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In New Zealand, a radiation of at least 63 species of Macropathinae has spread across the country from mountain to rocky shore. Within this single subfamily are a huge diversity of species placed within 18 genera. They all share the same flightless, nocturnal habit but range in size from 10 mm to 190 mm. None are known to make any sound, and all are without a tympanum. Some species are cave dwellers and tolerant of each other, forming clusters on the ceilings and walls of caves and tunnels (e.g., *Pachyrhamma*, fig. 3a,b). But many other species are forest specialists hiding among arboreal moss and lichen (*Maotoweta virescens*, fig. 3d), in holes in tree trunks (*Talitropsis sedelloti*, fig. 1b) or under bark (*Isoplectron armatum*). Other species have found shelter in damp sheds or cool basements (*Pleioplectron simplex*). A radiation of alpine species has resulted in eight camel cricket species living at high elevation. One species known as the Mount Cook flea (*Pharmacus montanus*) is almost completely black and is renowned for leaping out like showers of rain from rock crevices onto unsuspecting climbers (fig. 3e). All the *Pharmacus* species live above the tree line, where snow can cover the ground for half the year. The highest elevation where they have been recorded is 3,400 m above sea level. Due to the short alpine summers with cold nights, *Pharmacus* are often active during the day. They eat lichen and can be active even when the air temperature is below zero degrees. Peculiarly, New Zealand also has some species of camel cricket that feed by the sea, using coastal caves and rock crevices during the day and at night finding scraps at the high-tide line. However, the majority of New Zealand Rhaphidophoridae are small, secretive species of the forest (fig. 3f–h).

Figure 1 A glimpse into the morphological diversity of pygmy grasshoppers, Tetrigidae, showing members of 21 genera from all over the world. Specimens are not to scale. Source of images: Orthoptera species file, Museo Nacional de Ciencias Naturales Madrid, Josip Skejo and Josef Tumbrinck.

1.7 PYGMY GRASSHOPPERS: TAXONOMY UNDER CONSTRUCTION

by Josip Skejo and Niko Kasalo

Pygmy grasshoppers are a morphologically and ecologically unique group of tiny grasshoppers forming the large family Tetrigidae. With 2,000 described species assigned to almost 300 genera, they are the second-largest among 36 caeliferan families, second only

to Acrididae. New taxa at all levels are being described regularly, but there is still very little order. Although most of what we have are questions, some fascinating information has crystallized over this group's centuries-long but discontinuous history. In this chapter, we



Subfamily or tribe placement

Batrachideinae	n, r	Scelimeninae	h	a	Hymenotes	g	Trypophyllum	m	Cladoramus	s	Truncotettix
Cladonotinae	a, i, j, k, t	Tetriginae	e, l	b	Rhynchotettix	h	Discotettix	n	Paraselina	t	Deltonotus
Fijitettigini	u	Tripetalocerina	e-q	c	Potua	i	Cladonofus	o	Cota	u	Fijitettix
Metrodorinae	b, f, o, p, s, v	Xerophyllini	c, d, g, m	d	Royitettix	j	Nesotettix	p	Xistrella	v	Amorphopus
				e	Paratettix	k	Diotarus	q	Tripetalocera		
				f	Systolederus	l	Dinotettix	r	Scara		

will provide a short summary of the general diversity, distribution, and evolution of these insects.

For such small animals, an incredible morphological diversity has been observed among tetrigids. Their body length varies from the barely perceptible 6 mm of the New Caledonian *Nesotettix cheesmanae* to the comparatively gigantic 25 mm of the Jamaican *Phylotettix rhombeus*. The most important feature of any tetrigid is the pronotum, the shield that drapes over the insect's back like a stiff cape. It may be covered with dents, grooves, tubercles, and spines, but the most impressive feature is the median carina that extends over the entire length of the pronotum and can form impressive structures such as spines, wavy shapes, or dome-, fin-, and leaf-like elevations.

The head is often neglected in descriptions but has recently been shown to bear crucial information about the supposed deep divergences within the family due to the very different arrangements of facial elements. The vertex – the forehead – is especially interesting as it sometimes forms sizable horns or rostrums. On the other hand, legs seem to correspond more to ecology than to phylogeny and can be long and slender, robust and bumpy, or even oar-like.

Other grasshopper families have long forewings, called tegmina, which extend over the hindwings and protect them. In Tetrigidae, this function is carried out by the extended pronotum, while tegmina are reduced to two small, scaly structures. Although the pronotum is not movable, the species with elongated hindwings can use them for flight, some with impressive maneuverability. A good example is the Oceanian *Paratettix nigrescens*, which is present on islands such as New Caledonia, Vanuatu, and Palau, while its supposed close relatives are present in Fiji and Australia. This suggests that this tiny animal is able to fly across hundreds of kilometers of open ocean. On the other end of the spectrum, the above-mentioned islands house many local endemic species, which are usually completely wingless.

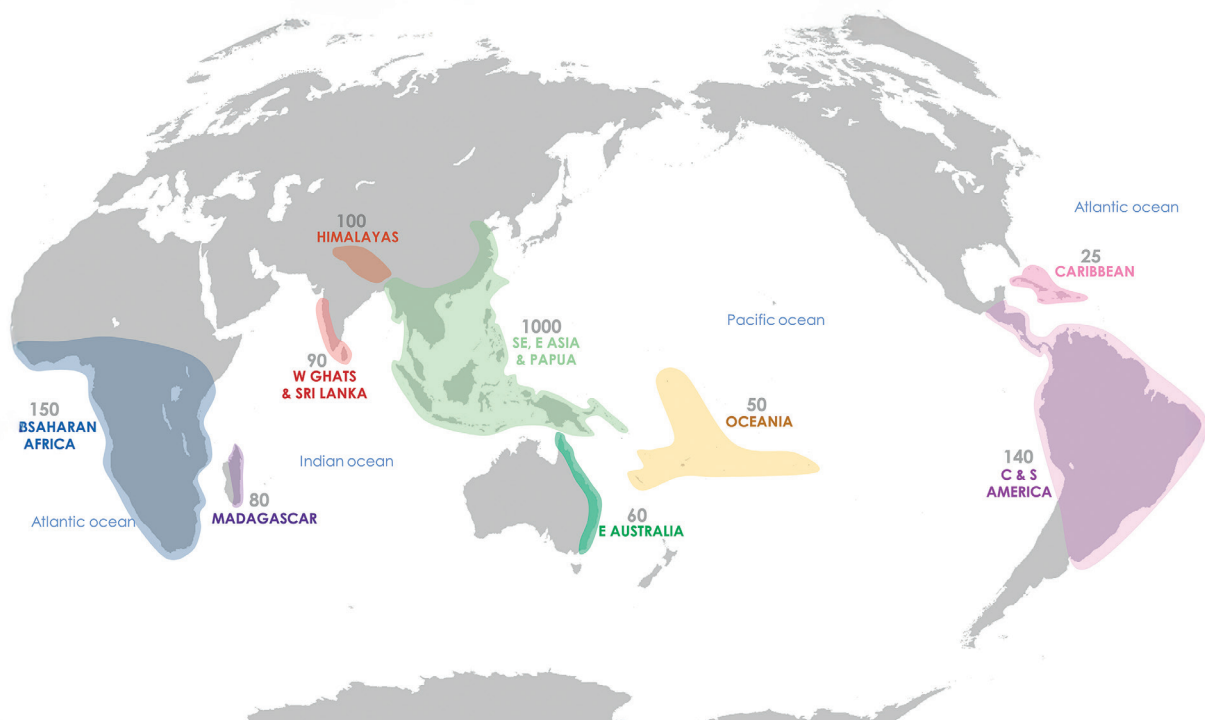
Pygmy grasshoppers are found on all continents except Antarctica. Curiously, despite exten-

sive research efforts, no tetrigids have ever been found in New Zealand. Their diversity is much larger in the tropical zones than in the temperate ones. Many genera of Tetrigidae are constrained to relatively small areas, with only two having a global distribution: *Tetrix* and *Paratettix*. It is, however, abundantly clear that the wide ranges of some taxa may in large part be due to taxonomic errors. This is not to say that there are no widely distributed genera or species, only that many things remain uncertain while revisions are underway.

