Chapter 4

Insects and Ecology

The term **ecology** is derived from the Greek word *oikoV*, meaning house or place to live. Ecology is defined as the study of relationships of organisms or groups of organisms to their environment, both the animate or **biotic** and inanimate, **abiotic** environment. Ecology can be further divided into **synecology** dealing with **communities** and **autecology**, having a look at single species. **Population ecology**, also referred to as **population biology** or **demecology** is the study of populations, their structures and dynamics. Population ecology is integrated by some authors in synecology, others consider it as equivalent to synecology and autecology.

The ecology of a pest species is important for the understanding of its feeding habits, natural enemies, spatial distribution, dispersal and population dynamics. Without this essential piece of information one can hardly develop and successfully apply pest management strategies.

This chapter introduces some aspects of ecology. One reason for the success of insects is their adaptation to all **trophic levels**. Therefore, the involvement of insects in the **food chain** as herbivores, carnivores and decomposers is outlined in this chapter.

The 'living together' or **symbiosis** between insects and other organisms is discussed, including the interactions between insects and plants, other animals and microorganisms. The relationships can be for the benefit of both or all involved species, a type of symbiosis known as **mutualism**. A relationship being for the benefit of one species without harming or benefiting the other partner is known as **commensalism**. We talk about **parasitism**, if one partner of the relationship benefits to the detriment of the other, but usually without causing its death. In the latter case, defence strategies have evolved in order to minimise the disadvantages and thus to secure survival.

Finally this chapter analyses insect populations with emphasis on various factors affecting the dynamics of insect populations.

4.1 Food Chain and Materials Triangle

Regarding the flow of matter and energy in a system, several distinct **trophic levels** can be found. The trophic levels of the **food chain** or **food web** are shown in the **materials triangle** or **pyramid of biomass** in **fig. 4-1**. **Producers** like **photoautotrophic** green plants use sunlight and minerals for the production of carbohydrates in a process known as **photosynthesis**. All other organisms are **heterotrophs** that occupy **consumer** levels. Primary consumers are **herbivores** or **phytophages**, feeding upon green plants. Primary consumers are the source of food for **secondary consumers**, like the various **carnivorous** predators and parasites as well as **omnivorous** scavengers. Any dead plant or animal matter like litter, decay, carrion and faeces is consumed by **decomposers** that finally recycle minerals for plants.

Insects can be found on all heterotrophic levels. Herbivorous insects act as primary consumers, whereas predacious, parasitic and scavenging insects are secondary consumers.

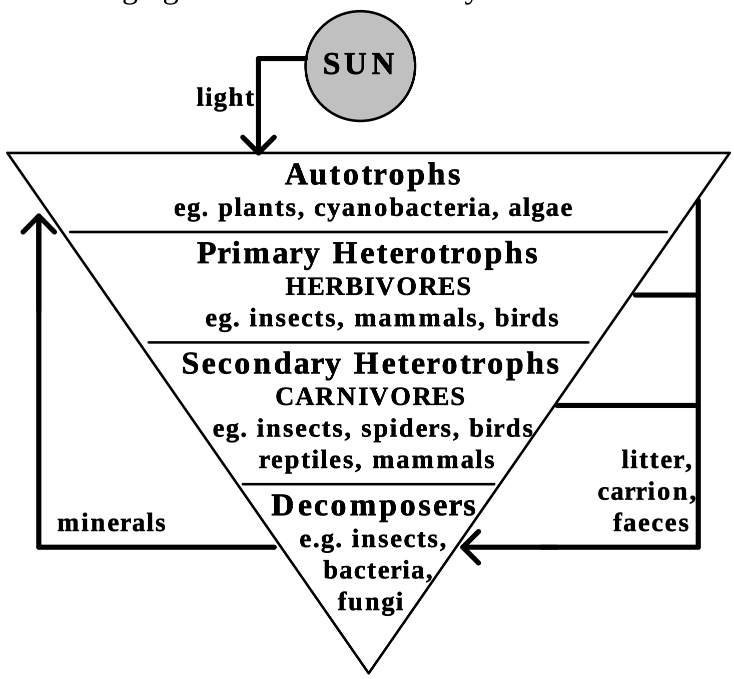

Fig. 4-1: Involvement of insects in the materials triangle as primary and secondary consumers and decomposers; see text for more details (graphic Schneider, M.F.)

Decomposing insects help to rapidly mineralise dead organisms, litter, etc. Therefore insects play a crucial role in food chains and contribute towards maintaining the natural balance between biotic and abiotic factors.

4.2 Insect-Plant Interactions

Plants and insects closely coevolved during the geological past leading to the success of both partners. The diversity of **Angiosperms** and **phytophagous** insects dramatically increased during the Jurassic period. The driving force of this coevolution and the advantage for flowering plants was their **pollination** by insects. However, the price for pollination paid by the plants is **herbivory**. Many plants became foodplants of phytophagous insects. Another reward for insects is nectar and pollen as food provided by flowers.

4.2.1 Herbivory

The majority of plants supply food for innumerable species of more or less specialised insects. **Monophagous** insects are **host-specific**, feeding on one particular taxon only. **Oligophages** have a few plant species to feed upon, whereas **polyphages** have a broad spectrum of host plants. About half the insect species are phytophagous and some taxa feed exclusively on plants like leaf-mining flies (**Agromycidae**), leaf beetles (**Chrysomelidae**), weevils (**Curculionidae**), butterflies and moths (**Lepidoptera**) and gall wasps (**Cynipidae**).
The different types of feeding like leaf chewing, mining, boring, sap sucking, seed predation and gall formation are discussed in **chapter 6.1**.
Of course, plants developed various defence strategies against herbivores. Physical defence strategies include spines, thorns, hairs, etc., but these seem to be more effective against the larger vertebrate herbivores. Chemical defence strategies of plants offer a large number of chemicals, especially to deter insects from feeding upon plants. These noxious or at least deterrent chemicals, also known as **secondary plant compounds**, **allelochemicals** or **phyto-chemicals**, include tannins, thiols, terpenoids (essential oils), alkaloids, cyanogenic glyco-sides and glucosinolates. Some of these com-pounds shown in **fig. 8-9** are end products of the plant metabolism. They are not eliminated from the plant tissues, if they possess deterrent properties and thus help the plant defend itself against herbivores. This kind of **constitutive defence** is usually only effective against less specific herbivores. Other chemical com-pounds are solely produced by the plant to defend against specific feeders. Since the synthesis of these chemicals requires energy, they are only produced, when feeding upon leaves occurs and thus to avoid further damage. This kind of chemical response is called **induced defence**.
Interestingly, there are a number of insects that have acquired the ability to resist toxic plant compounds. Even more, these insects might accumulate the ingested poisons in their bodies with the result of gaining protection from being consumed by predators. The phenomenon of chemical defence in insects is further outlined in **chapter 4.4.4**.
Defence strategies against insects developed by host-plants are also referred to as **plant resistance**. Plant resistance as an important tool in integrated pest management is further discussed in **chapter 8.4**.

In many cases herbivores are **pests** and negatively interfere with man's endeavour to grow various crops. However, the disastrous action of herbivores is sometimes desired. Particular beneficial herbivorous inset species can be used for the **biological control** of **weeds**. One outstanding example shown in **fig. 4-2**, is the weevil *Cyrtobagous salviniae* (**Curculionidae**) that has been introduced into PNG in order to control the water fern *Salvinia molesta* (**Salviniaceae**). During the climax of the *Salvinia* infestation in the early 1980s, approximately 2000 km² of the lower and middle Sepik were covered with a thick layer of the floating water fern. As a result of this, local transport by means of canoe was almost impossible and even engine-driven vessels could only be operated with difficulty. Apart

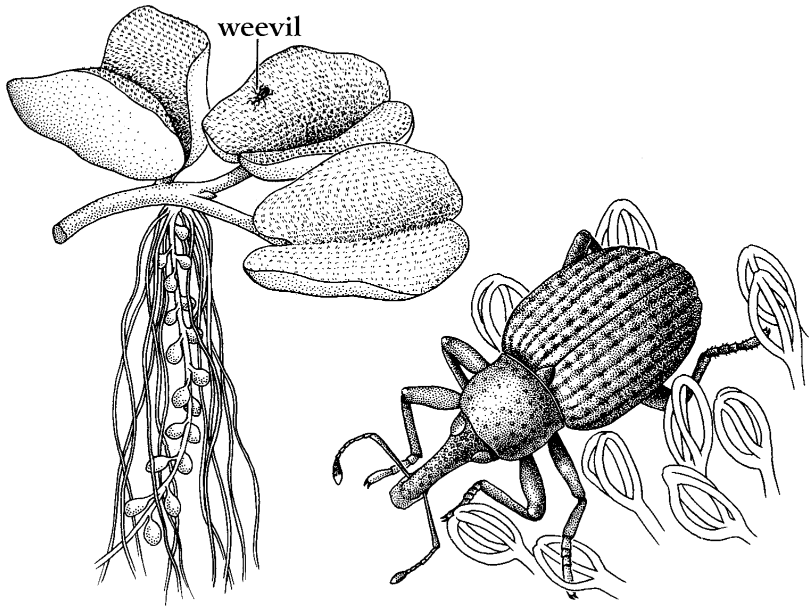

Fig. 4-2: The water fern *Salvinia molesta* and its natural control agent, the weevil *Cyrtobagous salviniae* (reproduced from Gullan, P.J. and Cranston P.S., 1994)

from disrupting the livelihood of the Sepik people, the ecological balance threatened to collapse, particularly the hundreds of lagoons which almost suffocated due to oxygen deficiency. Since *Salvinia* was accidentally introduced, there was no natural enemy to control the weed. The introduction of the weevil from its South American home and the establishment of its populations resulted in quick relief. The 2 mm long weevil perforates the water fern thus causing it to sink. Nowadays, both *Salvinia* and *Cyrtobagous* can be found along the Sepik river, however the water fern is perfectly controlled and kept in check by its natural enemy.

Some other insect species suitable as biological control agents against weeds are listed in **box 8-1**.

4.2.2 Pollination by Insects

Flowering plants are either pollinated by wind (**anemophily**) or by animals, mainly insects (**entomophily**). During pollination the pollen from male anthers is transferred to the female stigma of a flower of either the same plant (**self-pollination**) or a different plant of the same species (**cross-pollination**). The insects' ability to fly is fundamental for cross-pollination of flowering plants and the key for the success of Angiosperms. In comparison to wind, insects as pollinators

- increase pollination efficiency
- reduce pollen wastage
- pollinate successfully under conditions unsuitable for wind
- and are able to specifically pollinate rare plant species.

The reward for pollination is pollen and nectar as food for the pollinating insects (**plate 8 F**, **G**). Nectar is produced in **intra-** or **extrafloral nectaries** and consists of a solution of sugars such as fructose, glucose and sucrose. Pollen is mainly composed of proteins, sugars, starch, fat and traces of vitamins and minerals.

The production of pollen and nectar requires energy, therefore plants developed strategies to reward only pollinating insects and to prevent pollen and nectar being stolen by non-pollinators. The shape of flowers is often highly modified to allow access only to the specific pollinators. Only particular bees or wasps for instance can open an orchid flower and access the nectar hidden inside. Other examples are long, slender tubular flowers whose nectar can be recovered only by means of a long lepidopteran proboscis.

Specific odour and colours attract insects to the flower and furthermore guide them into it. That is why butterflies sometimes accidentally approach a colourful shirt or *bilum*. The flowers of some plants such as orchids even imitate the pollinator with the result that males might attempt to mate with the flower. This behaviour is called **pseudo-copulation**.

