ily cere-
cahier

pretenders

matthew gandy

Moth

Matthew Gandy

REAKTION BOOKS

7 Pretenders

> . . . he told me about these magic masks of mimicry; about the enormous moth which in a state of repose assumes the image of a snake looking at you; of a tropical geometrid coloured in perfect imitation of a species of butterfly infinitely removed from it in nature's system . . .
>
> Vladimir Nabokov[1]

The life of a moth is fraught with danger at every stage of its life cycle. The co-evolutionary dynamics of moths and their predators has long been a source of cultural and scientific fascination. Moths have developed a remarkable diversity of survival strategies to fool, hide from or even ward off other animals that might want to eat them, including various kinds of crypsis (camouflage and other tactics to avoid being seen) and mimicry (resemblance to other species with similar or superior defences). The astonishing intricacy of these survival strategies has even provoked reflections on whether the degree of aesthetic, and even behavioural, perfection that these moths have achieved in imitating other organisms confounds the utilitarian basis of evolutionary theory.

Even eggs, the smallest and most inconspicuous stage in a moth's life cycle, are subject to predation. Despite the fact that they are often hidden (laid in bark crevices, under leaves, in the axils of stems) or protected by discarded hairs or web-like fragments of cocoons, these tiny beads of life are hunted down by small insects such as ants or targeted by parasitoid wasps that search by smell rather than by sight. It is at the caterpillar stage where moths begin to deploy the full diversity of protective strategies. Not only do birds consume huge quantities of caterpillars, especially in the spring in order to feed their young, but beetles, bugs, lizards and small mammals will eat them. Caterpillars are also susceptible to viral, bacterial or fungal attacks (except for the highly poisonous burnet caterpillars of the family Zygaenidae, which seem to repel even viruses). There are also some caterpillars, such as those of the Silky Wainscot, *Chilodes maritima*, that are known to attack each other, or caterpillars of other species, but instances of cannibalism are restricted to just a few species, and tend to occur in situations of food stress.

Among the most pervasive threats that caterpillars face are the relentless attacks of parasitoid wasps and flies. These predatory insects lay their eggs either in, on or near their prey, and their larvae then proceed to gradually devour their host, keeping them alive just long enough to provide sustenance. Such strategies have their logic: not only is the caterpillar kept 'fresh' but it continues to behave relatively normally so that its usual defences against larger predators such as birds protect the growing parasites within.[2] Many species of wasps are able to pierce the body of the caterpillar with a sharpened ovipositor, while parasitic flies generally lay their eggs on leaves that the unsuspecting caterpillar will ingest. Even underwater caterpillars such as those of the China-mark moths in the Crambidae family are not completely safe since there are wasps that can dive down to reach them.[3] Nor are caterpillars that are hidden inside the branches and trunks of trees safe: some wasps possess specialist drill-like ovipositors capable of cutting through wood to reach their prey.

It is a strange sight to see not a moth or butterfly emerging from a pupa but a menacing-looking wasp. Since these predators almost invariably kill their host they are referred to as 'parasitoids' to distinguish them from the relatively few 'true parasites' of Lepidopetera, such as mites, that live in less deadly relation with their host. So significant is this evolutionary relationship between moths and parasitoids that there are over 20,000 species of tachinid flies, over 40,000 species of braconid wasps, over 60,000 species of ichneumonid wasps, and more than 400,000 chalcidoid wasps, that prey on caterpillars.[4]

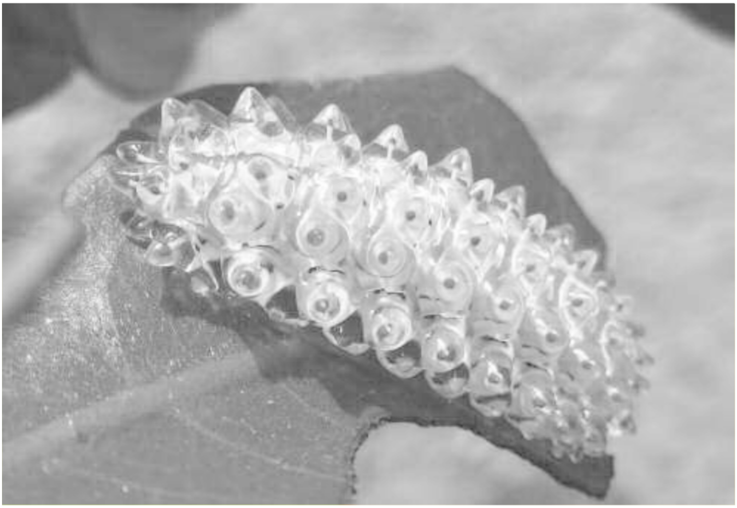
There is a progressive sequence in the eating habits of many parasitoids, which begins with less important tissues before finally devouring the key organs of their host (even more advanced animals such as toads are vulnerable to a similarly grisly fate). Among the ghoulish distinctions between these predators are the neatness of wasps versus the messiness of flies. However, we should not forget that many parasitoid larvae can themselves be targeted as hosts for yet smaller larvae of so-called 'hyper-parasites' (or 'secondary-parasitoids') so that the chain of predation is extended yet further.[5]

In his book *Creative Evolution* (1907) the French philosopher Henri Bergson draws on the earlier scientific observations of the entomologist Jean-Henri Fabre to discuss the troubling relationship between the parasitoid wasp of the genus *Ammophila* and its caterpillar prey. The wasp is able to paralyse its host with a series of clinically targeted stings to the main nerves passing through each segment of its body. Bergson wonders how a wasp can have such precise knowledge, and compares the understanding of its prey with that of the entomologist who can only know the caterpillar from the 'outside'. For Bergson, the 'hereditary transmission of contracted habit' is an insufficient explanation for the wasp's apparent intelligence. He therefore posits a different explanation based on the idea that 'caterpillar' and 'wasp' should be considered as relational activities rather than different organisms.[6]

For Bergson, the more distant working relationship between scientist and object of study compares badly with the skill of the wasp in relation to the caterpillar, which he ascribes to some kind of vital force or *élan vital* inherent to the natural world and not reducible to evolutionary genetics and the role of heredity in behaviour. While vitalist philosophy à la Bergson remains a highly contentious epistemological field, and is rejected by most modern biologists, the original observations of wasp behaviour by Fabre remain a source of fascination.[7]