Molecular phylogenies place the origin of Tetrigidae at the end of the Paleozoic (Permian) or the beginning of the Mesozoic (Triassic) some 250 MYA, but more work needs to be done to refine this estimate. Few fossil specimens have been found, mostly from different ambers formed in the Cenozoic. Most of the fossil representatives belong to Batrachideinae, the oldest tetrigid subfamily, but some Cretaceous fossils elude interpretation – they may represent a new family related to Tetrigidae.

Barring a few molecular studies, the current system of Tetrigidae classification is based on morphology and is a direct continuation of the system established in the 19th century. This system is plagued with groups that are composed of superficially similar morphologies but do not form true evolutionary groups. The modern approach to taxonomy places a big emphasis on examining type specimens, studying the wider context of the region being worked on, and clearly identifying evolutionary significant characters. Although future molecular phylogenies may bring further insights, we are now finally at a point where we can offer some broad hypotheses on the evolution of the tetrigid subfamilies.

The subfamily Batrachideinae is well-supported by molecular phylogenies, which reconstruct it as a sister group to all the other tetrigids. The members of this subfamily have some shared morphological peculiarities – most notably, a spine at the front edge of the pronotum, and antennae with more than 20 segments. This cosmopolitan and ancient group may even be proven to represent a separate family. The distribution of Batrachideinae will be important for elucidating



the biogeographic patterns of Gondwanan insects, since the current distribution of its members in South America, Africa, southeast Asia, and Australia implies an origin on that ancient continent. The subfamily Cladonotinae resembles Batrachideinae in its distribution and general morphology. Unfortunately, the taxonomy of this group is in urgent need of revision. Lately, the prevailing hypothesis has been that Cladonotinae and Batrachideinae are both ancient and are in some way related.

Figure 2 Tetrigidae world biodiversity hot spots with an approximate number of species living in the region, according to the Orthoptera Species File. Altogether, 80% of known pygmy grasshopper species live in the marked regions. Map modified from Wikimedia Commons (adapted from https://commons.wikimedia.org/wiki/File:World_map_Pacific_Center.svg).

The subfamilies Metrodorinae, Scelimeninae, and Tetriginae are thought to be younger than Batrachideinae and Cladonotinae, and may have a Laurasian origin. Most Scelimeninae are clearly identifiable by their pronotal projections, and they likely stem from a common ancestor. On the other hand, Tetriginae and especially Metrodorinae are commonly considered to be the most difficult to work with due to the many disparate morphologies that are assigned to them. The work on these groups is underway, and many new, smaller subfamilies may be found hiding within them.

Lophotettiginae (South America) and Tripetalocerinae (southeast Asia) are examples of small subfamilies, each encompassing only two genera, but are nonetheless problematic. They resemble each other at first glance, due to their leaf- or fin-like crests and expanded antennal segments, but they are not closely related. While Lophotettiginae resem-



ble Metrodorinae and likely form an evolutionary unit with them, there is no clear candidate for the sister taxon of Tripetalocerinae.

Throughout the long history of Tetrigidae research, only a few people have worked on this group at any given time. Most of them did not have access to all the previous material and publications, and new material kept pouring in from around the world. The modern epoch in tetrigidology has been mostly focused on resolving inherited problems and producing a practical framework for future research. There is still a tremendous amount of work to be done on all fronts: from making the type specimens more accessible and establishing more local research teams to diversifying the topics of research to include molecular and ecological data. Even south-east Asia, in which nearly half of all described species live and which could represent the ancient homeland of Tetrigidae, is severely understudied. Even there, many more species await discovery.

There has never been a better time for studying Tetrigidae. The myriad of problems are awaiting young and eager researchers with open arms, and any of the possible answers promises to impart to us a greater understanding not only of this extraordinary family, but also of the ecosystems these creatures have been witnessing for hundreds of millions of years.

Figure 3 Tetrigidae also includes species with very unusual shapes, such as this *Ophiotettix rohwedderi* from Papua New Guinea. Photo: Philipp Hoenle, CC0 1.0 Universal.

Figure > Like in all insects, molting represents an essential part of the life cycle of Orthoptera. This raspy cricket (Gryllacrididae) is just completing its final molt to the adult stage. Photo: Chien C. Lee.

2 BIOLOGY AND ECOLOGY



THE STAR PARADE: A PECULIAR FORM OF COURTSHIP IN GRASSHOPPERS

by Paolo Fontana and Roberto Scherini

Many species of Orthoptera are known to exhibit varying degrees of gregariousness. More than a century ago, Australian entomologist Walter Wilson Froggatt (1858–1937) reported a strange behavior for the plague locusts *Chortoicetes terminifera* (not *C. australis*, as reported by Chopard); he observed many males (up to 30 to 50) of the mentioned species, living in Australia, assisting the egg-laying of a conspecific female. Two males in particular remained in antennal contact with the egg-laying female. A similar behavior was observed in Italy for the Oedipodinae *Acrotylus patruelis*, a non-gregarious species never cited as harmful. The first time we observed this phenomenon was in Tuscany (central Italy) in 2002. Many males were arranged in a star shape around an ovipositing female. All males were in antennal contact with each other and with the female, and from time to time, they moved their posterior femora up and down all together for a period of one or two seconds. The female occasionally also moved the posterior femora in the same way and at the same time as the males. These movements did not appear to produce any sounds: a highly sensitive microphone was placed in close proximity to the specimens involved. The phenomenon was observed for over 40 minutes, during which time some males abandoned the choreography and others

joined in, always remaining in number from six to eight. The final result of this behavior was not observed by these authors, who called it a “star parade”.

We recently observed the star parade for *A. patruelis*, also in Lombardy (northern Italy). On a warm day (20°C) at the end of October 2022, four star parades were observed a few meters apart in the fields on the edge of a town. In each of these star parades, a laying female was surrounded by eight to ten males. The males rhythmically moved their hind legs and palps. In turns, some males would emerge from the formation to attempt mating with the female. On the same site, the behavior was observed until the beginning of November and again, in 2023, at the end of October. A similar behavior, although involving a small number of males (two to four), was observed in *Oedipoda caerulea* by Buzzetti (personal communication).

Other pseudo-gregarious behaviors are known in the literature, all linked to the oviposition of Caelifera. Yuri Alexandrovich Popov observed groups of females of *Acrotylus longipes*, a non-gregarious species, laying eggs together, assisted by some males. A similar behavior is reported by D.P. Clark for the Australian species *Austroicetes pusilla*. This behavior is frequent for gregarious spe-



cies, such as *Locusta migratoria migratoria* and *Schistocerca* species, as reported by Boris Uvarov. In other Acridids – for example, in *Doclostaurus maroccanus*, as observed in Libya by Bruno Massa – the males often mate with females who have just completed oviposition; this may explain the gathering of males around a female. Even if the case studies for this behavior do not allow us to advance solid inter-

pretations, the star parade could be a phenomenon linked to sexual competition between males, perhaps in the presence of an unbalanced sex ratio for some reason, such as greater predation of the larger and less mobile females, especially during oviposition.

