Ethology Ecology & Evolution 3: 73-77, 1991

Predator avoidance and antipredator mechanisms: distinct pathways to survival

E.D. BRODIE JR[1], D.R. FORMANOWICZ JR[1] and E.D. BRODIE III[2]

[1] *Department of Biology, The University of Texas at Arlington, UTA Box 19498, Arlington, Texas 76019, U.S.A.*

[2] *Department of Ecology and Evolution, University of Chicago, 940 East 57th Street, Chicago, Illinois 60637, U.S.A.*

Received 28 September 1989, accepted 28 June 1990

Prey may respond evolutionarily to predator pressure either by removing themselves from the foraging microhabitat of the predators (predator avoidance mechanisms) or by reducing the probability of successful predation when they are within the perceptual field of the predators (antipredator mechanisms). These two categories of survival mechanisms are under different selective regimes and the evolution of one type of prey survival mechanism reduces selection on the other.

KEY WORDS: antipredator, predator avoidance, survival.

There are two distinct categories of mechanisms mediating prey survival that may result from different selective environments. First, there are characteristics that enhance the survivorship of prey by reducing the probability that they will occupy the foraging microhabitat of potential predators (*predator avoidance mechanisms*). Second, there are characteristics of prey that reduce the probability of successful predation when they occupy the foraging microhabitat and are within the perceptual field of would-be predators (*antipredator mechanisms*).

Different types of predators can exert qualitatively and quantitatively different evolutionary pressures on prey populations. Some predators have the ability to eliminate local populations of prey (HEYER & MUEDKING 1976); here refered to as «complete» predation. Such selective pressures can have the result of favoring predator avoidance mechanisms but cannot lead to the evolution of antipredator mechanisms. Other predators may reduce prey populations but do not cause their elimination (HEYER 1976, FORMANOWICZ & BRODIE 1982); here refered to as «incomplete» predation. Unsuccessful predation is necessary for the evolution of antipredator mechanisms (VERMEIJ 1982) but also can confer selective advantages to predator avoidance mechanisms. Thus, antipredator and predator avoidance mechanisms are under somewhat different selective regimes.

Predator avoidance mechanisms eliminate the risk of predation by a specific predator by removing the prey from the foraging microhabitat of that predator and may evolve under either complete or incomplete predation of local prey populations. These mechanisms are typically patterns of behavior exhibited by prey species, such as occupying refugia (e.g., a burrow or dense vegetation), altering their foraging habitats (spatial avoidance), or adjusting their activity periods (temporal avoidance) (EDMUNDS 1974, SIH 1985). Recent studies have documented the survival advantage of predator avoidance mechanisms (e.g., SIH et al. 1988).

Antipredator mechanisms reduce the probability that a predation sequence, which begins when a prey enters the perceptual field (*sensu* JAMIESON & SCUDDER 1979, FORMANOWICZ 1987) of a predator, will go to completion (ENDLER 1986). Such mechanisms can only evolve if predation on prey populations is incomplete (VERMEIJ 1982, 1985). A variety of morphological and behavioral traits of prey are antipredator mechanisms, including: crypsis or immobility which reduce the probability of detection by a predator; speed or protean movement allowing a prey to escape a pursuing predator; shells, spines, claws, biting, autotomy, and distastefullness which allow a prey to repulse predators; and aposematic and pseudoaposematic traits which communicate repulsiveness to predators (BRODIE 1983, ENDLER 1986, GREENE 1988). Morphological and behavioral antipredator traits often interact synergystically to increase the probability of surviving a predator attack (BRODIE 1983).

The evolution of either antipredator or predator avoidance mechanisms reduces the selective pressures on the other. The effect of one type of prey survival mechanism on the evolution of the other may be examined with a simple model. Three distinct factors affect the probability of survival (S) for a prey individual: the probability that a prey avoids the foraging microhabitat of a predator (V, predator avoidance mechanisms); the probability that a prey is within the perceptive field of a predator (C) multiplied by the probability that the predation sequence is interrupted by some trait of the prey (A, antipredator mechanisms); and the probability that a prey within the foraging microhabitat will not come within a predator's perceptual field ($1\text{-}C$). The latter two factors are conditional on the probability of a prey occurring within a predator's foraging microhabitat ($1\text{-}V$). Thus, we can express the probability of survival as the sum of these factors:

$$S = V + (1\text{-}V)^{*}[(1\text{-}C) + (C^{*}A)] \qquad (1)$$

The probability that a prey avoids the foraging microhabitat of the predator (V) and the conditional probability that a prey survives within the perceptual field of the predator [$(1\text{-}V)^{*}(C^{*}A)$] are properties of the prey individual and therefore may evolve through selection by the predator. However, the probability of not coming within the perceptual field of a predator while within the foraging microhabitat of the predator [$(1\text{-}V)^{*}(1\text{-}C)$] is the result of unpredictable density-dependent properties of the predator-prey interaction and not the result of actions or traits of the prey. As such, the probability of not coming within the perceptual field of a predator cannot evolve through selection by the predator.