Caterpillars are by no means passive in the face of these enemies. Hairiness is one defence mechanism, acting as a physical barrier to prevent eggs from being laid either in or on the caterpillar. Additionally, specialized types of hairs, such as extensible barbs laden with poison, may provide a further line of defence. As they grow in size some caterpillars develop various appendages that they can flail around like clubs or whips to fend off predators. To avoid olfactory detection caterpillars may also fling their droppings (known as 'frass') as far away as possible, thus putting would-be predators off the scent. Some caterpillars also have internal defences that enable them to isolate and destroy eggs or small larvae within their bodies, an action not dissimilar to that of antibodies that bind to threatening micro-organisms.[8] Parasitized caterpillars are also known to bask in the sun in order to use heat as a weapon against their internal intruders. Perhaps most astonishing of all, there is evidence that some caterpillars will self-medicate by chewing poisonous leaves in order to destroy the deadly parasitoids lurking within their bodies.[9]

To defend against larger predators that hunt by sight, many caterpillars have evolved mechanisms to avoid visual detection. Caterpillars from the Geometridae, or 'loopers', sometimes resemble thorns or broken twigs, resting motionless at an angle by day only to resume feeding by night. Kent's Geometer, *Selenia kentaria*, occurring in the forests of North America, is among the most intricate of the twig mimics, even growing subtle bark-like protuberances.[10] The caterpillar of the Showy Emerald, *Dichorda iridaria*, also found in North America, mimics dead leaves with a row of 'dorsolateral flanges' that resemble the plant on which it feeds:



Jewel caterpillar, *Acraga coa*, from the Dalceridae family, photographed in Mexico.

Caterpillar from the *Mahanta* genus of the Limacodidae (slug moths) with stinging hairs, from Pu'er, Yunnan, China.

OPPOSITE TOP
Caterpillar of the Spotted Apatelodes moth, *Apatelodes torrefacta*.

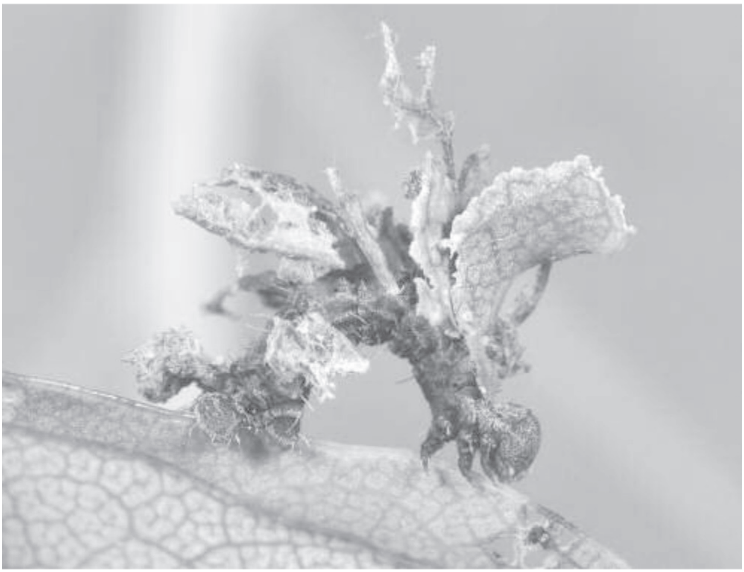
OPPOSITE BOTTOM
Caterpillar of the Flannel Moth, *Megalopyge opercularis.*

> The caterpillar resembles a withered sumac leaflet. It may rest with the anterior portion of its body raised and looped or crooked to one side, adding to its guise as an aged, browning sumac leaflet. Emerald caterpillars have a single gear – slow. If disturbed, their caterpillars often quaver from side to side, much like loosely attached leaves being pushed about by a light breeze.[11]

The thorn mimic caterpillar of the Swallow-tailed Moth, *Ourapteryx sambucaria*, that intrigued Roger Caillois and other early 20th-century sceptics of Darwinian evolution.

The caterpillar of *Pygaera timon* tries to merge with the twig it is clinging to.

In a similar fashion, the Blotched Emerald, *Comibaena bajularia*, a striking denizen of oak woods in temperate zones across much of Europe and eastwards to Japan, has a caterpillar that disguises itself by attaching fragments of leaves to its body so that it can creep along the stems of its foodplant unseen, not unlike the advancing trees of Birnam Wood in Shakespeare's *Macbeth*. In North America, there are several 'loopers' of the genus *Synchlora* that adorn their bodies with petals to become mobile flower mimics, leading the entomologist David L. Wagner to describe



The caterpillar of the Blotched Emerald, *Comibaena bajularia*, attaches fragments of leaves to its body as a form of camouflage.

The caterpillar of the Elephant Hawk-moth, *Deilephila elpenor*, is a snake mimic with false eyes.

Eumorpha labruscae is also a snake mimic: note the fake fangs and small reflections in its 'eyes'.

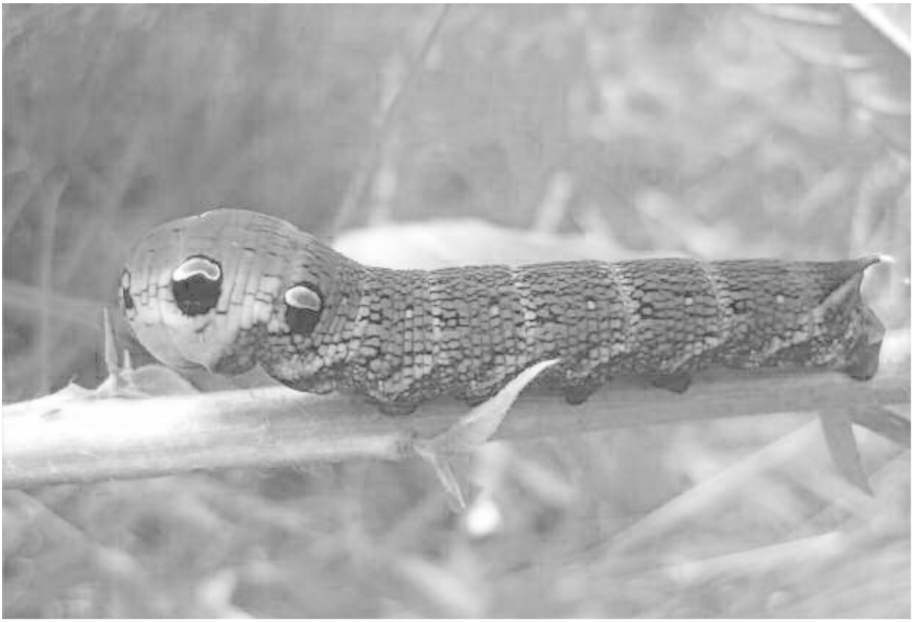
them as 'a Mardi Gras caterpillar that is out of costume only after a molt'.[12]

Other caterpillars, such as the red underwings of the genus *Catocala*, prefer to slink along crevices in bark or wrap their bodies so tightly around stems that they are all but impossible to spot (often aided by rows of 'shadow elimination hairs' that help them to disappear from view). But if disturbed, some of these larger *Catocala* caterpillars can switch to feigned attack mode by making darting movements of their head that 'bump' potential predators with pretend bites.[13] Other caterpillars, and even adult moths, will also contort their bodies to reveal intersegmental rings that resemble banded forms of warning colouration.