Figure 1 Males of *Acrotylus patruelis* surrounding a female and forming a star shape. Photo: Paolo Fontana.

2.1 EAT AND BE EATEN: THE ROLE OF ORTHOPTERA IN FOOD WEBS

by Sebastian König and Jens Schirmel

FEEDING IN ORTHOPTERA

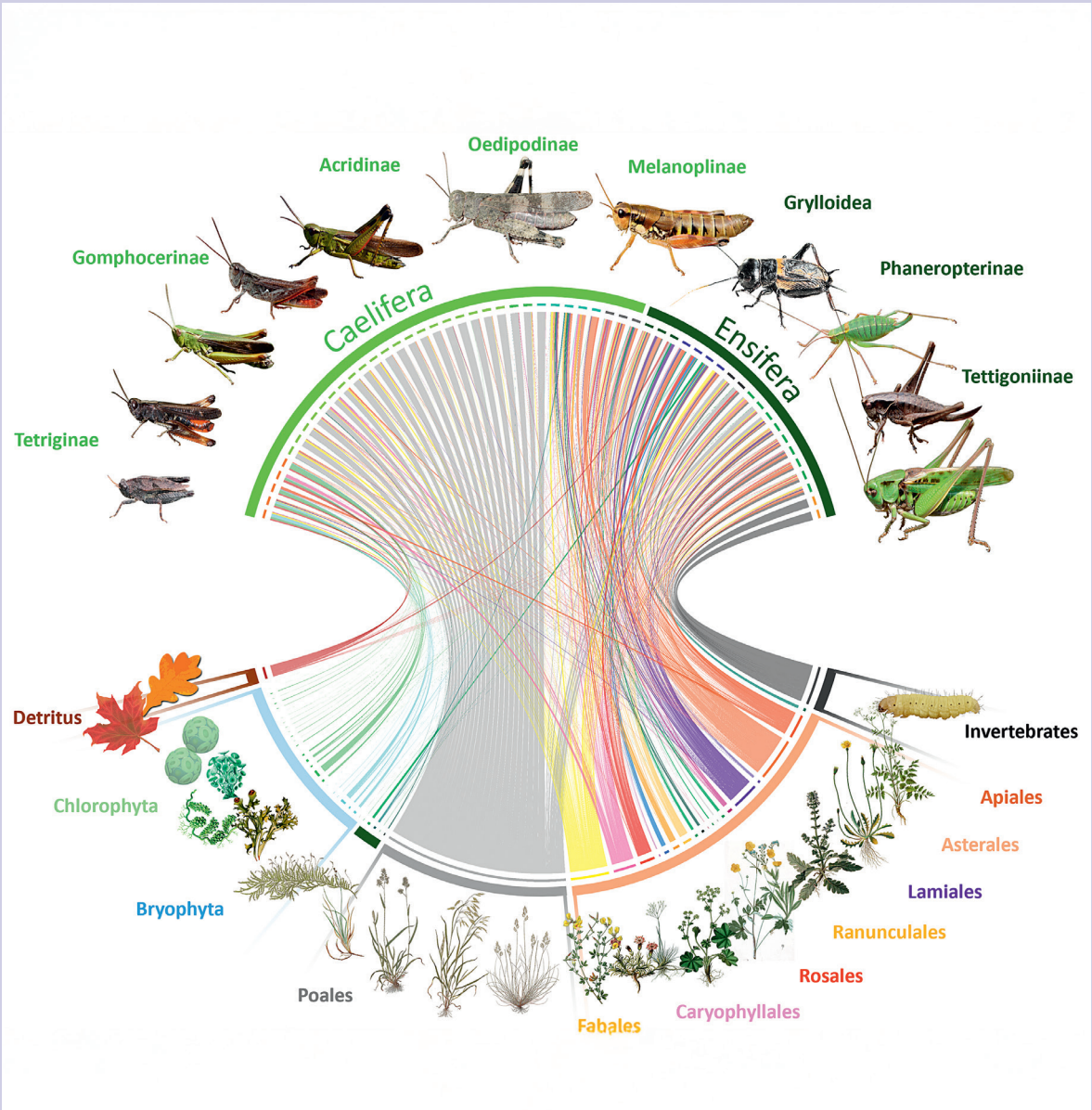
Not a single green leaf remains when voracious locusts clear entire stretches of land of any plant, including agricultural crop plantations (see chapter 7.1, Conserving Orthoptera diversity). As we think about Orthoptera feeding habits, such phenomena bring back memories for those concerned; however, most will regard grasshoppers in the meadows as harmless, polyphagous herbivores that mainly chew on a range of grasses and herbs. While both perceptions are true, the feeding strategies of Orthoptera are far more multifaceted (fig. 1); yet much remains to be understood. Since observing feeding interactions in nature can be challenging, collecting gut content or fecal samples are alternative approaches to unravel the mysteries of resource use and dietary preferences through morphological determination or by means of molecular genetic methods.

There are marked differences between Ensifera and Caelifera in terms of feeding habits. On one hand, most caeliferans are indeed vegetarians and feed mainly on grasses, herbs, and other plant material with a certain degree of selectivity (fig. 2). Compared to the high number of specialized phytophagous insects of other groups, however, the average dietary niche of a grasshopper is quite broad. While some can utilize an astonishing spectrum of different host plants, others prefer a narrow range of closely related food plants, such as grasshoppers (Gomphocerinae) feeding on grasses and sedges (order Poales), the cactus-feeding species in North America (e.g., *Chloroplus cactocaetes*) or the euphorb-feeders (e.g., *Acrostira euphorbiae*) on the Canary Islands. A special case are the tetrigids,

which consume detritus, mosses, lichens, and algae, which they may even graze on underwater.

The feeding behavior of ensiferans is even more diverse. The diet of many bush crickets and katydids contains plant material. Which part of the plant is consumed is specific to certain feeding groups; some feed on flowers and seeds; others prefer the leaves. Thus, some Orthoptera may even be important seed dispersers and pollinators, as has been demonstrated in gryllacridids (e.g., genus *Glomeremus*) visiting orchid flowers (see chapter 2.5, Raspy crickets as pollinators of orchids), while some Australian species are even specialized feeders of pollen and nectar (e.g., *Anthophiloptera dryas*). Crickets are often detritivores, and many ensiferans supplement their diet with other arthropods, especially soft-bodied ones such as caterpillars. Even opportunistic cannibalism is not a rare phenomenon. This goes as far as some groups, such as the oak bush crickets (e.g., genus *Meconema*) and the predatory bush crickets (Saginae), being strict carnivores, preying exclusively on other insects, including grasshoppers. The proportion of plants or arthropods in the diet can vary during their development. In some extreme environments, such as harsh deserts, species may only feed on detritus blown by the wind. As for the species with a more hidden lifestyle, mole crickets (Gryllotalpidae) can be pests in gardens under certain circumstances, as they feed on the roots of vegetables and other plants, in addition to ground-dwelling arthropods that they find in their underground tunnels. In similar tunnels, pygmy mole crickets (Tridactylidae) mainly consume detritus. Finally, cave crickets (Rhaphidophoridae) scavenge on dead arthropods, but also eat fungi, plants, or live insects in caves.

Figure 1 Schematic overview of feeding interactions from central European grassland sites. Dietary interactions were reconstructed based on observations and meta-barcoding of the DNA content in fecal pellets. Modified figure from König et al. (2022).





