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## Summary

Individuals that are not killed before the end of their reproductive period are likely to leave more offspring than individuals that can not avoid being killed. Therefore, selection is expected to favour traits that increase the likelihood of escaping predation. One means by which prey may reduce their predation risk is by displaying antipredator behaviour. However, avoiding predators entails costs, since it goes at the expenses of other fitness-determining activities. Therefore, prey should tune its behaviour to the risk of being killed. Moreover, predators may pose risks that differ in their spatial or temporal characteristics. Therefore, the efficient display of antipredator behaviour requires that the prey perceive the risk of being killed. In this thesis, I investigate the factors that affect the predation rates of plant-inhabiting arthropods as well as when and how antipredator behaviour is displayed.

The first part of the thesis tackles some factors that affect predation risk. In Chapter 2, I investigate the life-history consequences of the foraging behaviour of two predatory mites that are spatially segregated within cassava plants: *Typhlodromalus manihoti* occurs on the middle leaves of the plant, whereas *T. aripo* is restricted to the apices during the day and moves to the upper leaves at night. Field data show that the spatial distribution of their shared prey, the herbivorous Cassava Green Mite (CGM) within plants is also heterogeneous: more prey are found on the middle leaves of cassava than in the apices. Moreover, prey densities fluctuate temporally. Laboratory experiments demonstrate that the life histories of the predators differ such that *T. aripo* has a higher growth rate than *T. manihoti* at low prey densities, whereas the growth rate of *T. manihoti* is higher than that of *T. aripo* at high prey densities. Moreover, *T. aripo* survives longer than *T. manihoti*, which has a higher fecundity than *T. aripo*. Therefore, the life-history strategies of these two predators are tuned to the prey densities that they experience on the plants, resulting in prey individuals being exposed to different predation risks on different plant strata.

Predation rates may vary within a single plant, but they may also differ according to the species of plant. In Chapter 3, the effect of host plants on the diet choice of omnivores is investigated. It has been shown that omnivores kill more herbivores on host plants of low quality than on high-quality host plants. However, omnivores may also kill the predators of the herbivores and the total predation risk of herbivores on plants of high and low quality will thus depend on killing of their own predators by

omnivores. Omnivorous Western Flower Thrips feed on plants, such as cucumber and sweet pepper, but they also eat eggs of herbivorous spider mites (*Tetranychus urticae*) and eggs of a predatory mite (*Phytoseiulus persimilis*) that attacks the spider mites as well. Spider mites compete with thrips for the plant and produce a web that hampers the mobility of predators. Total predation by thrips on the eggs of the two species is higher on sweet pepper, a host plant of low quality, than on cucumber, a high-quality host plant. The web produced by spider mites does not affect predation rates on cucumber, but it hampers the predation on spider-mite eggs on sweet pepper. As a result, more eggs of predatory mites than eggs of spider mites are killed in damaged and webbed discs of this host plant. A model on the local dynamics of spider mites and predatory mites is used to predict the effects of intraguild predation by thrips on the dynamics of the mites on the two host plants. The model predicts a small effect of the total predation rate, but a large effect of the relative predation rate, resulting in much higher levels of infestation by spider mites on sweet pepper than on cucumber. Therefore, plants of low quality do not always benefit from the presence of omnivores. Moreover, the predation experienced by each of the prey of the thrips varies with the host plant where the interaction occurs.

Given this variation in predation risk, prey should avoid predators when predation risk is sufficiently high and invest in other activities otherwise. Additionally, they should respond specifically to predator species that pose different risks. The second part of the thesis concerns these behavioural responses of arthropods to variation in predation risk. Chapter 4 describes the antipredator behaviour of CGM, the prey of the two predators investigated in Chapter 2. Because the predators are restricted to particular plant strata, the prey may find a refuge from predation in predator-free strata. Indeed, CGM were found to avoid predators by vertically migrating within the plant. This response is mediated by odours produced by the predators. Moreover, the response of the prey is specific to each predator species: when exposed to odours associated to *T. manihoti*, the leaf-dwelling predator, CGM migrate upwards, while they migrate downwards when exposed to *T. aripo*, the predator occurring in the apices. CGM always move up when exposed to *T. manihoti*, a predator that occurs always on the middle leaves, but their response to *T. aripo*, a predator that shows a diurnal pattern of migration, is flexible: when *T. aripo* occurs in the apices, CGM move downwards, whereas they move to the upper strata when *T. aripo* occurs in the middle leaves. CGM do not respond to *Euseius fustis*, a predator that poses a low predation risk. Hence, the prey may find a refuge from predation within a single plant and stage a specific response to each predator species.

