THE EVOLUTION OF MULTI ANTI-PREDATOR CHARACTERISTICS AS ILLUSTRATED BY TIGER BEETLES (COLEOPTERA: CICINDELIDAE)

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ABSTRACT

Tiger beetles as a family show a broad spectrum of morphological, behavioral and physiological mechanisms by which their enemies are deterred. This phenomenon of multiple anti-predator mechanisms is also evident within species and individuals. Although multiple anti-predator mechanisms have been widely recognized among most if not all insects groups, general models and broad theoretical studies of predator-prey interactions have largely ignored this confounding pattern. Based on experiments and observations of tiger beetles, six theories are presented that explain the evolution of multiple anti-predator characters: 1) several characters must operate in concert to minimize predation, 2) each anti-predator character is largely or uniquely targeted against one of several distinct foraging phases used by the predator, 3) increasingly potent lines of defense may be used as a predator overcomes the primary ones, 4) separate anti-predator characters are directed at each of several different types of predator, 5) an individual prey is the result of a phylogenetic or ontogenetic accumulation of anti-predator characters, and 6) competing or counterselective forces may override or supplement the effectiveness of some anti-predator characters.

RESUMEN

Las cicindelas, como familia, demuestran amplios espectros morfológicos, de comportamiento y de mecanismos fisiológicos por los cuales sus enemigos son disuadidos. Este fenómeno de mecanismo múltiples anti-depredador, también es evidente entre las especies y entre individuos. Aunque mecanismos múltiples anti-depredadores han sido reconocidos ampliamente entre la mayoría si no de todos los grupos de insectos, modelos generales y amplios estudios teoréticos sobre la interacción entre depredadores y su presa, han practicamente ignorado estos patrones desconcertantes. Basado en experimentos y observaciones de cincindelas, se presentan seis teorías que explican la evolución de caracteres múltiples anti-depredadores: 1) varios caracteres deben de operar al mismo tiempo para disminuir depredación, 2) cada carácter anti-depredador es mayormente, o es el blanco único, contra una de las distintas fases forageras usadas por el depredador, 3) aumentando la potencia de las lineas de defensa pudieran ser usadas a medida que el depredador sobrelleva las primarias, 4) caracteres separados anti-depredadores son divigidos hacia cada uno de los diferentes tipos de depredadoves, 5) una presa individual es el resultado de una acomulación filogenética o ontogenética de caracteres anti-depredadores, y 6) fuerzas competitivas o contra-selectivas pudieran sobrellevar o suplementar la efectividad de algunos caracteres anti-depredadores.

It is likely that the vast majority of prey species exhibit multiple anti-predator characters (Pearson 1985, Endler 1988). However, most general models and mathematical theories of predator-prey interactions assume, at least implicitly, that prey have only single anti-predator characters. This single character assumption has great potential for misleading and invalid results.

At least six theories predict the evolution of multiple anti-predator characteristics within a single individual prey: 1) *Some characters may function in concert to minimize predation.* For instance, aposematic coloration and distasteful compounds are frequently associated. A complication with this category is that each of these characters may not effectively deter predation by itself, and if they only or usually function in combination, they may technically be considered one character. Tiger beetles use body size, brightly-colored abdomens exposed in flight, and defense chemicals against robber fly predators. The per cent deterrence by these characters is greatest for larger beetles with bright orange abdomens and benzaldehyde released from their defense glands (Pearson 1985). As each of these characters is eliminated from models presented to wild robber flies, the deterrent effect is reduced. Some characters such as large body size are more important by themselves than other single characters, but the greatest protection is derived from a combination of all three together. Tropical forest tiger beetles use nocturnal communal roosts that apparently rely on gregariousness to enhance defense compound potency (Pearson and Anderson 1985).

2) *Some anti-predator characters may be largely or uniquely targeted against each of the distinct foraging phases of a predator (Endler 1986).* Predator behavior can be divided into distinct stages such as search, pursuit, capture and processing (Holling 1966). Among tiger beetles anti-predator characters like crypsis (Willis 1967) are primarily effective against the searching phase, rapid flight against the pursuit phase (Pearson 1985), chemical defense such as benzoyl cyanide (Pearson et al. 1988) against the capture phase, and sharp mandibles together with enzymes in extradigestive juices against the processing phase. Most individual tiger beetles have all these characters, and together they provide protection from either a single predator or several different predators through all these foraging phases.