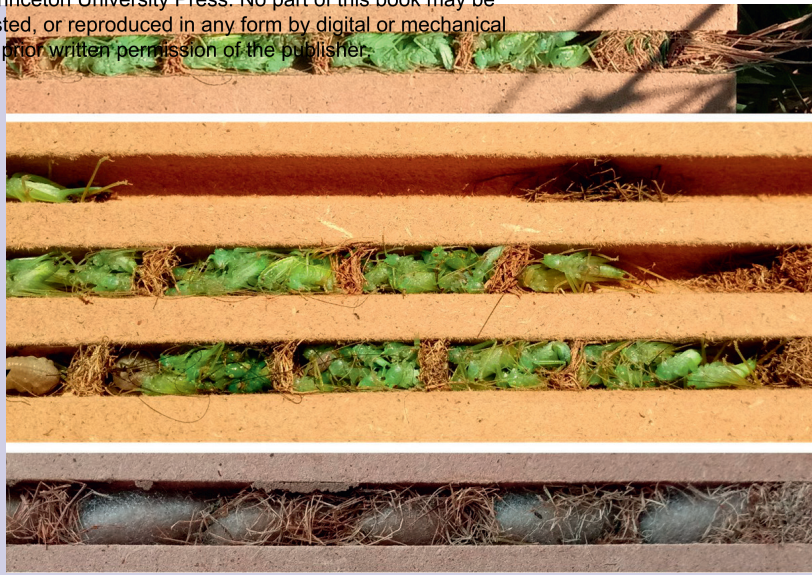
Since most feeding links between Orthoptera and plants are rather loose, they are anticipated to respond directly to changes in micro- and macro-climatic conditions in their habitats by range shifts.

NATURAL ENEMIES OF ORTHOPTERA

The majority of Orthoptera are relatively large and soft-bodied insects, making them an important source of protein for a diverse range of predators, including humans (see chapters 8.4, Grasshoppers as traditional royal food and modern protein source in Madagascar, and 8.5, Salt, lime, and chapulines). Insectivorous birds, reptiles, and amphibians are among the predators of Orthoptera. The white stork (*Ciconia ciconia*) is perhaps the best-known example of a grasshopper-eating bird. In Europe, white storks exhibit a selective feeding behavior, feeding primarily on larger grasshoppers. They have been observed to

Figure 2 Most Caelifera are herbivores, while Ensifera can be omnivores or carnivores. (left side above) A male of the Siberian grasshopper *Gomphocerus sibiricus* feeding on moss, (left side below) a black color morph of the green mountain grasshopper *Miramella alpina* feeding on herbs, (right side above) an upland green bush-cricket *Tettigonia cantans* eating flowers and (right side below) a predatory bush-cricket *Saga pedo* devouring, in turn, a *T. cantans*. Photos: (left side) Sebastian König, (right side above) Martin Husemann, (right side below) Christian Roesti.





consume several hundred individuals within minutes. Gregarious locusts frequently constitute the principal food source for migrating white storks returning to Africa. In North America, the grasshopper sparrow (*Ammodramus savannarum*) is an example of a specialized grasshopper predator. Other birds that frequently feed on Orthoptera include shrikes (*Laniidae*), bee-eaters (*Meropidae*), and several birds of prey, such as the common kestrel (*Falco tinnunculus*). Furthermore, mammals are also known to consume Orthoptera. New World monkeys belonging to the Cebidae family, such as capuchin and squirrel monkeys, are known to prey on Orthoptera. In some cases, they have even learned to avoid toxic grasshoppers, such as stick grasshoppers (*Proscopiidae*), which employ a rare form of chemical defense as a predator-avoidance strategy (see chapter 5.5.5, The endemic jumping sticks from Meso- and South America). In addition to insectivorous vertebrates, Orthoptera are prey to a variety of invertebrates, with spiders, especially orb-weavers, representing significant predators. The wasp spider (*Argiope bruennichi*), for instance, is highly adapted for capturing grasshoppers with its nets, which are strategically placed at the optimal height for jumping grasshoppers. Other insects – such as mantids, wasps, ants, and even other Orthoptera – may also feed on Orthoptera. In particular, predatory bush-crickets (genus *Saga*) can be important predators.

However, not only crawling, jumping, and flying Orthoptera are eaten, but also their immobile eggs. The larvae of dipterans, such as bee flies (*Bombyliidae*), are known to prey on eggs, as are the larvae of beetles, particularly those of blister beetles (*Meloidae*, genera *Mylabris* and *Epicauta*). Additionally, some generalist predatory insects, such as ground beetles (*Carabidae*) and rove beetles (*Staphylinidae*), are capable of attacking grasshopper eggs.

Parasites, parasitoids, and pathogens represent further natural enemies of Orthoptera and can attack all life stages. Ectoparasites of Orthoptera adults or nymphs include larvae of some wasps (e.g., *Rhopalosomatidae*) and red velvet mites (*Trombididae*). Typical endoparasites include some dipterans,

Figure 3 (left) A female sphecid wasp *Isodontia mexicana* carrying a paralyzed oak bush cricket *Meconema meridionale* individual to her nest. (right) The breeding chambers may be full of paralyzed crickets stored as larval food. In the middle, a larva of *I. mexicana* can also be seen (arrow); it has already consumed all bush crickets in the chamber. Cocoons after pupation of the larvae are shown in (below). In most cases, 6 to 8 Orthoptera individuals (here mostly nymphs of *Meconema* spp.), but sometimes up to 16, were deposited into a breeding chamber. Photos: (left) PJT56/Wikimedia Commons/CC BY-SA 4.0; (right) modified figure from Schirmel et al. 2020.



such as tachinid flies (Tachinidae) and flesh flies (Sarcophagidae). Flies deposit their eggs or larvae on Orthoptera, which penetrate the cuticle and develop within the body. Some of these flies (e.g., *Ormia ochracea*) exhibit phonotaxis – that is, the attraction to Orthoptera songs. Some sphecid wasps (Sphecidae) are well-known and specialized predators of Orthoptera. For instance, the Mexican grass-carrying wasp (*Isonotia mexicana*) preys on Ensifera, transporting the paralyzed, yet still alive, individuals to its nest in hollow branches, where the larvae feed on them. *I. mexicana* is native to Central and North America but has become established in large parts of Europe, where it frequently feeds on tree crickets (Oecanthinae) and oak bush crickets (genus *Meconema*, fig. 3). Further-

more, different entomopathogenic fungi infest Orthoptera. The globally distributed complex *Entomophaga grylli* has a broad host spectrum of mostly short-horned grasshoppers (Acrididae). The infestation of the fungus alters the behavior of grasshoppers, causing them to climb up and remain in higher vegetation. The fruiting bodies of the fungus emerge from the body of the grasshopper, and spores are released and can be distributed from the exposed location of the grasshopper. Finally, some nematomorphs (horse-hair worms) are known to be specialized endoparasites of Orthoptera. As these cause infected grasshoppers to enter water bodies, they can influence the food web and energy flow in riparian systems.