Flowers that are pollinated by beetles (**cantharophily**) are often small, dish- or bowl-shaped, of white or dull coloration. They emit an unpleasant or at least strong odour and the plant's ovaries are hidden from the mouthparts of the beetles. Pollinating beetles like scarabs (**Scarabaeidae**), jewel beetles (**Buprestidae**), longicorn beetles (**Cerambycidae**) and soldier

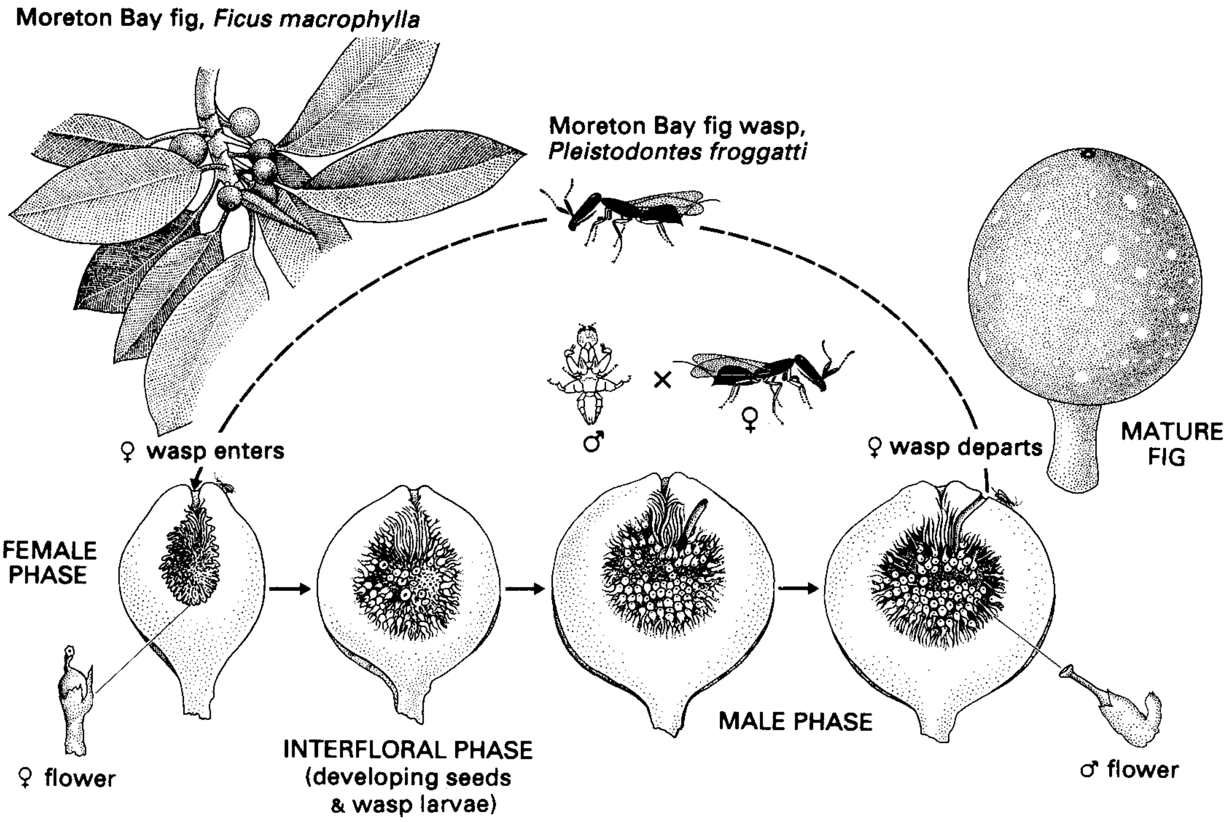

Fig. 4-3: Highly specialised pollination of figs (Moraceae) by fig wasps (Agaonidae). For details see text (reproduced from Gullan, P.J. and Cranston P.S., 1994)

beetles (**Cantharidae**) mainly harvest pollen from flowers.

Pollinating flies (**myophily**) usually prefer less conspicuous flowers releasing an unpleasant smell.

Pollination by wasps is known as **sphecophily**. An outstanding example for the specific and obligatory association of the development of figs and fig wasps is shown in **fig. 4-3**. A female fig wasp enters the **syconium** of a fig, pollinates female flowers and at the same time lays eggs in some of the female flowers. The larvae develop in the ovaries of the flowers. When the adult male wasps emerge, they mate with females that are still in the ovaries. The female wasps leave the syconium, when the male flowers have opened. Thus, a bit of pollen gets stuck to the female wasp and is carried to the next syconium to complete the cycle.

Pollination by ants (**myrmecophily**) is less common, but bees are the most important pollinators (**melittophily**). Their preferred flowers are often of bright yellow or blue colours, emitting a sweet, for humans pleasant scent. The flowers have guide-lines, that are often only visible in ultraviolet (**UV**) light, directing the bees to the nectaries. Bees are most valuable agricultural pollinators annually worth several billion Kina in the United States alone. However, the bees' endeavour can also cause severe ecological problems due to competition with native pollinators for nectar.

The tubular shaped, sweet-smelling flowers visited by butterflies and moths (**Lepidoptera**) have been mentioned already. Flowers pollinated by moths (**phalaenophily**) usually open during the night, hang downwards and are of light colours like white. The upright flowers visited by butterflies (**psychophily**) however, open during the day and are of bright yellow, red or blue colours.

4.2.3 Seed Dispersal by Insects

Seed dispersal by insects is less common, but might occur, if seeds are collected for the purpose of storage and then lost accidentally. However, particular ants actively collect seeds and disperse them, a phenomenon called

myrmecochory. The usually very hard thus inedible seeds are associated with fruit bodies or **elaiosomes**. The elaiosomes are edible and offered by the plant as a reward for dispersing seeds.

4.2.4 Other Symbiotic Interactions

There are a large number of other symbiotic interactions between plants and insects. The mutualistic interactions between particular ants and antplants (**myrmecophytes**) are outlined in **chapter 3.2.3**. Another example of a relationship for the benefit of both involved species is shown in **fig. 4-4**. The bull's-horn acacia provides shelter for ants in hollow thorns and offers food from **Beltian bodies** as well as nectar produced by **extrafloral nectaries** (**EFN**). In return, the resident ant protects its myrmecophyte from grazing mammals, herbivorous insects and keeps the antplant free from epiphytes and vines.

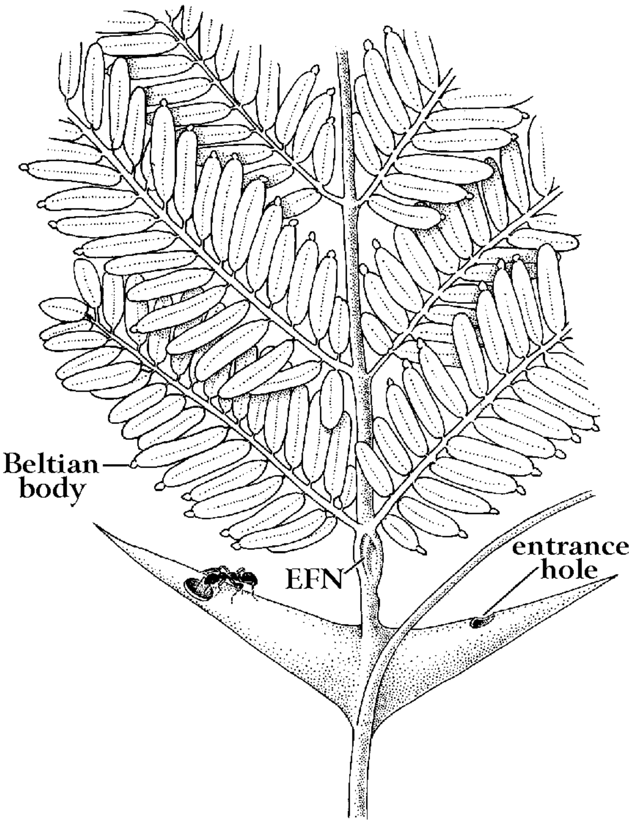

Fig. 4-4: The bull's-horn acacia, *Acacia sphaerocephala* and its resident ant, *Pseudomyrmex spp*. EFN: extrafloral nectaries. For details see text (reproduced from Gullan, P.J. and Cranston P.S., 1994)

Fig. 4-5: The insectivorous sundew *Drosera sp.* (photo Schneider, M.F.)

Parasitic interactions for the detriment of insects and the benefit of plants can be found as well. For instance insectivorous plants such as sundew, Venus fly traps and pitcher plants trap and digest insects and other small arthropods. The plants mainly extract the nitrogen compounds of insects, thus allowing the plant to grow on nitrogen deficient soils. 'The Future Eaters' by Flannery, T.F. (1994) offers interesting further reading on this topic.

Modified leaves of sundew, shown in **fig. 4-5**, possess sticky hairs. Insects are lured by the yellow colour of the leaves and by a specific scent. Once an insect sits on a leaf it becomes immediately stuck and can't escape. The hairs move the prey towards the centre for digestion. A genus of sundew occurring in Papua New Guinea is *Drosera*.

Venus fly traps work similarly, however the leaf consists of two hinged valve-like parts like a mussel, as shown in **fig. 4-6 A**. When an insect sits on the opened leaf, the two halves instantly close, thus trapping the insect for digestion. The leaf margins are armed with an array of spines, that prevent the insect from escaping (**fig. 4-6 B**).

Pitcher plants, as shown in **fig. 4-7**, have bowl-like modified leaves that are filled with liquid containing digestive enzymes. Prey is lured by

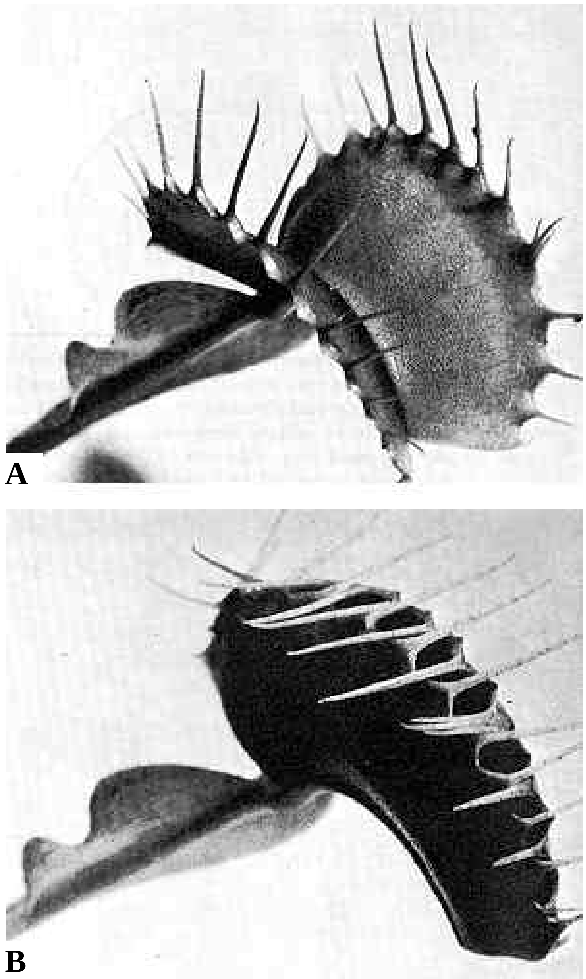

Fig. 4-6: The insectivorous Venus fly trap *Dinoaea muscipula*, open in (A), closed in (B) (photo Heath, B.J.W.)

nectar, colour and scent of the pitcher. Once an insect is trapped, it cannot escape and finally drowns. The inner walls of the pitcher are wax-coated and thus slippery. Furthermore, downwards directed guard hairs prevent the prey from escaping. Interestingly, there are quite a number of insects and other arthropods that can survive and even make their living in the pitcher's inhospitable environment without being harmed. **Inquilines** like mosquitoes and midge larvae as well as spiders inhabit pitchers and live together with the pitcher plant in a mutualistic relationship. The inquilines do not compete with the pitcher plant for prey, because the inquilines digest trapped prey and release the nutrients as faeces, in a readily available form for the plant. Pitcher plants belong the genus *Nepenthes* and also occur in Papua New Guinea.

4.3 Interactions between Insects and other Animals

This section talks about **symbiotic** interactions between insects on the one hand and other insects or animals in general or man on the other hand. The relationship can be either of a mutualistic, commensalistic or parasitic nature. Humans are molested by various parasites like mosquitoes, bed bugs, lice and sand flies. If the interaction is for the benefit of these parasites but without disadvantage for human beings we talk about **commensalism**. But if bedbugs continuously suck blood so that this eventually causes anaemia, then the relationship is **parasitic**, because it is for the detriment of the human being.

Insect predation and parasitism, a key for the understanding of biological pest control, are discussed in this section. Other mutualistic interactions, for instance between ants and aphids or scale insects were already mentioned in **chapter 3.2.3**.

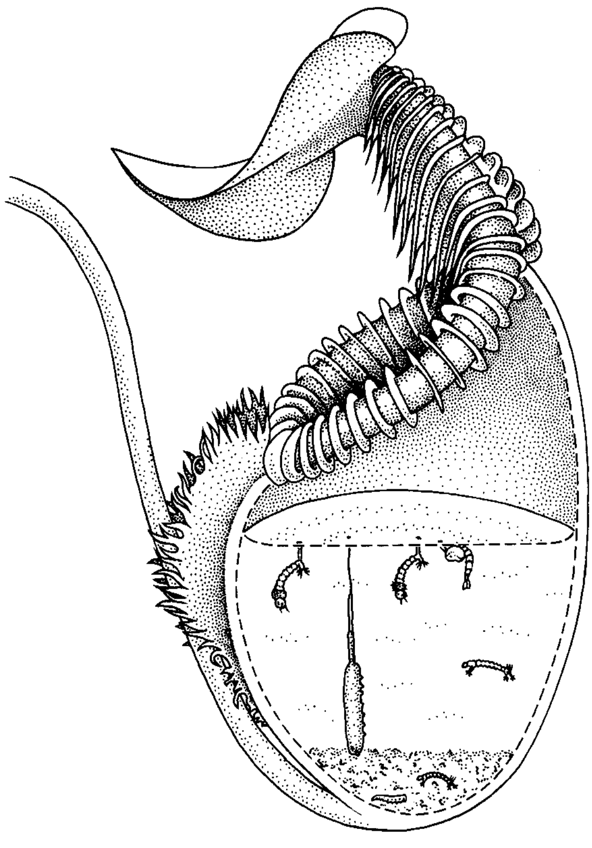

Fig. 4-7: Insectivorous pitcher plant with inquilines. See text for more details (reproduced from Gullan, P.J. and Cranston P.S., 1994)

4.3.1 Predation

Predation is defined as the **parasitic** interaction between a **predator** and its **prey**. The predator usually kills and consumes several prey animals during its life. Insects can either act as predators or fall prey to an **insectivore** or **entomophage**. Non-insect predators of insects are spiders and spider-like animals, fish, birds, reptiles, amphibians and mammals amongst others. Insectivorous plants like sun dew, Venus fly traps or pitcher plants can be considered as predators of insects, too.
Predacious insects are recruited from various insect orders or groups. These are for instance many ant and wasp species (**Hymenoptera**), leaf beetles, adult and larval lady bird beetles, ground beetles, rove beetles (**Coleoptera**), all damsel and dragon flies (**Odonata**), some true flies (**Diptera**), ear wigs (**Dermaptera**), some cricket species (**Orthoptera**), the larvae of lace wings, the ant lions (**Neuroptera**), cicadas and various bugs, eg. assassin bugs (**Hemiptera**), alder and dobson flies (**Megaloptera**), praying mantids (**Mantodea**, **plate 3 A**) and snake flies (**Raphidioptera**).

