

# CHAPTER 12-4

## TERRESTRIAL INSECTS:

### HEMIMETABOLA – ORTHOPTEROIDEA

---

#### TABLE OF CONTENTS

ORTHOPTERA – Grasshoppers and Crickets .....	12-4-2
Tetrigidae – Pygmy Grasshoppers .....	12-4-4
<i>Tetrix</i> .....	12-4-4
Color Morphs – Thermoregulation or Camouflage? .....	12-4-4
Gause's Law and Bryophyte Dwellers .....	12-4-5
<i>Discotettix</i> .....	12-4-6
Vibration Sites .....	12-4-6
Reproduction .....	12-4-6
Food Consumption .....	12-4-8
Age and Seasonal Differences .....	12-4-11
Mandibular Abrasion .....	12-4-11
<i>Potua sabulosa</i> .....	12-4-12
Acrididae – Grasshoppers .....	12-4-12
<i>Melanoplus</i> .....	12-4-13
<i>Chorthippus</i> .....	12-4-15
<i>Nicarchus</i> .....	12-4-16
<i>Sciaphilacris</i> – Moss and Lichen Mimics .....	12-4-16
<i>Myrmeleotettix maculatus</i> .....	12-4-16
Food .....	12-4-17
Oviposition .....	12-4-18
Gryllidae – Crickets .....	12-4-18
Rhaphidophoridae – Camel Crickets, Wetars .....	12-4-19
Tettigoniidae – Katydid .....	12-4-20
Camouflage .....	12-4-21
<i>Paraphidnia</i> .....	12-4-23
<i>Balboana tibialis</i> .....	12-4-24
<i>Arachnacris tenuipes</i> – Emperor Bush Cricket .....	12-4-24
PHASMIDA – Walking Sticks .....	12-4-25
<i>Antongilia laciniata</i> (Bacillidae) .....	12-4-29
<i>Phanocles</i> (Diapheromeridae) .....	12-4-29
MANTODEA – Preying Mantids .....	12-4-29
Liturgusidae .....	12-4-31
Mating .....	12-4-32
BLATTODEA – Cockroaches and Termites .....	12-4-33
ISOPTERA – Termites .....	12-4-33
EMBIOPTERA – Webspinners .....	12-4-36
Summary .....	12-4-36
Acknowledgments .....	12-4-36
Literature Cited .....	12-4-36

# CHAPTER 12-4

## TERRESTRIAL INSECTS:

### HEMIMETABOLA - ORTHOPTEROIDEA



Figure 1. **Orthopteran** moss mimic, blending with surrounding bryophytes. Photo courtesy of Matt von Konrat.

The **Orthopteroidea** (Figure 1) comprise a group of insects that used to be in the order **Orthoptera**. The group has recently been split into multiple orders, one of which is still called **Orthoptera**.

#### **ORTHOPTERA – Grasshoppers and Crickets**

Most grasshoppers are big, and in fields of tall grasses and **forbs** (non-grass herbaceous plants) they seem to be everywhere (Paranjape *et al.* 1988). But do they inhabit or use bryophytes? And what can bryophytes offer them?

At least some grasshoppers eat mosses (Appelqvist 1997). Uvarov (1977) suggested that the grasshoppers might eat mosses for their water content. But some seem to subsist primarily on mosses (Hochkirch *et al.* 2007). And some have color patterns that hide them well against the patterned moss surface (Figure 2-Figure 3) (Forsman & Appelqvist 1998). Others choose bryophytes for laying eggs (Langmaack 1997), presumably providing them with some protection (concealment) from predators and decreasing the danger of desiccation.



Figure 2. Forest grasshopper of Ecuador with liverwort color patterns on its sides and a moss hanging from its head. It appears that this hopper can help in dispersal. Photo by Arthur Anker, with permission.





Figure 3. Juvenile grasshopper in Ecuador with markings that look like leafy liverworts that are so common on tropical leaves. Photo by Arthur Anker, with permission.

Any increase in niches is likely to increase insect diversity, and bryophytes can play this role for some of the **Orthoptera**. Noting that the grasshopper family **Tetrigidae** (pygmy grasshoppers) included mosses in their diet (Hochkirch *et al.* 2000), Hochkirch *et al.* (2007) experimented with members of this family to determine how **sympatric** (having overlapping geographic distribution) species might co-exist. They used the mosses *Rhytidiadelphus squarrosus* (Figure 4) and soil algae as food sources. *Tetrix ceperoi* (Figure 5) and *T. subulata* (Figure 6), both sometimes moss inhabitants, were cultured together in the lab experiments. *Tetrix ceperoi* exhibited substantial decrease in copulations with its own species when in the presence of *T. subulata*. The males attempted more mating events with females of *T. subulata*, but the females rejected them. Although none of these two-species matings was successful in the lab, they substantially reduced the success of *T. ceperoi* in field experiments. It required much denser populations to have similar depression effects on *T. subulata*. Hochkirch *et al.* (2007) surmised that to prevent such reproductive interference the species may evolve different mating signals or different habitat preferences, spatial patterns, or temporal segregation. Having bryophytes in the habitat provides differences in available niches, including moisture and food item differences (Figure 7).



Figure 4. *Rhytidiadelphus squarrosus*, an acceptable food source for *Tetrix* species. Photo by Michael Lüth, with permission.



Figure 5. Mating grasshoppers, *Tetrix ceperoi*, on the moss *Atrichum subulatum* in the Czech Republic. Holes appear in the leaves where they have been eaten. Research continues on feeding preferences of these insects. Photo by Petr Kočárek, with permission.



Figure 6. *Tetrix subulata* female, a species that eats bryophytes and uses them for perching sites during mating. Photo by Joy Markgraf, with permission.

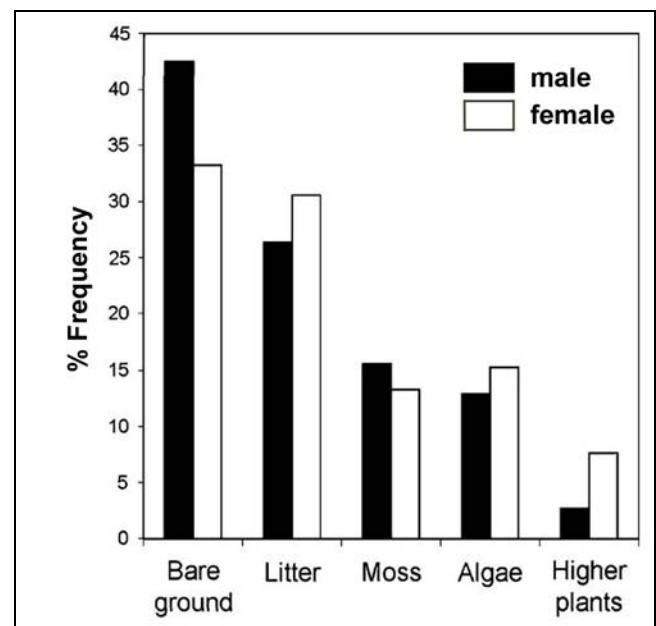


Figure 7. *Tetrix ceperoi* (Figure 5) frequency of perching on moss compared to other perching sites in its habitat. Modified from Hochkirch *et al.* 2007.



## Tetrigidae – Pygmy Grasshoppers

The pigmy grasshoppers (Figure 8) are common moss dwellers and moss consumers (Hancock 1902; Chopard 1951; Bastow *et al.* 2002).

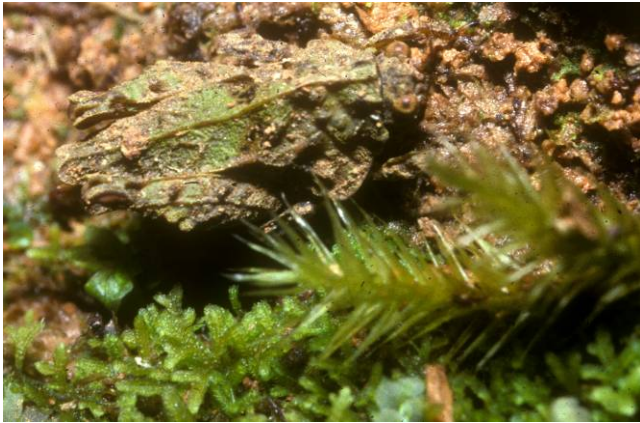


Figure 8. This grasshopper appeared to have protonemata cultured on its back. At the very least, it has cryptic coloration that makes it nearly invisible among these mosses – until it jumps! Photo by Janice Glime.

### *Tetrix*

*Tetrix granulata* in Oregon, USA, lives in shaded meadows with damp mossy ground and short grass (Fulton 1930). Buckell (1921) noted that *Tetrix brunneri* (Figure 9) in the Chilcotin District of British Columbia, Canada, was present only in a small area where it lived among leaf litter and mosses under birch (*Betula*) and willow (*Salix*) surrounding an upland spring. This species occurs as high as 3,300 m among boulders in Colorado, USA (Alexander 1964). But the most widespread of these moss dwellers in North America is *Tetrix subulata* (Figure 6) (Rehn & Grant 1955).



Figure 9. *Tetrix brunneri*, a species that seems to prefer mossy areas. Photo by Lynette Schimming, through Creative Commons.

*Tetrix subulata* (Figure 6) has the somewhat unusual character of having both **brachypterous** (short-winged) and **macropterous** (large-winged) forms (Lock *et al.* 2006). There is a tradeoff in these insects between dispersal and reproduction, with the short-winged forms reproducing faster and the long-winged ones travelling farther and colonizing new habitats. The long-winged form consumes significantly more energy and exhibits a significantly higher protein content compared to the short-winged form. Carbohydrate and lipid content do not differ. The males have higher protein content and consume more energy than females, providing males with the energy needed to search for females.

### Color Morphs – Thermoregulation or Camouflage?

Many grasshoppers exhibit color morphs (Nabours 1929; Rowell 1971; Holst 1986; Forsman 1999, 2000). *Tetrix subulata* is able to exhibit a variety of morphs (Figure 6, Figure 10-Figure 11) even within a single clutch (Forsman 2000). *Tetrix subulata* occurs in damp places on the soil surface where it eats mosses, algae, and humus (Forsman 1999) and is widespread in Europe (Holst 1986). This species exhibits discontinuous color morphs that could affect body temperature or protection from predation (Forsman 1997). Forsman (1997) found that black morphs had up to 49% higher **temperature excess** (difference between ambient and body temperature) compared to white morphs in the same external conditions. Forsman (2000) found that females preferred higher body temperatures than did males. Dark morphs both attain higher temperatures and prefer higher temperatures compared to paler morphs.



Figure 10. *Tetrix subulata* as a dark variant, with somewhat shortened wings. Photo from Biopix, through Creative Commons.



Figure 11. *Tetrix subulata* as a grey variant, with long wings. Photo from Biopix, through Creative Commons.

### Gause's Law and Bryophyte Dwellers

When multiple species in the same genus occupy the same area, one must ask what keeps the species from competing – and out-competing (**Gause's Law**)? Gause (1934) described this "law" and experiments to support it in his "Struggle for Existence." This "law" has become known as the **competitive exclusion principle**. Based on many plant experiments, Gause put forth the principle that competition begins due to the reaction when plants are spaced in such a way that the reaction of one affects the response of the other by **limiting** it. He used this base to suggest that animal experiments are needed, demonstrating that when there is growth a number of individuals of a first and a second species will compete for common food. "At a certain moment food will have been consumed, or toxic waste products will have accumulated, and as a result growth of the population will cease. Competition will take place for utilization of a certain **limited** amount of energy." I have emphasized "limited" because this part of Gause's argument is often ignored. If food and space are unlimited or in excess, competitive exclusion need not apply.

Gause built his famous law upon the work of many other ecologists. In his comprehensive treatment of competitive exclusion (Gause's Law), Gause again emphasized the importance of experiment, providing guidance on the types of experiments needed. Levin (1970) presented it somewhat differently: "No stable equilibrium can be attained in an ecological community in which some  $r$  of the components are limited by less than  $r$  limiting factors. The limiting factors are thus put forward as those aspects of the niche crucial in the determination of whether species can coexist." If each species is limited by an independent combination of predation and resource limitation, it is possible for them to coexist. "If the two have comparable threshold values, which is certainly possible, any equilibrium reached between the two will be highly variable, and no stable equilibrium situation will result."

Here is where proving the competitive exclusion principle gets messy. Two species may co-exist because the environment is constant and advantages for survival may shift as the weather shifts. As a result of this and other problems with the complex relationship, Gause's law has come under close scrutiny, with many researchers providing examples that appear to disprove it. For example, Simberloff (1982) stated that it "has not helped us to understand how nature works. It has generated predictions that are either practically untestable, by virtue of immeasurable parameters or unrealizable assumptions, or trivially true."

Simberloff (1982) recognized the inherent problems with our use of Gause's law and offered an explanation. "When species do compete with one another, effects are usually moderated by other factors (e.g., weather, predators, pathogens) that keep populations below levels at which exclusion would occur, or else each competitor is favored in a different set of times and/or places and this fact combined with normal individual movements keep all species in the system."..."Chance plays a major role in many potentially competitive interactions, and there is good evidence that many species that do compete with one another do so rarely or intermittently, and at most times their population dynamics are governed by other forces."

While this explains why closely related species are able to co-exist, it does not disprove Gause's law.

But in many of the examples that seem to refute Gause's law, the requirement of competition for a limiting resource or being preyed upon by a common predator is often missing because neither population has reached a limiting state for the needed resource. Levin (1970) attempted to improve upon our understanding of the "law" by suggesting three considerations:

1. Eliminate the restriction that all species are resource-limited, a restriction persistent in the literature.
2. The results relate in general to periodic equilibria rather than to constant equilibria.
3. The nature of the proof relates to the crucial question of the behavior of trajectories near the proposed equilibrium, and provides insight into the behavior of the system when there is an insufficient number of limiting factors.

Vance (1978) added further to the explanation of seeming exceptions. He took the position that one means by which two closely related species can co-exist is by having "suitable differences in spatial refuges from the predator, differences in appearance and/or location which induce frequency-dependent predation, and a difference in energy allocation between competitive and predatory defense." Vance concluded that "Gause's Law is just as true when predators are common and important as when they are absent. Most of those prey in nature whose coexistence is known to depend on predation differ in resource use; i.e., these prey appear to partition environmental resources just as is expected of coexisting species in predator-free systems. A large proportion of cases of coexistence of similar species in nature probably results not from resource partitioning alone or from predation alone but from both mechanisms operating simultaneously."

Hanski (1983) carries this argument somewhat farther to include the role of a patchy environment. He concludes that two possible outcomes of regional competition are (1) a decrease in the fraction of habitat patches occupied by the competing species and (2) an increase in the proportion of regionally rare species, some of which may ultimately go extinct. This study has implications for bryophytes as a habitat because of the often patchy nature of their distribution within a habitat. This patchiness can especially affect invertebrate species that have limited dispersal ability.

Caesar *et al.* (2010) examined the application of Gause's Law within the moss-dwelling pygmy grasshopper genus *Tetrix*. According to Gause's Law, if two species are in the same genus, then their niches are likely to be similar, but one might be expected to be better in that niche, out-competing the other. An often overlooked part of this law is the part "if any factor is limiting."