GRASSHOPPERS OF KEY IMPORTANCE IN (GRASSLAND) FOOD WEBS

Although Orthoptera do not rank among the most diverse groups of insect herbivores, they play a substantial role in food webs of many ecosystems worldwide, with a particular importance in grassland ecosystems. Here, grasshoppers often reach high densities and constitute more than 50% of the total arthropod biomass. Studies have shown that grasshoppers can consume about one-third of their body mass in food per day. Thus, they often represent the dominant insect herbivore group in many grassland ecosystems and can consume up to 20% of the net primary

Figure 4 (left) The red bulbs visibly attached under the pronotum of this Alpine dark bush cricket *Pholidoptera aptera* are parasitic mites. (right) The ornate bright bush cricket *Poecilimon ornatus* is normally green. The abdomen of this unfortunate and still living individual is completely infested with the fungus *Entomophaga grylli*. Photos: (left) Sebastian König; (right) Roberto Battiston.



production and up to 30% of the standing phanerogam biomass – for example, in central European Alpine meadows. Of course, these rates are highly variable and depend on grasshopper densities. These numbers can fluctuate year by year, depending on the weather conditions, ranging from fewer than one to more than 10 grasshoppers per square meter; under certain circumstances, grasshoppers may have even larger impacts and can be severe pests (see chapter 7.1, Conserving Orthoptera diversity).

Through their feeding activity, grasshoppers have a top-down impact on the vegetation structure and plant composition of grasslands. Although most grasshoppers are generalist herbivores, they often select specific plants (see above). Species preferentially feeding on fast-decomposing plants can reduce annual overall plant production, whereas those preferentially feeding on slow-decomposing plants, such as grasses, can increase nitrogen availability and productivity. In both cases, nutrient cycling and, therefore, ecosystem processes and functioning are affected. By experimentally increasing grasshopper density in a high-elevation system to simulate conditions under a warming climate, researchers were able to show that the enhanced herbivore density may

even lead to a promotion of plant coexistence by reducing the dominant high-stature grasses. While Orthoptera influence the plant community composition, they are, in turn, affected by the nutritional and structural characteristics of these communities.

Through their consumption – but also through the waste of uneaten plant material (grasshoppers can be wasteful feeders) and their feces – grasshoppers play an important role in the energy budget of grasslands. Their high biomass makes them an important source of protein for many predators. Therefore, grasshoppers are key organisms in grassland food webs worldwide.

Figure 5 Many animals feed on Orthoptera. The red-backed shrike *Lanius collurio* even hoards them by impaling its prey, such as this great green bush cricket *Tettigonia viridissima*, to thorns of plants. Photo: Wolfgang Brandmeier.

2.2 CRYPSIS, MASQUERADE, AND MIMICRY: ORTHOPTERA HIDING IN PLAIN SIGHT

by Chien C. Lee and Oliver Hawlitschek

Stick and leaf insects of the insect order Phasmatoidea are widely known for mimicking parts of the plants they live on. Orthopterans are less famous for their mastery of this art, but the camouflage of some species, especially in the tropics, rivals that of the phasmids – or goes even further.

All orthopterans, whether they are herbivores or predators, face a whole army of natural enemies. Most are able to escape via jumping or flight, but many species of grasshoppers and katydids have evolved other means of defense, such as spines or chemical substances (see chapter 5.4.4, African gaudy grasshoppers: Pretty poisonous pests). Others rely on stealth to avoid being caught and eaten. The biological term for any strategy of an animal to avoid detection by another animal is called crypsis. Visual crypsis is also called camouflage.

The most common type of camouflage is background matching, which means that the animal's color pattern makes it resemble its surroundings. This can be comparatively simple and intuitive: a green katydid is generally difficult to spot when sitting among the leaves of a tree or bush, as is a gray grasshopper resting on a gravel bed or rock (chapter 1.3, fig. 2b). A very high number of orthopteran species have evolved this form of camouflage. Some, however, have taken it further. Species living on the bark of trees or on lichens are often colored in a way that dissolves their outline against the background of their habitat. Many species have evolved body structures that complement the camouflage and make them even harder to spot (and, at the same time, harder to ingest, as often these body structures are spines; fig. 1).

Camouflage may also be supported by behavior. In addition to staying on a substrate that matches the cryptic coloration, some species are

able to flatten their bodies and hide their legs to further dissolve their shapes. Others completely look like a living or dead leaf, in some cases even a half-eaten one. This form of crypsis, in which the animal resembles a specific structure or item of its surroundings, is called masquerade or mimesis (figs. 2, 3). Other than leaves, some orthopteran species masquerade as a pebble, a patch of lichen, or even a twig.

Some orthopterans even pose as different kinds of animals. The biological term for an animal masquerading as a different species of animal is mimicry (figs. 4, 5). Model species for mimicry (i.e., species that are mimicked by another species) are typically not very attractive to a potential predator because they have some kind of defense mechanism. Stinging wasps and ants or beetles with a tough exoskeleton are common models for mimicry by other insects, such as Orthoptera. As with camouflage, mimicry is often supported by behavior: the mimic not only looks like its model, but also moves like it.

Most, but not all of these spectacular forms of camouflage occur among tropical species, often tree-dwelling katydids, possibly because the population densities of the orthopterans in these habitats are lower than in temperate zones and grassland or bushland areas, and a single individual is subject to a particularly strong predation pressure. Species from different tropical regions of the world show remarkably similar forms of camouflage, even though they are not closely related to each other. These highly specialized forms are striking examples of convergent evolution (see chapter 1.4, Convergent evolution in band-winged grasshoppers) and make us aware of the enormous selective pressures driving the evolution of Orthoptera.



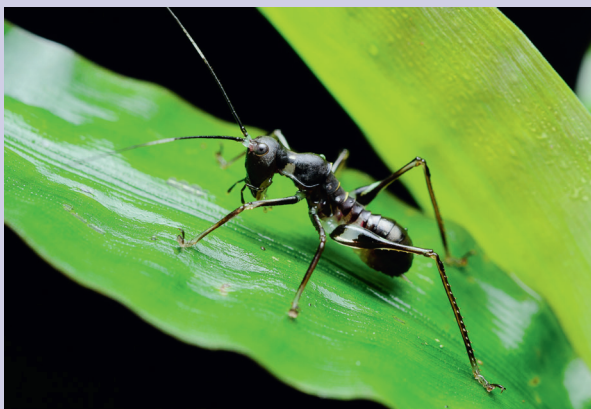
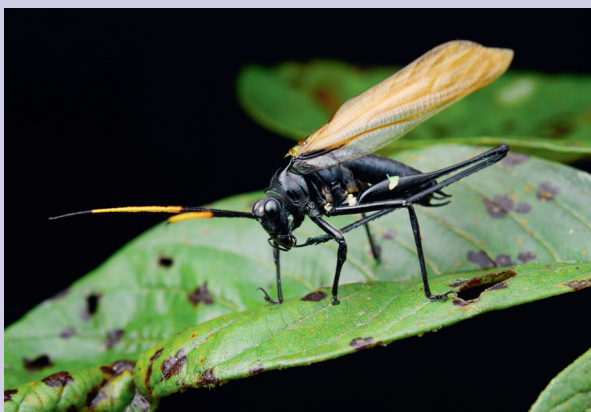


< **Figure 1** The peacock katydid *Pterochroza ocellata* occurs widely throughout the Amazonian rain-forest region. Like many other katydids, this species masquerades as foliage, but it also has a secondary defense if this crypsis fails. When threatened, the insect raises its wings in dramatic fashion, exposing two large eyespots that resemble the eyes of a large animal. This startling sight has certainly scared more than one would-be predator away. Photos: Chien C. Lee.

Figure 2 (above left) Central American *Championica*, such as this *C. montana* from Costa Rica, are masters of disguising themselves as the moss growing on the bark of trees and leaves in humid forests. Not only their color, but also the array of spines on their body and legs matches the structure of their microhabitat. (above right) In the southeast Asian tropics, *Sathrophylliopsis longepilosa* and related species have evolved similar camouflage that is also effective when remaining flat against tree bark or other surfaces. Photos: Chien C. Lee.



