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Antipredatory behaviour: a "hot spot" of evolutionary ecology of the nineties

To enjoy a delicious dinner or to have a date with someone you like is nice. But if this means that you risk to getting into a dangerous situation or even being killed, you would have to think about how important these things are and maybe change your preferences, and avoid activities or places with such a high risk. The same is true for various aspects of animal behaviour. As a link of a food web most organisms live with a permanent conflict between different demands, and must optimise foraging and breeding and avoid being attacked by a predator at the same time.

The "hot spots" of special interest among evolutionary and behavioural ecologists have changed over the years, from the island biogeography and population ecology of the seventies, and the predation and competition theories of the eighties to the behavioural ecology of today, including trade-offs, plasticity, and sexual selection. Beside the last topic — which currently forms the major part of the presentations of behavioural ecology conferences — the antipredatory needs of individuals have gained an increasing interest among empirical researchers and theoreticians. An individual is often susceptible to predation when foraging, trying to attract a mate, or caring for offspring, and predation should be a strong selective force for evolving adaptations to minimise the risks. Recent reviews of the behaviour of animals under risk of predation (Lima & Dill 1990, Magnhagen 1991) document the progress of research activities in this field during the eighties.

The plans for the present special issue, focusing on antipredatory behaviour of individuals, were launched at a Nordic Council for Ecology course, held at the Konnevesi Research Station 25–29 November 1991. During this intensive week, nine invited lecturers from Canada, Israel, England, USA, Sweden and Finland and twenty graduate students from the Scandinavian countries discussed various aspects of the evolution and ecological significance of antipredatory behaviour. The talks given at this course have formed the bases for most of the articles presented in this special issue, which focus on theory and modelling of antipredatory behaviour as well as on empirical data on mammals, birds, fish and invertebrates. Here we attempt to form a package of the current knowledge and on-going research in this interesting field, to give the reader access to some new experimental studies on both terrestrial and aquatic organisms, to future perspectives of advanced researchers in the field of antipredatory adaptations, and to recent literature on antipredatory behaviour documented in several review papers. Our goal was to publish an issue with fresh ideas, reviews and good empirical data on both invertebrates and vertebrates from different habitats and continents. We think we have succeeded in our efforts, at least regarding the last point, since the empirical studies describe antipredatory mechanisms in a range of aquatic and terrestrial invertebrates and vertebrates inhabiting areas from the South American pampas to Finnish Lapland.

Andy Sih (Kentucky, USA) starts the issue with a broad review where he strongly argues for an integrative approach in ecological research. His empirical work is drawn from studies of antipredatory adaptations of salamander larvae. His ideas about the evolution of antipredatory

traits in the behaviour of salamander larvae are thought-provoking and will definitely be discussed further among ecologists.

The two following empirical studies deal with antipredatory adaptations of rodents against their main predators in desert environment and boreal forests. Burt Kotler, Leon Blaustein and Joel Brown (Sede Boker, Israel; Chicago, USA) test the predation facilitation hypothesis experimentally, using gerbils of the Negev desert and their predators the eagle owl and the sand viper as subjects. In the carefully planned enclosure experiment the authors illustrate the dilemma of individual prey in a multipredator environment: they cannot be safe from two types of predators at a time. "The fangs of a snake drive gerbils into the talons of owls".

The bank vole is a common rodent species in the boreal and deciduous forests of Europe and the predator community around it is probably more diverse and geographically variable than that of the gerbils of Negev. The authors of the third paper, Hannu Ylönen, Bogusia Jędrzejewska, Wlodek Jędrzejewski and Jari Heikkilä (Białowieża, Poland; Jyväskylä and Helsinki, Finland) have separately been working on antipredatory behaviour of the bank vole and its "close relatives" for several years. In their review they sum up the knowledge on short- and long-term changes in the behaviour of bank voles under high risk of predation and also present some new results from their experimental studies. If the evolution of the bank vole's antipredatory adaptations can be described with the analogy of David's and Goliath's fight, the most dangerous Goliath in the environment of this vole species seem to be a very small one, i.e. the weasel.

Previous articles dealt with a prey species in a multi-predator environment, and showed that there seem to be differences in the coevolutionary relationship of the prey and its various predators. This subject is discussed further in the theoretical paper by Steve Lima (Terre Haute, USA) dealing with antipredatory vigilance in a multi-predator system. He addresses the importance of different approaches to study antipredatory behaviour in a single vs. multi-predator environment. Most studies tend to follow the response of prey individuals to the most dangerous predators and ignore the — often great number — of less important predators. Lima's approach is important in integrating behavioural studies with the predator-prey interactions going on in natural multipredator communities.