*Tetrix subulata* (Figure 6) not only differs within the species by differences in color pattern, but also in form, behavior, and physiology (Caesar *et al.* 2010). Caesar and coworkers tested the interactions of these factors, using the moss *Polytrichum* sp. (Figure 12) as food. Individuals climbed the moss to feed and to find the best combination of moisture, light, and temperature. Survival is higher in low density of mothers than in high density. In high



density, the intermediate color morphs survived best, but survival was independent of color diversity at low densities, presumably due to less intense competition. Mixed siblings had higher survival than mixes of non-siblings, suggesting some competitive advantage. The mosses in their natural habitat therefore provided not only food, but permitted the various morphs to find locations suitable to their temperature, moisture, and light needs as well as being the safest place for particular morphs.



Figure 12. *Polytrichum juniperinum*, an acceptable food source for *Tetrix subulata* (Figure 4). Photo by Janice Glime.

To demonstrate the advantages of certain color patterns against predators in grasshoppers, Forsman and Appelqvist (1998) likewise experimented with *Tetrix subulata* (Figure 6). By manipulating color patterns and exposing these pygmy grasshoppers to predation from domestic chickens they could determine prey advantages (Figure 13). They painted some black and others striped. The striped individuals experienced enhanced survival when reaction distance was short and jumping performance was poor, but when the reaction required a long distance jump with high performance, their survival decreased compared to those individuals painted black. The advantage to the multiple color patterns seems to differ with circumstances, resulting in each morph surviving at different times and circumstances. The differences in form, behavior, and physiology make their specific habitat needs differ, hence defining different niches.

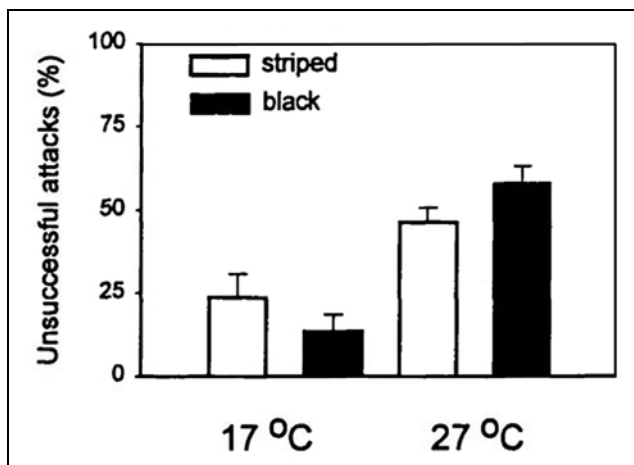


Figure 13. Comparison of *Tetrix subulata* (Figure 6) painted solid black and with stripes to determine the success of chickens preying upon them. Modified from Forsman & Appelqvist 1998.

### Discotettix

One species, *Discotettix belzebuth* (= *Tetrix belzebuth*; Figure 14), occurs on mossy tree trunks in the orient (Gen & Rahman n.d.). Rather than having its own cryptic coloration, this species is sometimes bedecked with small plants of bryophytes or algae (I was unable to independently verify this). This enables them to move about undetected while they eat the epiphytic mosses, plants, and detritus on the tree trunks. However, when I searched for a picture to demonstrate this, all representatives were clean. Nevertheless, as you can see in Figure 14, the species is well suited for culturing bryophytes and algae. Its surface has pits where they can cling and become established, and the "thorns" could even help to hold larger bryophytes in place. These same pits and thorns provide disruptive coloration that helps to camouflage the uninhabited ones.



Figure 14. *Discotettix belzebuth* showing the pits in the exoskeleton and the thorns, both of which could aid in establishment of mosses. Photo by Bernard Dupont, through Creative Commons.

### Vibration Sites

It seems a bit odd that females rest on mosses, but males do not call from mosses. But there is a very sound reason for that (pun intended!). Males attract females for mating by using vibrations (Kočárek 2010). But for vibrations to be effective, the hopper must be sitting on a suitable substrate, and that is not a moss. Moss, instead, can effectively absorb sounds. Rather, the males sit on bare ground, especially when exhibiting mating behavior. Sand is especially good at transmitting the sound, especially in the hearing range of frequencies between 300 and 400 Hz. And this is a choice mating substrate for males of *Tetrix ceperoi* (Figure 5), despite the increased risk of predation compared to resting on mosses or other vegetation. These vibrations are important in mate recognition in this species (Kočárek 2010).

Elias *et al.* (2004) examined the effectiveness of sound transmission from several substrates in their study of a jumping spider, *Habronattus dosseus*. They found that both rocks and sand quickly attenuated the sound, and that leaf litter was the most effective of the three for sound transmission. Furthermore, there is great variability among rock types. But mosses are more like a sponge, whereas



leaf litter has a large, nearly flat surface that can reflect and direct sound. I would hypothesize that at least some mosses would make effective sound-proofing. And different organisms make sounds with different tones and frequencies, so more study is needed to determine if mosses are good or bad for carrying mating sounds to females of any particular species. (See *Troglophilus neglectus* below.)

## Reproduction

Competition isn't the only problem for closely related species living together. Reproductive barriers are likewise needed to maintain species differences. These are especially important for **sympatric** (having overlapping distributions) species such as members of *Tetrix*. To be an effective barrier, there must be an isolating mechanism such as behavior, timing, habitat, morphology, or genetics.

Reproduction is energetically costly. It typically carries a cost in future ability to reproduce, growth, or survival (Forsman 2001). Age is important in determining **clutch** size [number of eggs deposited in single reproductive bout (Godfray 1994)], with **clutch** size decreasing progressively from the first to the third clutch (Forsman 2001). Furthermore, larger first clutches correlate with greater reduction in the size of the next clutch and increase the time to the next clutch.

Reproduction in **ectothermic** (temperature controlled by external environment) animals, including insects, can be modified by body temperature. Temperature in grasshoppers affects both activity levels and physiological performance. Forsman (2001) compared four different color morphs under two different temperatures in *Tetrix subulata* (Figure 6). Different colors absorb different amounts of heat, whereas white reflects it. Warmer females were more likely to oviposit, had earlier first clutches, produced more clutches, and had decreased intervals between clutches compared to females kept at cooler temperatures. Some color morphs produced larger clutches with fewer clutches per unit time. No differences in relative fat content existed between dark and pale individuals in either sun or shade exposures. The data suggest that the differences in color morphs were advantageous in camouflage against predators rather than providing any reproductive advantage.

Forsman (1999) examined reproductive performance in five of these morphs, noting variation in body size and reproductive life-history characteristics. These lived in an area characterized by bare rocks and boulders, with bryophytes [*Ceratodon purpureus* (Figure 15), *Pohlia nutans* (Figure 16-Figure 17), *Polytrichum commune* (Figure 18), *P. juniperinum* (Figure 12)] and some tussock sedges (*Carex* spp.) dominating the vegetation. Season played a major role, with number of females with eggs declining significantly as the season progressed from mid-May (100%) to mid-June (40%). However, seasons had no effect on body size, clutch size, or egg size. On the other hand, morphs differed from each other in body size, and these size differences accounted for differences in clutch and egg size.



Figure 15. *Ceratodon purpureus* on bare rock, home for *Tetrix subulata* in Norway. Photo by Michael Lüth, with permission.



Figure 16. *Pohlia nutans* on expanse of rocks, forming a suitable habitat for *Tetrix subulata*. Photo by Michael Lüth, with permission.



Figure 17. *Pohlia nutans* bare rocks, a suitable habitat for *Tetrix subulata*. Photo by Michael Lüth, with permission.





Figure 18. *Polytrichum commune*, home and probably food for *Tetrix subulata* on rocks. Photo by David T. Holyoak, with permission.

The ratio of egg size to clutch size also differed among the morphs (Forsman 1999). These factors suggest that different color morphs may have different reproductive strategies. The color differences may be responsible for variation in thermoregulation, but they also most likely affect the ability to avoid predation due to cryptic coloration. This implies that predation would differ among the morphs.

### Food Consumption

Most grasshoppers are not moss consumers. In Bavaria, all tested grasshoppers except *Tetrix* (Figure 1, Figure 11, Figure 30-Figure 31, Figure 34) rejected mosses, but in 80% of the fecal pellets of *Tetrix* there were leaves of the moss *Hypnum* (Figure 19) and rhizoids and protonemata of a variety of mosses (Verdcourt 1947). Kaufman (1965) likewise found that *Tetrix* sp. fed on mosses, whereas other grasshopper genera in that study fed on **forbs** (non-grass herbaceous flowering plants).



Figure 19. *Hypnum cupressiforme* with young sporophytes. Fecal pellets of *Tetrix* contained leaves from this genus. Photo by Dick Haaksma, with permission.

*Tetrix ceperoi* (Figure 5) is among the moss consumers in the **Tetrigidae** (Kočárek *et al.* 2008a, b). Kočárek and coworkers examined the gut of 21 males and 18 females of this species. Of the nine mosses [*Amblystegium serpens* (Figure 20), *Barbula convoluta* (Figure 21), *Brachythecium albicans* (Figure 22), *B. velutinum* (Figure 23), *Bryum argenteum* (Figure 24), *B. caespitium* (Figure 25), *Ceratodon purpureus* (Figure 15), *Funaria hygrometrica* (Figure 26), *Plagiomnium undulatum* (Figure 27)] in their sandy habitat, all nine appeared in at least one gut. The most frequent species was *Bryum argenteum* (in 81% of specimens). At least one fragment of moss occurred in 92% of the specimens, *i.e.* only 8% had not consumed mosses. **Tracheophytes** (in this case grasses) were in 20%, all females, and algae were in 25%. The average number of species of mosses per gut was three, but some contained as many as six. Hence, mosses appeared to be the preferred food, but there seemed to be only limited preference for any particular moss.



Figure 20. *Amblystegium serpens*, a species found in the guts of *Tetrix ceperoi* (Figure 5). Photo by David T. Holyoak, with permission.



Figure 21. *Barbula convoluta*, a moss found in the guts of *Tetrix ceperoi* (Figure 5). Photo by Janice Glime.





Figure 22. *Brachythecium albicans*, food for *Tetrix ceperoi* (Figure 5) in Europe. Photo by Michael Lüth, with permission.



Figure 25. *Bryum caespiticiun* males, a species eaten by *Tetrix ceperoi* (Figure 5) in Europe. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 23. *Brachythecium velutinum*, a species eaten by *Tetrix ceperoi* (Figure 5) in Europe. Photo by Michael Lüth, with permission.



Figure 26. *Funaria hygrometrica* young female plants, a species eaten by *Tetrix ceperoi* (Figure 5). Photo by Janice Glime.



Figure 24. *Bryum argenteum*, a species eaten by *Tetrix ceperoi* (Figure 5) in Europe. Photo by Dick Haaksma, with permission.



Figure 27. *Plagiommium undulatum*, a species eaten by *Tetrix ceperoi* (Figure 5). Photo by Michael Lüth, with permission.



Based on the gut analysis of *Tetrix ceperoi* (Figure 5), Kočárek *et al.* (2008c) found its "favorite" to be *Bryum caespiticium* (Figure 25), but this was also the most common moss in the area with a 70% cover (Table 1). Other commonly consumed mosses included *Bryum argenteum* (Figure 24), *Ceratodon purpureus* (Figure 15), and *Barbula convoluta* (Figure 21) and/or *B. unguiculata* (Figure 28). Only the females had grasses in their diet, whereas 94% of females and 86% of males had at least one fragment of moss in the gut. Males had an average of 1.5 moss species and females had an average of 2, whereas the maximum number of species in any gut was 4 (Figure 29). It was not unusual to find three species in the crop at one time. Kočárek and coworkers offer three explanations for this behavior:

1. A mixed diet promotes better health, development, and survival for grasshoppers than a single-food diet (Chapman & Sword 1997).
2. Mosses often contain toxic secondary compounds (Zinsmeister *et al.* 1991; Becker 1994; Markham *et al.* 2006) and must thus be consumed only in small quantities.
3. The multiple species indicate that the grasshoppers move around a lot and are able to sample the high diversity of mosses present in the area.

Table 1. Frequency of moss species in guts of 39 specimens of *Tetrix ceperoi* (Figure 5). From Kočárek *et al.* 2008c.

Moss species	T. ceperoi specimens					
	♂(ind.)	♂(%)	♀(ind.)	♀(%)	Σ(ind.)	Σ(%)
Barbula sp. (B. convoluta or/and B. unguiculata)	6	31.6	6	35.3	12	33.3
Bryum argenteum	4	21.1	6	35.3	10	27.8
Bryum caespiticium	15	78.9	17	100	32	88.9
Ceratodon purpureus	6	31.6	7	41.2	13	36.1



Figure 28. *Barbula unguiculata*, a moss present in the gut of *Tetrix ceperoi* (Figure 5). Photo by Michael Lüth, with permission.

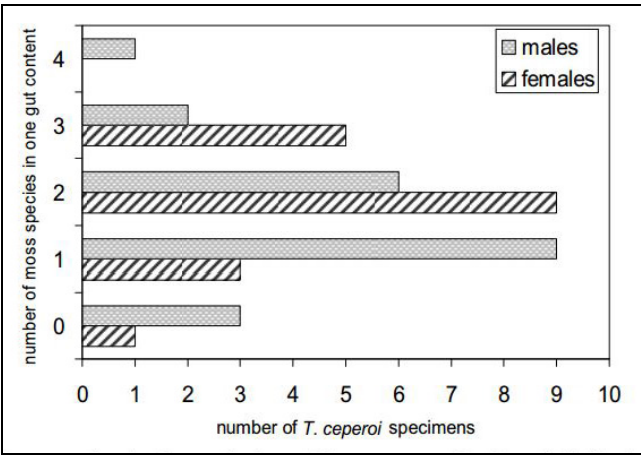


Figure 29. Comparison of mosses in guts of one individual in males and females of *Tetrix ceperoi* (Figure 5). Modified from Kočárek *et al.* 2008c.

Like the aforementioned species of *Tetrix*, *T. bolivari* (Figure 30) eats primarily detritus and mosses (Kočárek 2011). The main mosses consumed in this European study were *Bryum caespiticium* (Figure 25) and *B. argenteum* (Figure 24), but at least eight different species were consumed. Like the other species, these were sensitive to temperature and were most active at warmer temperatures. However, their activities were negatively correlated with humidity, suggesting that mosses were most likely not important in maintaining a humid environment for them.



Figure 30. *Tetrix bolivari*, a moss eater. Photo by Petr Kočárek, with permission.

The moss eater *Tetrix undulata* (Figure 31) eats mosses throughout its life (Hodgson 1963). As it gets older, it is able to eat coarser food. Both young and old eat mosses, humus, lichens, and algae, but adults add **tracheophytes** (lignified vascular plants) such as grass to their diet.





Figure 31. *Tetrix undulata*, a moss eater on moss. Photo by Gilles San Martin, through Creative Commons.

Paranjape (1985) compared the diets of three subfamilies of the **Tetrigidae** and found that not only mosses, but also liverworts and hornworts are consumed (Figure 32).