Figure 4 (top) Some species of bush crickets have evolved mimicry of other animals, such as this *Aganacris velutina* from Ecuador (left), which resembles a wasp of the genus *Pepsis* (right). Potential predators that avoid wasps will likely also leave a wasplike katydid alone. Photos: Chien C. Lee.



< **Figure 3** The genus name *Mimetica* speaks for itself. The various species of this tropical Central and South American genus, such as this *M. incisa*, masquerade as leaves of all sizes, colors, or states of decay or consumption. Members of the southeast Asian genus *Systella* follow a similar strategy, also resulting in an effective form of camouflage. Unlike *Mimetica*, which are katydids and belong to Ensifera, *Systella* are grasshoppers that belong to Caelifera. Photos: Chien C. Lee.

Figure 5 (bottom) Some katydids follow different strategies throughout their lives, mimicking other animals as nymphs and later masquerading as leaves as adults. This nymph of a member of Amblycoryphini resembles a stinging ant (*Diacamma* sp.) (right), but as the katydid matures, it sheds this appearance in favor of camouflage. Photos: Chien C. Lee.

2.3 ANT CRICKETS: A LIFE IN CHEMICAL DISGUISE

by Thomas Stalling

Ant crickets (Myrmecophilidae, Myrmecophilinae) often elude the eye of the grasshopper expert because of their small size and their secretive, specialized way of life. With a size of 1.5 mm to 8 mm, they are the smallest known species in the order Orthoptera. The first species of ant cricket was discovered as early as 1799 in Germany (fig. 1), but was thought to be and was described as a cockroach at the time. This is not surprising, as these inconspicuous brown, wingless crickets, with their oval body shape, their conspicuous cerci, and their darting movements, resemble the nymphs of cockroaches.

Ant crickets occur in North and Central America, the northwestern part of South America, the central and southern parts of Europe, North Africa, middle, southern and southeast Asia, and Australia, and on various tropical and subtropical islands, but they are absent in sub-Saharan Africa, the main part of South America, and the northern regions of the Holarctic. Globally, there are currently 67 described species in 3 genera, but it seems there are still many species that remain undescribed. After an initial revision of the European species in the 1960s, the subfamily Myrmecophilinae has recently been studied more intensively, and numerous new species have been described in Europe and Asia. All 11 species in Europe belong to the genus *Myrmecophilus*, including *M. quadrispinus*, which usually occurs in tropical and subtropical areas and was presumably introduced to Malta together with invasive ants. The different species can be identified by their coloration, type of setae, and shape of the ovipositor, for which a stereomicroscope is usually required due to their small size.

Ant crickets occur in various habitats, from moist alluvial forest habitats to semi-open landscapes with evergreen scrub and woodland to semi-deserts. They can also be found in the centers of

large cities, such as Berlin, Copenhagen, and Lima, where they live in fallow areas at railroad tracks or in gardens. All known species live as kleptoparasites in ant nests, which they rarely leave, taking advantage of the stable conditions in the nests. They share this life strategy with other myrmecophilous – that is, ant-parasitizing – species of various arthropod groups, such as silverfishes, beetles, (larvae of) hoverflies, and butterflies. Ant crickets avoid attacks from their hosts through their great physical agility and by using chemical camouflage. Ants recognize their nest mates by their specific cuticular hydrocarbons, which the crickets glean from the ants to coat their own bodies, preventing recognition as intruders. Their diet comprises discarded matter – the “waste” of the ant nest, ant eggs, ant larvae, and food obtained from ants by begging them to feed them directly through trophallaxis.

Studies by Japanese scientists have shown that there are ant cricket species that specialize in one or a few host species and others that use a wide range of host ants. Perhaps the most extreme example is the species *Myrmecophilus albicinctus*. This species is found in southeast Asia and Japan and lives exclusively on the ant species *Anoplolepis gracilipes*. Due to its specialized mouthparts, it cannot feed itself, but is exclusively fed by the ants. Other species, such as the common ant cricket *Myrmecophilus acervorum* (fig. 2), are host-generalists and live in nests of many different ant species from various genera and subfamilies (fig. 3).

Most ant crickets reproduce sexually, but the common ant cricket, which is widespread throughout Europe and large parts of Asia, reproduces parthenogenetically, as is also known from other Orthoptera species, such as the common predatory bush cricket *Saga pedo*. Recently, males of the common ant cricket were found for the first time in

a small part of the distribution area. The occurrence of males in southeastern Europe is a typical case of geographical parthenogenesis, which means that asexual individuals have a larger distribution area than their sexual relatives.

There are still many unanswered questions regarding the systematics, ecology, and biology of this interesting orthopteran group, which can be researched in the coming years.

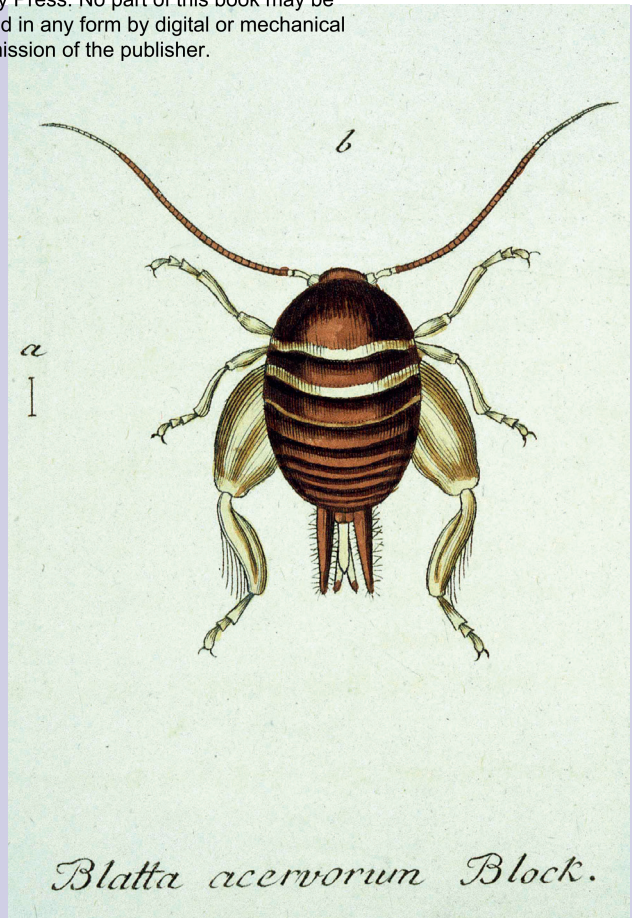


Figure 1 First-ever illustration of an ant cricket from Panzer 1799, originally described as a cockroach, *Blatta acervorum*. Illustration: Public domain.



Figure 2 Adult female of *Myrmecophilus acervorum*. November 2019, La Roque-sur-Pernes, France. Photo: Thomas Stalling.

Figure 3 Nymph (left) and adult female (right) of *Myrmecophilus acervorum* in a nest of *Lasius* sp. November 2019, La Roque-sur-Pernes, France. Photo : Thomas Stalling.