The caterpillars of the Elephant Hawk-moth, *Deilephila elpenor*, will contract the front of their body to create a false head with eyes, so they appear as snakes to predators. So intricate are these false eyes that in some species they contain tiny white dots to resemble light reflections. In other species this 'snake's head' can even protrude a foul-smelling tongue-like protrusion, or the caterpillar may use behavioural mimicry such as swaying its body from side to side in a menacing way.

Another defence is for caterpillars to cluster together so that they appear to be one much larger organism snaking its way across tree trunks, vegetation or even open ground. The so-called processionary moths, for example, adopt this strategy as they move in formation in search of new sources of food. The young larvae of the Buff-tip, *Phalera bucephala*, feed together gregariously and, when disturbed, will all rear their heads simultaneously until the danger has passed (the wing pattern of the similarly ingenious adult moth enables it to disguise itself as a broken birch twig).

One of the most remarkable caterpillar defence strategies of all is that of Harris's Three-spot, *Harrisimemna trisignata*, a moth



The caterpillar of Harris's Three-spot, *Harrisimemna trisignata*, is among the most unappetizing-looking of all.

encountered in marshy woodlands from southern Canada to Florida and Texas. 'By almost any measure,' writes David L. Wagner, 'this is an exceptional animal – the caterpillar resembles a bird dropping, a pile of debris, a moldy cadaver, a spider, and who knows what else.' Among its more curious features the caterpillar retains the discarded head capsules from its previous moults, suspended on long hairs jutting out from behind its head, to create a kind of 'mace', which it thrashes against predators, batting away flies, wasps and other enemies in this manner. 'In addition,' notes Wagner, 'if molested, the caterpillar will rock its body with blurring rapidity – the effect is much like that of a spider rapidly tugging on its web (stabilimentum).'[14]

Instead of hiding, some caterpillars adopt a strategy of making themselves as conspicuous as possible with various forms of warning colouration against would-be predators. The striking black-and-yellow striped caterpillars of the Cinnabar moth, *Tyria jacobaeae*, for example, feed on the highly poisonous plant ragwort, *Senecio jacobaea*, and concentrate the alkaloid toxins in their bodies as a defence mechanism. In effect, the Cinnabar and many other distasteful moths have succeeded in unravelling the chemical defence strategies of plants and then using the acquired compounds for their own protection. This use of warning colouration is known as 'Müllerian mimicry' (named after the German biologist Fritz Müller): the appearance signals to predators that the caterpillar is unpalatable or poisonous and thus not worth eating.

The caterpillar of the Cinnabar moth, *Tyria jacobaeae*, concentrates toxins in its body from its larval foodplant and is an unpalatable Müllerian mimic with yellow- and black-banded warning colouration.

Some caterpillars deploy both crypsis and mimicry at different stages of their development. The caterpillar of the Alder Moth, *Acronicta alni,* resembles a bird dropping until its final moult when it is transformed into a brightly coloured black-and-yellow striped creature, complete with a set of black 'paddles' to flail at predators, although it is not poisonous and is therefore an example of 'Batesian mimicry', whereby a harmless organism resembles one that is best avoided. One possible reason for this switch in strategy adopted by the Alder Moth and many other species is that as the caterpillar grows in size it becomes more difficult to remain unseen, so there is a gradual or even sudden development of frightening protuberances, spikes, spines or other features.

Still more remarkable is the Hag Moth, *Phobetron pithecium*, also known as the Monkey Slug because of the curious shape of the caterpillar, found in orchards and woodlands from Quebec to Arkansas. This caterpillar has an extremely odd appearance: from above it resembles a strange kind of spider, a dead leaf furred with mould or, most probably, a discarded tarantula skin (although these spiders are absent from North America, the *Phobetron* genus is well represented south of Mexico). If turned upside down the caterpillar enhances its apparent unpalatability further by strange internal contortions of its abdomen, which make it appear as if a large *Alien*-like grub is squirming around within its body. If all these visual tricks should fail, a final line of defence is present in the shape of stinging hairs that can cause serious discomfort or irritation. As for the adult moth, the female looks like a bee, complete with yellow tufts on its legs resembling pollen baskets, while the male is a wasp mimic, so that we must contend with a moth that mimics several kinds of organisms or unpalatable objects at different stages of its life cycle.[15]

The greatest threat to adult moths that fly by night is bats. Many species have evolved specialized tympanal (hearing) organs that

The caterpillar of the Alder Moth, *Acronicta alni*, mimics bird droppings during its early instars. After its final moult the caterpillar is transformed into a dramatic yet harmless Batesian mimic with characteristic aposematic (warning) colouration.

The extraordinary caterpillar of *Phobetron hipparchia* is related to the Monkey Slug found in North America.

can detect the echolocation calls of these predators, producing involuntary neurological responses that cause the moth to fold its wings and fall directly to the ground.[16] Additionally, some species of Tiger Moths such as the Dogbane Tiger, *Cycnia tenera*, found in North America, produce ultrasonic sounds in response to the echolocation calls of bats to effectively jam or confuse their hunting strategies. There are even moths that adopt a form of Batesian acoustic mimicry for courtship as well as protection.[17] Colour may also play a role in evading nocturnal predators: it is possible that the high visibility of white or pale-coloured moths, which are easily spotted at dusk, is a type of protective warning colouration against bats.[18]

The caterpillars of the *Phobetron* genus are among the strangest of all, with weird appendages and contorted body shapes. This specimen was found in São Bernardo do Campo, São Paulo, Brazil.

Adult moths of the *Phobetron* genus can resemble miniature frogs or even monkeys.