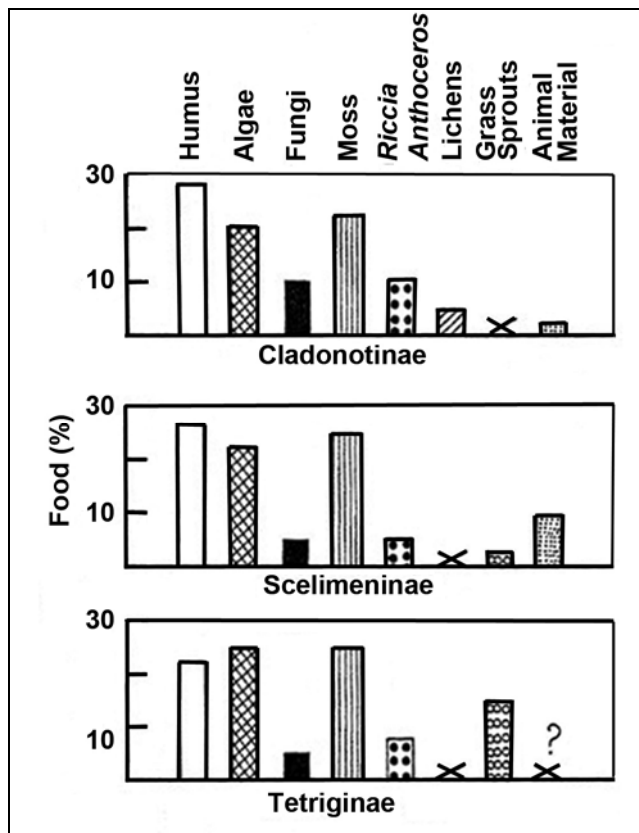


Figure 32. Diet of three subfamilies of **Tetrigidae**. Note that in addition to mosses, they consume the liverwort *Riccia* and the hornwort *Anthoceros*. Modified from Paranjape 1985.

### Age and Seasonal Differences

Tough foods require strong mandibles and teeth to break through the lignin in vascular tissue. The strength can change as the nymphs age, so diets can change or expand as the organism matures. Similarly, moss tissues can change with the seasons, becoming tough when dry and soft when wet. These factors can affect the diet of the consumers.

*Tetrix tenuicornis* specializes on mosses and detritus (Kuřavová & Kočárek 2015). This species maintains its moss diet throughout the growing/feeding season. But the moss species change. More moss species occur in the alimentary tract in spring and summer compared to autumn. Females eat more food than males, and the diet changes with developmental stage. Furthermore, the rate of consuming detritus is affected by ambient temperature (most at 19-21°C), whereas the rate of moss consumption is primarily affected by relative humidity (lowest at 67-72%, highest at 90% or higher). Detrital consumption increases as body size increases.

These groundhoppers do not seem to specialize on any part of the mosses, consuming leaves, gemmae, and rhizoids (but apparently not stems) (Kuřavová & Kočárek 2015). Furthermore, they show little preference for moss species, consuming all of those present except *Pohlia nutans* (Figure 16-Figure 17) and *Bryoerythrophyllum recurvirostrum* (Figure 33). Nevertheless, an individual never contained more than 3 moss species, with the average being 1.9. Moss consumption was considerably less than that of detritus, with one population having 12% moss in the gut and the other only 3%. The amount of moss consumption is linearly related to the amount of moss available. Kuřavová and Kočárek suggest that keeping the moss consumption low prevents poisoning by secondary compounds produced by mosses. A reduction in moss consumption near the end of the growing season supports this hypothesis. Mosses increase their production of secondary compounds in autumn in preparation for the freezing conditions of winter (Cornelissen *et al.* 2007).



Figure 33. *Bryoerythrophyllum recurvirostrum*, a moss that seems to be avoided as food by *Tetrix*. Photo by Hermann Schachner, through Creative Commons.

It is also possible (probable?) that the choice of food is more a choice of habitat as the environmental conditions change. Low or high temperatures could drive the groundhoppers to the more stable conditions of the moss cushions. Furthermore, unfavorable conditions most likely reduce activity, resulting in lower consumption.

### Mandibular Abrasion

*Tetrix tenuicornis* (Figure 34) avoids eating grasses, instead eating mosses [16.3%; *Barbula convoluta* (Figure 21), *Brachythecium albicans* (Figure 22), *Bryum caespitium* (Figure 25), *Campylopus introflexus* (Figure 54), and *Ceratodon purpureus* (Figure 15)] and detritus (83.7%) (Kuřavová *et al.* 2014). But it still exhibits

increased mandible abrasion with age, with females showing more age-related abrasion than males, perhaps due to greater frequency of feeding. On the other hand, Hence, even detritus and bryophytes cause wear on groundhopper mandibles.



Figure 34. *Tetrix tenuicornis*, a species whose mandibles show wear from eating bryophytes. Photo by B. J. Schoenmakers, through Creative Commons.

It is interesting that the diet of males and females may differ. Hochkirch *et al.* (2000) found that *Tetrix subulata* (Figure 6) males fed exclusively on algae and mosses, but females consumed grasses and forbs as well, perhaps accounting for the greater mandibular abrasion in females of *T. tenuicornis* observed by Kuřavová *et al.* (2014). Temperature also plays a major role in feeding, with only 1% feeding on a cool day but 24.7% feeding on the warmest day of the study (Hochkirch *et al.* 2000). When not feeding, the grasshoppers preferred sitting on the more open, warmer locations. These resting locations differed significantly from the feeding locations, which included mosses, suggesting that a color morph might be at a disadvantage in one of those locations.

### *Potua sabulosa*

This pygmy grasshopper (Figure 35) is also a moss consumer, having mosses, especially *Funaria* (Figure 26), as its preferred food (Bhalerao *et al.* 1987). It lacks the molar dentes that are used for eating tracheophyte leaves, making it difficult to eat these foods as an alternative food source. For example, female adults fed on only "paddy" sprouts died within 5-6 days. The species overwinters as an adult. During the cold winters and hot, dry periods in summer it does not eat.



Figure 35. *Potua sabulosa*, a moss consumer that lacks polar dentes. Its roughened body helps it to blend with its surroundings. Photo by Jason Weintraub, through Creative Commons.

These tiny grasshoppers can jump 25-35 cm (Paranjape & Bhalerao 1985). In southwest India they hang out among mosses, being protected by their cryptic coloration. They also eat the mosses, as well as humus, and are capable of making an entire clump of moss disappear (Paranjape 1985). In the summer they survive the heat and drought by burrowing into soil, where they can remain for at least two months without food (Paranjape & Bhalerao 1985). When it is time for egg laying, the females dig a small burrow (~2 mm) in the soil or between the dense moss tufts, using their ovipositors. Their 23-25 eggs are laid in a loose cluster, hatching 10-12 days later at 23-25°C.

## Acrididae – Grasshoppers

*Akris* is the Greek word for locust and is the basis for the name of the family that contains them (Acrididae 2015). More than 10,000 species comprise this family. The species are medium to large, as grasshoppers go. They are **diurnal** (day-active) and typically travel by jumping in their preferred open habitats. They often have cryptic coloration, but some are brightly colored. And many prefer "mossy" habitats.

"Three years ago there was a grasshopper 'explosion' in some central British Columbia grassland sites" (Terry McIntosh, pers. comm. 6 September 2013). "In the Gilpin Grasslands, they completely cleaned up most of the broad-leaved herbaceous plants (and ignored the grasses by the way), then started browsing on some shrubs, including, at one site, poison ivy! Later that day, I noticed a peculiar *Grimmia* on an outcrop. On closer inspection, the reason it look odd was because the whole moss face (mainly *G. ovalis*) had been grazed by the 'hoppers.' Not one plant in some 10 square meters had any leaf tips left." And the capsules were eaten too. (See discussion of other moss eaters under Food below.)





Figure 36. *Grimmia ovalis* growing on a rock outcrop where it may serve as food for grasshoppers during outbreaks. Photo by Michael Lüth, with permission.



Figure 38. *Melanoplus islandicus* male, a shoreline inhabitant where there are short grasses and mosses. Photo by David Kleiman, through Creative Commons.

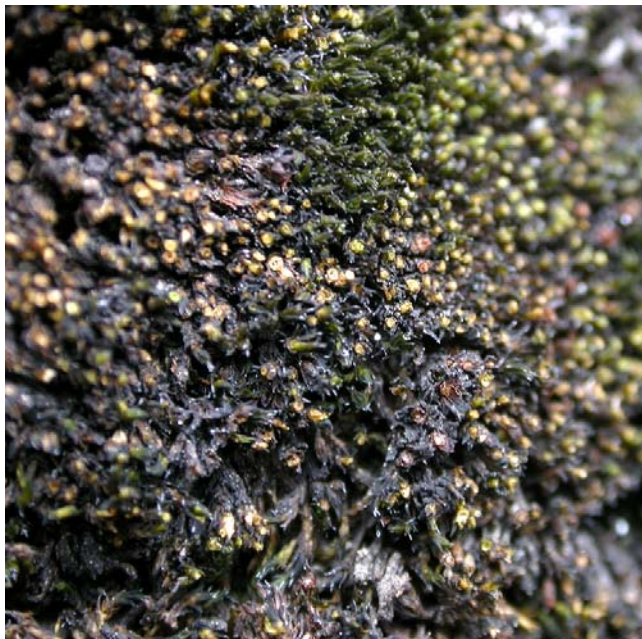


Figure 37. *Grimmia ovalis* grazed by grasshoppers. Note the absence of white tips on the leaves. Photo courtesy of Terry McIntosh.

### ***Melanoplus***

Although this genus (Figure 38-Figure 44) does not exhibit the close food association exhibited by the **Tetrigidae**, at least several members prefer mossy habitats. *Melanoplus lovetti* lives in damp mossy ground, avoiding taller grasses (Fulton 1930). *Melanoplus islandicus* (Figure 38) in Michigan, USA, occurs along damp shorelines of pools where vegetation includes short grasses and sedges as well as mosses and organic debris (Bland 1989).

*Melanoplus borealis* (Figure 39) is well camouflaged among the mosses near Fairbanks, Alaska, USA. Kaufmann (1971) recounts seeing an adult that jumped/flew away from the approaching human. Once it landed, it became invisible among the moss-covered field where its color pattern blended with both the colors and spongy texture of the mosses. This species, like others in the genus, avoided areas of tall grass, apparently requiring areas where they could rest in the sun.



Figure 39. *Melanoplus borealis* male, a species well camouflaged among the Arctic mosses. Photo by Denis Doucet, with permission.

This genus has a variety of feeding strategies. Kaufmann (1968) found that *Melanoplus differentialis* (Figure 40) in Maryland, USA, prefers *Taraxacum officinale* (dandelion), but will also feed on grasses. They also eat dried plants, even when fresh ones are present. Kaufman found that the habitat was more important in the



choice of food (light, temperature, plant orientation) than the foods themselves. The mandibles are typical of grasshoppers that eat forbs, but the maxillae are similar to the moss feeders in the genus *Tetrix*.



Figure 40. *Melanoplus differentialis*, a grasshopper that eats mostly forbs but has maxillae similar to those of moss feeders. Photo by Rob Curtis, through Creative Commons.

*Melanoplus femurrubrum* (Figure 41-Figure 43), like many of the grasshoppers, has many color forms (Figure 41-Figure 43). This species has been studied to determine the effect of food absence on survival. As you may know, grasshoppers will eat their own appendages when starved for days. Bland (1981) found that nymphs survived up to 113 hours with no food. But hatchlings required food within 48 hours to insure their continued survival and growth. This species tends to eat the first suitable food it encounters, using olfactory senses to find it.



Figure 41. *Melanoplus femurrubrum* in Zion National Park, showing an olive-green form. Photo by Leyo, through Creative Commons.



Figure 42. *Melanoplus femurrubrum* grayish green color form. Photo by Sheryl Pollock <[www.discoverlife.org](http://www.discoverlife.org)>, with permission.



Figure 43. *Melanoplus femurrubrum* reddish form. Photo by Sheryl Pollock <[www.discoverlife.org](http://www.discoverlife.org)>, with permission.

It appears that members of this genus have not been tested for sensitivity to secondary compounds in mosses. In tests of compounds in tracheophytes on nymphs of *Melanoplus sanguinipes* (Figure 44), a species that does not typically eat mosses, many elicited no response, but several compounds caused a reduction in mean weight (Westcott *et al.* 1992). Saponin decreased survival and seven compounds significantly decreased both survival and mean weight. Vanillic acid significantly increased mean weight. This leaves the intriguing question of the effects of secondary compounds of bryophytes. Investigations into the chewing apparatus and digestive response to bryophytes compared to preferred foods may help us to understand why some insects choose bryophytes while others avoid them.



Figure 44. *Melanoplus sanguinipes* female, a forb feeder that benefits from vanillic acid in forbs. Photo by Lynette Schimming, through Creative Commons.



Not only do populations of *Melanoplus* (Figure 40-Figure 44) differ in coloration, but their physiology can differ as well. Fielding (2006) demonstrated **facultative diapause** (resting period that can change based on conditions) in the widely distributed *Melanoplus sanguinipes*. In an Idaho population, diapause in this species was facultative, with pre-diapause embryos averting diapause when held at 5°C for 90 days. On the other hand, this same population entered diapause in the late stage of development if held at 22°C for 30 days or more (Figure 45). The subarctic Alaskan populations had obligate diapause and entered diapause in a late stage of development. Chilling in the pre-diapause stages had no effect on diapause. These differences in life cycle strategies permit this species to occupy its wide distribution and are likely to be important for some of the moss-dwelling species as well.

### *Chorthippus*

Langmaack (1997) found that mosses were important in the reproduction of some grasshoppers. *Chorthippus montanus* (Water-meadow Grasshopper; Figure 46) and *C. parallelus* (Figure 47) (*Acrididae*), both flightless, clearly selected moist mosses for depositing their egg pods.

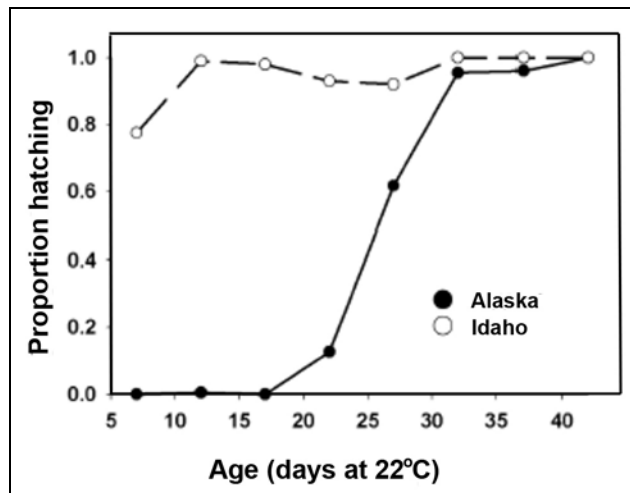


Figure 45. Comparison of proportion of eggs from Alaska and Idaho populations of *Melanoplus sanguinipes* that hatched after exposure to 5°C for 90-100 days following incubation at 22°C for different times.  $n > 200$  observations at each point. Modified from Fielding 2006.



Figure 46. *Chorthippus montanus*, a flightless grasshopper that selects moist mosses for egg deposition. Photo by Gilles San Martin, through Wikimedia Commons.



Figure 47. *Chorthippus parallelus* male, a flightless grasshopper that selects moist mosses for egg deposition. Photo by Atlasroutier, through Wikimedia Commons

*Chorthippus montanus* (Figure 46) is a flightless wetland species and therefore it is likely to become rarer because its habitat is disappearing. Using a mark-recapture technique, Weyer *et al.* (2012) found that this species travels on average only 23.5 m, with a maximum of 104 m. This is not sufficient to permit its dispersal among widely fragmented wetland landscapes, and even the requirement to replace a drained wetland with another (somewhere else) will not solve this dispersal problem. Even if it could travel farther, it has restricted habitat requirements and is unable to traverse unsuitable habitats.