In order to examine selection on predator avoidance and antipredator mechanisms, we can examine the relationships between variation in these traits and variation in survival. This is similar to a selection gradient analysis where the trait in question is either predator avoidance or antipredator effects and survival is used as an estimate of fitness. This can be done by taking the derivatives of equation (1) with respect to each of the types of mechanisms:

$$dS/dV = C(1\text{-}A) \quad (2)$$

$$dS/dA = C(1\text{-}V) \quad (3)$$

The resultant derivatives are analogous to selection gradients and describe the selection pressure on prey survival mechanisms.

The selective pressure on predator avoidance mechanisms (*V*) and antipredator mechanisms (*A*) can be estimated from (2) and (3) respectively and decreases linearly as a function of the other type of mechanism (Fig. 1a-b). The *y*-intercept of these relationships is *C* and the slope is negative *C*. Thus, the probability of a prey coming within the perceptual field of the predator (*C*) defines the upper limit of selection pressure on *A* or *V* and determines the rate of change in selection with increases or decreases in *V* or *A*. Greater values of *C* allow for stronger selective pressures and a more profound effect of *A* on *dS/dV* (Fig. 1a) and of *V* on *dS/dA* (Fig. 1b). For any given *C*, selection pressure increases with decreases in *V* or *A* (Fig. 1a-b). When the probability of being in the perceptual field is zero, there is no selection for either antipredator ($dS/dA = 0$) or predator avoidance mechanisms ($dS/dV = 0$). When this probability is one, selection on these two mechanisms simplifies to:

$$dS/dV = (1\text{-}A) \quad (4)$$

$$dS/dA = (1\text{-}V) \quad (5)$$

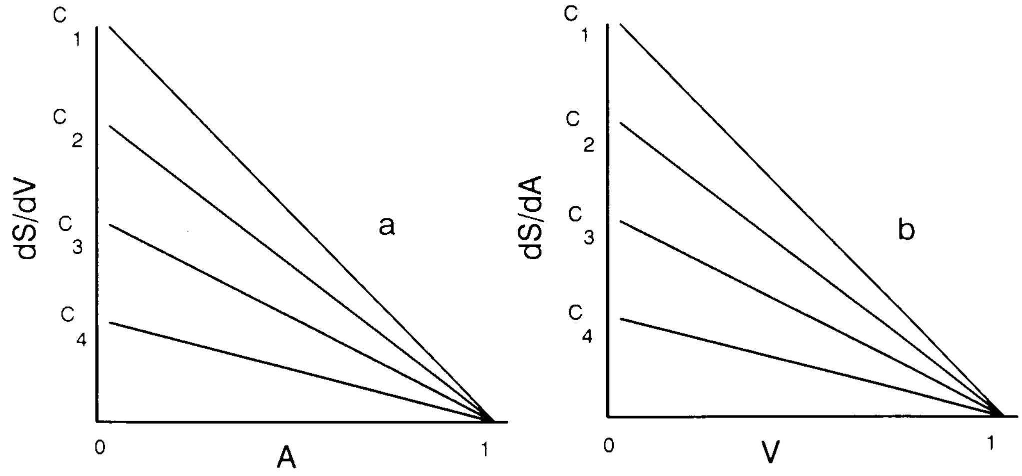

Fig. 1. — A graphical representation of the relationship between (a) selection on avoidance mechanisms (*dS/dV*) and the efficacy of antipredator mechanisms (*A*) and (b) selection on antipredator mechanisms (*dS/dA*) and the efficacy of avoidance mechanisms (*V*). The *y*-intercept and slope of the curve are determined by the probability that prey come within the perceptual field of the predator (*C*). The curves drawn are for different values of *C* ($C_1 = 1$, $C_2 = 0.75$, $C_3 = 0.5$, $C_4 = 0.25$). When $C = 0$, the curve lies along the *x*-axis.

Under these conditions, selection on predator avoidance mechanisms (dS/dV) is inversely proportional to the efficacy of antipredator mechanisms (A) and selection on antipredator mechanisms (dS/dA) inversely proportional to the efficacy of avoidance mechanisms (V). In general, selection on prey survival mechanisms (dS/dV or dS/dA) is the result of the interaction between the probability of the prey coming within the perceptual field of the predator (C) and the effectiveness of the other type of mechanism (A of V). This interaction can be illustrated by examining how the limits of A and V affect selection.

Case 1: Perfect avoidance or antipredator mechanisms.

If prey, as the result of some predator avoidance mechanism, never occur within the foraging microhabitat of the predator, then $V = 1$ (that is $1\text{-}V = 0$; Equation 1). The overall probability of survival is one and there is no selection on antipredator mechanisms ($dS/dA = 0$) or any additional predator avoidance mechanisms. If prey always survive coming within the perceptual field of a predator, then $A = 1$ and the selection on predator avoidance mechanisms (dS/dV) goes to zero. The probability of survival is one and, intuitively, selection on antipredator mechanisms is zero. When either type of mechanism is perfectly effective, there can be no selection on either because of the absence of successful predation.