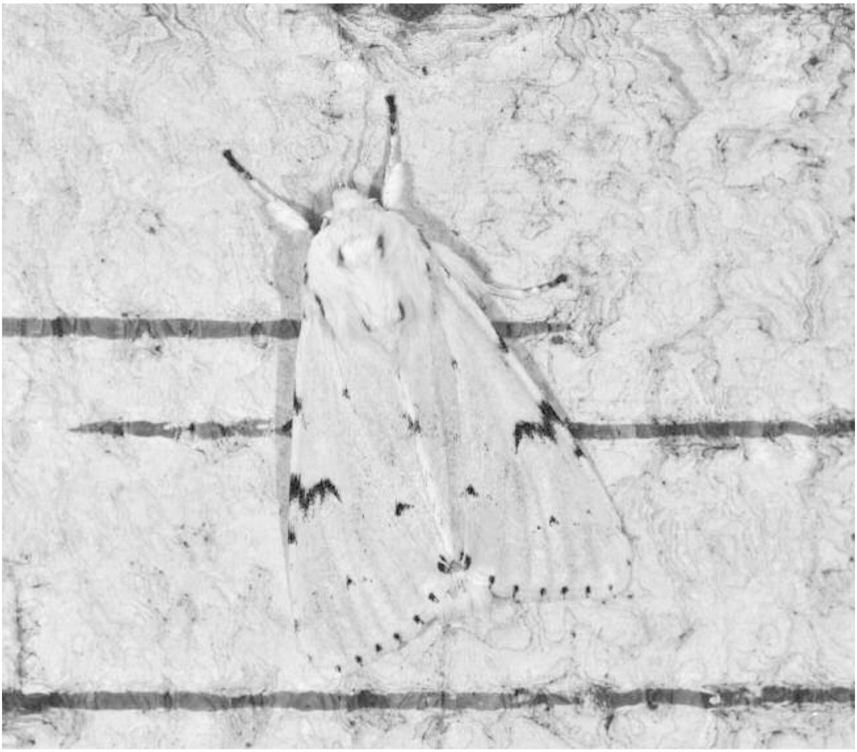
Other diurnal behavioural defence strategies include feigning death, the release of unpleasant chemicals, the emission of strange or unexpected sounds (in addition to anti-bat defences), erratic flight, 'flash colouration' from brightly coloured hindwings or the sudden display of eyespots to surprise potential predators such as

birds.[19] The Eyed Hawk-moth, *Smerinthus ocellatus*, for example, often rests on tree trunks by day with its 'bunched' wings resembling dry leaves; if disturbed, however, it flashes two bright blue eyespots on its pinkish hindwings in order to startle predators. The possession of eyespots is also used for 'body mirroring' so that an insect may appear to have two heads, thereby encouraging the predator to pounce on the false one. The presence of high levels of polymorphism, where one species has different forms, also serves as a defensive mechanism against the searching strategies of predators. The scarcity of a particular form can reduce levels of familiarity among predators, as can a high level of sympatric (same place) species diversity: in North America alone, for example, there are over 100 different red underwing species of the genus *Catocala* with often very subtle differences in their markings. 'Though birds learn when relationships are simple and systematic,' suggests the American entomologist Theodore Sargent, 'diversity makes for complex and unpredictable relationships which only confound the avian brain.'[20] If we add into the mix the short lifespans of many moths, then it becomes even harder for predators to remember their prey.

For most palatable species of moths that fly by night – unless they are Batesian mimics – the main survival strategy by day is to hide. To remain unseen, moths use a huge diversity of resting poses and wing patterns to produce a bewildering variety of cryptic defence strategies. The disguises adopted include wing patterns that resemble leaves, broken twigs or lichen-encrusted rocks. The patterns are often quite specific, such as the resemblance of the Miller moth, *Acronicta leporina*, to the bark of birch trees on which it rests by day. Wing patterns may also include stripes or spots that break up the wing outline and make the moth harder to spot. In addition, unusual resting postures or strangely shaped wings can help the moth to blend into its

The Eyed Hawk-moth, *Smerinthus ocellatus*, flashes its dramatic 'eyes' at would-be predators.

The spectacular *Antitrygodes divisaria* is found in South and East Asia. Its broken pattern might resemble dappled light within the forests where it is found.



The Miller moth, *Acronicta leporina*, rests by day on the bark of birch trees. This specimen was found in Spreewald, Brandenburg, Germany.

surroundings. The moth *Tarsolepis sommeri* of the family Notodontidae, which is found in Borneo and other parts of the Malaysian Peninsula, has a wing pattern that resembles an empty space through which a broken twig protrudes (this moth is also known to be lachryphagous, or tear drinking, in its feeding habits since it has been observed drinking from around the eyes of forest animals such as tapirs). The curiously marked *Macrocilix maia*, a type of Drepanid moth found in China, Japan, Korea and elsewhere in East Asia, appears to have two flies on its wings that are feeding off bird excrement or some other kind of putrefied yellow liquid. And just in case this visual pattern fails to convince, the moth also emits a smell similar to bird droppings as an additional olfactory line of defence.

Moths not only seek out rocks, tree trunks or other surfaces but take care to position themselves carefully on them to make themselves as inconspicuous as possible, though whether the background

The lachryphagous (tear drinking) species of prominent moth, *Tarsolepis taiwana*, appears to include a void space in its wing pattern to radically break up its outline. This photograph is from Pu’er, Yunnan, China.

preferences of cryptic moths are actively 'chosen' rather than automatically adopted remains uncertain. This tendency to seek protection against different background colours or surfaces has been the source of some of the most remarkable research into what the British geneticist Michael Majerus termed 'evolution in action'.[21] A particular focus of interest has been the phenomenon of melanism – the prevalence of dark pigmentation – which occurs naturally but began to confer specific competitive advantages during the nineteenth century for many species occurring in soot-covered urban and industrial environments. The story of the Peppered Moth, *Biston betularia*, begins with the discovery in 1848, in a Manchester garden, of a black *carbonaria* form of what is normally a lightly speckled white moth. By the 1890s, nearly 90 per cent of the Peppered Moths in the Manchester area were black and, in 1896, the British entomologist James Tutt suggested the 'differential

The Drepanid moth *Macrocilix maia* has what appears to be two flies feeding off its wings. This moth was found in Fushan, Taiwan.