Based on fecal analyses, *Chorthippus pullus* (Figure 48) has a varied diet that includes dicotyledons, monocotyledons, and bryophytes (Steiner & Zettel 2006). The bean *Astragalus onobrychis* was the most consumed food in the Steiner and Zettel study. Moss consumption, including the moss *Dicranoweisia crispula* (Figure 49), formed a greater part of the diet in seasons and locations when other herbs were less abundant, despite having mandibles adapted for eating grasses. At one location *D. crispula* comprised 45% of the diet. Contrary to the suggestion of Uvarov (1977) that grasshoppers eat mosses for their water content, the water content of this moss was the lowest among the top four foods consumed, suggesting that the grasshoppers derived some other value from eating it.



Figure 48. *Chorthippus pullus*, a species that lays its eggs in moss **polsters** (cushions) in Austria. Photo by Gabriele Kothe-Heinrich, through Creative Commons.



Figure 49. *Dicranoweisia crispula*, a species that can form as much as 45% of the diet of *Chorthippus pullus* (Figure 48). Photo by Michael Lüth, with permission.

In the Lake Salzburg area of Austria, *Chorthippus pullus* (Figure 48) lays its eggs in June and July as an **ootheca** (egg case; Figure 50) in sand or moss polsters (Schwarz-Waubke 2001). This species deposits an average of 75 eggs during its lifetime. Each ootheca contains an average of 6.1 eggs. These moss polsters are especially important in rocky areas where they supply protection in an otherwise hostile environment.



Figure 50. Insect **ootheca**. Photo by Gilles San Martin, through Creative Commons.

### *Nicarchus*

The genus *Nicarchus* (Figure 51) is flightless and lives on tree trunks (Rowell 2009). These grasshoppers are adapted to their habitat by having a wider thorax with reduced sternal lobes, the latter correlating with the reduced wings and flightless condition. This reduction in wing muscle provides additional space for a larger than typical **crop** (part of digestive system in which food is stored before digestion). Like other members of this group of tree trunk orthopterans (**Ommatolampinae**), their adaptations include cryptic coloration that mimics mosses, lichens, or bark; roughened cuticle or spines, again mimicking their substrate; strongly protuberant eyes; pronotum with bumpy projections; widely separated metasternal lobes; nodular antennae; 7 external spines on hind tibia; all but *Sciaphilacris* (Figure 52) flightless. They live on the trunks and major branches of tropical forest trees in the Amazon basin and in Central America. Among this group, only *Nicarchus* is known to feed on mosses, a habit that is probably favored by the enlarged crop.



Figure 51. *Nicarchus erinaceus*, a species that lives among mosses on tree trunks and branches in the tropical forest and feeds on mosses. Photo by Frank through What's that Bug <<http://www.whatsthatbug.com/2014/01/19/orthopteran-costa-rica/>>.

### *Sciaphilacris* – Moss and Lichen Mimics

*Sciaphilacris* (Figure 52) lacks many of the modifications noted for *Nicarchus* and is the only member of **Ommatolampinae** that is not flightless (Rowell 2009). Nevertheless, despite having somewhat reduced wings, it rarely flies. Little seems to be known about it – it lives in South and Central America and most likely spends part of its time among the mosses, blending well.



Figure 52. *Sciaphilacris alata*, a good moss mimic. Photo by Arthur Anker, with permission.

### *Myrmeleotettix maculatus*

Interactions with mosses is not always positive, and *Myrmeleotettix maculatus* (Figure 53) would most likely agree. In Europe it is a species of acidic coastal dunes. However, these dunes are being invaded by the exotic moss *Campylopus introflexus* (Figure 54). In a comparison of invaded dunes vs non-invaded dunes, Schirmel (2010) found that the mean number of captures of this species in non-invaded (native) plots was significantly higher than that in the invaded plots. Schirmel suggested that this difference may have been due to the higher proportion of grasses as food, more appropriate shelter, or more favorable microclimate in the native plots, leading to a higher mortality in the invaded plots. On the other hand, the mean number of young and older nymphs did not differ between the two habitats, suggesting that the invaded sites were suitable for oviposition but in some way detrimental to adults.





Figure 53. *Myrmeleotettix maculatus* female, a species that is disappearing in European coastal dunes due to the invasion of the moss *Campylopus introflexus* (Figure 54). Photo by Brian Eversham, with permission.



Figure 54. *Campylopus introflexus*, an invasive moss that may destroy grasshopper habitat in Europe. Photo by Michael Lüth, with permission.

## Food

Kaufman (1965) found that the feeding rate of *Acrididae* grasshoppers in Bolivia increased greatly with temperature. Feeding habits seem to correspond with mandibles and maxillary laciniae. These mouth parts can be divided into the graminivorous (grass) type, the forb-feeding type, and the moss-feeding type. Even the gastric caeca can be divided into four types based on diet preference. Nevertheless, experiments with *Euthystira brachyptera* (Figure 55) suggest that feeding on several different species, in this case of grasses, improves mortality, longevity, fecundity, and body weight.



Figure 55. *Euthystira brachyptera* female, a species that feeds on grasses but thrives best on mixed species. Photo by Gilles San Martin, through Creative Commons.

Position of the food can be important (Kaufman 1965). *Chorthippus parallelus* (Figure 47) prefers to feed on vertical grass blades. Passage time for the food in the alimentary tract differs not only in different species, but also depends on food plant, individual differences, and developmental stage. And males seem to assimilate more of the food they eat than do females.

Patterson (1984) demonstrated differences in shape and arrangement of dentes resulting in different mandibular ratios among members of the *Acrididae* with different feeding choices. Patterson (1984) and Kaufman (1965) pointed out the need for comparative studies among the moss-feeding species. Some of the species in this family are *stenophagous* (having narrow range of suitable foods) (Philippe 1991). For example, whereas *Trimerotropis saxatilis* (Figure 56-Figure 57) is specialized on eating mosses, *Boottettix punctatus* (Figure 58) specializes on *Larrea tridentata*, an evergreen shrub.



Figure 56. *Trimerotropis saxatilis* nymph well camouflaged among the grey lichens. Photo by Ted C. MacRae <beetlesinthebush.wordpress.com>, with permission.



Figure 57. *Trimerotropis saxatilis*, a specialist for eating mosses, is conspicuous here on mosses. Photo by Ted C. MacRae <beetlesinthebush.wordpress.com>, with permission.





Figure 58. *Bootettix argentatus*, a specialist on the shrub *Larrea tridentata*. Photo by Margarethe Brummermann, through Creative Commons.

In the southeastern United States lichen grasshoppers, also known as rock grasshoppers (*Trimerotropis saxatilis*; Figure 56-Figure 57), are important consumers in desert-like rock outcrops (Duke & Crossley 1975). This small species consumes 27.25 mg of the moss *Grimmia laevigata* (Figure 59), an **apparent** (conspicuous) moss, per day, totalling 391 mg m<sup>-2</sup> per year in this harsh habitat. This grasshopper species has a variety of color patterns that help it blend with its lichen and moss environment (Morse 1907). Although Morse says that *T. saxatilis* is restricted to bare rock surfaces, as its name implies, it has to eat somewhere, and it is a vegetarian. Do the math!



Figure 59. *Grimmia laevigata* on a rock outcrop, common habitat for *Trimerotropis saxatilis* (Figure 56-Figure 57). Photo by Michael Lüth, with permission.

### Oviposition

Knowing that some grasshoppers eat mosses, it is not hard to imagine that they also lay their eggs among mosses. *Chorthippus pullus* (Figure 48), in Salzburg, Austria, is endangered in Europe (Schwarz-Waubke 2001). Despite this rarity, in the proper habitat of wild river landscape near Taugl it is a **eudominant** [>10% (Bick 1989)] among 12 other members of the **Saltatoria** (suborder of **Orthoptera**

including grasshoppers, crickets, and related forms). This species lays its eggs as an ootheca (Figure 50) in sand or moss clumps during June and July.

Some species of *Chorthippus* seem to have an inexplicable combination of oviposition habitats. For example, *C. albomarginatus* (Figure 60), *C. montanus* (Figure 46), and *C. parallelus* (Figure 47) prefer vertical plant surfaces for oviposition (Langmaack 1997). But *C. parallelus* and *C. montanus* also use moist mosses for egg deposition, a quite different type of structure. Rather than structure, it seems that height is important, with *C. albomarginatus* preferring 2-6 cm, *C. montanus* 0.5-2 cm, and *C. parallelus* 0-0.5 cm. Langmaack suggested that these preferences may indicate different requirements for moisture and temperature during development. *Chorthippus albomarginatus*, the species ovipositing at the greatest height, has the greatest desiccation resistance and highest temperature requirement for its eggs. Eggs of both *C. parallelus* and *C. montanus* have low desiccation resistance and a low temperature requirement.



Figure 60. *Chorthippus albomarginatus* female, a species that prefers higher positions of 2-6 cm above the ground for its egg deposition, including moss locations. Photo by Gilles San Martin, through Creative Commons.

### Gryllidae – Crickets

The common names of the families of "crickets" have been hopelessly confused among the continents (Alexander *et al.* 1972), and me, so I will stay with only scientific names for most of these. The males are the callers in these groups, but in some the female may also call. The crickets make their well known chirps by rubbing together the leathery forewings. These chirps increase in frequency as the temperature increases. Overlapping species may have "songs" that we cannot distinguish, but they can be distinguished by instrumentation – and other crickets. Females are attracted to the calls and go to the males for mating. We know that frogs use mosses to modulate their calls, so it is appropriate to ask how grasshoppers might use them.

Alexander *et al.* (1972) report *Eunemobius melodius* singing in a *Sphagnum* bog (Figure 61) in Michigan, USA. Strang (2015) states that the sphagnum ground cricket (*Neonemobius palustris*; Figure 62-Figure 64) is not found outside of *Sphagnum* bogs. Some crickets make nests in *Sphagnum* (Vickery 1969). Crickets don't seem to be commonly known from mosses, but in captivity with



predators like frogs and lizards they will typically hide among the mosses. Does that happen in nature as well?



Figure 61. *Sphagnum* blanket bog where one might hear the song of *Eunemobius melodius*. Photo through Creative Commons.



Figure 62. *Neonemobius palustris* male (sphagnum ground cricket) on *Sphagnum*, its only known home. Photo by Brandon Woo, with permission.



Figure 63. *Neonemobius palustris* female on *Sphagnum*, its only known home. Photo by Brandon Woo, with permission.



Figure 64. *Neonemobius palustris* nestled among *Sphagnum* of bog. Photo by Carl Strang, with permission.

## Rhaphidophoridae – Camel Crickets, Wetas

These **Rhaphidophoridae** like it dark, living in forests, caves, animal burrows, under stones, in wood, and in cellars (Rhaphidophoridae 2015). They occur on all seven continents, where they are usually active at night and rely on their sense of touch to identify things in their environment. Wetas are characterized by lack of wings, lack of auditory organs, long, compressed tarsi with no pads, small bodies, and long hind legs and antennae (Richards 1961). They are primarily scavengers, often eating plant debris that is washed into the cave and left stranded on the cave walls, but they also eat bryophytes.

Johns and Cook (2014) found the new genus and species *Maotoweta virescens* (Figure 65-Figure 66) hidden in a moss forest in New Zealand. This mottled green weta is inconspicuous among the mosses; *maoto* is the Maori word for fresh green. Johns and Cook reported the difficulty of finding this weta on the mossy tree trunks during their night-time activity; it required 16 person hours for them to locate only 5 individuals. The only female collected was in copulation – on a moss.



Figure 65. *Maotoweta virescens* on bryophytes, a recently described weta that is well camouflaged among bryophytes. Photo by Tony Jewell, with permission.





Figure 66. Green weta (cf. *Maotoweta virescens*) in its mossy habitat. Photo by George Gibbs, with permission.

In the caves of New Zealand, one might find *Pallidoplectron turneri* feeding on the thallose liverwort *Marchantia* that grows near the electric lights, but I cannot verify the reference and my new Zealand colleagues and I suspect it was really fern prothalli being eaten.

*Troglophilus* (Figure 67-Figure 69) species exhibit cryptic coloring with shades of marble brown, green, or grey (Karaman *et al.* 2011). These color patterns blend well with the forest background and the lichen and moss-covered rocks where they hide during the day.

One consideration for crickets of all kinds is the need to call in order to connect with a mate. But all calls are not equal (Stritih & Čokl 2012). The surroundings modify the calls, and mosses have a different resonance than that of grasses or bushes. The *sympatric* (occupying overlapping distributions) *Troglophilus neglectus* (Figure 67-Figure 68) and *T. cavicola* (Figure 69-Figure 70) use vibratory signalling to distinguish the opposite sex of their own species. *Troglophilus neglectus* uses abdominal vibrations, whereas this behavior is absent in *T. cavicola*. Both species use whole-body vibrations after copulation. Although they most frequently use bark for both signalling and mating, mosses are often used as well. The signalling frequency depended on the substrate. On rocks, the intensity of *T. neglectus* is below the detection range for this species and therefore could not be heard if they signal from within a cave. The frequency extends up to 600 Hz on mosses, whereas its highest frequency on stone was below 250-300 Hz. This difference explains the movement from the caves to bark, or less often moss, for mating calls, with mosses and litter providing suitable vibratory substrate (Magal *et al.* 2000; Elias *et al.* 2004).



Figure 67. *Troglophilus neglectus* female in cave. Photo by Florin Rutschmanni, through Creative Commons at <[www.orthoptera.ch](http://www.orthoptera.ch)>.



Figure 68. *Troglophilus neglectus* female with green and brown cryptic coloration. Photo by František Chládek, with permission.



Figure 69. *Troglophilus cavicola* male with marbled brown coloration that blends with mosses and litter. Photo by Walter P. Pfliegler, with permission.



Figure 70. *Troglophilus cavicola* on moss. Photo by Stefan Pluess, through Creative Commons.

## Tettigoniidae – Katydids

Katydids can be abundant and diverse. At only three collecting sites in Loreto Province, Peru, Nickle and Castner (1995) found more than 370 species of Tettigoniidae.

Many katydid males offer a large gelatinous spermatophore to the female during mating (Del Castillo & Gwynne 2007). This is energy expensive and the larger the



reward offered, the less calling is done, another energy expensive activity. Size of the spermatophore and of the male do not seem to play any role in mate selection, but larger females seem to be favored over smaller ones.

Bogs seem to be the most common place for moss-associated katydids. The bog bush cricket *Metrioptera brachyptera* (Figure 71-Figure 72) is frequent in southern England heaths and bogs, but in northern England it is rare and in Scotland it has been found only once (Aucheninnes 2011). *Neonemobius palustris* (Figure 62-Figure 64) in Canada is rare, confined to *Sphagnum* (Figure 61) bogs (Johnstone & Vickery 1970; Kevan 1979), and feeds on the *Sphagnum* (Kevan 1979). Not only are the various *N. palustris* populations distinct genetically, but their **phenotypes** (sets of observable characteristics of individuals resulting from interaction of genes with environment) differ as well because interbreeding is rare if not non-existent between populations in different locations. Both *Neonemobius palustris* and *Allonemobius fasciatus* (Figure 73) lay their eggs on *Sphagnum* (Gerson 1969). Only these two species are considered to be characteristic peatland species in Canada (Marshall & Finnamore 1999).



Figure 71. *Metrioptera brachyptera*, a green bog bush cricket. Photo by Gilles San Martin, through Creative Commons.