Predators and pests can't be regarded in isolation, each on its own. Moreover, predator and prey usually have developed a close and specific relationship during evolution.
Predators follow various ways to catch, overwhelm and eventually kill prey. A time-consuming possibility requiring little energy is to hide and wait for prey to come along. This is done for instance by camouflaged praying mantids shown in **fig. 4-8** or antlions, hidden in their craters, as shown in **fig. 4-9**. The other extreme which is less time-consuming but requires a lot of energy is to actively hunt for prey. Ground beetles (**Carabidae**) for instance run after their prey and dragon and damsel flies (**Odonata**) chase prey whilst in flight.
The prey sooner or later evolves defence strategies in order to avoid being eaten, as outlined in **chapter 4.4**. The predator then has to catch up with the prey's novel strategy in order to secure supply of prey and ensure survival. This kind of interaction between two or more organisms is called **coevolution**.

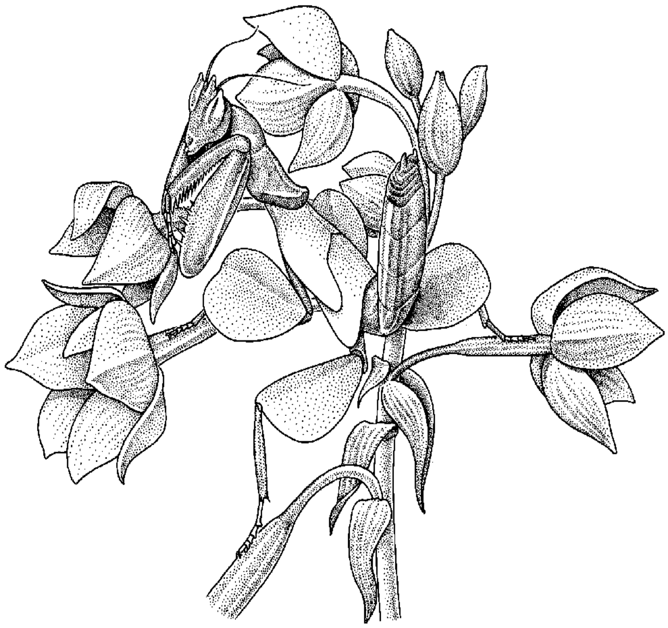

Fig. 4-8: Camouflaged praying mantis (Mantodea) waiting for prey (reproduced from Gullan, P.J. and Cranston P.S., 1994)

The predator-prey relationship is particularly important for the development of effective biological pest control strategies. The idea is to identify a suitable predator that more or less specifically feeds upon an undesired pest. The next step is to establish the population of the predator so that it is then able to significantly reduce and control the pest population. The dynamics of predator and prey populations are shown in **fig. 4-26**, the practical implications for biological control as well as further perspectives are discussed in **chapter 8.7.2**.

4.3.2 Parasitism

Parasitism is a relationship between a **parasite** and its **host**. The interaction benefits the parasite at the expense of the host, but usually without killing the latter. In contrast to that, **parasitoids** eventually kill their host. According to whether a parasite or parasitoid lives internally or externally, we add the prefix **endo**- or **ecto**-. An ectoparasite for instance is a parasite living externally on the host. **Super-parasitism** is the occurrence of more than one parasitoid within a particular host. **Hyper-parasitism** is the condition of a secondary

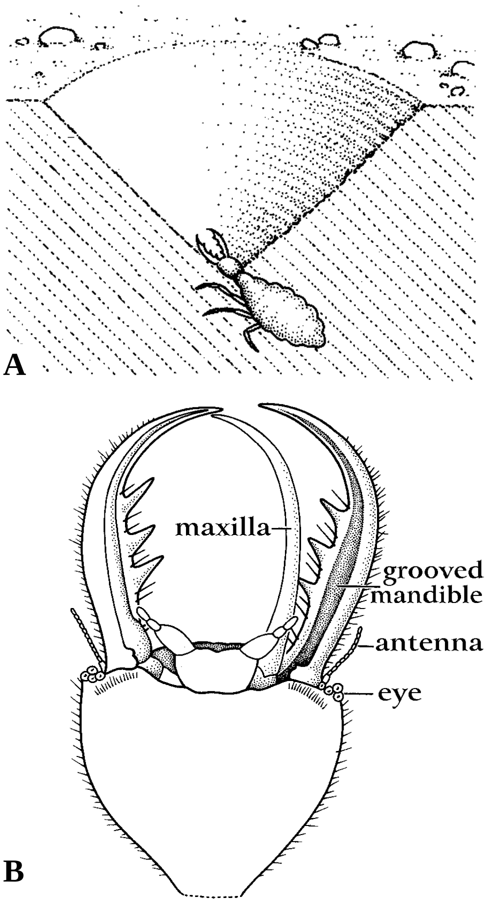

Fig. 4-9: The lacewing larva, called antlion (Neuroptera), is abundant in very dry sandy, poor soils such as under houses. There it builds a small crater of 4 to 5 cm in diameter and buries itself in the centre (A). A trespassing ant might cause a few sand grains to drop from the rim into the crater. Once the antlion realises the ant is there, it throws sand towards the prey, eventually triggering an avalanche that forces the ant down into the crater, where it is grabbed by the antlion with its claw-like jaws (B) (reproduced from Gullan, P.J. and Cranston P.S., 1994)

parasite or parasitoid developing upon another parasite or parasitoid. Finally, multiparasitism defines parasitization of a host by two or more parasites or parasitoids.

Apart from a large number of bacteria, fungi, and protists, several insects and allies such as mites (**Acari**), stylops (**Strepsiptera**), many species of parasitic flies (**Diptera**) and wasps (**Hymenoptera**), and a few others are parasites or parasitoids of insects. These are then referred to as **entomoparasites** and **entomoparasitoids**, respectively (see **fig. 4-10**).

Insects and allies that harm other insects, animals or man as parasites or parasitoids can be found amongst mites and ticks (**Acari**), lice (**Phthiraptera**), true bugs (**Hemiptera**), fleas (**Siphonaptera**) and flies (**Diptera**). These are of medical or veterinary importance, if they interfere with humans, livestock or pets. Some are even vectors for severe diseases, caused by microorganisms. Fleas of rodents for instance transfer bacteria causing pestilence in humans and mosquitoes transfer malaria or dengue fever as further outlined in **chapter 5.6.3.26**.

There is no sharp distinction between predators and parasites but in general, parasites are much smaller and seem to be more specific than predators. **Host preference** of one host over another is lower in ectoparasites but often highly specific in endoparasites. Hosts are often located by means of chemical communication (see **chapter 3.1.3**). Some parasites trace their hosts by following their sex attractants. Blood-sucking parasites often locate their hosts by detecting carbon dioxide and other volatile gases exhaled by the host. Many parasites of phytophagous hosts use

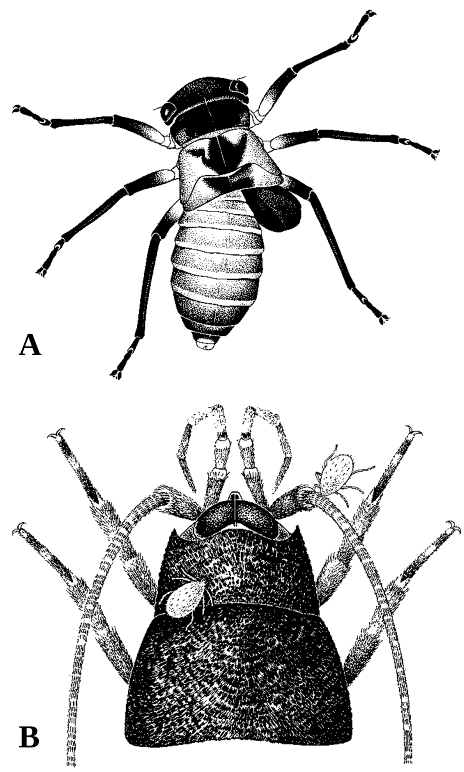

Fig. 4-10: Ectoparasites of insects on their hosts: (A) parasitic wasp on a homopteran bug, (B) larval mites on the head of a bristletail (reproduced from CSIRO, 1991)

synomones for host location. Synomones are released by a plant when attacked by the phytophage or otherwise stressed.

Similar to predator-prey relationships, the interactions between parasite and host are subject to continuous coevolution. One of the host's major interests is to develop suitable and effective defence strategies against the parasite. The host's immune system usually responds and is able to eliminate endoparasites. Therefore endoparasites evolved several ways to escape from the effects of the host's immune system by encapsulation, molecular mimicry or interference with the host's immune system so that it is no longer effective against the parasite.

Entomoparasites and parasitoids are invaluable biological control agents, if pest species are parasitized. A number of true flies (**Diptera**) and wasps (**Hymenoptera**), especially of the family **Trichogrammatidae** are effective parasitoids of eggs and other stages of their host's life cycle. These are further discussed in **chapter 5.6.3.30** and **8.7.2**.

4.4 Insect Defence

Various organisms, including insectivorous plants depend more or less on insects as a source of food. Since insects can be found everywhere in abundance and since they have quite a high nutrient value, they are suitable and easy prey for innumerable predators. Therefore insects had to evolve strategies to avoid being eaten. Protective coloration, scare tactics, chemicals as well as morphological and behavioural adaptations protect insects and thus secure their survival.

Many insects make use of **chemical defence** strategies and are disastrous or even toxic. Being unpalatable or otherwise distasteful is often associated with warning or **aposematic coloration**. During the night however, this does not help nocturnal insects very much, because it is dark and a predator like a bat for instance can't see the warning coloration. Therefore it is advantageous to develop an additional defence strategy, that protects the insect during the night. This is the case in some tiger moths (**Arctiidae**). The moths interfere or disturb the echolocation system of bats by emitting a rapid series of ultrasonic clicks. However, that doesn't help in all cases, because some bats then simply change the frequency and are thus able to detect their prey. Some poisonous tiger moths even tell the bat via an ultrasonic signal: '*I am distasteful, don't touch me*'.

The knowledge of the type of defence strategy used by a particular pest species can save a lot of time and money when biological control strategies against the pest have to be developed. If the pest uses aposematic coloration for its defence, then it is in general effectively protected from day-time predators. Therefore, the use of a predator as a biocontrol agent is quite likely to fail. Since warning coloration is not effective against parasitoids, it is definitely more promising to search amongst parasitoids for a suitable biocontrol agent.

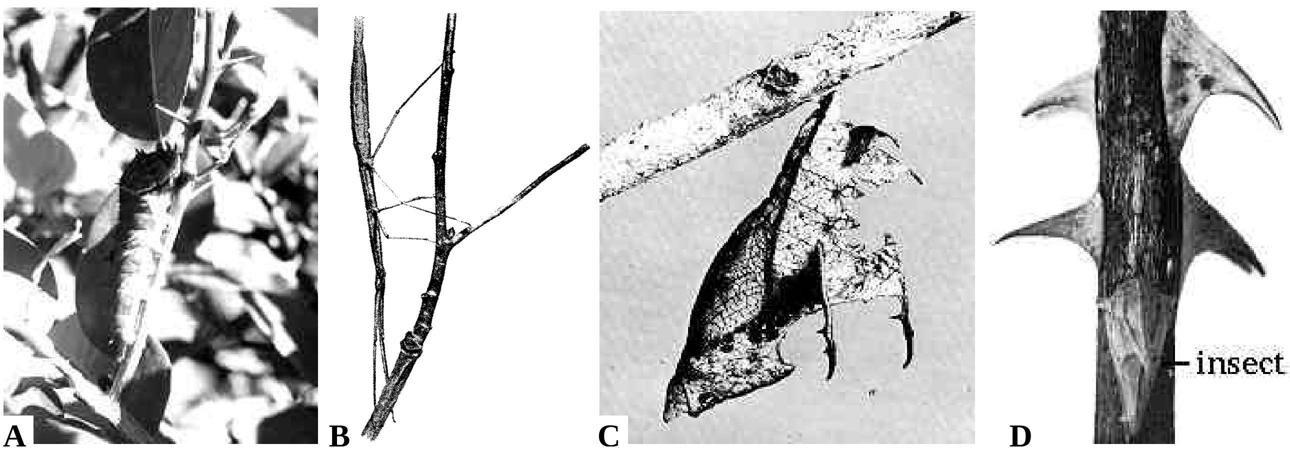

Fig. 4-11: Defence Strategies of Insects: (A[†]) camouflaged *Papilio aegeus* caterpillar, (B[‡]) stick insect imitating a twig, (C[‡‡]) moth pupa imitating a dry leaf, (D[††]) pupa imitating a thorn (photos Schneider, M.F. [†]; British Museum, Natural History[††]; Tweedie, W.F. [‡‡]; reproduced from Ross, H.H., 1982[‡])

Fig. 4-12: 'Sinister' face of a smaller mammal on the forewings of the Sphingidae moth *Psilogramma menephron* (photo Schneider, M.F.)