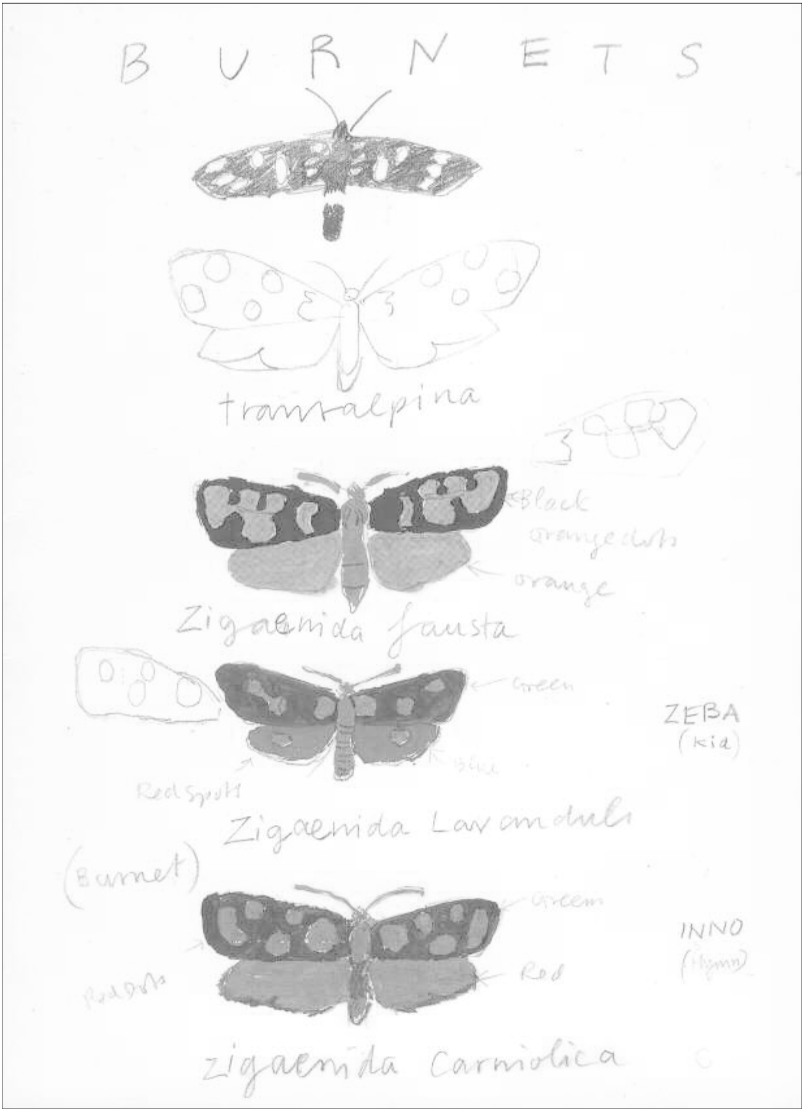
The rise of the melanic form of the Peppered Moth, *Biston betularia*, has been the focus of intense research and also controversy surrounding the effects of bird predation on evolution.

bird predation hypothesis' to account for this increase in the frequency of a previously rare form.[22] His basic thesis, investigated in field experiments by the British geneticist Bernard Kettlewell during the 1950s, was that the dark form had less chance of being spotted by birds when resting against soot-covered trees or buildings than the lightly speckled *typica* form. Further evidence for melanism in industrial areas was also provided by the increasing frequency of dark forms for many other species of moths found in urban and industrial areas of Europe and North America.[23]

More recently, however, these early studies of melanism have been criticized for methodological weaknesses, such as the deliberate placing of darker moths against pale surfaces to prove their vulnerability. It is now believed that this 'bird feeder' research design exaggerated the results, ignoring the ability of moths to seek appropriate substrates to hide against by day, even making small adjustments in their position in relation to bark striations or other patterned surfaces. Critics of Kettlewell's work note that little is known about how these species conceal themselves in natural situations since many Geometrid moths hide on the underside of leaves within tree canopies. Other concerns include the rise of melanism in *rural* areas of Europe and North America over the twentieth century, which cannot be explained by bird predation alone.

The scientific uncertainties over industrial melanism were heightened by the publication of Judith Hooper's book *Of Moths and Men: Intrigue, Tragedy, and the Peppered Moth* (2002), which alleged that Kettlewell's research had been not only flawed but fraudulent.[24] Creationists in the USA latched onto the controversy with glee and a leading biology textbook quietly dropped the Peppered Moth as an example of evolution.[25] In order to address this mounting scientific controversy, Michael Majerus undertook the original field experiments again over a seven-year period between 2001 and 2008 in order to address the weaknesses in Kettlewell's original research design. The study was carried out with a painstaking thoroughness and concern for eliminating the possibilities for bias introduced by placing moths in unnatural resting positions by day, and revealed that differential bird predation was indeed the critical factor in determining the relative dominance of pale and dark forms of the Peppered Moth, although the causal mechanisms are more complex than originally thought.[26] A further factor in the scientific mix is the fact that the Peppered Moth is strongly attracted to streetlights and other artificial sources of illumination, and will frequently settle on nearby surfaces such as walls where it is easily picked off by birds the next day.

A page of watercolours from the notebook of Joe Tilson in 1997 depicting various burnet moths (*Zygaena* spp.), which are among the most poisonous species of all.


B U R N E T S
transalpina
Black
orange dots
orange
Zigaenida fausta
Green
ZEBA
(kia)
Blue
Red Spots
Zigaenida Lavandulæ
(Burnet)
Green
INNO
Red
Red Dots
zigaenida Carniolica

In contrast to the melanic disguise of the Peppered Moth, there are many moths that seek protection in visibility, relying on their ability to use aposematic (warning) colouration to deter predators. These colour patterns are typically simple, consisting of brightly coloured bands, stripes or spots of two or three colours, which may also extend to the thorax or abdomen. The presence of Müllerian mimicry, whereby several, unpalatable forms adopt the same pattern or colouration, ensures that the colour combinations are straightforward and easily learnt by predators. Moths are able to use a wide variety of chemical compounds to produce toxins, either derived from the larval foodplant or synthesized in the body of the adult moth. The effect on predators varies from the merely distasteful to the highly toxic. For example, the brightly coloured burnet moths, of the family Zygaenidae, are among the most poisonous of all (they self-synthesize hydrogen cyanide). In contrast, various tiger moths from the subfamily Arctiinae use somewhat different chemical defences such as pyrrolizidine alkaloids and cardiac glycosides. In the case of the Garden Tiger, *Arctia caja*, some of the defence chemicals are derived from larval foodplants whereas others are self-synthesized by the adult moth. Research into Tiger Moths has also revealed that the caterpillars' consumption of pyrrolizidine alkaloids and iridoid glycosides produces specific morphogenetic effects, impacting on the development of the larvae, in an illustration of how these chemicals are woven into virtually every aspect of the insect's life cycle.[27]