Figure 72. *Metrioptera brachyptera* female, a black bog bush cricket. Photo by Robert Vlk, through Creative Commons.



Figure 73. *Allonemobius fasciatus*, a cricket that lays its eggs on *Sphagnum*. Photo through Creative Commons.

### Camouflage

Like the previous **Orthoptera**, katydids exhibit cryptic coloration. *Haemodiasma tessellata* (Figure 74-Figure 75), known as a moss mimic katydid, exhibits a mix of brown and green with a roughened light and dark surface (Thorman 2008) that helps it blend not only with mosses but also with leaf litter. But *Steiroxys strepens* (Figure 76), with a nearly solid green coloration, was sitting on damp mossy ground where it most likely blended better with the short grasses there (Fulton 1930).



Figure 74. This katydid (*Haemodiasma tessellata*) from Costa Rica was billed as a moss mimic katydid (Thorman 2008), but it seems to resemble a tracheophyte leaf more than it does a moss. It does have markings that would blend with epiphyllous bryophytes. Photos by Mary Thorman, permission pending.





Figure 75. *Haemodiasma tessellata* showing its cryptic coloration that could blend with leaves or bryophytes. Photo by Bernard Dupont, through Creative Commons.



Figure 76. *Steiroxys strepens* male, illustrating the solid colors typical of most katydids. Photo by Jim Johnson, with permission.

Nickle and Castner (1995) summarized the strategies used by katydids in the rainforests of northeastern Peru to protect themselves against daytime predators. These included primary defenses – camouflage, concealment within leaf parts or litter, territoriality by defending roosting sites against other katydids; secondary defenses used when making contact with predators – colorful displays by distasteful species (Figure 77), aggressive counterattacks, **aposematic** (serving to warn or repel) wasp mimicry, visual or acoustical alarm displays. They seem to return to the same daytime locations, suggesting they may be aware of their camouflage in those surroundings. Of the 378 species, 71.4% had general color patterns of green (208 spp.), brown (46 spp.), and both green and brown (19 spp.). Another 13.8% were more specific, mimicking wasps, bark, twigs, leaves, or lichens. Another 4.8% hid from view within vegetation or litter. Nickle and Castner did not distinguish any as having bryophyte camouflage, but some patterns that work well among leaf litter also work well among bryophytes (Figure 75).



Figure 77. *Acanthodis* sp. female showing startle display in Campana Highlands, Panama. Photo by Arthur Anker, with permission.

In Columbia, *Championica bicuspidata* (Figure 79) feeds on mosses and mimics them (Cardona Granda 2012). This genus has a number of moss mimics, including *C. pallida* (Figure 78-Figure 80). *Acanthodis curvidens* (see Figure 77) is also a moss mimic and rests prostrate to avoid detection (Robinson 1991). In addition to its camouflage, on Barro Colorado Island, Panama, this katydid avoids predation by bats when it is calling by maintaining a low frequency of calls (Belwood 1988). Bats locate katydids that produce frequent calls in about 26 seconds, immediately flying directly from their perch to the singing insect. In contrast, bats require nearly 34 minutes to locate the katydids (*Acanthodis curvidens*) that call less often (about once per minute), typically flying about seemingly randomly.



Figure 78. *Championica pilata* blending with a leaf and its epiphylls. Photo by Arthur Anker, with permission.





Figure 79. *Championica* sp. in Ecuadorian Amazon, illustrating its cryptic coloration that hides it on mosses. Photo by Geoff Gallice, through Creative Commons.



Figure 80. *Championica pilata* blending with a dead leaf. Photo by Arthur Anker, with permission.

### ***Paraphidnia***

*Paraphidnia* (Figure 81-Figure 85) is known as the moss katydid. Its markings look like leafy liverworts and lichens, making it blend well with its rainforest habitat, where it lives among and eats mosses and lichens (Ferrari 2015).



Figure 81. *Paraphidnia* sp. (lichen katydid) with markings that resemble leafy liverworts. Photo by Andreas Kay, through Creative Commons.



Figure 82. *Paraphidnia* sp. (lichen katydid) mimicking a stick that has bryophytes and lichens. Photo by Andreas Kay, through Creative Commons.



Figure 83. *Paraphidnia* sp. (mossy katydid) mimicking a stick with leafy liverworts. Photo by Arthur Anker, with permission.





Figure 84. *Paraphidnia* sp (mossy katydid) on bryophytes, mimicking a stick with leafy liverworts. Photo by Arthur Anker, with permission.



Figure 86. *Balboana tibialis* male with mosses on a branch covered with lichens. Photo by Arthur Anker, with permission.



Figure 85. *Paraphidnia* sp. from Ecuador, mimicking a stick with leafy liverworts. Photo by Arthur Anker, with permission.

### ***Balboana tibialis***

Like many tropical species, little seems to be known about *Balboana tibialis* (Figure 86-Figure 87). And like many katydids, it most likely benefits from its cryptic coloration.



Figure 87. *Balboana tibialis* in Gamboa, showing camouflage markings suitable for living on bryophytes. Photo by Arthur Anker, with permission.

### ***Arachnacris tenuipes* – Emperor Bush Cricket**

A big thank you to Nick Garbutt for allowing me to use his image to show *Arachnacris tenuipes* (Figure 88) eating a moss. This is a species that may reach 12 cm (Hincks 1956), and it has the largest wingspan (27.4 cm) in the **Orthoptera** s.s. (Cowardine 2008). Its size is limited by temperature (Makarieva *et al.* 2005). Because of increases in metabolism with increasing temperature, the maximum length increases approximately twofold for each 10°C increase in ambient temperature. Hence, larger **poikilotherms** (those with temperature controlled by the environment) occur farther north, with smaller individuals in the tropics. *Arachnacris tenuipes* (syn. *Macrolyrstes imperator*) is known from Malaysia and Indonesia, but its distribution may be wider. This may be the first report that it eats mosses.





Figure 88. *Arachnacris tenuipes*, an emperor bush cricket (katydid) eating moss. Photo by Nick Garbutt, with permission.

"Endless forms most hidden." Thus is the title of an article by Kikuchi *et al.* (2017) in *Ecology* regarding katydids that mimic mosses. A katydid, *Adeclus* cf. *trispinosus* (Cadena-Castaneda 2011), was discovered as a short-winged adult male, presenting a wing pattern and coloration with legs and other parts that made it resemble a moss (Kikuchi *et al.* 2017). The katydid that became famous in *Ecology* uses three strategies of concealment: background matching, disruptive coloration, and masquerade. A member of the **Pleminiini**, it joins many other species that resemble mosses. Other moss mimics in the **Tettigoniidae** include *Panacanthus varius* (Figure 89) and *P. intensus* (Montealegre-Z & Morris 2004). This type of mimicry seems to have evolved multiple times in the **Orthoptera** (Mugleston *et al.* 2013).



Figure 89. *Panacanthus varius*, a moss mimic. Photo by Andreas Kay, through Creative Commons.

## PHASMIDA – Walking Sticks

The common name of walking stick indicates that the **Phasmida** is a group of mimics. While looking like a stick is cool, looking like a hanging moss is awesome! And some members in the rainforests do just that (Figure 90), resembling pendent mosses in both color and appearance (Robinson 1969). The genus *Acanthoclonia* (**Pseudophasmatidae**) exhibits this moss-mimicking appearance (Gutiérrez & Bacca 2014).



Figure 90. Moss mimic walking stick. This one moves with a swaying, vibrating motion that mimics the movement of moss branches in the wind. Photo by Neil Bell, permission pending.

This kind of camouflage has been named in different ways, including **Batesian mimicry** and **crypsis**. But these terms may both be misleading conceptually (Skelhorn *et al.* 2010). Rather, the term **masquerade** has been applied to them (Figure 91). One problem in naming and understanding this phenomenon is the paucity of evolutionary studies on it, perhaps because its greatest representation is in the tropics where our level of understanding the systematics is much less than in other parts of the world. The term **masquerade** was introduced to describe those organisms that cause misidentification by other organisms.



Figure 91. A walking stick in Peru that looks like a twig with mosses growing on it. Photo by Arthur Anker, with permission.

### *Trychopeplus laciniatus*

An incredible insect, *Trychopeplus laciniatus* (**Diapheromeridae**; Figure 92-Figure 98), is a montane Neotropical rainforest walking stick that looks like strands of mosses and leafy liverworts. Its range includes the mountainous forests of Costa Rica, Nicaragua, Panama, and Colombia. It "sways" its way through its mossy habitat, a behavior scientists have suggested resembles the moving of mosses in the wind. Regarding its presence in Monte Verde, Costa Rica, Ryan Burrows (Bryonet 14 April 2010) states that it "would be a perfect match to the habitat there." This phenomenal insect bears such resemblance to the mosses on the cloud forest tree trunks that it is virtually



undetectable to an untrained eye. It is flightless and slow moving, and has no means of defense (Simon 2015). Hence, this invisibility is its only means of protection.



Figure 92. An immature walking stick, *Trychopeplus laciniatus*, from Nectandra Cloud Forest Garden in Balsa, Costa Rica. Photo by Diane Lucas, with permission.



Figure 93. *Trychopeplus laciniatus* in Costa Rica. Photo by Dorothy Allard, with permission.



Figure 94. Bryophytes in Monte Verde, Costa Rica, Nectandra cloud forest where *Trychopeplus laciniatus* lives. Photo by Diane Lucas, with permission.



Figure 95. *Trychopeplus laciniatus*, a walking stick that mimics bryophytes, on twig in Costa Rica. Photo by David Meagher.



Figure 96. Bryophytes in Monte Verde, Costa Rica, Nectandra cloud forest where *Trychopeplus laciniatus* lives. Photo by Diane Lucas, with permission.



Figure 97. *Trychopeplus laciniatus* on bark. Photo by Dan Doucette through Project Noah, with permission.





Figure 98. *Trychopeplus laciniatus*, clearly masquerading as a bryophyte. Photo by Dan Doucette through Project Noah, with permission.

Another observer (Anonymous 2015) describes the mating in more detail. *Trychopeplus laciniatus* is a herbivore and uses its mossy appearance to hide among the mosses while it feeds. Instead of laying its eggs in a cluster like most mantids, it lays them singly and loosely on the trees. The eggs subsequently fall to the forest floor where the nymphs hatch and develop.

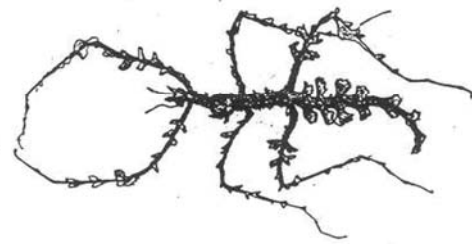
Ng (2015) reports a moss mimic stick insect that laid eggs among mosses in the Botanical Garden of the Kinabalu Park, Malaysia (film is available on website). In China, *Pericentrus* (Phasmatidae; possibly synonym of *Trychopeplus laciniatus*, Error! Reference source not found.-Figure 98) has coloration of green and brown that makes it look like mosses and lichens (Hennemann *et al.* 2008). It moved its body back and forth from side to side as it laid the eggs, occasionally releasing the ovipositor and re-inserting. It is likely that variants of these mimics exist in many locations in the tropics. Some may have been transported along with mosses, but their lack of wings would limit their distribution once they arrived. This kind of isolation promotes the formation of new species through the **founder principle** and **genetic drift**. For example, Belt figured one of these masqueraders in 1888 (Figure 99). But Tilgner (2002) disagrees with this explanation, suggesting instead that the multiple locations of such masquerading phasmids is the result of **convergent evolution**.

In Puerto Rico, *Lamponius nebulosus* (Pseudophasmatidae; Figure 100), a spiny green and brown mantid, represents the mimics (Nico Franz & Ines Sastre-de Jesus, Bryonet 15 April 2010). Those moss "leaves" you see are the spiny cuticle projections. This species is endemic to the cloud forest in the Luquillo Experimental Forest (Tilgner *et al.* 2000; Tilgner 2002) and has only been known for a short time. Its host plants include *Miconia* sp. and *Guzmania*, both likely to have associated mosses where it can rest undetected. In this group, activity is typically restricted to only certain times of day; when they are resting they are well camouflaged (Willig *et al.* 1993; Basset 2000; Berger 2004). But this species has two backup plans if it is discovered – it can exhibit **catalepsy** (trance state) or regurgitate fluid from its mouth.

#### T. Belt 1888

382 THE NATURALIST IN NICARAGUA. [Ch. XXI.

related genus (*Pterochroza*), imitate leaves in every stage of decay, some being faded-green, blotched with yellow; others, as in the species figured, resemble a brown withered leaf, the resemblance being increased by a transparent hole through both wings that looks like a piece taken out of the leaf. In many butterflies that resemble leaves on the under side of their wings, the wings being raised and closed together when at rest so as to hide the bright colours of the upper surface, there are similar transparent spots that imitate holes; and



MOSS INSECT.

others again are jagged at the edge, as if pieces had been taken out of them. Many chrysalides also have mirror-like spots that resemble holes; and one that I found hanging from the under side of a leaf had a real hole through it, formed by a horn that projected from the thorax and doubled back to the body, leaving a space between. Another insect, of which I only found two specimens, had a wonderful resemblance to a piece of moss, amongst which it concealed itself in the daytime, and was not to be distinguished except when accidentally shaken out. It is the larval stage of a species of *Phasma*.

Figure 99. "Moss insect" from Nicaragua as illustrated in "The Naturalist in Nicaragua" by Thomas Belt 1888. Photo by Rob Gradstein, with permission.



Figure 100. *Lamponius nebulosus*, a moss mimic. Photo courtesy of Alfredo D. Colon Archilla <alfredocolon.zenfolio.com>.

Even egg shape may contribute to adaptations for living among bryophytes (see Hennemann 2008). *Parasthenobea foliculata* (Diapheromeridae) has many



irregular pale green, straw, or brown markings and speckles that give it good camouflage among lichens and mosses. *Parastheneboea exotica* (Figure 101) and *P. imponens* (Figure 102-Figure 103) have elongate, cylindrical, bullet-shaped eggs with conical polar ends. The **operculum** (lid) is surrounded by a collar of **setae** (hairs). This egg shape is usually associated with taxa having an appendicular ovipositor that is suitable for laying eggs into soil, moss, and bark crevices.



Figure 101. *Parastheneboea exotica*, a species with good camouflage among lichens and mosses. Photo by Albert Kang through Project Noah, permission pending.



Figure 102. *Parastheneboea imponens*, a moss and lichen mimic. Photo by Albert Kang through Project Noah, permission pending.



Figure 103. *Parastheneboea imponens* is blending here among the mosses. Photo by Albert Kang through Project Noah, permission pending.

In *Cnipsus rachis* (Phasmatidae; Figure 104) the thorn pads consist of a single pair (Buckley *et al.* 2010). Projections along the body resemble moss leaves. Some of the New Caledonian species prefer ferns for food, but it seems that New Zealand species do not feed on ferns.



Figure 104. Mantid *Cnipsus rachis* from Costa Rica – and New Caledonia. Photo by Louis Thouvenot, with permission.

### *Neoclides laceratus*

*Neoclides laceratus* is a stick insect from Sumatra, Kalimantan, and Sarawak (Meagher 2022). In the swampy forests of Borneo it resembles creeping moss or the liverwort *Jungermannia* (Figure 106) with the insect's olive-green color and leaf-like projections.