4.4.1 Protective Colour Patterns

There are several ways of protecting insects by the use of colour patterns. **Cryptic** coloration usually makes the bearer invisible and thus hidden from a predator. **Camouflage** can be gained by resembling the background or disrupting one's own silhouette. There are many examples like green grasshoppers, stick insects, leaf insects, the upper sides of the forewings of moths, the under side of the wings of butterflies, as shown in **fig. 4-11 A**, **plate 1 A** to **C** and **plate 3 C**. Another form of cryptic coloration is the resemblance of an object in the environment, that is of no interest and relevance for the predator. This strategy is called **mimesis** or **masquerade**. Insects developed the ability to mimic an endless variety of objects such as leaves, twigs, thorns and bird droppings. Some examples are shown in **fig. 4-11 B** to **D** and **plate 1 D** to **F.** Camouflage is not only used for protective purposes, but it is also important for predators to be invisible to prey whilst waiting for it, as shown in **fig. 4-8**. Apart from crypsis, being hidden by means of camouflage and mimicry, some insects use **scare tactics**. **Sinister faces** and **false eye spots** act as deterrents, scaring an approaching predator that will eventually give up the intention to attack the insect. Sinister faces shown in **fig. 4-12** and false eye spots shown on **plate 2 A** and **B** can be found on wings of moths like **Noctuidae** and **Sphingidae** and butterflies of the families **Papilionidae** and **Nymphalidae**. Noctuid moths are also called '**underwings**', because many of them have brightly coloured eye spots on the uppersides of their hindwings (see **plate 2 B**). These 'underwings' are invisible during rest because they are covered by the camouflaged forewings. Upon disturbance, these moths open up the forewings, display the false eyes and thus scare away an intruder.

4.4.2 Morphological Defence

Defence is not only used against predators, but also helps during territorial fights for instance, to successfully defeat an opponent. Various morphological adaptations like particular body shapes of ectoparasites contribute to avoid being scratched off the host. This can be found in laterally compressed fleas, making it difficult for a dog to get rid of the nuisance. Morphological structures such as the cuticle or its extensions or modified mouthparts are used by many insects for defence. Other examples include the heavily sclerotized exoskeleton of beetles and fleas, protective shield-like pronota as found in cockroaches, sharp and pointed claws of many beetle species, hardened forewings (**elytra**) of beetles, spines and spurs for instance on the legs of grasshoppers or all over particular stick insects (see **fig. 4-13 A**). Hairs of caterpillars, as shown in **fig. 4-13 B** and on **plate 2 C** and **D**, sometimes irritating, are left untouched by bigger predators because it is almost impossible to swallow such an armed caterpillar. Mandibles are suitable weapons and bites can be easily experienced when improperly handling grasshoppers or beetles. The use of shelters for defence is common in larval caddis flies (**Trichoptera**). The larvae are hidden in cases made from little stones or plant material spun together with silk, shown in **fig. 5-47**. The

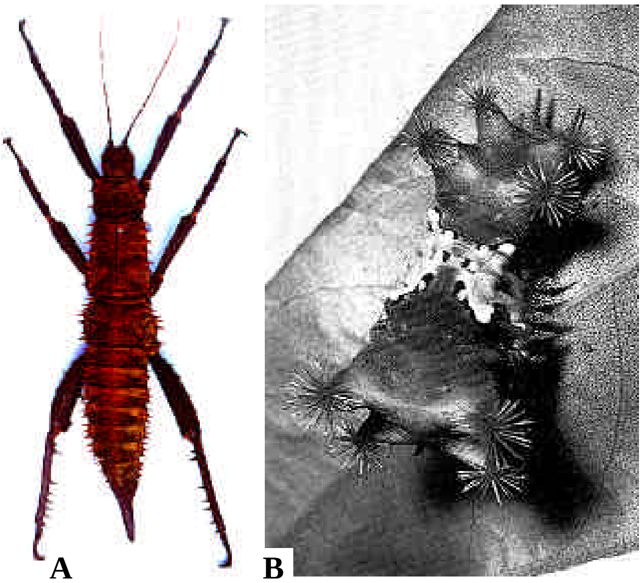

Fig. 4-13: Protective structures: (A†) spines on the stick insect *Eurycantha horrida* ♂ (Phasmatidae), (B††) stinging spines of the cupmoth caterpillar *Doratifera vulnerans* (Limacodidae) (photos Schneider, M.F.†, CSIRO, 1991††)

pupae of many moths like silk moths (**Bombycidae**) are protected by cocoons. Scale insects, woolly aphids, white flies and many other **Hemiptera** produce shields and other protective structures from wax, powder, spittle, etc. (**figs. 5-25 C**, **E**, **F**, **H**, **6-3 J**, **6-7**, **box 6-1 N**). The scales of moths and butterflies come off easily. When a 'scale wing' gets trapped in a spider web, only some scales get stuck, the rest of the animal has a fair chance of escape. Particular ant soldiers have plug-shaped heads, that are used to block entrance holes of their

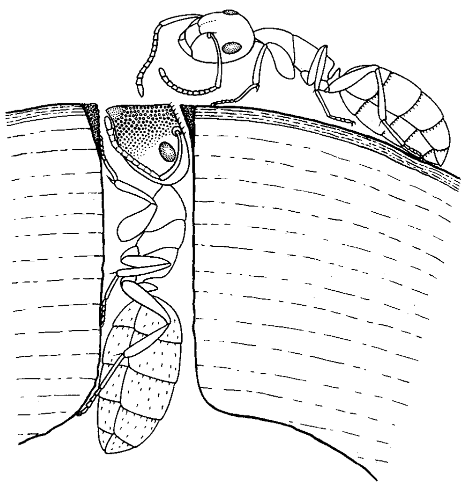

Fig. 4-14: Nest-blocking of a soldier of the European ant *Colobopsis truncata* (reproduced from Gullan, P.J. and Cranston P.S., 1994)

nest, as shown in **fig. 4-14**. **Autotomy** is the shedding of appendages, such as legs for the purpose of defence. This is done by some praying mantids (**Mantodea**) and stick insects (**Phasmatodea**) that sacrifice a leg grasped by a predator. The lost leg can be regenerated by immature stick insects during the next moult.

4.4.3 Behavioural Defence

Behavioural defence strategies comprise escaping by crawling, jumping, flying, hiding or dropping upon disturbance. Dropping down is a common strategy of many beetles and some moths when attacked. **Noctuidae** moths for instance are able to hear ultrasound of the echolocation system of an approaching bat. A moth drops out of the range of the bat's radar system as a reflex to escape from being eaten. Shamming death, called **thantosis**, is a common defence strategy amongst beetles, in particular in weevils (**Curculionidae**). The animal remains motionless and stiff, thus the predator loses interest in the apparently dead prey or can't locate its prey any more. Click beetles (**Elateridae**, **plate 3 R**) have a muscular articulation between prothorax and mesothorax that enables the beetle to snap its body. As a result, the beetle skips and clicks in a scaring way. **Sphingidae** moths avoid contact with bats, their predators, by being active during the early morning, when bats are already asleep.

4.4.4 Chemical Defence

The importance of chemicals for insect communication is outlined in **chapter 3.1.3**. Chemicals also play a major role in the defence of insects against predators. The number of chemicals used for this purpose is diverse and can be categorised into **noxious** and **antifeedants** or **deterrents**.

Noxious chemicals act as emetics, inducing vomiting, or hurt, irritate, poison or paralyse an aggressor, either immediately or some time after contact. Noxious chemicals are recruited from the groups of cardenolides, alkaloids and cyanogenic glycosides that often originate from poisonous foodplants.

The second class of chemicals, the antifeedants and deterrents are usually not noxious and are used as a warning sign for the predator. Antifeedants and deterrents are volatile acids, ketones, aldehydes, terpenes, quinones, etc. They are generally produced by the insect itself and are of bitter taste or have an unpleasant smell. In low concentrations a number of noxious chemicals also act as deterrents.

Many disastrous insects use a mixture of both classes of chemicals, deterrents to warn the predator and poisons to eventually teach it a lesson, if the warning is ignored. The chemicals are in many cases derived from food plants, that contain the poison. Larval *Danaus plexippus* (**Nymphalidae**, Danainae), shown on **plate 2 K**, for instance feed on poisonous milkweeds *Asclepias spp.* (**Asclepiadaceae**) that contain cardenolides. The caterpillars accumulate the poison in their bodies, become poisonous themselves and thus gain protection. The poison can even be found in eggs, pupae and adults, shown on **plate 2 L** and **M**, that do not feed on the poisonous plants. Other examples of caterpillars and their poisonous foodplants are

- birdwing butterflies *Ornithoptera spp.* (**Papilionidae**) feeding on *Pararistolochia* and *Aristolochia* vines (**Aristolochiaceae**) containing aristolochic acid
- moths of the families **Aganaidae** and **Arctiidae** (Tiger moths) and
- other **Danainae** (**Nymphalidae**) butterflies whose larvae feed on **Apocynaceae** and **Asclepiadaceae** containing cardenolides, alkaloids and cyanogenic glycosides.

More examples are shown in **box 5-6**. However, preliminary results of my own studies have revealed that none of the above insects collected in PNG contained poisons in concentrations, that could harm a predator, as assumed by various scientists. It seems that PNG insects are rather the exception than the rule.

In a number of insects, poisonous compounds of plants are actually not incorporated but stored 'outside' the body. For instance some **Pergidae** wasps (**Hymenoptera**) and many **Oecophoridae** moths (**Lepidoptera**) feed on eucalyptus leaves containing poisonous essential oils. These are stored in diverticles of the guts (the guts are considered as outside!) and exuded upon disturbance. Other insects excrete and store the chemicals in prothoracic glands. This is the case in the distasteful Tiger moth *Rhodogastria crokeri* (**Arctiidae**) that produces a pungent foam-like secretion containing pyrazines, when disturbed. Such an animal is shown on **plate 2 J**. Many stink bugs and cockroaches have stink glands for the production of deterrents.

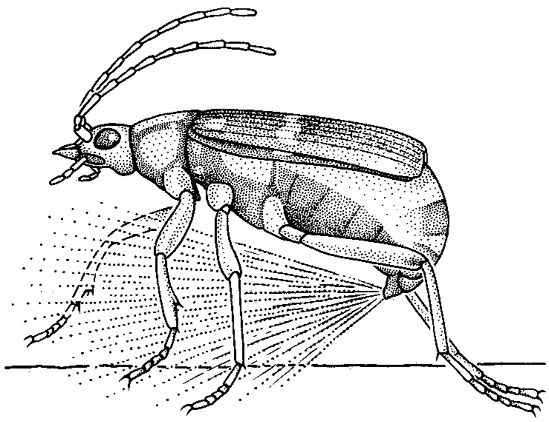

Fig. 4-15: Chemical defence: adult bombardier beetles (Carabidae) ignite a binary weapon made from hydrogen peroxide and hydroquinones in an abdominal combustion chamber. The resulting explosion launches the beetle out of the reach of the antagonist. Furthermore, the audible 'pop' of the explosion scares away the attacker. Lastly, the product of the chemical reaction, a p-benzoquinone, directed at the aggressor, acts as a tear gas, resulting in temporary blindness (reproduced from Gullan, P.J. and Cranston P.S., 1994)

The peculiar and multiple defence mechanism of the bombardier beetle is described in **fig. 4-15**. Formic acid, a strong organic acid is used for defence by **Formicidae** ants like the red arboreal ant *kurakum*. The ants spray formic acid on intruders, causing painful irritations of the skin (see **chapter 5.6.3.30**). Venomous bites and stings are used by spiders, scorpions, bees and bumblebees as well as by some wasps and ants for self defence and for killing or paralysing prey. The venoms contain one or several of the following pharmacologiaclly active chemicals: **polypeptide enzymes** such as hyaluronidases, phosphoesterases and phospholipases; **biogenic amines** like histamine, noradrenaline, adrenaline, dopamine, serotonine; and **alkaloids**. Caterpillars of **Papilionidae** butterflies, eg. of the genera *Troides* and *Ornithoptera* possess eversible stink glands called **osmeteria**. An osmeterium is a thoracic pouch into which toxins of the poisonous food plants are excreted. The osmeteria are everted upon disturbance, as shown on **plate 2 I**.

Being disastrous or unpalatable is often closely correlated with a conspicuous warning or **aposematic coloration**. Aposematism makes use of contrasting, bright red, orange or yellow colours and is sometimes associated with audible signals. Warning signals together with a bad experience for a predator for instance a sting or the bitter taste of the prey, trigger a learning process. Thus, the aggressor will avoid prey of that particular coloration in future. Aposematism is often associated with gregarious or aggregated animals.

4.4.5 Mimicry

Mimicry is defined as the close resemblance of two or more unrelated species. The disastrous species serves as a **model** that is imitated by the **mimic**. The mimic gains protection by looking like the disastrous model. Thus the mimic benefits from this relationship. Mimicry can be divided into **Batesian mimicry** and **Müllerian mimicry**.