By contrast, the palatable Batesian mimics adopt visual or even behavioural mimicry of other distasteful or dangerous organisms, including bees, wasps and other stinging insects. The various 'spider moths' found in rainforests appear to have multiple eyes and venomous fangs. The Lygodium Spider Moth, *Siamusotima aranea*, first described from northern Thailand in 2005, reveals leg-like markings across its wings when spread against a pale background. Some

species even elude spider predators not just by resembling them but also through adopting aspects of their behaviour: the *Brenthia* genus of metalmark moths confronts their jumping spider predators by pretending to be an aggressive adversary.[28] With Batesian mimicry, however, the number of palatable mimics must remain relatively low or the model itself is potentially placed in danger (which may partly explain the relative scarcity of some of these mimics). In practice, however, a spectrum of mimicry strategies between a 'pure' Batesian or Müllerian model can be observed with varying degrees of unpalatability and vulnerability (that may also be affected by the degree of hunger experienced by predators).[29]

Historically, the degree of perfection displayed by some mimics has provoked uncertainty over the limits to Darwinian evolution.

The Garden Tiger, *Arctia caja*, with its bright aposematic (warning) colours, sequesters plant toxins and also manufactures its own additional toxins.

The Clearwing Moth, *Negotinthia myrmosaeformis*, from the family Sesiidae is a hymenopteroid mimic complete with yellow tufts on its legs that resemble pollen baskets. This specimen was found in Chaskowo, Bulgaria.

Among the most influential critics of the reductionist aspects to evolutionary theory is the novelist Vladimir Nabokov, who suggested that there must be something more than mere natural selection involved given the exquisite degree of refinement of many insect mimics. In his autobiography, *Speak, Memory*, for example, Nabokov reflects on a caterpillar that is shaped like a larva caught in the jaws of an ant:

> Consider the tricks of an acrobatic caterpillar (of the Lobster moth) which in infancy looks like bird's dung, but after molting develops scrabbly hymenopteroid appendages and baroque characteristics, allowing the extraordinary fellow

> to play two parts at once (like the actor in Oriental shows that *becomes* a pair of intertwisted wrestlers): that of a writhing larva and that of a big ant seemingly harrowing it.[30]

Nabokov continues, marvelling at the excess of detail in nature:

> When a certain moth resembles a certain wasp in shape and colour, it also walks and moves its antennae in a waspish, unmoth like manner. When a butterfly has to look like a leaf, not only are all the details of a leaf beautifully rendered but markings mimicking grub-bored holes are generously thrown in. 'Natural selection,' in the Darwinian sense could not explain the miraculous coincidence of imitative aspect

The caterpillar of the Lobster moth, *Stauropus fagi*, inspired Vladimir Nabokov's doubts over the degree of refinement achievable under Darwinian evolution.

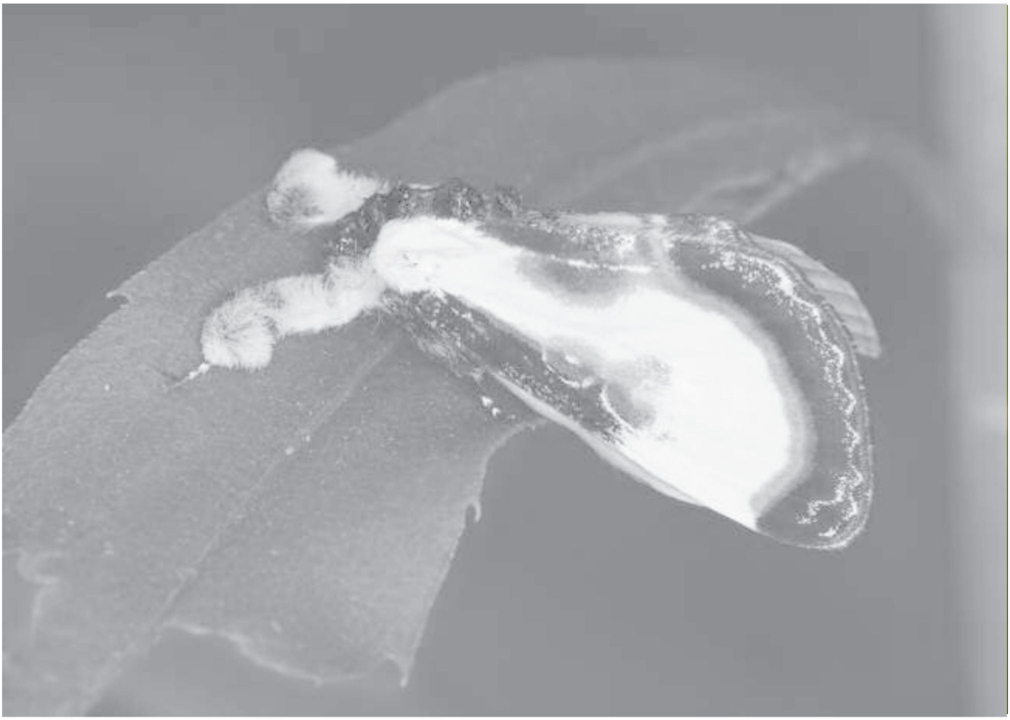
> and imitative behaviour, nor could one appeal to 'the struggle of life' when a protective device was carried to a point of mimetic subtlety, exuberance, and luxury far in excess of a predator's power of appreciation. I discovered in nature the nonutilitarian delights that I sought in art. Both were a form of magic, both were a game of intricate enchantment and deception.[31]

These reflections, along with some brief passages from *The Gift* (1963), are all that remains of Nabokov's lost essay on the limits to Darwinian theory.[32] But what are we to make of Nabokov's claim that natural selection cannot account for the refinement of mimicry in the natural world? Nabokov was no creationist, but he did incline towards vitalism, searching (like Bergson) for some kind of life force beyond the mere mechanics of what he understood to be population genetics. Although defenders of Nabokov have tried to place him in the vanguard of post-Darwinian approaches to evolution, his perspectives on mimicry lie closer to a transitional phase in late nineteenth-century scientific thought when the apparent simplicity of Darwinism was still being widely contested. Nabokov's own research, undertaken at Harvard's Museum of Comparative Zoology in the 1940s, remains a respected contribution to taxonomy (especially in relation to Lycaenid butterflies, known as 'the blues'), but it seems that he never developed a sophisticated grasp of population genetics or articulated an alternative theory of evolution that could have gained wider scientific credence.[33]

There are, however, parallels between Nabokov's focus on the 'nonutilitarian delights' of insect mimicry and the surrealist writer Roger Caillois' anti-Darwinian stance developed in his essay 'Mimicry and Legendary Psychasthenia', first published in 1935.[34]Among Caillois' examples are the leaf- or petal-mimicking mantises, the Eyed Hawk-moth (*Smerinthus ocellatus*), and also various Geometrid caterpillars that resemble thorns. Like Nabokov, Caillois finds that 'imitation is pushed to the smallest details', and he draws on a striking passage from Rémy Perrier's *Cours élémentaire de zoologie*, first published in 1899, to illustrate his point:

> the wings bear gray-green spots simulating the mold of lichens and glistening surfaces that give them the look of torn and perforated leaves: 'including spots of mold of the sphaeriaceous kind that stud the leaves of these plants; everything, including the transparent scars produced by phytophagic insects when, devouring the parenchyma of the leaves in places, they leave only the translucid skin.