Figure 105. *Neoclides laceratus* camouflaged perfectly among bryophytes on wood in Costa Rica. Photo by David Meagher.





Figure 106. *Jungermannia atrovirens*, in a liverwort genus that is mimicked by the stick insect *Neoclides laceratus*. Hermann Schachner, through Creative Commons.

### ***Antongilia laciniata* (Bacillidae)**

The moss mimic stick insect *Antongilia laciniata* (Figure 107) blends well with mosses in its aerial habitat. Although there are several images of this mimic online, there seems to be little information about its life.



Figure 107. *Antongilia laciniata* showing its moss-like camouflage in Madagascar. Photo by Frank Vassen, through Creative Commons.

### ***Phanocles* (Diapheromeridae)**

The genus *Phanocles* (Figure 108) is distributed in Central and South America (Gutiérrez & Bacca 2014) where it blends in with the epiphytic and epiphyllous bryophytes due to its markings and its shape like a twig.



Figure 108. *Phanocles* sp. nymph resembling a twig with adnate mosses, liverworts, and lichens in Panama. Photo by Arthur Anker, with permission.

## **MANTODEA – Preying Mantids**

This group of mantids are predators, hence the name preying mantis, but they also look like they are praying, so you will see the name spelled both ways. I still recall seeing my first mantid as a child. I thought at first someone had dropped a pocket knife, then realized it was the largest insect I had ever seen. These insects usually are safely camouflaged while at rest (Figure 109), but when they are searching for food or attacking prey they become more visible (Figure 110). Some are able to secrete a nasty spray that can blind the predators ("Steve" on Fellowship of the Minds 6 May 2013).



Figure 109. Mantid moss mimic among mosses on tree trunk. Photo by Nick Garbutt <[www.nickgarbutt.com](http://www.nickgarbutt.com)>, with permission.



Figure 110. *Polytrichum strictum* capsules with a mantid. Photo by Michael Lüth, with permission.



But they are not all so large – Zborowski (1993), in *Animals in Disguise*, illustrates mantids from Borneo that are no more than a cm long. Coyne (2013) discusses *Pogonogaster tristani* (Thespidae; Figure 111-Figure 112), described in 1918 but reported only a few times since. Others in this genus are present in Colombia (Gutiérrez & Bacca 2014). This is one of the minute preying mantids that mimics mosses.



Figure 111. *Pogonogaster tristani*, one of the many moss mimics in this genus. Photo by Oscar Blanco, through Creative Commons.



Figure 112. Mantid that resembles mosses. Photo by Evelyne Lennette.

Not all camouflage involves morphology of the insect. Some mantids carry their own flora around with them. Two species of the shield mantis, *Choeradodis rhombicollis* (Figure 113) and *C. rhomboidea* (Figure 114-Figure 115) (Mantidae) in Costa Rica have **epizoic** (growing on animals) leafy liverworts and lichens growing on them (Lücking *et al.* 2010). Of the 84 individuals Lücking and coworkers examined in the lowland rainforests, 60 of them had epizoites, comprised of five liverwort species, 23 lichen species, and several unidentified fungi (Figure 116). These epizoites grew mainly on the enlarged pronotum, but some also grew on the forewings. The liverworts were all in the family

*Lejeuneaceae* and were all species typical as **epiphylls** on leaves, especially *Leptolejeunea elliptica* (Figure 117). These pronotal inhabitants were more pronounced in *C. rhombicollis* than in *C. rhomboidea*, and more in females than in males (Figure 116). One female of *C. rhombicollis* also had the leafy liverworts *Diplasiolejeunea brunnea* (Figure 118), *Cololejeunea gracilis* (Figure 119), *C. camillii* (Figure 121), and *Colura tortifolia* (Figure 120). The researchers suggested that the longer life span of females may account for the greater development of liverworts there. This camouflage permits these large mantids to rest undetected among the leaves with their own flora of "epiphylls."



Figure 113. *Choeradodis rhombicollis* showing the large hood that resembles a leaf. Photo by Andreas Kay, through Wikipedia Commons.



Figure 114. *Choeradodis rhomboidea* carrying a flora on its back like the leaves it inhabits. Photo by Andreas Kay, through Creative Commons.





Figure 115. *Choeradodis rhomboidea* showing its hood thorax (=enlarged pronotum) that resembles a leaf – in this case a damaged one. Photo by Andreas Kay, through Creative Commons.

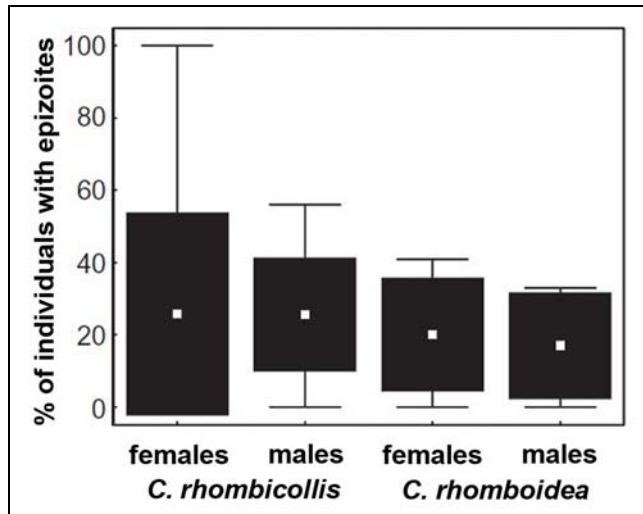


Figure 116. Comparison of males and females of two *Choeradodis* species showing percentage with liverwort, lichen, and fungus epizoids. Modified from Lücking *et al.* 2010.



Figure 117. *Leptolejeunea elliptica* epiphylls. Photo by Yan Jia-dang, through Creative Commons.



Figure 118. *Diplasiolejeunea brunnea* on leaf in Ecuador. Photo courtesy of Tamás Pócs.



Figure 119. *Cololejeunea gracilis* var. *linearifolia*, a tiny liverwort that can grow on larger liverworts as well as leaves of evergreen plants. Photo courtesy of Tamás Pócs.



Figure 120. *Colura tortifolia*, an occasional epizoite on *Choeradodis rhombicollis*. Photo by Michaela Sonnleitner, with permission.





Figure 121. *Cololejeunea camillii* on leaf in Panama. Photo courtesy of Tamás Pócs.

### Liturgusidae

Members of the genus *Majangella* can even resemble liverworts – a common group of bryophytes in the tropics. *Majangella moultoni* (Figure 122) has a green and brown patterned coloration with various protuberances that give it good camouflage when it is among mosses and liverworts. This species is tropical southeast Asian from Borneo, Indonesia, Malaysia, and Sumatra where it is inconspicuous in its rainforest habitat (Svenson & Vollmer 2014).



Figure 122. *Majangella moultoni* closely resembling the bryophytes beneath it. Photo by Hee Jenn Wei, with permission.

### Mating

The mantids are well known for their mating behavior (Figure 123). The male is smaller than the female, and the female needs to be well fed before producing her egg case with eggs (Figure 124). Perhaps this is why the katydid males have evolved to offer a gelatinous spermatophore before mating. In short, it isn't safe to be the male mantid – you might get eaten! The predatory females see the smaller males as food (Figure 125), so males must make their moves carefully.



Figure 123. *Mantis religiosa* couple mating. Note that the smaller, brown mantid is the male. Photo by Zwentibold, through Creative Commons.



Figure 124. *Mantis religiosa* egg case. Photo by Hans Hillewaert, through Creative Commons.



Figure 125. *Polyspilota* sp female chewing on the head of the male while mating with him. Photo by Arthur Anker, with permission.



## BLATTODEA – Cockroaches and Termites

You would most likely prefer not to think of cockroaches and termites as moss dwellers. If so, it may please you to know that the Australian wood-boring cockroach *Panesthia australis* (Blaberidae; Figure 126) prefers odors of individual tracheophyte species over the odor-neutral *Sphagnum* (Figure 61) (Billingham *et al.* 2009).



Figure 126. *Panesthia australis*, a cockroach that avoids mosses as a food item. Photo by Toby Hudson, through Creative Commons.

But the tables can be turned. Bernard Dupont photographed the ootheca (Figure 127) of a cockroach that was deposited on bryophytes and that had leafy liverworts growing up onto the ootheca. And Chatervedi sent me a picture of a cockroach that was hiding under the thallose liverwort *Dumortiera hirsuta* (Figure 129).



Figure 127. Cockroach ootheca with leafy liverworts growing on it. Photo by Bernard Dupont, through Creative Commons.



Figure 128. Cockroach on ventral surface of *Dumortiera hirsuta*. Photo courtesy of Chatervedi.



Figure 129. *Dumortiera hirsuta*, a hiding place for cockroaches. Photo by David T. Holyoak, with permission.

## ISOPTERA – Termites

Termites have lost their status as an order and are now included as an infraorder within the **Blattodea**. Termites have a division of labor much like that of the ants.

There are some bizarre habitats occupied by bryophytes, and these include termite mounds (Figure 131-Figure 133). One of these is the preferential occurrence of four species of *Fissidens* (*F. gymnostomus*, *F. hornschurchii*, *F. scariosus*, and *F. subulatus*) on termite structures in the Amazon (Reese & Pursell 2002). In one case, *F. allionii* co-occurred with *F. subulatus* on mounds in Amazonian Brazil. In another *F. pellucidus* var. *pellucidus* (Figure 130) and *F. prionodes* both occurred on one mound.



Figure 130. *Fissidens pellucidus* var. *pellucidus*, a termite mound colonizer. Photo by Scott Zona, with permission.





Figure 131. Termite mounds in the Bungle Bungle Range in Western Australia. Photo by Ouderkraal, through Creative Commons.



Figure 132. *Nasutitermes triodiae* in Northern Territory, Australia. Photo by J. Brew, through Creative Commons.

These organically enriched structures may benefit from the mosses through erosion control, while the mosses benefit from enrichment by feces, saliva, and other substances (Reese & Pursell 2002). The raised mounds serve in the same way as tree roots and soil banks by elevating the substrate above the leaf litter accumulation. Nevertheless, few other mosses and liverworts seem able to live in this habitat.

It appears that *Fissidens* may actually help the termites (Reese & Pursell 2002). One can observe fishbone-like patterns on some kinds of termite nests, and *Fissidens* provides such a pattern on nests it occupies. This pattern most likely facilitates drainage of rainfall. Furthermore, the mosses can serve to bind the particles that comprise the nest as well as softening the blow as raindrops strike.

*Fissidens termitarum* in Bolivia and Brazil occurs almost exclusively on termite structures (Reese & Pursell 2002). In the Amazon Churchill (1998) recorded 13 of the

38 *Fissidens* taxa on termite structures, but none were found there exclusively. In Rondônia, Brazil, Lisboa (1993) found 7 of the 15 *Fissidens* taxa associated with termite nests.



Figure 133. Termite mound with mosses at base. Photo by Izuchukwu Ezukanma, with permission.

*Fissidens* is also known from termite mounds in Africa (Potier de la Varde 1928, 1936; Bizot & Pócs 1979; Bizot *et al.* 1990; Bruggeman-Nannenga 1993). Likewise, Catcheside and Stone (1988) reported this genus from termite mounds in northern Australia. Even Mitten (1869) referred to *Fissidens pellucidus* (Figure 130) on "ant mounds," but Reese and Pursell (2002) considered that these were most likely termite mounds.

Other species of mosses are rare on the termite structures. Reese (2001) reported several species of *Calymperaceae* on termite structures. Churchill (1998) has the largest number of collections noted, including *Calymperaceae*: *Syrrhopodon cryptocarpus* (Figure 138), *S. ligulatus*, *S. xanthophyllus*; *Pilotrichaceae*: *Brymela parkeriana*; *Stereophyllaceae*: *Pilosium chlorophyllum*. Reese and Pursell (2002) found *Phyllocladus falcifolium* (*Phyllocladaceae*) with *Fissidens* on one termite structure in the Amazon. Nevertheless, none of these non-*Fissidens* species seems to frequent the nests. Ezukanma (in prep) found 5 species (none included above) on termite nests in the Eastern Nigeria highlands: *Campylopus savannarum* (Figure 134), *Daltonia angustifolia* var. *angustifolia* (Figure 135), *Philonotis hastata* (Figure 136), *Rhachitheciopsis tisserantii*, and *Sematophyllum brachytheciiforme*.





Figure 134. *Campylopus savannarum*, a species that occurs on termite nests in the Eastern Nigeria highlands. Photo by A. J. Ramalho, through Creative Commons.



Figure 135. *Daltonia angustifolia*, a species known from Nigerian termite mounds, shown here growing on the weevil *Gymnopholus reticulatus*. Photo courtesy of Rob Gradstein.

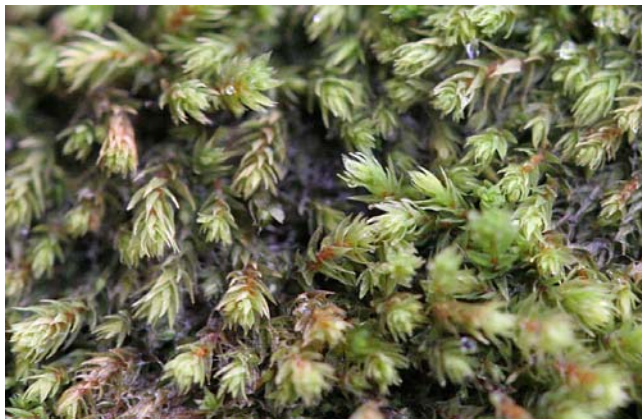


Figure 136. *Philonotis hastata*, a species known from Nigerian termite mounds. Photo by Michael Lüth, with permission.

Termites are generally unable to digest mosses (Bush 2015). Their guts have protozoa that facilitate their digestion of cellulose and lignin, hence their ability to eat wooden houses. Some people have considered termites to actually be a deterrent to mosses. Bush (2015) refers to a study in Ontario, Canada, that compared various types of

mulch on termite mortality. When used as the only source of food, peat moss starved the termites to death. Another study showed that subterranean termites tended to avoid travelling through peat, but only if the peat was moist. Dry peat seemed to have no effect.

Nevertheless, *Hospitalitermes umbrinus* (Termitidae; Figure 137) has "food balls" that contain bryophytes, but it prefers lichens (Collins 1979). This species forms foraging parties of roughly 500,000 soldiers and workers that leave the nest in the evening and return in the morning carrying these food balls.



Figure 137. *Hospitalitermes umbrinus*, a species that makes food balls containing bryophytes. Photo by Budak, through Creative Commons.

Termite mounds are an interesting ecosystem engineering feat. The termites actually benefit the ecosystem. The structure of these mounds cause more water to be absorbed into the soil and thus provide oases where green plants are able to subsist, preventing desertification (Bonachela *et al.* 2015; Hance 2015).



Figure 138. *Syrrhopodon* sp. Several species in this genus are known from termite mounds. Photo by Blanka Shaw, with permission.



## EMBIOPTERA - Webspinners

This is a little-known order of tropical and subtropical net spinners. The name *embio* refers to the fluttery wings (*ptera*) of the first one described (Meyer 2009). One must wonder why one net spinner was collected from a moss cushion in Israel (Gerson 1982), but the image (Figure 139) below from Brazil supports it.



Figure 139. **Embioptera** from Brazil with net on mosses. Photo by Arthur Anker, with permission.