Another example of antipredator behaviour that is specific for different predator species is found in *T. urticae*. This spider mite produces a web that hampers the mobility of most predators, resulting in a decrease in

predation rate (cf. Chapter 3). The predatory mite *Iphiseius degenerans* is a predator species hampered by this web. However, some predators, such as the predatory mite *P. persimilis*, can easily cope with the web and are even arrested by it. In Chapter 5, we investigate the fitness consequences of moving outside webbed areas or staying inside the web for spider mites that were exposed to either *P. persimilis* or to *I. degenerans*, or in absence of predators. The two predators indeed show opposite predation patterns: *P. persimilis* forage and kill prey mainly inside the web, whereas *I. degenerans* pose a higher predation risk to spider mites outside the web than in webbed areas. In absence of predators, spider mites have lower oviposition rates inside the web than outside of it. These costs and benefits are incorporated in the calculation of fitness associated with each behavioural option (staying inside the web or moving to clean areas) for each scenario (absence of predators or presence of one of them). Fitness is measured as the number of dispersing offspring produced per female prey during a local predator-prey interaction, because populations of spider mites exhibit a metapopulation structure. A simple model of the local predator-prey interaction predicts that spider mites should move outside the web in absence of predators or when exposed to *P. persimilis*, and remain in the web when in the presence of *I. degenerans*. Spider mites behave according to these predictions, thus perform a specific antipredator behaviour to each predator species.

In more complex food webs, predators may feed on the same resource as their prey, a phenomenon known as intraguild predation. Like in simple predator-prey systems, prey are also expected to avoid being killed by their intraguild predators. Moreover, even if the predator would concentrate all its foraging efforts on the shared resource and thus pose no direct predation risk to the prey, prey may still avoid patches with the predator to avoid competing with them. The predatory bug *Orius laevigatus* and the predatory mite *Neoseiulus cucumeris* are involved in such intraguild predation: they both feed on Western Flower Thrips, but *Orius* also kills *N. cucumeris*. In Chapter 6, we show that *N. cucumeris* avoids patches with its intraguild predator. This avoidance is mediated by volatile cues associated with the diet of *Orius*. Indeed, olfactometer experiments show that *N. cucumeris* avoid *Orius* that has fed on thrips, but not those that have been feeding on other diets, including a diet of conspecifics predatory mites. On a patch with thrips, *N. cucumeris* forages less and captures less thrips when perceiving odours of *Orius* that have fed on thrips than when perceiving odours of *Orius* having fed on moth eggs. However, *Orius* that have fed on thrips did not pose a higher predation risk to *N. cucumeris* than *Orius* having fed on other diets. Therefore, the cues used by *N. cucumeris* to recognize their predators are not associated to a situation of higher risk, but probably reflect the conditions under which the two predators encounter each other in the field.

Chapters 4, 5 and 6 are examples of antipredator behaviour in which prey avoid predators by escaping. This is indeed the most known example of antipredator behaviour. However, prey have other behavioural options to reduce their predation risk. For instance, instead of escaping themselves, they may induce predators to escape. This is what larvae of the Western Flower Thrips do: by killing the eggs of the predatory mite *I. degenerans*, they deter the adults of this species which pose a high predation risk on thrips larvae. Such counterattacks result in a lower predation risk for the thrips larvae. Predators avoid patches with killed eggs probably because they are deterred by sites where their offspring will run a high risk of being killed. However, when predators are on patches with their own offspring, they may defend their young by killing the counterattacking prey. Indeed, *I. degenerans* females kill more thrips in patches with their offspring than elsewhere (Chapter 8). This results in fewer eggs of *I. degenerans* being killed on those patches. This protective parental care can be seen as a special case of antipredator behaviour.

Prey may reduce the risk of being killed by using refuges where their predation risk is reduced. The web of spider mites is such a refuge, as was shown in Chapter 5. Western Flower Thrips may also use this refuge to reduce their risk of being killed by *N. cucumeris*, a predatory mite that is hampered by the web. However, thrips pay a cost for using this refuge, since both thrips and spider mites feed on the host-plant tissue. This results in a slower development of thrips inside spider-mite web. This affects the vulnerability of thrips to predation by *N. cucumeris*, which kills the young thrips instars only. Therefore, it is not obvious that thrips will benefit from moving inside the web. Chapter 9 focuses on the consequences of using the web for the populations of thrips exposed to predation by *N. cucumeris*. Populations of thrips on plants with web and damage inflicted by spider mites grow slower than populations of thrips on clean plants, but finally reach higher numbers than on clean plants and on plants with spider-mite damage but without web. This suggests that the use of spider-mite web as a refuge has a positive effect on thrips densities. By means of a stage-structured model yielding good predictions for this system, we show that incorporating the cost of refuge use as a lower developmental rate and the benefits as a decrease in predation is sufficient to predict the dynamics observed.

In summary, it can be concluded that predation risk varies in time as well as space, and that the arthropod prey studied here can cope with this variation due to their flexible antipredator behaviour. Prey reduce predation risk by displaying several types of antipredator behaviour, such as escaping, hiding in refuges, or by counterattacking the predators, and they may even reduce the predation risk of their offspring through protective parental care. These behaviours have important consequences for the co-evolution of predators and prey as well as for the dynamics of populations. The results presented in this thesis also show that predator-