3) *Increasingly potent lines of defense may be used as a predator overcomes the initial ones.* The primary lines of defense function regardless of whether the predator has been perceived by the prey, and they are likely to be energetically cheap (crypsis). The secondary lines are initiated by an encounter with a predator and are generally more energetically expensive (chemicals) (Robinson 1969, Rotheray 1986). Tiger beetle colors that may serve as camouflage (Schultz 1986) or in mimicry of stinging hymenopterans (Acorn 1988) are always present and take no extra energy to protect the beetle. Flight and pygidial chemicals are only used when the primary defenses have been breached.

4) *Prey encountering several different types of predators may need a separate anti-predator character targeted at each predator (Downes 1987).* This phenomenon compounds problems interpreting results from over-simplified experimental design as well as makes models of frequency-dependent predation extremely complex (Endler 1988). Tiger beetle adults use flight as an important mechanism to escape predation from insectivorous lizards. However the instant they fly up from the ground, they become susceptible to predation by robber flies, most of which can only take flying prey items (Lavigne 1972. Pearson 1985). Specific defense chemicals like benzaldehyde are targeted at robber flies. In addition, tiger beetles are the only beetles known to possess tympana, and many species are thus apparently able to hear and respond to ultrasounds produced by the wings of attacking robber flies (Spangler 1988). Tiger beetles respond to these sounds with an instant contraction of abdominal muscles that in flight disrupts aerodynamics and causes the beetle to fall to the ground where it is again susceptible to the reptilian ground predators.

Tiger beetle body size is also related to reduction of predation from various predator types. Small tiger beetles (<8 mm are more readily taken by insectivorous lizards and spiders than are larger beetles. Large tiger beetles (>15 mm), however, are more likely to be taken by insectivorous birds. Intermediate size tiger beetles are taken by robber flies (Pearson 1985). As with flight, body size that provides protection against one type of predator automatically makes the prey more susceptible to another type of predator.

5) *Selective forces on one stage of the life cycle or direct ancestors can be carried over into other stages or descendants (Endler 1986, Downes 1987), and the resultant individual may be a composite of anti-predator characters derived from predators on all life cycle stages and ancestors.* Larval tiger beetles have several highly specialized parasitoid enemies (Pearson 1988). Large sized larvae need considerably more time than do smaller congeners to sequester sufficient food to advance through their three instars and pupal stage (Pearson & Knisley 1985). They are thus exposed longer to mortality from parasitoids than are small larvae and are at an adaptive disadvantage. However, selection for large size in the larval stage is probably at least partially the result of adaptive advantages for large individuals as adults (Pearson & Knisley 1985).

Closely associated with this theory of an ontogenetic composite of multiple anti-predator characters is a theory that explains a composite individual based on historical factors (see Edwards & Reddy 1986), evolutionary lag times, and differential genetic lability of various characters. Among tiger beetle species, it is apparent that body color for camouflage and mimicry can evolve relatively quickly (Schultz 1986). Chemical defenses, however, evidently are extremely conservative and evolve very slowly (Pearson et al. 1988). These differential evolutionary rates could result in an accumulation of slowly evolving characters adapted for different predators over time. Some of these characters may have served as pre-adaptations against subsequent predator(s), and others may have taken on other functions such as in thermoregulation, competition or courtship.

6) *Additional factors may supplement selection for anti-predator characters or even be counter-selective (Pearson 1988).* This multiplicative or synergistic potential tremendously complicates a simple understanding of the function and evolution of multiple anti-predator characters and this complicating factor can impinge on all the preceding theories. Thermoregulation, competition, courtship and a host of additional factors can supplement the function of anti-predator characters or be counter selective (Endler 1987, Kingsolver & Wiernasz 1987). Among larval tiger beetles, for instance, the longer it takes to capture sufficient food to molt into the subsequent instars and finally imagoes, the greater the probability of mortality to parasitoids (Pearson & Knisley 1985).

Body size among endothermic and ectothermic insects can have a significant effect on heating and cooling rates (May 1976, Heinrich 1981). Body size may also help minimize interspecific competition (Pearson & Mury 1979, Pearson and Stemberger 1980, Pearson 1980, Pearson & Lederhouse 1987). If small body size to maximize thermoregulation and minimize competition overrides the disadvantages accrued by susceptibility to predation, small body size is likely to be selected regardless of the increased costs to predation. The ambiguities of character function involving several types of adaptation besides predation is likely a common phenomenon.

Considerations for investigating the role of multiple anti-predator characters:
1) *Determine all the potential predators and the relative risks to lifetime fitness by each predator (Endler 1988).*
2) *Identify the rate of susceptibility and mortality in all life cycle stages.*
3) *Validate the target of each anti-predator character or suite of characters.*
4) *Establish the reduction of successful predation produced by each character.*
5) *Determine alternative functions of the anti-predator characters such as courtship, thermoregulation, competition, etc.*

Endnotes

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