The bird dropping mimic *Eudryas grata* is found in North America.



The superb dead leaf mimic *Uropyia meticulodina* photographed in Taiwan.

> Imitations are produced by pearly spots that correspond to similar spots on the upper surface of the wings.'[35]

For Caillois, these forms of mimetic adaptation go far beyond chance, as intimated by the French biologist Lucien Cuénot.[36] Caillois draws on a modified Lamarckian theory of inherited traits to suggest the existence of 'environmental mirroring', whereby an organism reproduces its environment in its body in a manner that is considered analogous to a kind of three-dimensional photography:

> Morphological mimicry could then be, after the fashion of chromatic mimicry, an actual photography, but of the form and the relief, a photography on the level of the object and not on that of the image, a reproduction in three-dimensional space with solids and voids: sculpture-photography or better

> teleplasty, if one strips the word of any metapsychical content.[37]

However, far from seeing this as an effective adaptation, Caillois does not accept that visual mimicry can be a dependable form of defence since it only works against predators that rely on sight rather than smell (we now know this is incorrect, since various forms of olfactory mimicry do exist). This leads him to conclude, with Cuénot, that the 'epiphenomenon' of mimicry is of little practical utility to an organism and may even create new dangers:

> We are thus dealing with a luxury and even a dangerous luxury, for there are cases in which mimicry causes the creature to go from bad to worse: geometer-moth caterpillars simulate shoots of shrubbery so well that gardeners cut them with their pruning shears.[38]

Instead, Caillois suggests that imitation is a kind of biomorphic relic from a more primitive state of nature. He interprets mimicry as a form of residual magic left over from an earlier evolutionary phase when organisms possessed a greater degree of 'plasticity'. For Caillois, the phenomenon of mimicry in insects 'would thus be accurately defined as *an incantation fixed at its culminating point* and having caught the sorcerer in his own trap'.[39] This invocation of 'magic' in nature has affinities with Nabokov's search for an explanation that lies beyond the utilitarian realm of population genetics. Yet many of these concerns with the meaning of mimicry do not ultimately stem from scientific disputes over evolution but rather from a cultural ambivalence towards the aesthetic characteristics of modernity.

More recently there has been scientific recognition of the limitations to more simplistic accounts of evolution. Greater emphasis has been placed on the detailed timescales and mechanisms involved in the development of mimicry and polymorphism.[40] In terms of mimicry, a two-step evolutionary process is now widely acknowledged in which a random major mutation that confers some degree of advantage in Batesian or Müllerian terms is subsequently refined by further minor mutations to produce some of the spectacular examples found in nature.

Timeline of the Moth

146–100 MYA	100–90 MYA	60–50 MYA	4,900 BCE
First definitive Lepidoptera fossils found in amber (oldest from the Mesozoic/Lower Cretaceous period)	Fossil leaf mines found in Mid-Cretaceous Dakota Formation. Rapid co-evolution of Lepidoptera with the rise of angiosperms (flowering plants)	Co-evolution of moths and bats during the Early Tertiary era	Neolithic cultures in what is now eastern China begin silk production

1705	1734–42	1758	1763
Maria Sibylla Merian publishes *Metamorphosis insectorum surinamensium*	René-Antoine Ferchault de Réaumur publishes *Mémoires pour servir à l'histoire des insectes*	Carl Linnaeus introduces the modern binomial system of nomenclature for Lepidoptera in his *Systema naturae*	Giovanni Antonio Scopoli publishes *Entomologia carniolica*

1878	1896	1950s
Fritz Müller proposes the concept of Müllerian mimicry, based on poisonous organisms sharing similar types of colours or patterns	James Tutt suggests that the rise of melanism in moths in industrial Manchester might be caused by differential bird predation	Growing use of Robinson-type moth traps expands the scope and effectiveness of fieldwork including long-term sampling of population change

77–79 CE

Pliny the Elder describes several species of moths in his *Natural History*

1602

Ulisse Aldrovandi publishes *De animalibus insectis*

1634

Posthumous publication of *Theatrum insectorum* by Thomas Moffet and other scholars

1669

Jan Swammerdam publishes *Historia insectorum generalis*

1766

Moses Harris publishes *The Aurelian or Natural History of English Insects: Namely, Moths and Butterflies. Together with the plants on which they feed*

1775

Michael Denis and Ignaz Schiffermüller publish *Ankündung eines systematischen Werkes von den Schmetterlingen der Wienergegend*

1848–59

Henry Walter Bates observes insect mimicry in Amazonia, after which 'Batesian mimicry' is termed. Bates's work is a major influence on Charles Darwin

1980s

Daniel Janzen and his colleagues develop parataxonomy in Costa Rica in order to rapidly expand knowledge of biodiversity

1990s

The use of DNA barcoding reveals the presence of many cryptic species, challenging existing approaches to taxonomy

2000s

Various studies show significant declines in moth abundance that may parallel bee decline