### Summary

The **Orthopteroidea** include grasshoppers, pygmy grasshoppers, crickets, wetas, katydids, walking sticks, preying mantids, cockroaches, ice crawlers, and **Embioptera**. Among this group are many forms of camouflage and mimicry, and some of these are adaptations to living among bryophytes.

The pygmy grasshoppers (**Tetrigidae**) include many species that live among bryophytes and eat them. Some species have multiple morphs, permitting the species to occupy a variety of habitats. Many in this family also lay eggs there, as do many members of the **Acrididae**, a family that also includes bryophyte feeders. *Discotettix beelzebuth* has bryophytes growing on it, providing camouflage.

Mosses contribute a variety of patchy habitats that enable grasshoppers to remain separated spatially, supporting **Gause's** law by coexisting in the same environment but failing to compete due to the spatial separation.

**Gryllidae** (crickets) are rare among bryophytes, with bogs being the primary bryophyte habitat for them. Wetas are often found with bryophytes in caves or among them on tree trunks.

**Rhaphidophoridae** (camel crickets and wetas) include cave dwellers and other species that have color patterns blending with bryophytes. Some of the cave crickets also eat bryophytes.

**Tettigoniidae** (katydids) are good leaf mimics and some blend well with bryophytes by having a more broken color pattern. Some feed on *Sphagnum* and some lay their eggs there.

Walking sticks (**Phasmida**) are the master of disguise, mimicking pendent mosses in their rainforest homes. This type of mimicry, in which the insect can be mistaken for a hanging moss, may more

appropriately be termed **masquerading**. This type of mimicry has recently been termed masquerading. Some of these seem to have egg shapes adapted for oviposition among bryophytes.

The mantids (**Mantodea**) can have bryophyte camouflage and blend well, but their broad bodies prevent them from being mimics of pendent bryophytes. However, some do an excellent job of mimicking leaves with epiphylls living on them, including liverwort epiphylls, by having their own garden of bryophytic epizoots.

Cockroaches (**Blattodea**) seem to avoid mossy habitats, but one image shows the **ootheca** on bryophytes with liverworts growing onto the ootheca. Termites, formerly **Isoptera**, are members of the **Blattodea**. They often build mounds, especially in Australia, Africa, and the Amazon. These mounds are suitable habitats for a number of species of *Fissidens*, some of which seem to prefer that habitat. Few other bryophyte species occupy the mounds.

The **Embioptera** are probably not moss dwellers, although they were reported among mosses once.

## Acknowledgments

Pavel Drozd helped me obtain some of the grasshopper photos. Heino Lepp and Judith Curnow introduced me to the tiny moss-mimicking mantids from Borneo. Jessica Beever, Thomas Buckley, and Sven Bradler helped me to get the identity of *Trychopeplus laciniatus*. Ryan Burrows helped me find web sites with information and the scientific name of the walking stick, *Trychopeplus laciniatus*. Louis Thouvenot sent me the image of another mantid mimic, *Cnipsus rachis*. Rob Gradstein provided me with the story of liverworts on *Choeradodis* (Mantidae). Matt Renner provided the reference on using the term masquerade. Thank you to all the photographers who gave me permission to use their images or placed them in Creative Commons. Three professional photographers gave me permission to use their images in this chapter – thank you to Nick Garbutt for the mantis moss mimic, Tony Jewell for his picture of *Maotoweta virescens*, and Alfredo D. Colon Archilla for his picture of *Lamponius nebulosus*. Tomás Pócs took pictures of Lejeuneaceae just for use in this chapter. Allan Fife helped me make contacts to try to understand the role of bryophytes for cave wetas. Petr Kočárek kindly sent me images of *Tetrix* spp. and *Discotettix beelzebuth* on mosses. Izuchukwu Ezukanma showed me an advance copy of his manuscript that documented termites on Eastern Nigerian highlands mosses on termite mounds.

## Literature Cited

- Acrididae. 2015. Wikipedia. Accessed 5 July 2015 at <<https://en.wikipedia.org/wiki/Acrididae>>.
- Alexander, G. 1964. The Orthoptera of the Boulder Region. Natural History of the Boulder Area. University of Colorado Museum Leaflet 13: 70-74.
- Alexander, R. D., Pace, A. E., and Otte, D. 1972. The singing insects of Michigan. Great Lakes Entomol. 5: 33-69.



- Anonymous. 2015. The Moss Mimic Stick Insect. Accessed 30 June 2015 at <<http://ryanstaffanthropoda.weebly.com/moss-mimic-stick-insect.html>>.
- Appelqvist, S. 1997. Hoppor som äter mossor. [Hoppers who eat mosses.]. *Myrinia* 7: 16-17.
- Aucheninnes Moss. 2011. Accessed 15 June 2011 at <<http://www.buglife.org.uk/conservation/Scotland/Saving+Sites>>.
- Basset, Y. 2000. Insect herbivores foraging on seedlings in an unlogged rain forest in Guyana: Spatial and temporal considerations. *Studies Neotrop. Fauna Environ.* 35: 115-129.
- Bastow, J. L., Sabo, J. L., Finlay, J. C., and Power, M. E. 2002. A basal aquatic-terrestrial trophic link in rivers: Algal subsidies via shore-dwelling grasshoppers. *Oecologia* 131: 261-268.
- Becker, H. 1994. Secondary metabolites from bryophytes in vitro cultures. *J. Hattori Bot. Lab.* 76: 283-291.
- Belwood, J. J. 1988. Critically-Endangered Species. *Bats Mag.* 6(2): <[http://www.batcon.org/resources/media-education/bats-magazine/bat\\_article/323](http://www.batcon.org/resources/media-education/bats-magazine/bat_article/323)>.
- Berger, J. 2004. Ecology of Phasmids (Phasmatodea) in a Moist Neotropical Forest: A Study on Life History, Host-Range and Bottom-Up Versus Top-Down Regulation. Ph. D. Dissertation. Dissertation zur Erlangung des naturwissenschaftlichen Doktorgrades der Technischen Universität Kaiserslautern, 113 pp.
- Bhalerao, A. M., Naidu, N. M., and Paranjape, S. Y. 1987. Some observations on the nutrition-reproduction correlation in grouse locusts (Orthoptera: Tetrigidae). *Proc. Anim. Sci.* 96: 323-327.
- Bick, H. 1989. *Ökologie*. Verlag G. Fischer, Stuttgart.
- Billingham, Z. D., Chapple, D. G., Sunnucks, P., and Wong, B. B. M. 2009. Chemical cues and group association preferences in a subsocial cockroach, *Panesthia australis*. *Austral. J. Zool.* 57: 385-390.
- Bizot, M. and Pócs, T. 1979. East African bryophytes, III. *Acta Bot. Acad. Sci. Hung.* 25: 223-261.
- Bizot, M., Pierrot, R. B., and Tixier, P. 1986-1987. Reliquiae Bizotianae. Nanobryaceae et Fissidentaceae (Bryophyta) en République Centrafricaine, récoltes by R. P. E. Assel. *Bull. Inst. Fond. Afrique Noire Sér. A Sci. Nat.* 46: 250-273.
- Bland, R. G. 1981. Survival and food detection by first-instar *Melanoplus femurrubrum* (Orthoptera: Acrididae). *Great Lakes Entomol.* 14: 197-204.
- Bland, R. G. 1989. An annotated list of the Orthoptera of Beaver Island, Lake Michigan. *Great Lakes Entomol.* 22(1): 39-44.
- Bonachela, J. A., Pringle, R. M., Sheffer, E., Coverdale, T. C., Guyton, J. A., Caylor, K. K., Levin, S. A., and Tarnita, C. E. 2015. Termite mounds can increase the robustness of dryland ecosystems to climatic change. *Science* 347: 651-655.
- Bruggeman-Nannenga, M. A. 1993. Taxonomic results of the BRYOTROP Expedition to Zaire and Rwanda. 15. Fissidentaceae. *Trop. Bryol.* 8: 141-148.
- Buckell, E. R. 1921. Notes on the ecological distribution of some Orthoptera from the Chilcotin District of British Columbia. *J. Entomol. Soc. Brit. Columb.* 18: 32-38.
- Buckley, T. R., Attanayake, D., Nylander, J. A., and Bradler, S. 2010. The phylogenetic placement and biogeographical origins of the New Zealand stick insects (Phasmatodea). *Syst. Entomol.* 35: 207-225.
- Bush, Joshua. 2015. Peat Moss & Termites. Accessed 25 July 2015 at <<http://homeguides.sfgate.com/peat-moss-termites-46744.html>>.
- Cadena-Castañeda, O. J. 2011. El género *Adeclus* (Orthoptera: Tettigoniidae): Claves, distribución y notas biológicas. *J. Orthop. Res.* 20: 43-49.
- Caesar, S., Karlsson, M., and Forsman, A. 2010. Diversity and relatedness enhance survival in colour polymorphic grasshoppers. *PLoS One* 5(5): e10880.
- Cardona Granda, J. M. 2012. Grasshoppers of Colombia - A photo Guide Vol. 1 (western fauna). Barnes & Noble, 124 PP.
- Castillo, R. C. Del and Gwynne, D. T. 2007. Increase in song frequency decreases spermatophore size: Correlative evidence of a macroevolutionary trade-off in katyids (Orthoptera: Tettigoniidae). *J. Evol. Biol.* 20: 1028-1036.
- Catcheside, D. G. and Stone, I. G. 1988. The mosses of the Northern Territory, australia. *J. Adelaide Bot. Gard.* 11: 1-17.
- Chapman, R. F. and Sword, G. A. 1997. Phytophagy in the Acridomorpha. In: Gangwere, S. K., Muralirangan, M. C. and Muralirangan, M. (eds.). *The bionomics of grasshoppers, katyids and their kin*. CAB International, Wallingford, New York, pp 143-172.
- Chopard, L. 1951. *Orthoptéroïdes*, Vol. 56. Lechevalier, Paris.
- Churchill, S. P. 1998. Catalog of Amazonian mosses. *J. Hattori Bot. Lab.* 85: 191-238.
- Collins, N. M. 1979. Observations on the foraging activity of *Hospitalitermes umbrinus* (Haviland), (Isoptera: Termitidae) in the Gunong Mulu National Park, Sarawak. *Ecol. Entomol.* 4: 231-238.
- Cornelissen, J. H. C., Lang, S. I., Soudzilovskaia, N.A., and During, H. J. 2007. Comparative cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry. *Ann. Bot.* 99: 987-1001.
- Cowardine, M. 2008. *Animal Records*. Sterling Publishing Co., Inc., New York, p. 230.
- Coyne, Jerry. 2013. Moss-mimicking mantid. Why Evolution Is True. Accessed 30 June 2015 at <<https://whyevolutionistrue.wordpress.com/2013/11/13/moss-mimicking-mantid/>>.
- Duke, K. M. and Crossley, D. A. Jr. 1975. Population energetics and ecology of the rock grasshopper, *Trimerotropis saxatilis*. *Ecology* 56: 1106-1117.
- Elias, D. O., Mason, A. C., and Hoy, R. R. 2004. The effect of substrate on the efficacy of seismic courtship signal transmission in the jumping spider *Habronattus dosseus* (Araneae: Salticidae). *J. Exper. Biol.* 207: 4105-4110.
- Ferrari, Andrea. 2015. Beauty of the Beast. Accessed 14 July 2015 at <[http://www.animamundimag.com/ANIMA\\_MUNDI/pdf/AM16%20-%20Grasshoppers%20-%20LTC\\_animaMundi01.pdf](http://www.animamundimag.com/ANIMA_MUNDI/pdf/AM16%20-%20Grasshoppers%20-%20LTC_animaMundi01.pdf)>.
- Fielding, D. 2006. Optimal diapause strategies of a grasshopper, *Melanoplus sanguinipes*. *J. Insect Sci.* 6: 2-; DOI: <[http://dx.doi.org/10.1673/1536-2442\(2006\)6\[1:ODSOAG\]2.0.CO;2](http://dx.doi.org/10.1673/1536-2442(2006)6[1:ODSOAG]2.0.CO;2)>.
- Forsman, A. 1997. Thermal capacity of different colour morphs in the pygmy grasshopper *Tetrix subulata*. *Ann. Zool. Fenn.* 34(3): 145-149.
- Forsman, A. 1999. Reproductive life history variation among colour morphs of the pygmy grasshopper *Tetrix subulata*. *Biol. J. Linn. Soc.* 67: 247-261.
- Forsman, A. 2000. Some like it hot: Intra-population variation in behavioral thermoregulation in color-polymorphic pygmy grasshoppers. *Evol. Ecol.* 14: 25-38.