The resemblance of two or more disastrous or inedible organisms is called **Müllerian mimicry**. It causes enhanced learning in predators, which having once tried the one species will avoid the other, too. A remarkable example is the moth *Alcides agathrysus* (**Uraniidae**), that is imitated by the swallowtail butterfly *Papilio laglaizei* (**Papilionidae**). The day-active *Alcides* often occurs in flocks of ten or so animals. A closer look might reveal one particular animal, whose flight is more clumsy and different from the others. This animal is *Papilio laglaizei* that intermingles with the moths. **Plate 2 E** to **H** show the striking resemblance of under- and uppersides of both species. The characteristic orange spot on each side of *Alcides*' abdomen is lacking on *P. laglaizei*. However, the latter has the two orange spots on the underside of the hindwings, evoking the impression that the spots are on the abdomen.

Many edible or otherwise defenceless organisms gain protection by imitating the warning coloration, shape and patterns of a distasteful, poisonous or inedible organism like some beetles or wasps. This kind of mimicry is called **Batesian Mimicry**. Many hover flies (**Diptera**: **Syrphidae**) for instance have a yellow and black banded abdomen, like their models, the venomous wasps. Some other examples are shown in **fig. 4-16**.

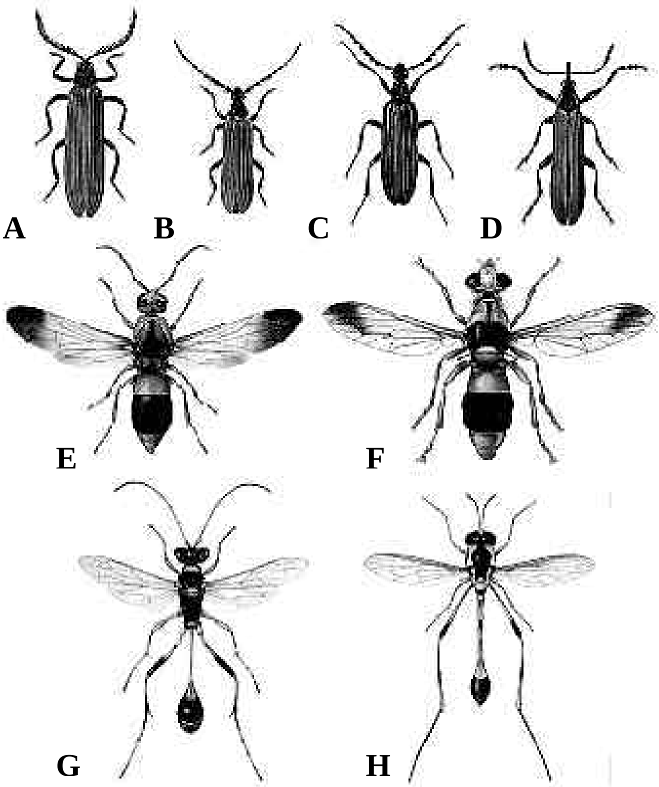

Fig. 4-16: Mimicry: (A) the poisonous beetle *Metiorrhynchus spp.* (Lycidae) is imitated by the harmless beetles (B) *Eroschema spp.* (Cerambycidae), (C) *Tmesidera spp.* (Meloidae) and (D) *Rhinotia spp.* (Belidae); (E) the venomous wasp *Pseudabispa spp.* (Vespidae) is imitated by the non-venomous fly (F) *Chrysopogon spp.* (Asilidae); (G) the venomous wasp *Sceliphron spp.* (Sphecidae) is imitated by the innocuous fly (H) *Systropus spp.* (Bombyliidae) (reproduced from CSIRO, 1991)

4.5 Interactions between Insects and Microorganisms

There are mutual and parasitic interactions between many insects and a wide range of microorganisms like bacteria, fungi and protista. These are either **symbionts** or **pathogens** of insects or serve as a source of food for **fungivorous** insects.

A large number of microorganisms live in close mutual association with insects, for the benefit of both partners. The relationships are subject to coevolution between insects and their **symbionts**. Extra- and intracellular symbionts provide enzymes for the digestion of otherwise unusable resources or predigest diet into assimilable substances, that can be further metabolised by the insect. For example cellulase, an enzyme to break down cellulose, the major compound of wood, is produced by protozoan symbionts of termites. Intracellular symbionts are often associated with the fat body, the major metabolic organ in insects and the gonads. The latter are important, because intracellular symbionts are ‘inherited’.

Fungivores or **mycophages** are fungus eating mites (**Acari**), **Collembola** and insects like cockroaches (**Blattodea**), termites (**Isoptera**), book lice (**Psocoptera**), bugs and allies (**Hemiptera**), thrips (**Thysanoptera**) and a large number of beetles (**Coleoptera**), wood wasps and leaf-cutting ants (**Hymenoptera**) and flies (**Diptera**). Some decomposing fungi make use of resources like wood, that usually can’t be used by the insect itself. Some insects like leaf-cutting ants in their fungus gardens literally cultivate ectosymbiotic fungi. **Ambrosia beetles** have their name from the ambrosia fungus (**Ascomycota**) that is cultivated by the beetles in galleries excavated in wood. The beetles feed upon specialised cells of the fungus, the yeast-like palisades. The digestion of fungi however requires a special enzyme called **chitinase**, to break down the chitin of the fungal cell walls. Fungivorous ants, termites and ambrosia beetles are further discussed in **chapters 3.2**, **6.2.1** and **6.2.5**.

Insects are attacked by a large number of internal as well as external **entomopathogens**. Examples are **bacteria** such as *Bacillus thuringiensis*, entomopathogenic fungi of the genera *Nosema*, *Entomophthera*, *Metarhizium*, *Beauveria* and *Aspergillus*, **viruses** like *Baculo* virus and **protista**. These are potentially lethal for insects, therefore they contribute towards the natural regulation of insect populations. This property is used by mankind to screen for entomopathogens that are suitable biological control agents for the regulation of pest species. Applied aspects of entomopathogens are further outlined in **chapter 8.7.1**.

4.6 Insects as Decomposers

Decomposition is defined as the action of **heterothrophic** organisms, breaking down dead organic matter to simpler organic or inorganic material. Dead organic matter is the source of food for various organisms like decomposing fungi, bacteria, protista, insects, arthropods, nematodes, etc. Organic matter can be derived from vegetation, ie. fallen leaves, flowers, fruits, twigs and wood, called **litter**. Apart from plant debris, the dead organic matter can be of animal origin, like faeces or **dung** and **carrion**.

The major task of decomposing insects and other arthropods is to physically break-down organic matter, thus increasing the surface area for the further impact of microorganisms. At the end of the decomposition process, minerals re-enter the nutrient cycle of plants.

The decomposing fauna, shown in **fig. 4-17**, can be further divided into large decomposers like earthworms, woodlice and millipedes and smaller decomposers such as a large number of mites (**Acari**) and **Collembola**. The latter organisms are also referred to as **microfauna**.

Since dead organic matter is mostly associated with the upper layers of soil - the litter and humus layer - most decomposers can be found there. Soil-dwelling insects usually are adapted to this kind of life. Mole crickets (**Orthoptera**: **Gryllotalpidae**), scarab beetles (**Coleoptera**: **Scarabaeidae**) as well as nymphal cicadas

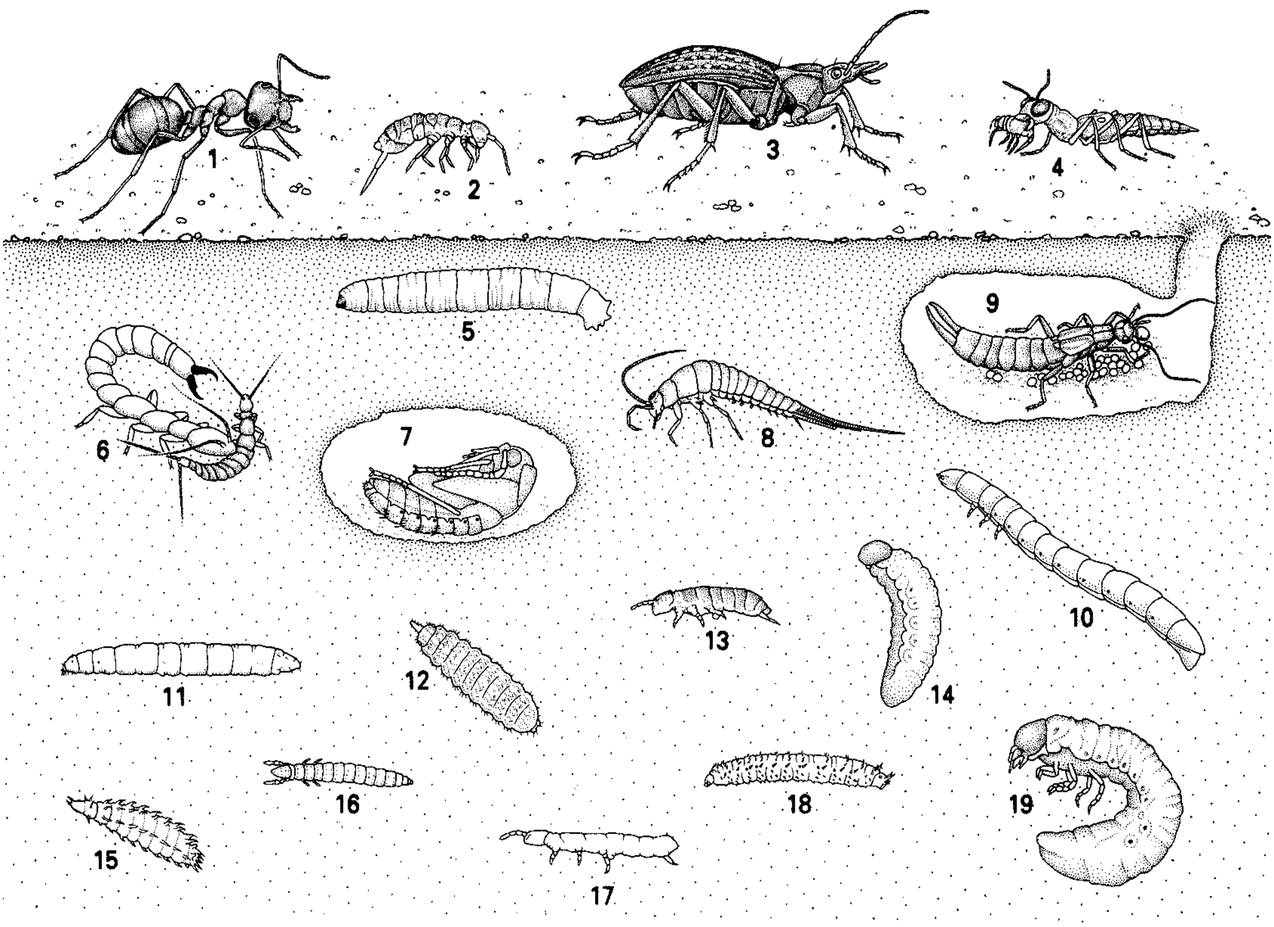

Fig. 4-17: Insects and allies of litter and soil: (1) worker ant (Hymenoptera: Formicidae), (2) springtail (Collembola), (3) ground beetle (Coleoptera: Carabidae), (4) rove beetle (Coleoptera: Staphylinidae) eating a springtail, (5) larval crane fly (Diptera: Tipulidae), (6) dipluran (Diplura: Japygidae) attacking a smaller campodeid dipluran, (7) pupa of ground beetle (Coleoptera: Carabidae), (8) bristletail (Archaeognatha: Machilidae), (9) female earwig (Dermaptera: Labiduridae), (10) wireworm, larva of a tenebrionid beetle (Coleoptera: Tenebrionidae), (11) larva of a robber fly (Diptera: Asilidae), (12) larva of a soldier fly (Diptera: Stratiomyiidae), (13) springtail (Collembola: Isotomidae), (14) weevil larva (Coleoptera: Curculionidae), (15) larva of a muscid fly (Diptera: Muscidae), (16) proturan (Protura: Sinentomidae), (17) springtail (Collembola: Isotomidae), (18) larval march fly (Diptera: Bibionidae), (19) larval scarab beetle (Coleoptera: Scarabaeidae) (reproduced from Gullan, P.J. and Cranston, P.S., 1994)

(**Hemiptera**: **Cicadidae**) have fossorial legs adapted for digging, as shown in **fig. 2-20 E**. Other soil-dwellers are wingless like **Diplura**, **Collembola** and **Archaeognatha** or at least have reduced wings like termites (**Isoptera**) and **Staphylinidae** beetles or their wings are protected and covered by **elytra** like in most beetles. The dark and moist conditions in the soil suit the requirements of mainly blind and unpigmented soil-dwelling arthropods.

Some specialised feeders of litter, carrion and dung are briefly outlined below.

Fungivorous soil-dwelling decomposers like wood-eating (**xylophagous**) beetles and termites are discussed in the **chapters 3.2.1**, **4.5** and **6.2.1**.

Some **Chrysomelidae** beetles and the larvae of many **Oecophoridae** moths feed on leaf litter of eucalyptus, containing poisonous essential oils. In areas where Eucalyptus was introduced, leaf litter piles up if the specialised decomposers do not occur naturally. This is, because there are no other decomposers that can handle the high content of essential oils.

Saprophages or **scavengers** feed upon dead animals. Many species of true flies like bow flies (**Diptera**: **Calliphoridae**), house flies (**Diptera**: **Muscidae**), as well as beetles of the families **Histeridae**, **Silphidae**, **Cleridae**, **Dermestidae** and **Staphylinidae** colonise and subsequently disintegrate carrion. One amazing example is the 'grave digger' *Necrophorus* (**Coleoptera**: **Silphidae**), occurring in Europe. A pair of the beetles digs away soil from under the body of a dead small bird or mammal. Slowly but continuously the body sinks and once it is completely buried, the female lays eggs onto the body. The larvae eat up the body during their development.