1 Vladimir Nabokov, *The Gift* (London, 1981 [1963]), p. 105.
2 David L. Wagner, *Caterpillars of Eastern North America* (Princeton, NJ, 2005).
3 Norman Riley, *Some British Moths* (London, 1944).
4 Wagner, *Caterpillars of Eastern North America*, pp. 22, 24.
5 Michael Majerus, *Moths* (London, 2002), p. 178.
6 Henri Bergson, *Creative Evolution*, trans. Arthur Mitchell (Mineola, NY, 1998 [1907]), pp. 173–4.
7 See also Hugh Raffles, *Insectopedia* (New York, 2010).
8 Wagner, *Caterpillars of Eastern North America*.
9 M. S. Singer, K. C. Mace and E. A. Bernays, 'Self-Medication as Adaptive Plasticity: Increased Ingestion of Plant Toxins by Parasitized Caterpillars', *PLOS ONE*, IV/3 (2009).
10 Wagner, *Caterpillars of Eastern North America*, p. 179.
11 Ibid., p. 198.
12 Ibid., p. 200.
13 Ibid., p. 224.
14 Ibid., p. 305.
15 Ibid.
16 J. E. Barber and William E. Conner, 'Tiger Moth Jams Bat Sonar', *Science*, CCCXXV (2009), pp. 325–7.
17 William E. Conner, Nickolay I. Hristov and Jesse R. Barber, 'Sound Strategies: Acoustic Aposematism, Startle, and Sonar Jamming', in *Tiger Moths and Woolly Bears: Behaviour, Ecology, and Evolution of the Arctiidae*, ed. William E. Conner (New York, 2009), pp. 177–92.
18 Miriam Rothschild, 'British Aposematic Lepidoptera', in John Heath and A. Maitland Emmet, *The Moths and Butterflies of Great Britain and Ireland* (Colchester, 1985), vol. II, pp. 9–62.
19 Theodore D. Sargent, *Legion of the Night: The Underwing Moths* (Philadelphia, PA, 1976), p. 147.
20 Ibid., p. 181.
21 Michael Majerus, *Melanism: Evolution in Action* (Oxford, 1998).
22 Graeme D. Ruxton, Thomas N. Sherratt and Michael P. Speed, *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals, and Mimicry* (Oxford, 2004), p. 10.
23 Theodore D. Sargent, 'Behavioural Adaptations of Cryptic Moths', *Animal Behaviour*, XVII/4 (1969), pp. 670–72.
24 Judith Hooper, *Of Moths and Men: Intrigue, Tragedy, and the Peppered Moth* (London, 2002).
25 Jaape de Roode, 'The Moths of War', *New Scientist*, CXCVI (8 December 2007).
26 L. M. Cook et al., 'Selective Bird Predation on the Peppered Moth: The Last Experiment of Michael Majerus', *Biology Letters*, VIII (2012), pp. 609–12.

27 Malcolm J. Scoble, *The Lepidoptera*: *Form, Function and Diversity* (New York, 1992).
28 Jadranka Rota and David L. Wagner, 'Predator Mimicry: Metalmark Moths Mimic Their Jumping Spider Predators', *PLOS ONE*, I/1 (2006).
29 Ruxton, Sherratt and Speed, *Avoiding Attack,* p. 164.
30 Vladimir Nabokov, *Speak, Memory* [1951] (London, 1969), p. 98.
31 Ibid.
32 See Brian Boyd, *Vladimir Nabokov: The American Years* (Princeton, NJ, 1991).
33 See also Stephen Jay Gould, 'No Science Without Fancy, No Art Without Facts', in *I Have Landed: Splashes and Reflections in Natural History* (London, 2003); Charles Lee Remington, 'Lepidoptera Studies', in *The Garland Companion to Vladimir Nabokov*, ed. Vladimir E. Alexandrov (New York, 1995), pp. 274–83.
34 Roger Caillois, 'Mimicry and Legendary Psychasthenia', trans. John Shepley, *October*, XXXI (Winter 1984), pp. 16–32.
35 Ibid., p. 22.
36 See Lucien Cuénot, *Les Moyens de défense dans la série animale* (Paris, 1892).
37 Caillois, 'Mimicry and Legendary Psychasthenia', p. 23.
38 Ibid., p. 25.
39 Ibid., p. 27.
40 See, for example, Stephen Jay Gould and Niles Eldredge, 'Punctuated Equilibria: The Tempo and Mode of Evolution Reconsidered', *Paleobiology*, III (1977), pp. 115–51.

Published by
REAKTION BOOKS LTD
Unit 32, Waterside
44–48 Wharf Road
London N1 7UX, UK
www.reaktionbooks.co.uk

First published 2016

Printed and bound in China by 1010 Printing International Ltd

A catalogue record for this book is available from the British Library

ISBN 978 1 78023 585 1

notes:

ily cere- cahiers is a collection of texts(fragments). it is a branch of the collective *it is part of an ensemble*. these texts function as starting points for dialogues within our practice. we also love to share them with guests and visitors of our projects.

the first copy of *ily cere- cahier 49* was printed in september 2026

1	the artist as producer in times of crisis	okwui enwezor
2	the carrier bag theory of fiction	ursula k. le guin
3	arts of noticing	anna lowenhaupt tsing
4	whatever & bartleby	giorgio agamben
5	notes toward a politics of location	adrienne rich
6	the intimacy of strangers	merlin sheldrake
7	the zero world	achille mbembe
8	why do we say that cows don’t do anything?	vinciane despret
9	nautonomat operating manual	raqs media collective
10	on plants, or the origin of our world	emanuele coccia
11	hydrofeminism: or, on becoming a body of water	astrida neimanis
12	the gift and the given	eduardo viveiros de castro
13	the three figures of geontology	elizabeth a. povinelli
14	what lies beneath	george monbiot
15	sculpture not to be seen	elena filipovic
16	the onion	kurt schwitters
17	tentacular thinking	donna j. haraway
18	toward a symbiotic way of thought	vincent zonca
19	living with birds	len howard
20	why look at animals?	john berger
21	quantum listening	pauline oliveros
22	politics of installation	boris groys
23	some notes on drawing	amy sillman
24	depiction, object, event	jeff wall
25	cyber-teratologies	rosi braidotti
26	love your monsters	bruno latour
27	arts of living on a damaged planet	multiple authors
28	what is it like to be a bat?	thomas nagel
29	dazzling diversity: the biology of chiroptera	tessa laird
30	what is an owl?	stephen moss
31	the gender of sound	anne carson
32	the euphio question	kurt vonnegut
33	listening to the tree of life	karen bakker
34	organic music societies	multiple authors
35	klittenbandjes	hay wijnhoven
36	a fable for tomorrow	rachel carson
37	listening music	john maus
38	wolf trilogy	angela carter
39	over leven	sander turnhout
40	hele dagen tussen levende wezens	estelle zhong mengual
41	the earthly community	achille mbembe
42	riding the blinds	maggie nelson
43	notes on gesture	giorgio agamben
44	the living mountain	nan shepherd
45	the ecological crisis as a crisis of sensibility	baptiste morizot
46	death of a moth	virginia woolf
47	the birds	aristophanes
48	anthropomorphism, anthropectomy and anthropocentrism	susana monsó
49	pretenders	matthew gandy
50	finding the mother tree	suzanne simard