2.4 SECRETS OF BUSH-CRICKET MATING BEHAVIOR

by Gerlind U. C. Lehmann and Arne W. Lehmann

When it comes to reproduction, Orthoptera exhibit some fascinating behaviors. Bush crickets (Ensifera, Tettigoniidae), also known as long-horned grasshoppers or katydids, in particular, are famous for the huge physiological investment males make in their mating strategy. The French researcher and writer Jean-Henry Fabre, who described the mating in the wartbiter species *Decticus albifrons*, observed the occurrence of a huge, white, sticky mass transferred from the male to the female during mating, which he called the spermatophore (Greek for “sperm carrier”). Closer study of the spermatophore revealed that it consisted of two parts: the smaller ampulla, which contains the sperm, and a large white mass surrounding the ampulla (figs. 1 and 2). The latter is called the spermatophylax (Greek for “sperm guard”), produced by special glands inside the male’s body.

THE MALE NUPTIAL GIFT

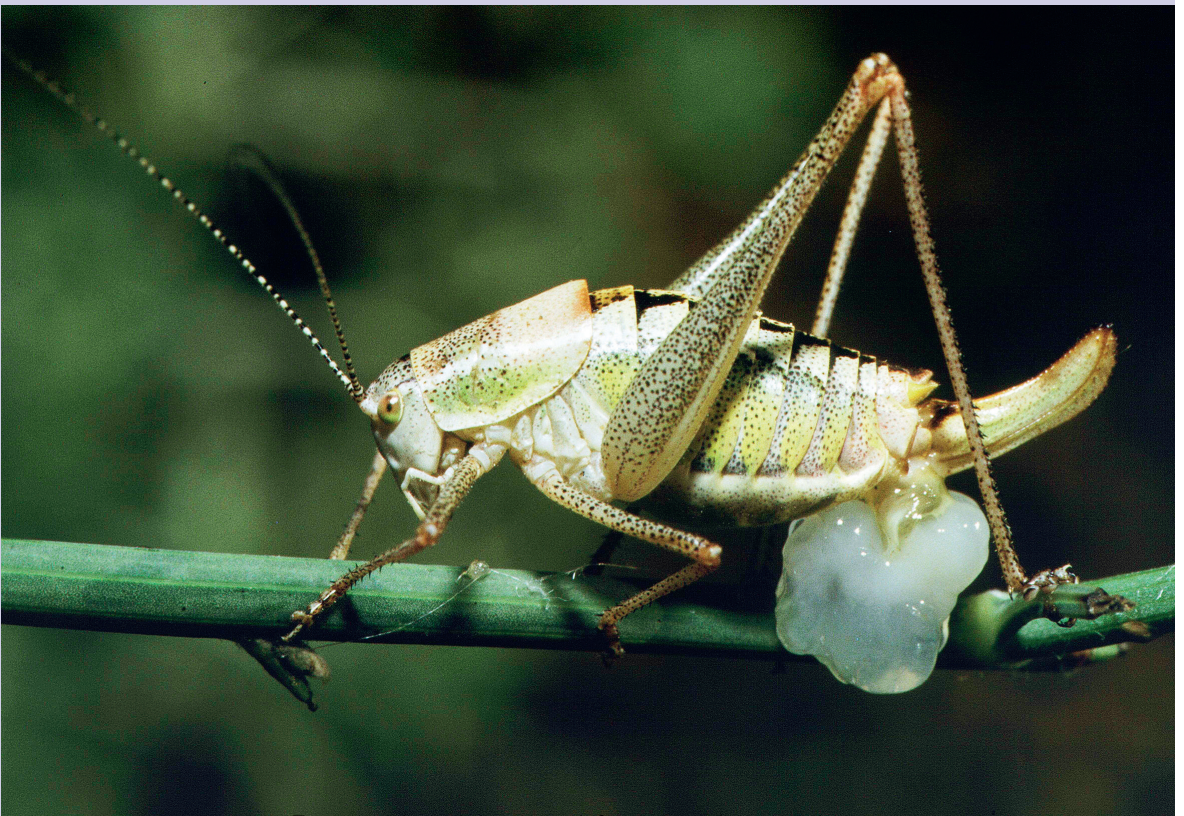
The spermatophylax is recognized as a “nuptial gift” (or “wedding present”). Males from a variety of insect orders provide such gifts prior to or during copulation. These gifts include prey items captured by the male, specifically adapted parts of the male’s body, or, in sexually cannibalistic species like mantids, the male itself. In bush crickets, the male spermatophylax represents a substantial investment: bush-cricket males sacrifice up to one-third of their body mass. The spermatophylax contains, aside from 80% water, which itself can be a valuable resource for egg production, hundreds of different proteins. This massive effort involved in producing the spermatophylax can only be understood in the light of sexual selection; therefore, the evolution of courtship feeding has been extensively studied by biologists. These studies have yielded evidence supporting a role both for increased male fertilization success and for male parental investment.

FERTILIZATION SUCCESS

Supporting male fertilization success, the spermatophylax is believed to have evolved to act as a sperm-protection device. After mating, females immediately start to feed on the spermatophore. The position and mass of the spermatophylax prevents females from consuming the ampulla, or at least until a substantial amount of the male’s sperm has entered the female’s body and been stored in the receptive organ, the spermatheca. Females of most bush-cricket species mate with several males, and the spermatheca can store the sperm of all these potential fathers. As in most insects, eggs are not fertilized directly after mating but only shortly before laying, so sperm from different males may compete for fertilization in the spermatheca. The larger the spermatophylax, the longer the female feeds on it before removing the ampulla, and this prolonged time span increases the number of sperm transferred. This, in turn, increases the chances that the male will fertilize more eggs. Furthermore, the spermatophylax is believed to transmit substances that make females temporarily unreceptive to other males. The length of this post-mating refractory period is variable, both within and between species, but typically stretches over several days. Within a species, its duration is positively associated with the attachment period of

Figure 1 Bush-cricket mating pair separating. The female, on top of the male, has received the “nuptial gift.” *Poecilimon gracilis*, collected from Slovenia and mated in a garden at the Humboldt University of Berlin. Photo: Gerlind U. C. Lehmann and Arne W. Lehmann.

Figure 2 Freshly mated female with the spermatophore, consisting of the yellowish ampullae and the white spermatophylax. *Poecilimon gerlindae* found in Domokos, Greece. Photo: Gerlind U. C. Lehmann and Arne W. Lehmann.





the spermatophore and thus the amount of sperm transferred. During the refractory period, females lay eggs fertilized only by the sperm already stored in their spermatheca. Thus, spermatophylax size is under positive selection to increase the chance of fertilization of eggs by a specific male.

PARENTAL INVESTMENT

At the same time, larger spermatophylaxes are beneficial to females since they form an easily digestible and nutritious meal (fig. 3). Ingredients in the spermatophore are incorporated into the somatic tissue by females and can be quickly metabolized. As a re-

sult, consuming the spermatophylax increases a female's survival probability and her reproductive output, in terms of both the number and size of eggs. Larger eggs are more resistant to desiccation and increase the survival of offspring. The size of the spermatophylax is positively correlated with male size and body mass. As a result, when given a choice,

Figure 3 Mated female feeding on the spermatophylax. *Poecilimon gracilis* from Slovenia. Photo: Gerlind U. C. Lehmann and Arne W. Lehmann.

females prefer heavier males over lighter ones. The males' potential for providing larger gifts seems to be signaled via their courtship song; when males have been artificially muted, females mate at random in regard to male body mass.