So far, only a few studies have dealt with antipredatory adaptations of individual animals as a direct fitness component. However, under certain environmental conditions it could be of advantage for an individual not to breed (e.g. Ylönen 1989). Studies on breeding and predation risk are rare, especially in mammals, which was pointed out in a recent review (1991) by Carin Magnhagen (Umeå, Sweden). In her present paper she concentrates on one aspect of fitness, on parental care, and deals in her review with the behaviour of fish. Factors of importance for how much risk a nest-guarding fish should take includes brood size and age, and parent age, influencing the reproductive value of the offspring and the parent's probability of future reproduction .

Aquarium experiments on prey inspection in fish have been carried out by several research groups on a number of species (e.g. Magurran & Pitcher 1987), and the first paper on TIT for TAT (Milinski 1987) is one of the citation classics in the study of antipredatory adaptations. These experiments have provoked a lot of theoretical thinking about the evolution of co-operation and general game theory. One of the recent researchers developing these ideas further is Lee Dugatkin (Kentucky, USA) who here, together with Jean-Guy Godin (Sackville, Canada), has reviewed costs and benefits of prey approaching predators. In their paper they also present a new game theory model based on the cost-benefit perspectives of approach behaviour and group size, predicting frequency of approachers and non-approachers as well as approach distance.

Two articles deal with crayfish predation by fish and backswimmers. Björn Söderbäck (Uppsala, Sweden) compared the effect of perch on behaviour and survival of two crayfish species, one native and one introduced. The two species responded in a similar way to predation risk. However, Söderbäck suggests that the native species may have a higher total risk of predation during the juvenile period due to a lower growth

rate, leading to a longer time spent in a vulnerable size. Heikki Hirvonen (Helsinki, Finland) has looked at the indirect effect of backswimmers on juvenile crayfish. The backswimmers do not kill the crayfish, but instead take their chelae. This results both in a reduced growth rate and survival of the crayfish.

The only paper dealing — at least partly — with chemical defence against predators is by Päivi Palokangas and Seppo Neuvonen (Turku, Finland) with experiments on two Chrysomelid beetles in Finnish Lapland. This paper describes preliminary results on differences in the predation vulnerability for two species of herbivorous insects living on host plants with different chemical composition and that larvae probably increase their abilities to produce defensive chemicals with increasing age.

For all researchers using live trapping techniques on rodents, their different — often strong — species-specific odours are well-known. *Microtus*-voles have strong odours but these are not used for chemical defence against predators. Instead, there could exist adaptations of social behaviour in different species that serve as antipredatory mechanisms. Harri Hakkarainen, Erkki Korpimäki, Päivi Palokangas and Tapio Mappes (Turku and Jyväskylä, Finland) have tested experimentally if the different social behaviour — living in groups or solitarily — exposes the two species differently to avian predation. The results are partly contradictory to field observations made by one of the authors (see Norrdahl & Korpimäki 1992), which expresses the difficulty in the planning of laboratory experiments in higher vertebrates, birds and mammals.

Marcelo Cassini and Monica Galante (Oxford, UK.; Buenos Aires, Argentina) report on a simple method to monitor the feeding behaviour of wild guinea pigs in an indirect way by counting the droppings of feeding animals. There exists a good correlation between the feeding sites of the guinea pigs and the vegetation height which can be explained by the nutritional value of young grass but also by the antipredatory behaviour of foraging guinea pigs.

A characteristic feature of the shrew behaviour is the high foraging frequency with short bouts of activity and resting due to their high energy demands. This sets limitations to antipredatory behaviour of shrews as can be seen in the study by Jarmo Saarikko (Helsinki, Finland). Individual variation in the change of foraging activity is extremely high and seemingly only large animals can afford to avoid a potential predator by decreasing their activity in predators presence.

Studies on the foraging behaviour of desert rodents have produced a number of good empirical and theoretical articles on topics discussed in the present issue. Therefore two papers on the patch use of individuals under predation risk by Joel Brown and his co-authors, Robert Morgan and Beverly Dow (Chicago, USA) are a good finale of this issue. Joel gave, during the Konnevesi symposium, three enthusiastic talks — based on his desert rodent studies. His method of estimating the trade-off between safety and foraging using seed trays (determination of giving-up densities) has been adopted in several other studies. In the present issue the theory and predictions are supported by the empirical data on fox squirrels.

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