Coprohagous insects use dung or faeces as a source of food. True flies like the house fly *Musca domestica* (**Diptera**: **Muscidae**) are attracted in large numbers to faeces to lay eggs into this substrate. This might cause unpleasant fly problems, but can become a health hazard too, since flies can carry diseases from faeces to new hosts.

Dung beetles (**Scarabaeidae**: **Coleoptera**) however, contribute to disturb dung, thus limiting fly-breeding. There are about 7,000 species of dung beetles, mainly found in Africa. Their importance for the decomposition of dung of larger mammals is outstanding. In Africa, dung beetles process about one ton of elephant dung per hectare each year. Dung balls are formed and dug by the beetles in burrows below the dung pad. Within the dung balls, the development of the beetles takes place. The dung ball is subsequently consumed by the larvae, as shown in **fig. 4-18**. Thus, dung beetles virtually 'plough' soil, loosen it and bring the remineralised dung to the close vicinity of the roots of plants. If dung beetles are not present, dung of cattle for instance can become a serious pest, smothering pastures and causing severe fly problems. Furthermore, particular husky grasses disliked by grazing cattle, become dominant around dung pads thus decreasing the availability of suitable fodder. Therefore, dung beetles had to be introduced to areas where cattle was introduced and where dung beetles did not occur naturally. For that purpose some species of dung beetles were deliberately introduced to Papua New Guinea, eg. *Ontophagus gazella* to Central, Oro, East Sepik and East New Britain Provinces in 1973, others like *O. binodus* and *O. obliquus*, *Onitis alexis*, *O. vanderkelleni* and *Sisyphus spinipes* were introduced later.

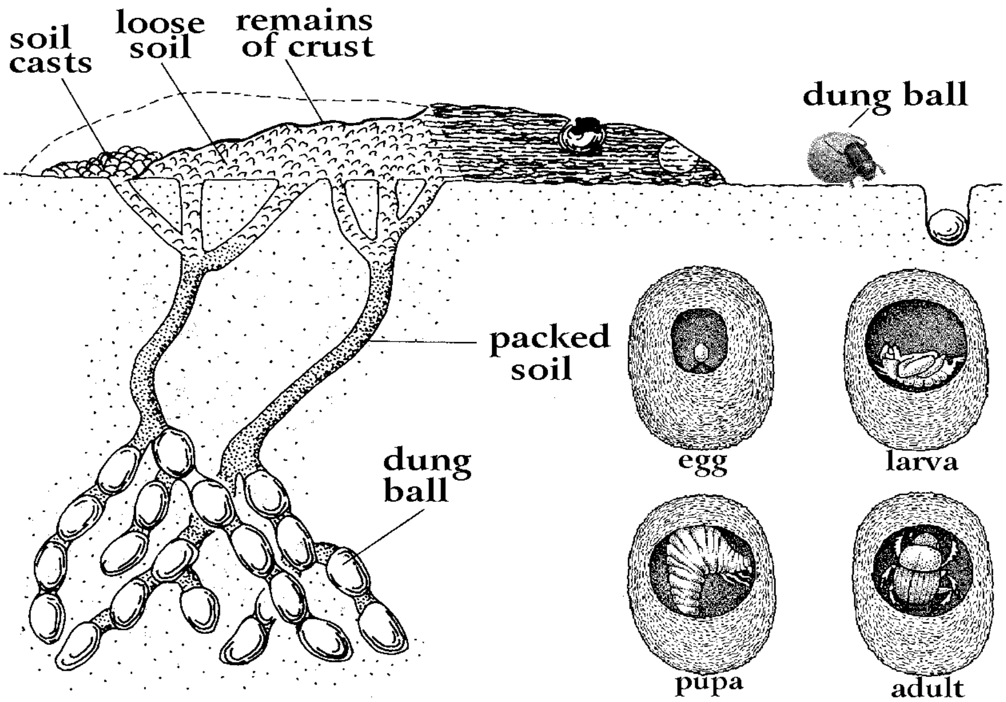

Fig. 4-18: Disintegration of dung by dung beetles: a pair of beetles digs a system of tunnels below a dung pad that are then filled with dung balls. Eggs, laid in each dung ball, develop as shown on the right (reproduced from Ross, H.H. et al., 1984)

4.7 Population Ecology

Population ecology or **population biology** studies the dynamics of populations, their structure and the various factors influencing the development of populations during the course of time. A **population** is defined as the entity of individuals of a particular species in a certain **habitat**, whereby the individuals of a population have to belong to the same reproductive community. The **population size** indicates the number of individuals of a certain population. The **population density**, also called **abundance**, expresses the number of individuals per area or volume. The change in size and structure of a population through time and space is the subject of **population dynamics**. A **population system** is the total of factors or **variables** having an impact on the dynamics of a population.

Population biology is a crucial subject in applied entomology. The population dynamics of a pest species as well as of its natural enemies have to be assessed regularly in order to predict outbreaks and to successfully apply control measures. Various assessment methods of insect populations are the subject of the **chapters 7.1** and **7.2**. An understanding of the variables that influence the ups and downs of populations open various ways for preventive control measures that keep pest species within tolerable limits.

4.7.1 Population Dynamics

The dynamics of an insect population is influenced by a large number of factors or variables. Complex mathematical models have to be used for the description of growth or decline of populations. Computer simulations are more suitable to model the effects of individual variables on the dynamics of a population. Thus, one might be able to predict the outbreak of a pest species, for instance as the result of abnormally changing factors. The complexity of population dynamics can be overcome by dividing the growth of a population into particular phases that can then be easily described by simple functions.

The basic mathematical model describing population growth without or at least with no constant limiting factors is **exponential growth**. It theoretically requires infinite space as well as a constant growth rate. Exponential growth usually occurs during a more or less short phase, the **exponential phase** of more realistic and natural growth curves, as shown in **figs. 4-21** and **4-22**. Exponential growth as shown in **figs. 4-19** or **4-20 A** is described by

$$N_t = N_0 \times e^{(r \times t)}$$

and in the logarithmic format as in **fig. 4-20 B**

$$\ln N_t = \ln N_0 + r \times t$$

where

N_t: number of individuals at a particular time **t_t**
N_o: number of individuals at starting time **t_o**
r: growth rate (birth rate - death rate)
t: time increment
e: exponential constant 2.718
ln: natural logarithm

For example a population with an annual increase of 40% due to birth and an annual decrease of 10% due to mortality has a net annual increase of 40% - 10% = 30%, a growth rate of r = 0.3. If the starting population N_o is 100, there are $N_1 = 100 \times e^{0.3} = 135$ individuals after one year, $N_2 = 100 \times e^{0.3 \times 2} = 182$ after two years, $N_3 = 100 \times e^{0.3 \times 3} = 246$ after three years and $N_{10} = 100 \times e^{0.3 \times 10} = 2009$ individuals after ten years and so on.

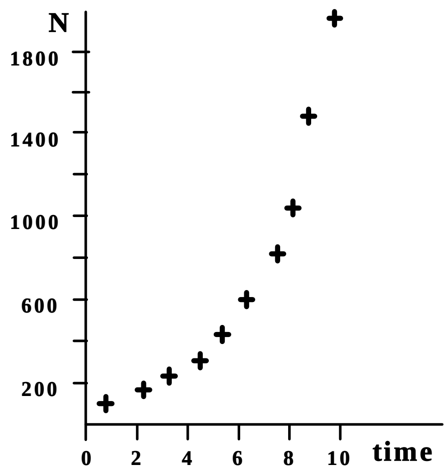

Fig. 4-19: Exponential growth of a population with **N** individuals during the course of time

For some purposes it is more convenient to use the logarithmic format. This has the advantage, that several x-values can be displayed along a relatively shorter logarithmic y-axis. Moreover, a decrease of the growth rate is not visible in the exponential format as can be seen in **fig. 4-20 A**, but it is conspicuous in the logarithmic format shown in **fig. 4-20 B**.

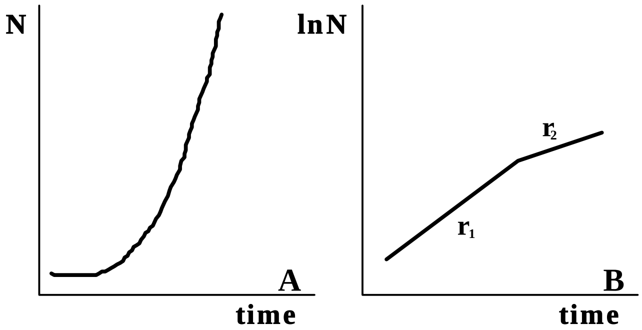

Fig. 4-20: Exponential growth of a population with **N** individuals displayed in exponential (A) and logarithmic form (B)

Logistic growth describes more realistically the dynamics of populations, because limiting factors like mortality or the availability of food are taken into account. Exponential growth increases *ad infinitum*, infinitely, but in nature usually space, food, light, etc. is limited. Thus the population number is driven asymptotically towards the maximum **capacity K**, as shown in **fig. 4-21** and described by

$$N_t = \frac{K}{1+e^{(a-r\times t)}}$$

Logistic growth shows an exponential phase, indicated in **fig. 4-21 B** in which the maximum reproductive rate and the maximum increase can be found. Although logistic growth considers particular factors related to real life it is still a theoretical model that only describes for instance the growth of bacteria during an initial phase of growth. For most other, higher organisms the influencing factors are so complex, that growth curves have to be drawn for each species and even then depend on various circumstances like location and climate. Some common naturally occurring growth curves are shown in **fig. 4-22**.

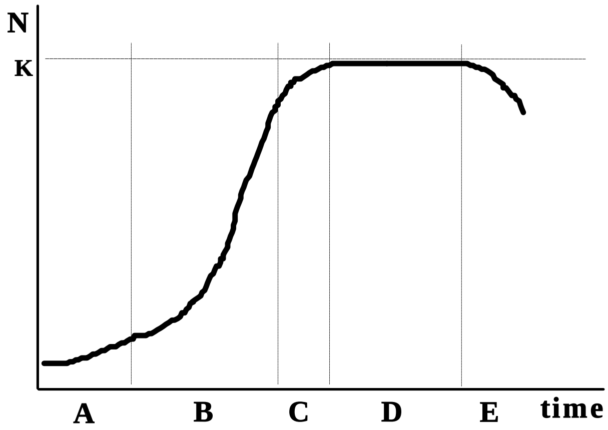

Fig. 4-21: Logistic growth of a population with **N** individuals during the course of time: (A) the population grows as reproduction increases, growth starts slowly because there are only a few reproductive individuals, that might be widely spread; (B) exponential phase: birth rate exceeds death rate resulting in maximum growth rate due to optimum environmental conditions; (C) population growth is decelerating because environmental resistance increases death rate and/or decreases birth rate; (D) equilibrium: death and birth rate balance each other; (E) growth rate drops, if conditions become increasingly unfavourable

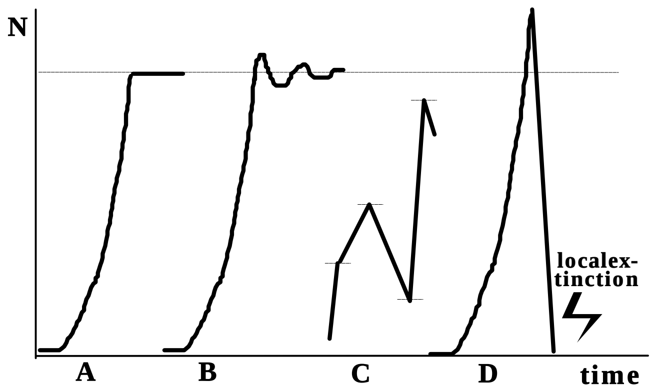

Fig. 4-22: Naturally occurring growth curves in populations with **N** individuals during the course of time: (A) the population grows exponentially until reaching a limiting density; (B) delayed density-dependent growth gradually approaches the limiting density and is then oscillating around it; (C) limiting density changes from year to year, depending on environmental factors like food and climate; (D) break-down of a population after its initial explosion, eg. outbreak of a pest and the sudden collapse or extinction of the population

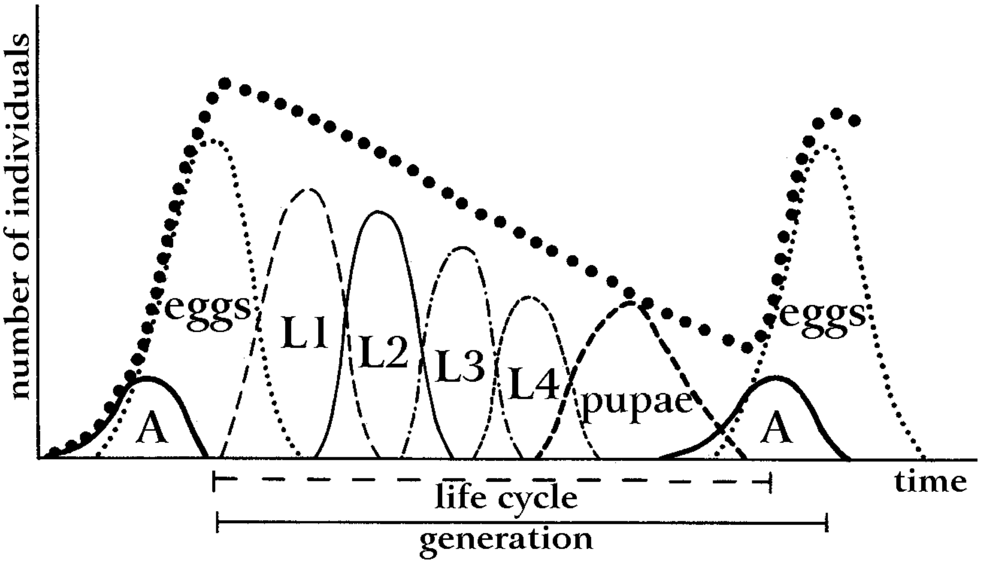

Fig. 4-23: Partial population curves for insect eggs, larval instars L1 to L4, pupae and adults (A); the thick dotted line indicates the total population curve, which is the cumulative number of insects of all life stages (reproduced from Coulson, R.N. and Witter, J.A., 1984)

4.7.2 Age Grading

The determination of the growth stages or ages of insects in a particular population, called **age-grading**, can be important for the prediction of outbreaks and for the modelling of insect populations. Due to the different instars, ie. egg stage, larval and pupal instars and adult stage, occurring during the life cycle of insects, there are two ways of expressing the number of individuals during the course of time, as shown in **fig. 4-23**. Individual **partial population curves** for each instar can be considered. The **total population curve** takes individuals of all life stages into account and is the sum of all partial population curves. The advantage of a more differentiated consideration of population growth as in the case of partial population curves is that the reproductive potential of insects becomes clearly visible. The population shown in **fig. 4-23** consists only of a relatively small number of adults, that however lay a large number of eggs. Furthermore, **fig. 4-23** illustrates the terms **generation time** and **life cycle**. The generation time is the interval between the production of eggs in one generation and the production of eggs in the following generation. The length of a life cycle is the time span that is required for the development of an insect from the egg stage to the adult stage.

