and easily examined the next morning.

the moth's biology, preferred habitat, host plants, nectaring preferences, and diel behavior to be successful.

Hunting and raising caterpillars of moths can be an engaging hobby, providing wonderful photographic opportunities, and offering much potential to yield new observations and discoveries. Such is especially true in the tropics and many regions of the southern hemisphere. Caterpillars are relatively easy to raise. Any such efforts are most valuable when you can confidently identify wild host plants; secure quality images of the early stages; photograph any issuing adults; and share your findings. Such life history data are lacking for most species of moths, and are critical to conservation and restoration efforts.

MOTH GARDENS

Butterfly and pollinator gardens are becoming exceedingly popular in home, community, nature center, and school gardens, and additionally are serving to drive interest in insect conservation matters more broadly. The idea of planting a garden for moths—for visitors that benefit after most people have gone in for the night—has only recently gained traction. While many good butterfly flowers, such as lantanas, buddleias, and milkweeds, are also good for moths, other moth flowers differ from those recommended for pollinator gardens. Moth flowers are often white and quite fragrant—think jasmine and honeysuckle. Many have a deep corolla tube that hides the nectar at the bottom so that only long-tongued moths, such as sphingids and noctuids, can easily access the nectar rewards. Various phlox, campions, and verbenas are examples. Four-o'clocks and evening primroses may not open their flowers until late afternoon or twilight (respectively), with moths clearly intended as their preferred pollinators. In addition to targeting the visitation of the adults, consider planting the larval hosts in insect gardens.

(continued...)

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Note: Superfamilies, families, and subfamilies are in Roman type; genera and species are in *italics*.