MALE MATING INVESTMENT

As a consequence, male bush crickets are under selection for increased body size due to female choice. However, body size is constrained by the amount and quality of available food and by the requirement of spending energy on courtship songs. The huge investment into the spermatophore also comes at a cost to the male's lifetime reproductive success. A large spermatophore takes longer to produce, so the periods between matings are greater. The remating period in male bush crickets is exceptionally long, lasting several days – a post-mating refractory period similar to that of females. Due to the high costs of reproduction, low-weight males are restricted in their investment capacities. This is well exemplified in bush crickets infected by a parasitoid fly. Such parasitized males produce smaller spermatophylaces and songs of lower quality. Females select against the songs of parasitized males. After mating with a parasitized male, females exhibit a shorter refractory period until remating with the next male. Consequently, parasitized males are less reproductively successful.

FEMALE MATING INVESTMENT

Compared with other crickets, bush-cricket eggs relative to female size are large, so females are comparatively large too because of the metabolic investment they make in reproduction. In insects and other animal groups, there can often be a significant size difference between males and females, which is called sexual size dimorphism. However, due to the selection for large spermatophores, bush-cricket males can be close in size to or even heavier than females. Comparison of a large number of different species demonstrates that males and females become more similar in body size if the male-derived spermatophore is larger.

FEMALE BUSH CRICKETS TYPICALLY TAKE LONGER TO REACH THE ADULT STAGE

As the body size in insects is fixed at adulthood, size differences between males and females are achieved during the nymphal development: female bush crickets have a longer nymphal period than their conspecific smaller males. The phenomenon that males mature earlier than females is named protandry. In the field, this effect is obvious, with males dominating at the start of the adult season and more females being alive at the end. The developmental difference and hence the level of protandry varies greatly between species, ranging from a few days to four weeks.

SUMMARY

Body size, developmental patterns, and spermatophore investment provide a complex picture of how selection has shaped the life histories of animals. Bush crickets became textbook examples for evolutionary biology as their reproduction has been extensively studied and is comparatively well understood. While the mating behaviors and strategies of bush crickets can differ from other animal groups, they provide an excellent subject to understand some of the selective forces shaping reproduction across the rest of the animal kingdom.

2.5 RASPY CRICKETS AS POLLINATORS OF ORCHIDS

by Sylvain Hugel

ORCHIDS OF THE GENUS *ANGRAECUM* AND DARWIN'S PREDICTION

Charles Darwin, one of the founders of the theory of evolution, famously had a fascination for orchids of the genus *Angraecum*. What intrigued him most was a Malagasy species of the genus, *Angraecum sesquipedale*, whose flowers have spurs about 25 cm long. Since only the tip of the spur contains nectar, Darwin hypothesized that there must be a (then unknown) species of pollinator in Madagascar with a proboscis of the same length. Alfred Russel Wallace, the "other" father of evolutionary theory, later speculated that this pollinator must be a hawk moth (Sphingidae). The species in question was not discovered until 1903 and was then named *Xanthopan morgani praedicta* to commemorate this prediction. This Malagasy subspecies was recently elevated to the species rank: *Xanthopan praedicta*.

The Mascarenes are a volcanic archipelago located to the east of Madagascar. This archipelago includes Réunion Island, Mauritius, and Rodrigues and harbors several species of orchids belonging to the genus *Angraecum*. In Réunion Island, three species of *Angraecum* have a spur not suitable for pollination by a hawk moth: it is very short and very wide (see fig. 1). The pollinators of these three orchid species have long remained a mystery. But what does this have to do with grasshoppers?

THE DISCOVERY OF THE POLLINATORS OF SHORT-SPURRED *ANGRAECUM*

These short-spurred orchids surprised Claire Micheau, Jacques Fournel, and Thierry Pailler from the University and the Herbarium of Réunion, who sought to find out who could ensure the pollination of these

strange plants. Using cameras during the day, they showed that two of these three species were regularly visited by birds endemic to the island. These birds carried the pollinia on their beaks and deposited them while visiting other flowers. The third orchid, *Angraecum cadetii*, was not pollinated during the day. After ensuring that this orchid was not self-fertilizing, the scientists used infrared cameras to monitor the orchids at night. To their surprise, these orchids were regularly visited by a small species of Orthoptera. These visitors came almost every night, systematically visiting the open flowers to consume the nectar. At that time, I was preparing an article describing new micropterous raspy crickets (Gryllacrididae) that I had just discovered in Réunion and Mauritius. One of these species corresponded to the unknown pollinator. For this reason, we named it *Glomeremus orchidophilus* (figs. 2 and 3).

AN ORCHID ADAPTED TO ITS POLLINATOR

As is often the case with orchids associated with a single pollinator, the dimensions of the flower opening correspond exactly to the width of the head of *G. orchidophilus*. Furthermore, the flower is tough and cannot easily be eaten by insects of this size. Interestingly, the consumption of a viscous liquid such as nectar involves a passage of the liquid through a particular space in the mouthparts of *G. orchidophilus*.

Figure 1 *Angraecum cadetii* in bloom in the forest of Sainte Rose, south of the island of Réunion. Note the very short spur (yellow arrow) and the short petals. Photo: Sylvain Hugel.

This space appears to have another function: through it, raspy crickets expel silk that they use to glue leaves together to form a hiding place for the day. The twofold use of this anatomical structure could therefore be an example of exaptation or pre-adaptation, in which the function of an adaptation is diverted to ensure a distinct function.

TWIN SPECIES IN MAURITIUS?

A raspy cricket very close to *G. orchidophilus* lives in Mauritius's neighboring Réunion Island. Because of

this morphological proximity, we named it *G. paraorchidophilus* and described both species in the same work. This Mauritian species has very distinct genitalia compared with its Réunionese sister species and a significantly smaller size. Interestingly, an orchid close to *A. cadetii* has just been discovered in Mauritius: *A. jeannineanum*. This orchid has a slightly smaller flower opening and could speculatively be pollinated by *G. paraorchidophilus*, which has a head dimension corresponding to that of the flower aperture.





A SPECULATIVE SCENARIO LEADING TO THE DESPECIALIZATION OF *ANGRAECUM* FOR POLLINATION BY HAWK MOTHS

Molecular phylogenetic data of *Angraecum* and their current pollinators suggest that pollination by hawk moths is ancestral and that the species from the Mascarene Islands derived from Malagasy ancestors. The ancestor of the short-spurred *Angraecum* from Réunion could therefore have reached the archipelago bearing a long and narrow spur. Moreover, data on the *Angraecum* phylogeny and their current pollinators also suggest that pollination of short-spurred

orchids by gryllacridid crickets is ancestral with respect to pollination by birds. Speculatively, the orchid-Gryllacrididae association could have selected for flowers with wide openings and short floral tubes; this de-specialization in regard to hawk-moths opens the way to other pollinators, such as birds. Such a scenario would be compatible with field observations. Indeed, the Gryllacrididae of the Malagasy region are often observed eating parts of flowers at night, in particular the stamens and pollen. The current association between orchids and Gryllacrididae could therefore have started with an initial phase of florivory.

Figure 2 An adult female of *Glomeremus orchidophilus* is clinging to an *Angraecum cadetii* in bloom in the forest of Plaine des Palmistes, on the island of Réunion. Note that the orchid is fruiting, indicating that it has been previously pollinated. Photo: Sylvain Hugel.

Figure 3 An adult male *Glomeremus orchidophilus* has recently visited a flower of *Angraecum cadetii* and has two pollinaria still attached on the head. Photo: Sylvain Hugel.

Figure > A flying swarm of the migratory locust on the Horombe Plateau, Madagascar. The density of locusts is such that the landscape is completely hidden. The farmers in the foreground seem understandably frightened by this mass of insects. Photo: Michel Lecoq.

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