4.7.3 Spatial Distribution

For the assessment of insect populations it is important to know how individuals of a certain species are distributed in an area in order to decide where and how many samples to take. **Fig. 4-24** shows the possible distributions or **spatial patterns** of individuals in an unlimited area. **Clumped** or **contagious distribution** is the most common case. **Random** or **normal distribution** is found only in a few soil-dwelling arthropod species. **Regular** as well as **clumped and regular distribution** usually do not occur in nature.

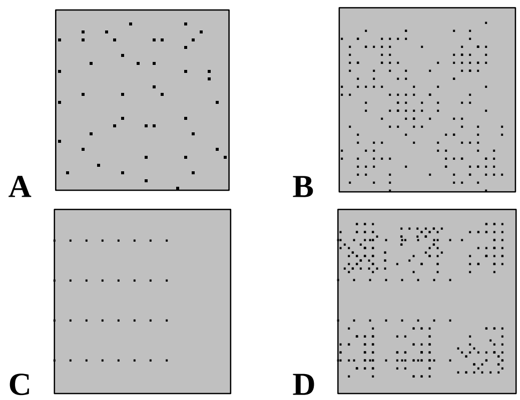

Fig. 4-24: Spatial distribution of individuals of a population: (A) random distribution or normal distribution; (B) clumped or contagious distribution; (C) negative contagious or regular or uniform distribution; (D) combination of clumped and regular distribution

Contagious or clumped distribution is the most common case, because insects often follow the clumped distribution of their respective food plants or are aggregated around their hosts. Moreover, communication chemicals promote the aggregation of insects like for instance sex attractants released by females or aggregation pheromones. These topics are discussed in the **chapters 3.1.3** and **4.4.4**.

Descriptive statistics can be used to decide how individuals of a population are distributed. Whether individuals are randomly distributed can be decided by comparing their distribution with the **normal** or **Poisson distribution**. The probability $\mathbf{p}_n$ of a particular unit or area containing **n** individuals where $\lambda_{\mathbf{n}}$ equals mean and variance can be calculated:

$$p_n = \frac{l_n \times e^{-l}}{n!}$$

The comparison with the negative **logarithmic** or negative **binomial distribution** is used to decide whether or not the distribution of individuals is clumped. If the variance **s** exceeds the mean **m** and for a mean **m** > 0.5 and with **k = m² / (s² - m)**, the probability $\mathbf{p}_n$ of a particular unit containing **n** individuals can be calculated:

$$p_n = \frac{k(k+1)...(k+n-1)}{n}\left(\frac{m}{m+k}\right)^n$$

4.7.4 Regulation of Population Growth

Irrespective of the kind of population growth, the dynamics of a population is described by a **demographic equation**. It considers the number of individuals of a population at a given time $\mathbf{N_t}$, the number of individuals of the starting population $\mathbf{N_0}$, the number of births **B**, the number of deaths **D**, the number of immigrants **I** and the number of emigrants **E**:

$$N_t = N_0 + B - D + I - E$$

The birth rate or **natality** is the reproductive rate of all females of a population, whereas **fecundity** describes the reproductive rate of a single female. **Fertility** is in general considering the reproductive rate of a female. The death rate is referred to as **mortality**. Birth rate and death rate are the result of a number of environmental factors, summarised in **fig. 4-25**, influencing the growth of a population in one way or another. Generally, these factors are divided into animate or **biotic factors** and inanimate or **abiotic factors**.

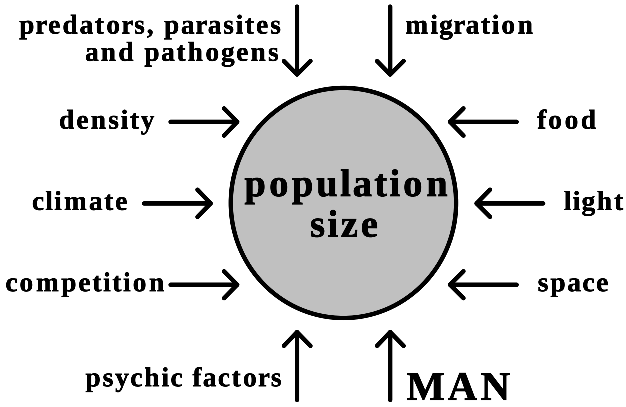

Fig. 4-25: Biotic and abiotic factors regulating population growth (graphic Schneider, M.F.)

4.7.4.1 Biotic Factors

Predators, Parasites and Pathogens

Predation and parasitism, outlined in **chapter 4.3.1** and **4.3.2** can have a major impact on prey or host populations, as indicated in **fig. 4-26**. If prey/host is abundant, the number of

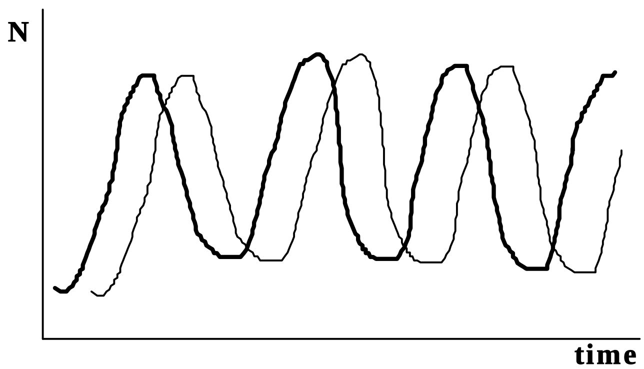

Fig. 4-26: Delayed regular cycling of a predator or parasite population (thin line) following the prey or host population (thick line) of **N** individuals during the course of time

predators/parasites increases due to a rich source of food. Predators/parasites living on prey/host are decreasing their number. As a result of the lower number of prey/host, the number of predators/parasites decreases too, because there is less for them to eat. Once the number of predators/parasites is low again, the prey/host population recovers and the whole game starts again from the beginning. An understanding of the complex predator-prey and parasite-host interactions is of special interest for the biological control of target species.

Competition

Competition is defined as interaction between organisms of the same trophic level for restricted resources to be shared such as food, light, space or mating partners. In general a distinction is made between **intraspecific competition** and **interspecific competition**. Intraspecific competition occurs within one species, for instance for **territory**. Territorial behaviour can be found where food or prey is dispersed or breeding sites have to be established like in the case of parasitic wasps.

Interspecific competition occurs between individuals of different species and is usually less severe or stressful than intraspecific competition. During the process of evolution competing species usually diverge. Organisms can share the same **habitat** (‘address’ of a species) but live in different **niches** (‘profession’ of a species) or develop a variety in using different food sources in order to escape competition.

Availability of Food

The availability of food is one of the most important factors for insect population growth and one of the driving forces for competition. If there is excess food, a particular population is fast growing. In this context factors like **host cross-over**, **host preference** and **introduction of attractive food** are of importance and are discussed in **chapters 8.5** and **8.7**

Dispersal and Migration

Spread is defined as local movements within a favourable area, whereas **dispersal** describes a movement of individuals or a population away from its birth site to other areas that are not necessarily suitable for the insects’ survival. Dispersal can be either active by means of flight, walking, floating, etc. or passive for instance by wind. The latter is done by insects and spiders that can’t fly or walk for long distances. Wind can carry small animals up as high as 3.5 km. Adult moths of the family **Lymantriidae** for instance are poor flyers that can hardly disperse by means of flight. Their caterpillars however, disperse along an anchored thread in a way that the air-borne caterpillar is carried by wind, as shown in **fig. 6-17**. Another strategy in contrast to **Lymantriidae** caterpillars, is used by some spiders that spin a loose thread into the wind. Once the thread gets entangled somewhere, the spider follows the newly established ‘short-cut’ along the thread. The dispersal of aphids (**Aphididae**) is described in **chapter 5.6.3.17**. **Migration** is a directed mass movement over a considerable distance from one favourable area to another, in the case of **immigration**, into an area, in the case of **emigration**, away. Dispersal and migration are important factors particularly for small populations and for animals with territorial behaviour. The driving force behind the effort to disperse or to migrate to other areas is usually to escape from competition. Thus, the migrants are able to colonise new habitats, to exploit new food sources or to enhance the probability of finding mating partners.

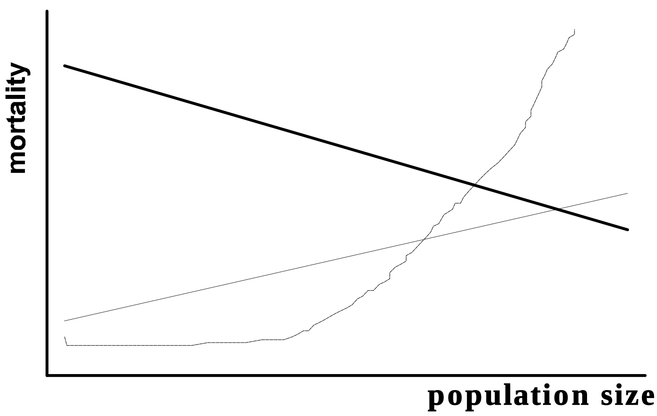

Fig. 4-27: Effects of direct (dashed line), delayed (dotted line) and inverse density-dependent factors (solid line) on a population

Population Density

The number of individuals of a population might be a direct or indirect control mechanism of the same population. Density-dependent regulation operates through negative feedback control, meaning that high density promotes the decrease of the population and vice versa. Direct density-dependent control is triggered for instance by intraspecific competition: many individuals in a population will cause high competition, eg. for food, thus causing higher mortality, once the source of food becomes scarce. Delayed density-dependent control can be due to natural enemies, whereas inverse density-dependent control can be the result of interspecific competition. The different types of density-dependent control mechanisms are shown in **fig. 4-27**.

Psychic Factors
Psychic factors like territorial behaviour, stress, and competition can be found in a number of species, but in general they are less important in the context of insects.

4.7.4.2 Abiotic Factors

Climate and Weather
Temperature and humidity are the most important abiotic factors regulating insect populations. The **temperature** of the surrounding environment directly effects the body temperature of **poikilothermic** or cold-blooded insects. The development of insects is temperature-dependent, an increase of the temperature by 10 °C usually doubles the velocity of chemical reactions. **Humidity** and **precipitation** greatly affect growth and health of food plants as well as the development of insects, their predators and parasites. High humidity for instance offers ideal conditions for particular fungal entomopathogens, thus reducing the number of host insects.

Space
The availability of space or habitat directly influences the availability of food, shelter, territory, etc. Therefore populations are subject to direct control by the available space.

Light
Light effects the day-and-night rhythm (**circadian rhythm**) of insects. But more importantly, light is a requirement for the growth of insects' host plants, thus having a substantial indirect effect on insect numbers.

Fire and Natural Disaster
These events are locally of major importance for the regulation of populations. A fire or land slide for instance can result in the local extinction of a population. Natural fire however, does not have the significance for insects, that it has for plant communities.