Case 2: No predator avoidance or antipredator mechanisms.

If prey never avoid the foraging microhabitat of the predator, then $V = 0$ and selection on antipredator mechanisms is equal to the probability of coming within the perceptual field of the predator ($dS/dA = C$; Fig. 1b). The evolution of predator avoidance mechanisms is possible as long as $C > 0$ and there is some successful predation ($A < 1$).

It is also possible that prey may have antipredator mechanisms that are effective against some predators but are totally ineffective against others. If prey were exposed to the latter type of predator, then $A = 0$ and selection on predator avoidance mechanisms is also equal to the probability of a prey coming within the predator's perceptual field ($dS/dV = C$; Fig. 1a). Antipredator mechanisms cannot evolve under these conditions because no prey survive coming within the perceptual field of the predator (VERMEIJ 1982). The above cases illustrate that the existence and efficacy of one type of prey survival mechanism can affect the strength of selection on the other. As used in our model, antipredator (A) and avoidance (V) mechanisms represent suites of characters that contribute to prey survival. Our intent is not to describe the evolution of specific prey survival traits; rather, it is to examine the conditions that allow the evolution of suites of antipredator or predator avoidance mechanisms.

The relationship between the strength of selection on either antipredator (A) or predator avoidance mechanisms (V) and the effectiveness of the other suite of mechanisms is determined by the probability of coming within the perceptual field of the predator (C). In our paradigm, these relationships are linear, but may take other forms. For example, variation in predator state (e.g., hunger level) or the existence of fitness costs associated with specific prey survival mechanisms may alter the shape of these curves. These additional parameters do not, however, alter the qualitative relationships between C, A, and V described above.

Previous considerations of antipredator and predator avoidance mechanisms have not distinguished between these aspects of prey survival. While in extreme cases either antipredator or predator avoidance mechanisms reduce the probability of the evolution of the other, it is likely that both contribute to survival in natural systems. Recognition of the differences between these two components of prey survival is critical to a full understanding of the evolution of adaptive responses of prey to predators. Predator-prey relationships are dynamic and depend upon learning and adaptation by predators to the antipredator and predator avoidance mechanisms of their prey. These factors as well as evolutionary constraints will influence the coevolution of predator-prey interactions.

ACKNOWLEDGMENTS

We thank P.K. Ducey for comments. This work was supported, in part by the Texas Advanced Research Program under Grant No. 3748 to Edmund D. Brodie Jr and NSF-BSR-87-14955 to Edmund D. Brodie III.

REFERENCES

Brodie E.D. Jr 1983. Antipredator adaptations of salamanders: evolution and convergence among terrestrial species, pp. 109-133. In: Margaris N.S. et al., Edits. Plant, animal, and microbial adaptations to terrestrial environment. *New York: Plenum Publishing Co.*

Edmunds M. 1974. Defence in animals: a survey of anti-predator defences. *London: Longman.*

Endler J.A. 1986. Defense against predators, pp. 109-134. In: Feder M.E. & Lauder G.V., Edits. Predator-prey relationships. *Chicago: University of Chicago Press.*

Formanowicz D.R. Jr 1987. Foraging tactics of *Dytiscus verticalis* larvae (Coleoptera: Dytiscidae): prey detection, reactive distance and predator size. *Journal of the Kansas Entomological Society* 60: 92-99.

Formanowicz D.R. Jr & Brodie E.D. Jr 1982. Relative palatabilities of members of a larval amphibian community. *Copeia*: 91-97.

Greene H.W. 1988. Antipredator mechanisms in reptiles, pp. 1-152. In: Gans C. & Huey R.B., Edits. Biology of the Reptilia. Vol. 16B. *New York: Alan R. Liss.*

Heyer W.R. 1976. Studies in larval amphibian habitat partitioning. *Smithsonian Contributions to Zoology* 242: III + 27 pp.

Heyer W.R. & Muedeking M.H. 1976. Notes on tadpoles as prey for naiads and turtles. *Journal of the Washington Academy of Science* 66: 235-239.

Jamieson G.S. & Scudder G.G.E. 1979. Predation in *Gerris* (Hemiptera): reactive distance and locomotion rates. *Oecologia* 44: 13-20.

Sih A. 1985. Evolution, predator avoidance, and unsuccessful predation. *American Naturalist* 125: 153-157.

Sih A., Petranka J.W. & Kats L.B. 1988. The dynamics of prey refuge use: a model and tests with sunfish and salamander larvae. *American Naturalist* 132: 463-483.

Vermeij G.J. 1982. Unsuccessful predation and evolution. *American Naturalist* 120: 701-720.

Vermeij G.J. 1985. Aptations, effects, and fortuitous survival: comment on a paper by A. Sih. *American Naturalist* 125: 470-472.