- Forsman, A. 2001. Clutch size versus clutch interval: Life history strategies in the colour-polymorphic pygmy grasshopper *Tetrix subulata*. *Oecologia* 129: 357-366.
- Forsman, A. and Appelqvist, S. 1998. Visual predators impose correlational selection on prey color pattern and behavior. *Behav. Ecol.* 9: 409-413.
- Fulton, B. B. 1930. Notes on Oregon Orthoptera with descriptions of new species and races. *Ann. Entomol. Soc. Amer.* 23: 611-641.
- Gause, G. F. 1934. Struggle for existence. Stechert-hafner, N. Y. 163 pp.
- Gen, I. T. O. and Rahman, H. n.d. A Guide to Orthoptera and Allied Insects. Self-published, 100 pp. Available at <<http://www.bbec.sabah.gov.my/overall/bbec21/orthoptera.pdf>>.
- Gerson, U. 1969. Moss-arthropod associations. *Bryologist* 72: 495-500.
- Gerson, U. 1982. Bryophytes and invertebrates, Chapt. 9. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman and Hall, New York, pp. 291-332.
- Godfray, H. C. J. 1994. *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, New Jersey.
- Gutiérrez, Y. and Bacca, T. 2014. Phasmatodea (Insecta) of the Nambí Natural River Reservation, Nariño, Colombia. *Boletín Científico. Centro de Museos. Museo de Historia Natural* 18: 210-221.
- Hance, Jeremy. 2015. How termites hold back the desert. Mongabay. Accessed 25 July 2015 at <<http://news.mongabay.com/2015/02/how-termites-hold-back-the-desert/>>.
- Hancock, J. L. 1902. *The Tettigidae of North America*. The Lakeside Press, R. L. Donnelly & Sons Company, Chicago, 188 pp.
- Hanski, I. 1983. Coexistence of competitors in patchy environment. *Ecology* 64: 493-500.
- Hennemann, F. H., Conle, O. V., Zhang, W., and Liu, Y. 2008. Descriptions of a new genus and three new species of Phasmatodea from Southwest China (Insecta: Phasmatodea). *Zootaxa* 1701: 40-62.
- Hincks, W. D. 1956. Dermaptera and Orthoptera. *Handbooks for the Identification of British Insects*. 1(5): 24 pp.
- Hochkirch, A., Gröning, J., Loos, T., Metzing, C., and Reichelt, M. 2000. Specialized diet and feeding habits as key factors for the habitat requirements of the grasshopper species *Tetrix subulata* (Orthoptera: Tettigidae). *Entomol. Gen.* 25(1): 39-51.
- Hochkirch, A., Gröning, J., and Bucker, A. 2007. Sympatry with the devil: Reproductive interference could hamper species coexistence. *J. Anim. Ecol.* 76: 633-642.
- Hodgson, C. J. 1963. Some observations on the habits and life history of *Tetrix undulata* (Swrb.) (Orthoptera: Tettigidae). *Proc. Royal Entomol. Soc. Lond. Ser A Gen. Entomol.* 38: 200-205.
- Holst, K. T. 1986. The Saltatoria of northern Europe. *Fauna Entomol. Scand.* 16: 1-127.
- Johns, P. M. and Cook, L. D. 2014. *Maotoweta virescens* new genus and new species; hidden in a moss forest (Orthoptera: Rhaphidophoridae). *Records of the Canterbury Museum*, 2013, Vol. 27: 11-17.
- Johnstone, D. E. and Vickery, V. R. 1970. Notes on the *palustris-cubensis* complex of the genus *Neonemobius* Hebard (Orthoptera: Gryllidae: Nemobiinae). *J. Georgia Entomol. Soc.* 5(4): 233-241.
- Karaman, I., Hammouti, N., Pavićević, D., Kiefer, A., Horvatić, M., and Seitz, A. 2011. The genus *Troglophilus* Krauss, 1879 (Orthoptera: Rhaphidophoridae) in the west Balkans. *Zool. J. Linn. Soc.* 163: 1035-1063.
- Kaufmann, T. 1965. Biological studies on some Bavarian Acridoidea with special reference to their feeding habits. *Ann. Entomol. Soc. Amer.* 58: 791-801.
- Kaufmann, T. 1968. A laboratory study of feeding habits of *Melanoplus differentialis* in Maryland (Orthoptera: Acrididae). *Ann. Entomol. Soc. Amer.* 61: 173-180.
- Kaufmann, T. 1971. Biology and ecology of *Melanoplus borealis* (Orthoptera: Acrididae) in Fairbanks, Alaska with special reference to feeding habits. *Mich. Entomol.* 4: 3-13.
- Kevan, D. 1979. Grylloptera. *Mem. Entomol. Soc. Canada* 111(S108): 318-321.
- Kikuchi, D. W., Kattan, G. H., Murcia, C., and Mntelegr-Z, F. 2017. Endless forms most hidden: Katydid that masquerade as moss. *Ecology* 98: 2479-2481.
- Kočárek, P. 2010. Substrate-borne vibrations as a component of intraspecific communication in the groundhopper *Tetrix ceperoi*. *J. Ins. Behav.* 23: 348-363.
- Kočárek, P., Grucmanová, Š., Filipcová, Z., Bradová, L., Plášek, V., and Holuša, J. 2008a. Mosses as a food component of groundhopper *Tetrix ceperoi* (Orthoptera: Tettigidae). In: Kočárek P., Plášek, V., and Malachová, K. (eds.). *Environmental Changes and Biological Assessment IV, Book of Abstracts*. Ostrava, Faculty of Science, University of Ostrava, pp. 43-44.
- Kočárek, P., Grucmanová, S., Filipcová, F., Bradová, L., Plášek, V., and Holuša, J. 2008b. Mosses as a food component of groundhopper *Tetrix ceperoi* (Orthoptera: Tettigidae). In: Shaw, B. and Golinski, K. (eds.). *Symposium Schedule, Abstracts, and List of Participants*. Alaska 2008. 4th International Meeting on the Biology of *Sphagnum*, August 1-11, 2008. Juneau, Anchorage, and Kenai Peninsula, Alaska, pp. 9-10.
- Kočárek, P., Grucmanová, Š., Filipcová, Z., Bradová, L., Plášek, V., and Holuša, J. 2008c. Bryophagy in the groundhopper *Tetrix ceperoi* (Orthoptera: Tettigidae): Analysis of alimentary tract contents. *Scripra Facultatis Rerum Naturalium Universitatis Ostraviensis* 186: 348-352.
- Kočárek, P., Holuša, J., Grucmanová, Š., and Musiolek, D. 2011. Biology of *Tetrix bolivari* (Orthoptera: Tettigidae). *Central Eur. J. Biol.* 6: 531-544.
- Kuřavová, K. and Kočárek, P. 2015. Seasonal variation in the diet of *Tetrix tenuicornis* (Orthoptera: Tettigidae). *Entomol. Sci.* 18: 489-501.
- Kuřavová, K., Hajduková, L., and Kočárek, P. 2014. Age-related mandible abrasion in the groundhopper *Tetrix tenuicornis* (Tettigidae, Orthoptera). *Arthropod Struc. Develop.* 43(3): 187-192.
- Langmaack, M. 1997. Eiablageort und Chorionstruktur bei 3 sympatrischen Grashuepferarten (Acrididae, Gomphocerinae) des Feuchtgruenlandes [Oviposition site and chorion structure of 3 sympatric fen grassland grasshopper species (Acrididae, Gomphocerinae).]. *Braunschweiger Naturkundliche Schriften* 5: 359-370.
- Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *Amer. Nat.* 104: 413-423.
- Lisboa, R. C. L. 1993. Musgos Acrocárpicos do Estado de Rondônia. *Museu Paraense Emilio Goeldi, Belém*.
- Lock, K., Verslycke, T., and Janssen, C. 2006. Energy allocation in brachypterous versus macropterous morphs of the pygmy



- grasshopper *Tetrix subulata* (Orthoptera: Tetrigidae). Entomol. Gen. 28: 269-274.
- Lücking, R., Mata-Lorenzo, J., and Dauphin L., G. 2010. Epizoeic liverworts, lichens and fungi growing on Costa Rican Shield Mantis (Mantodea: *Choeradodis*). Stud. Neotrop. Fauna Environ. 45(3): 175-186.
- Magal, C., Schöller, M., and Tautz, J. 2000. The role of leaf structure in vibration propagation. J. Acoust. Soc. Amer. 108: 2412-2418.
- Makarieva, A. M., Gorshkov, V. G., and Li, B. L. 2005. Temperature-associated upper limits to body size in terrestrial poikilotherms. Oikos 111: 425-436.
- Markham, K., Chalk, T., and Stewart, C. N. Jr. 2006. Evaluation of fern and moss protein-based defenses against phytophagous insects. Internat. J. Plant Sci. 167: 111-117.
- Marshall, S. A. and Finnamore, A. T. 1999. Canadian Peatlands. Chapt. 17, pp. 383-400. In: Batzer, D. P., Rader, R. B., and Wissinger, S. A. Invertebrates in Freshwater Wetlands of North America: Ecology and Management. John Wiley & Sons, Inc., New York, 1001 pp.
- Meagher, D. 2022. Two extraordinary stick insects that mimic bryophytes. Bryol. Times 154: 34.
- Meyer, John R. 2009. Embioptera. General Entomology, NC State University. Accessed 15 July 2015 at <<http://www.cals.ncsu.edu/course/ent425/library/compendium/embioptera.html>>.
- Mitten, W. 1869. Mjusc Austro-Americani. J. Linn. Soc. Bot. 12: 1-659.
- Montealegre-Z, F. and Morris, G. K. 2004. The spiny devil katydids, *Panacanthus* Walker (Orthoptera: Tettigoniidae): An evolutionary study of acoustic behaviour and morphological traits. Syst. Entomol. 29: 21-57.
- Morse, A. P. 1907. Further Researches on North American Acrididae. Carnegie Institution of Washington 68: 3-54 + Figures.
- Mugleston, J. D., Song, H., and Whiting, M. F. 2013. A century of paraphyly: A molecular phylogeny of katydids (Orthoptera: Tettigoniidae) supports multiple origins of leaf-like wings. Molec. Phylog. Evol. 69: 1120-1134.
- Nabours, R. K. 1929. The genetics of the Tettigidae (Grouse locusts). Bibliografia Genetica. M. Nijhoff, Den Haag, Netherlands, pp. 27-104.
- Ng, Murphy. 2015. Mt. Kinabalu Botanical Garden of Kinabalu Park. Posted 24 March 2015. Accessed 24 July 2015 at <<http://www.mysabah.com/wordpress/mt-kinabalu-botanical-garden-of-kinabalu-park/>>.
- Nickle, D. A. and Castner, J. L. 1995. Strategies utilized by katydids (Orthoptera: Tettigoniidae) against diurnal predators in rainforests of northeastern Peru. J. Orthoptera Res. 4: 75-88.
- Paranjape, S. Y. 1985. Behavioural analysis of feeding and breeding in orthopteran insects. Proc. Indian Acad. Sci. 94: 265-282.
- Paranjape, S. Y. and Bhalerao, A. M. 1985. Bioecological observations on a pigmy locust, *Potua sabulosa* Hancock (Tetrigidae: Orthoptera). Psyche 92: 331-336.
- Paranjape, S. Y., Naidu, N. M., and Braleras, A. M. 1988. Plant-animal association in relation to grouse locusts (Orthoptera: Tetrigoidea). Bull. Bot. Surv. India 28: 36-38.
- Patterson, B. D. 1984. Correlation between mandibular morphology and specific diet of some desert grassland Acrididae (Orthoptera). Amer. Midl. Nat. 111: 296-303.
- Philippe, L. G. 1991. Niche breadth and feeding in tropical grasshoppers. Internat. J. Trop. Insect Sci. 12: 201-208.
- Potier de la Varde, R. 1928. Mousses de l'Oubangui. Arch. Bot. Mém. 1(3): 1-152.
- Potier de la Varde, R. 1936. Mousses du Gabon. Mém. Soc. Sci. Nat. Cherbourg 20: 1-271.
- Reese, W. D. 2001. Substrate preference in Calymperaceae: *Calympeeres*, *Mitthyridium*, and *Syrrhopodon*. Bryologist 104: 582-593.
- Reese, W. D. and Pursell, R. A. 2002. The *Fissidens* flora of Amazonian forest floor termite structures. Bryologist 105: 185-188.
- Rehn, J. A. and Grant, H. J. Jr. 1955. *Tetrix subulata* (Orthoptera; Acridoidea; Tetrigidae) as occurring in North America. Proc. Acad. Nat. Sci. Phila. 107: 145-165.
- Rhaphidophoridae. 2015. Wikipedia. Accessed 3 July 2015 at <<https://en.wikipedia.org/wiki/Rhaphidophoridae>>.
- Richards, A. M. 1961. Some observations on New Zealand cave-wetas. Tuatara 9: 80-86.
- Richards, O. W. and Davies, R. G.. 1977. Imm's General Textbook of Entomology, 10th edn. Chapman and Hall, London.
- Robinson, M. H. 1969. The defensive behaviour of some orthopteroid insects from Panama. Trans. Royal Entomol. Soc. Lond. 121: 281-303.
- Robinson, M. H. 1991. Niko Tinbergen, Comparative Studies and Evolution. In: Dawkins, M. S., Halliday, T. R., and Dawkins, R. (eds.). The Tinbergen Legacy. Springer, Netherlands, pp. 100-128.
- Rowell, C. H. F. 1971. The variable coloration of the acridoid grasshoppers. In: Beament, J. W. L., Treherne, J. E., and Wigglesworth, V. B. (eds.). Advances in Insect Physiology, Vol. 8. Academic Press, London, pp. 145-198.
- Rowell, C. H. F. 2009. On the significance of changes in pterothoracic sternal morphology within the Vilerinae (Ommatolampinae, Acrididae). J. Orthoptera Res. 18(1): 1-4.
- Schirmel, J. 2010. Response of the grasshopper *Myrmeleotettix maculatus* (Orthoptera: Acrididae) to invasion by the exotic moss *Campylopus introflexus* in acidic coastal dunes. J. Coastal Conserv. 15: 159-162.
- Schwarz-Waubke, M. 2001. Zur Biologie und Vergesellschaftung von *Chorthippus pullus* (Philippi 1830) (Saltatoria, Acrididae) im Land Salzburg (Österreich). Linzer Biol. Beitr. 33: 997-1015.
- Simberloff, D. 1982. The status of competition theory in ecology. Ann. Zool. Fenn. 19: 241-253.
- Simon, Matt. 2015. *Trychopeplus laciniatus* (Phasmatodea: Diapheromeridae). Entomology Diary. Accessed 28 June 2015 at <<http://entomologydiary.typepad.com/home/trychopeplus-laciniatus-phasmatodea-diapheromeridae.html>>.
- Skelhorn, J., Rowland, H. M., and Ruxton, G. D. 2010. The evolution and ecology of masquerade. Biol. J. Linn. Soc. 99(1): 1-8.
- Steiner, A. and Zettel, J. 2006. Contributions to the nutritional ecology of the endangered grasshopper *Chorthippus pullus* (Philippi, 1830) (Orthoptera: Acrididae). Doctoral dissertation, Diplomarbeit Zoologisches Institut der Universität Bern, 43 pp.
- Strang, Carl. 2015. Sound Ideas: 3 Ground Crickets. Nature Inquiries. Accessed 23 July 2015 at <<https://natureinquiries.wordpress.com/2015/02/25/sound-ideas-3-ground-crickets/>>.
- Strith, N. and Čokl, A. 2012. Mating behaviour and vibratory signalling in non-hearing cave crickets reflect primitive



- communication of Ensifera. PLOS one DOI: 10.1371/journal.pone.0047646.
- Svenson, G. J. and Vollmer, W. 2014. A case of the higher-level classification of praying mantises (Mantodea) obscuring the synonymy of *Majangella* Giglio-Tos, 1915 (Liturgusidae, Liturgusinae) and *Ephippiomantis* Werner, 1922 (Hymenopodidae, Acromantinae). Zootaxa 3797: 103-119.
- Thorman, Mary. 2008. What's That Bug. Accessed on 14 April 2010 at <<http://www.whatsthatbug.com/2008/08/05/moss-mimic-walkingstick-from-costa-rica/>>.
- Tilgner, E. H. 2002. Systematics of Phasmida. Entomology. Ph. D. Dissertation, University of Georgia, Athens.
- Tilgner, E. H., Camilo, G. R., and Moxey, C. F. 2000. A new species of *Lamponius* (Phasmida: Phasmatidae). J. Orthoptera Res. 9: 37-39.
- Uvarov, B. 1977. Grasshoppers and Locusts, a Handbook of General Acridology, Vol. 2. Centre for Overseas Pest Research, London.
- Vance, R. R. 1978. Predation and resource partitioning in one predator - two prey model communities. Amer. Nat. 112: 797-813.
- Verdcourt, B. 1947. A note on the food of *Acridium* Geoff. (Orthopt.). Entomol. Month. Mag. 83: 190.
- Vickery, V. R. 1969. Two species of *Pteronemobius* previously unreported in Quebec (Orthoptera: Ensifera: Grylloidea: Nemobiinae). Ann. Soc. Entomol. Quebec 14: 22-24.
- Westcott, N. D., Hinks, C. F., and Olfert, O. 1992. Dietary effects of secondary plant compounds on nymphs of *Melanoplus sanguinipes* (Orthoptera: Acrididae). Ann. Entomol. Soc. Amer. 85: 304-309.
- Weyer, J., Weinberger, J., and Hochkirch, A. 2012. Mobility and microhabitat utilization in a flightless wetland grasshopper, *Chorthippus montanus* (Charpentier, 1825). J. Insect Conserv. 16: 379-390.
- Willig, M. R., Sandlin, E. A., and Gannon, M. R. 1993. Structural and taxonomic components of habitat selection in the neotropical folivore *Lamponius portoricensis* (Phasmatodea: Phasmatidae). Environ. Entomol. 22: 634-641.
- Zborowski, P. 1993. Animals in Disguise: A Journey into Nature's Deceptions. The Currawong Press, Sydney.
- Zinsmeister, H. D., Becker, H., and Eicher, T. 1991. Bryophytes, a source of biologically active, naturally occurring material. Angewandte Chemie 30: 130-147.