Impact of Man
Man interferes with populations of animals and plants in various ways. A large number of synthetic toxic substances are released into the environment and pollute air, soil, water, marine ecosystems, etc. As a result of pollution, susceptible organisms might die instantly or after some time. In Papua New Guinea, cyanide, mercury and other heavy metals from mining tailings or agrochemicals like pesticides and fertilisers cause already severe problems in certain areas. Some of these substances, especially pesticides, have a number of disadvantages, they are very persistent in the environment and accumulate in the food chain. These undesired side-effects of pesticides are further outlined in **chapter 8.8.2**.
The number one 'terminator' of animals and plants in Papua New Guinea however, is habitat destruction. Activities like logging, shifting cultivation and deliberately lit fires can completely change the environment and severely disturb or even destroy habitats, so that particular species become locally extinct. A sad example is one of PNG's proud national animals, the Queen Alexandra Birdwing *Ornithoptera alexandrae*. The establishment of oil palm plantations in Oro Province has resulted in a decrease of the number of *Aristolochia schlechteri*, one of the major larval foodplant of *O. alexandrae.* Thus, the number of this birdwing butterfly has decreased considerably in some areas and it has become extinct in other areas of the

province. Since the butterfly can be found only in Oro Province, it was necessary to protect the species by PNG and international legislation, as outlined in **chapter 1.3**. Another problem in PNG is the introduction of species that do not occur naturally. These might severely interfere with the subtle ecological balance of organisms. For instance, a possible adverse effect due to the introduction of the honey bee *Apis mellifera* is the competition with endemic pollinators for nectar and honey.

However, there are also some applied aspects of man interfering with insect populations. For the purpose of pest management, a habitat can be altered, so that it is no longer suitable for pest insects. Pest control in general intends to reduce the number of individuals of a pest species by using various control methods. These techniques are further outlined in **chapter 8**. Moreover, some insects are suitable indicators for the degree of pollution in the environment. The presence or absence of particular aquatic insects like the larvae of stoneflies (**Plecoptera**) allows an estimate of the soundness of a particular water body.

4.7.4.3 Influence of Abiotic and Biotic Factors on the Stability of Populations

The populations of most insect species remain more or less constant, with little alteration in the number of individuals during the course of time. Usually the population number oscillates around a threshold limit value shown in **fig. 4-28**. **Oscillation** is characteristic for feedback control systems and has the advantage of being able to react instantly in changing the density.

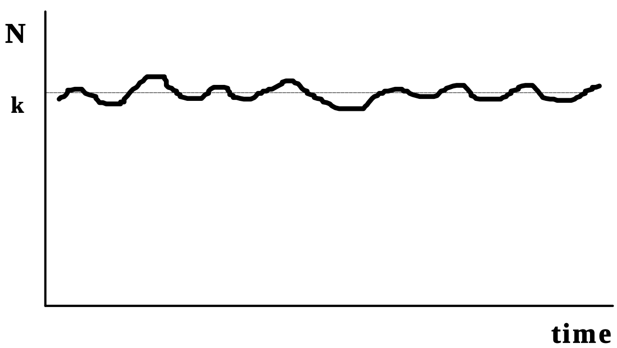

Fig. 4-28: Oscillation of the number of individuals **N** around a threshold limit value during the course of time

However, the populations of a few species can vary markedly in size. Their number might rise rapidly during an outbreak over one or two generations and then drop as quickly as it has increased. **Box 4-1** contrasts the influence of certain factors or variables on the stability of insect populations. For instance, unstable and unpredictable climate promotes unstable populations. Prolonged drought or unusual precipitation can easily unbalance a population causing its break-down or its explosion.

Agriculturalists and foresters desire to predict the effects of climate on crop and pest species, thus to allow an estimation of when pest-related problems can be expected. For instance a long period of time without rain affects the well-being of a crop and consequently results in a higher susceptibility to pest attack. If the critical amount of precipitation is known for a particular crop, a protectant application of a suitable pesticide might be helpful once precipitation is below this value. The problem however is the complexity of factors: the crop is not only affected by rain but also by the pest itself as well as its predators, parasites and pathogens. Furthermore, there are a number of other factors, having an effect on the crop and/or on the pest at the same time, for instance temperature, type of soil, nutrients and so on. Computers ease the task of predicting outbreaks and handling multifactorial systems. A number of software packages is available on the market like **Diagnosis for Crop Protection 2.1**™ and **Climex for Windows 1.0**™, listed below. Some of the software is interactive and allows the user to create scenarios for particular crops and their pests in a certain area with a characteristic climatic pattern.

Commonwealth Scientific and Industrial Research Organisation (CSIRO) and Cooperative Research Centre for Tropical Pest Management (1995): Climex; Computer software for predicting the effects of climate on plants and animals; Version 1.0; CD-ROM; Brisbane; Australia

Massey University and Cooperative Research Centre for Tropical Pest Management (1996): Diagnosis for Crop Protection; Multi-media software that teaches students to diagnose problems related to insects, diseases, nutrition and crop management practices; Version 2.1; CD-ROM; Brisbane; Australia

VARIABLE	UNSTABLE POPULATION	STABLE POPULATION
Climate:	**• uncertain, unpredictable**	**• constant, predictable**
Lifecycle:	**• short (some weeks)**	**• longer (several months)**
	• rapid development/growth rate	**• slower development/growth rate**
	• early reproduction	**• late reproduction**
	• small body size	**• larger body size**
	• many offspring	**• small number of offspring**
	• catastrophic mortality	**• mortality evenly distributed**
Population Size:	**• variable**	**• stable**
Competition:	**• low**	**• high**
Predator:	**• development slowly**	**• rapid and synchronous development**

Box 4-1: Influence of selected variables on the stability of insect populations

4.7.5 Insect Outbreaks

An outbreak of an insect population, also called **calamity**, is defined as a temporary condition that is characterised by excessive insect numbers as shown in **fig. 4-29**, and - if it is a pest species - injury to valuable materials or products. A **sporadic** calamity occurs suddenly, in a small, restricted area and vanishes after a short period of time. A **periodic** outbreak happens at more or less regular intervals, as is the case in plague locusts or the defoliating moth of *Pinus patula*, *Lymantria ninayi* (**Lymantriidae**).

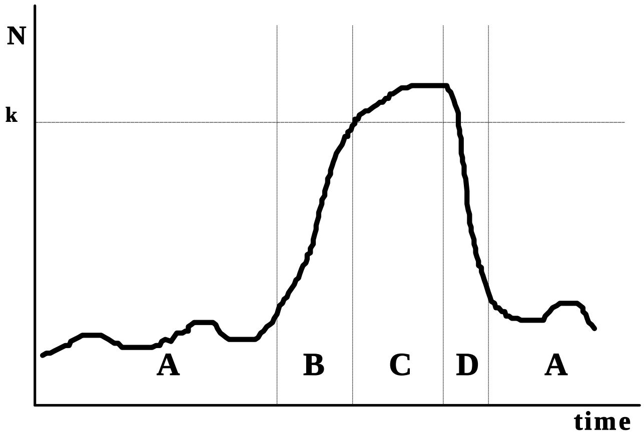

Fig. 4-29: Phases of a pest population with **N** individuals: (A) innocuous phase; (B) release phase; (C) outbreak; (D) decline phase

An outbreak is usually the result of an environmental condition, that temporarily disturbs the biotic balance. The populations of migrating grasshoppers for instance start to boom after unusually heavy rains. Higher moisture stimulates the development of dormant eggs in the soil, causing an unusually high number of locusts to hatch. At the same time, rain might have a positive feed-back on the growth of grass, the source of food for the grasshoppers. If there is enough grass to support the hatched locusts, then it is quite unlikely that predators or other natural enemies can effectively decrease the high number of locusts. Once the prey population reaches a threshold level **k**, shown in **figs. 4-29** and **4-30**, the predator population can’t catch up and thus is unable to keep prey in check any longer. This way, the grasshopper population escapes from its predator-prey cycle, as indicated in **fig. 4-30**. The outbreak will then continue until limiting environmental factors will have reduced the number of locusts and the natural balance has been restored at a lower population level.

The total of limiting environmental factors, also known as **environmental resistance**, is working against the **biotic potential** of reproduction in an optimum environment. The result of the reduced biotic potential is the **reproductive potential** that depends on fertility, length of life cycle and sex ratio. Environmental resistance restricts populations from growing indefinitely and getting out of control. A pair of flies could theoretically produce an incredible number of offspring in one season sufficient to cover the earth to a depth of 15 metres! Another example states that a single female plant louse (**Aphididae**) theoretically has the potential to produce 6,000,000,000 offspring in one year, which is equivalent to 600,000 kg or 10,000 humans, the number of people living in Bulolo. Luckily, this doesn’t happen due to the variety of environmental factors controlling the growth of insect populations.

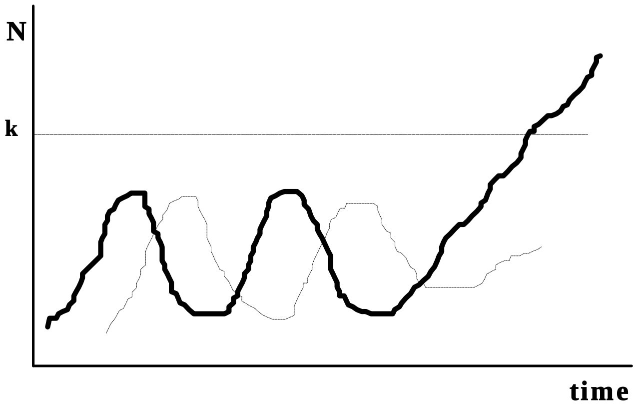

Fig. 4-30: Outbreak of a pest population of **N** individuals showing the pest's 'escape from its predator-prey-relationship

Further reading:

Abercrombie, M. et al. (1992[8]): Dictionary of Biology; Penguin Books; London; UK

Barbosa, P. and Schulz, J.C., (eds.) (1987): Insect Outbreaks; Academic Press; San Diego; USA

Bernays, E.A. (1991): Insect-Plant Interactions; CRC Press; Boca Raton, USA

Bernays, E.A. and Chapman, R.F. (1991): Host-Plant Selection by phytophagous Insects; Chapman and Hall; New York; USA

Commonwealth Scientific and Industrial Research Organisation (CSIRO) (1991[2]): The Insects of Australia - A Textbook for Students and Research Workers; Volume 1 & 2; Melbourne University Press; Carlton; Australia

Commonwealth Scientific and Industrial Research Organisation (CSIRO) and Cooperative Research Centre for Tropical Pest Management (1995): Climex; Computer software for predicting the effects of climate on plants and animals; Version 1.0; CD-ROM; Brisbane; Australia

Commonwealth Scientific and Industrial Research Organisation (CSIRO) (1996[2]): Insects - Little Creatures in a Big World; CD-ROM; CSIRO Publishing; Collingwood, Australia

Dean, J. and al. (1990): The defensive Spray of the Bombardier Beetle: A biological Pulse Jet; Science 248: 1219-1221

Eisenbeis, G. and Wichard, W. (1987[2]): Atlas on the Biology of Soil Arthropods; Springer Verlag; Berlin; Germany

Ewers, W.H. and Jeffrey, W.T. (1971): Parasites of Man in Niugini; Jacaranda Press; Milton; Australia

Flannery, T.F. (1995): The Future Eaters; Reed Books; Kew; Australia

Gullan, P.J. and Cranston, P.S. (1994): Insects - An Outline of Entomology; Chapman and Hall; London; UK

Hoydt, E. (1996): The Earth Dwellers - Adventures in the Land of Ants; Touchstone; New York; USA

Knipling, E.F. (1992): Principles of Insect Parasitism Analysed from New Perspectives; US Department of Agriculture, No. 693; USA

Lapedes, D.N. (ed.) (1978[2]): Dictionary of Scientific and Technical Terms; McGraw-Hill; New York; USA

Lawrence, J.F. and Milner, R.J. (1996): Associations between Arthropods and Fungi; in: Orchard, A.E. (ed.) (1996): Fungi of Australia; Vol. 1B Introduction - Fungi in the Environment; Australian Biological Research Studies (ABRC) and CSIRO; Canberra; Australia

Malcolm, S.B. (1990): Mimicry: Status of a classical evolutionary Paradigm; Trends in Ecology and Evolution 5: 57-62

Massey University and Cooperative Research Centre for Tropical Pest Management (1996): Diagnosis for Crop Protection; Multi-media software that teaches students to diagnose problems related to insects, diseases, nutrition and crop management practices; Version 2.1; CD-ROM; Brisbane; Australia

Monteith, S. in Monteith, G. (1990): The Life inside an Ant-Plant; Wildlife Australia 27(4): 5

Naumann, I.D. (1994): Systematic and Applied Entomology - An Introduction; Melbourne University Press; Melbourne; Australia

Pearson, I., (1978): English in Biological Science; Oxford University Press, Glasgow, UK

Price, P.W. (1975): Insect Ecology; Wiley; New York; USA

Roberts, M. B. V. (1985[4]): Biology - A Functional Approach; ELBS; Walton-o.-T.; UK

Robinson, W.H. (1996): Urban Entomology - Insect and Mite Pests in the Human Environment; Chapman and Hall; London; UK

Ross, H.H. et al. (1982[4]): A Textbook of Entomology; Wiley; New York; USA

de la **T**orre-Bueno, J.R. (1989[2]): The Torre-Bueno Glossary of Entomology; New York Entomological Society in Cooperation with the American Museum of Natural History; New York; USA

Varley, G.C. et al. (1975): Insect Population Ecology; Blackwell Scientific Publications; Oxford; UK

Waage, J. and Greathead, D. (eds.) (1986): Insect Parasitoids; Academic Press; San Diego; USA

Waterhouse, D.F. (1974): The biological Control of Dung; Scientific American 230(4): 100-109

Watt, A.D. et al. (1990): Population Dynamics of Forest Insects; Intercept; Andover; UK

Wickler, W. (1968): Mimicry in Plants and Animals; Weidenfeld and Nicolson; London; UK