

THERMAL EFFECTS ON THE ANTIPREDATOR BEHAVIOUR OF SNAKES: A REVIEW AND PROPOSED TERMINOLOGY

AKIRA MORI¹ AND GORDON M. BURGHARDT²

¹ *Department of Zoology, Graduate School of Science, Kyoto University, Sakyo, Kyoto 606-8502, Japan*

² *Departments of Psychology, and Ecology and Evolutionary Biology, University of Tennessee, Knoxville, 37996-0900 TN, USA*

The effects of temperature on the antipredator responses of snakes have been extensively studied during the last two decades. Several contradictory results have accumulated concerning the effects of temperature on the propensity of snakes to perform various behaviour patterns. We review this literature and discuss four possible factors related to these apparently contradictory results: (1) inconsistency in terms used to characterize antipredator behaviour; (2) erroneous citations; (3) interspecific differences; and (4) variable experimental designs. The last two factors reflect biologically important phenomena, whereas the first two are artificial “noise” that causes confusion and hinders scientific interpretation. To resolve inconsistency in wording, we propose a consistent terminology for the antipredator responses of snakes. Antipredator responses were characterized from three dimensions: (1) categorization from the viewpoint of whether prey animals move towards or away from predators (response is considered as either “approach”, “neutral”, or “withdrawal”); (2) categorization from the viewpoint of how much movement is involved in the behaviour (response is considered either “locomotive”, “active-in-place”, or “static”); and (3) categorization in terms of the apparent function (response is characterized as either “threatening”, “cryptic”, or “escape”). Antipredator responses of snakes, not only in relation to temperature but also in any situation, can be well characterized from these three perspectives using the proposed terminology.

Key words: defences, predator-prey interaction, reptile, temperature effect

INTRODUCTION

Various factors influence the antipredator responses that animals use when confronted with a predator. Although the behavioural repertoire and past experiences of the individual animal are important, much intraspecific variation is due to contextual factors such as the presence of conspecifics, the nature and number of the predators, the structure of the habitat, and climatic parameters such as light, humidity, and, especially for ectotherms, temperature (e.g. Burghardt & Schwartz, 1999; Magurran, 1999).

During the last two decades, more than a dozen experimental studies have explored the effects of temperature on the antipredator responses of snakes. Because performance capabilities of ectothermic animals are temperature-dependent (Stevenson *et al.*, 1985), antipredator responses that vary with temperature are usually considered adaptations for coping with physiological constraints. For instance, some snakes simply flee at high body temperature and exhibit less locomotive antipredator responses at low body temperature, because physiological mechanisms do not allow them to crawl fast enough to avoid predation (e.g. Hailey & Davies, 1986; Mori & Burghardt, 2001). However, in the past decade, contradictory results

concerning the effects of temperature on the performance of antipredator responses (e.g. striking) have appeared in the literature, even among closely related species (see below). Such variable results among the studies could be attributable to differences in terminology, responses measured, subject species, and experimental design. In the present paper we review and synthesize previous studies on temperature-dependent antipredator responses in snakes. In addition, we suggest a consistent terminology for characterizing antipredator responses of snakes to eliminate this confusion. This will aid communication between different researchers studying different species in varying ways and will help clarify the biologically significant sources of differences in antipredator responses among snakes.

REVIEW OF PREVIOUS PAPERS

We located twenty-four papers that mentioned or systematically examined thermal dependency of antipredator responses of snakes (Table 1). Most studies dealt with North American snakes: exceptions are *Natrix* in Europe, *Rhabdophis* in Japan, *Gloydius* in China, and *Pseudonaja* in Australia. Taxonomically, the subjects include colubrids – especially natricines – a few crotalines and one elapid. Except for a few earlier studies, the results are based on well-designed experiments conducted either in the field or in the laboratory.

The most overt discrepancy among the studies was the inclination of the snakes to exhibit strikes and/or

Correspondence: A. Mori, Department of Zoology, Graduate School of Science, Kyoto University, Sakyo, Kyoto 606-8502, Japan. *E-mail:* gappa@ethol.zool.kyoto-u.ac.jp

bites. Several studies found that snakes are more apt to strike at low temperature (Arnold & Bennett, 1984; Fitch, 1965; Goode & Duvall, 1989 [but only in pregnant females]; Heckrotte, 1967; Shine *et al.*, 2000), whereas others showed that snakes tend to strike at high temperature (Keogh & DeSerto, 1994; May *et al.*, 1996; Schieffelin & de Queiroz, 1991; Shine *et al.*, 2002). In addition, some studies failed to find any temperature effects on the tendency to strike, bite, or bluff (Gibbons & Dorcas, 2002; Goode & Duvall, 1989 (in males and non-pregnant females); Mori & Burghardt, 2001; Mori *et al.*, 1996; Scribner & Weatherhead, 1995; Whitaker *et al.*, 2000). These apparently contradictory results and associated confusion can be attributed to the following four factors.

(1) INCONSISTENCY OF WORDING CONCERNING THE CHARACTERIZATION OF ANTIPREDATOR RESPONSES

Many adjectives have been used to express the propensity to perform antipredator responses by snakes: "aggressive", "offensive", "defensive", "passive", "threatening", "static", "active", "retaliatory" and so on. Heckrotte (1967) used the term, "defensive" behaviour, apparently to indicate biting, and Goode & Duvall (1989) regarded the snakes that more rapidly escalated to striking as being more "defensive." On the other hand, Arnold & Bennett (1984) applied the term "defensive" to responses such as head-hide and body-ball. The term "defensive" behaviour has also been used as a synonym of antipredator behaviour, or even used for any kind of behaviour that protects an animal from conspecifics as well as predators (Edmunds, 1974; Immelmann & Beer, 1989).

Another example of confusion is found in the term "active". Arnold & Bennett (1984) used "active" defence for head-hide and body-ball, whereas Hailey & Davies (1986) used "active" defence for escape response and called balling a "static" defence. Kissner *et al.* (1997) labeled rattling by rattlesnakes as "active" defense in contrast to crypsis. Prior & Weatherhead (1994) considered biting an "active" defence.

(2) ERRONEOUS OR EQUIVOCAL CITATIONS

Keogh & DeSerto (1994) mentioned that the study by Arnold & Bennett (1984) showed an increased flight response of *Thamnophis radix* at higher temperature. In fact, Arnold & Bennett (1984) did not include a flight response in their variables; their experimental protocol did not allow them to record any kind of flight response (see below). Passek & Gillingham (1997) mentioned that their results are inconsistent with the findings of Schieffelin & de Queiroz (1991). However, both studies showed that energetically costly responses involving much movement are more frequently exhibited as temperature increases, and thus, their "inconsistency" is equivocal. As has already been pointed out by Schieffelin & de Queiroz (1991), a cursory examination of previous studies may lead to erroneous conclusions

and create a potential source of confusion in subsequent studies.

(3) INTERSPECIFIC DIFFERENCES IN RESPONSE TO TEMPERATURE

It is not surprising that different species may respond differently to changes in temperature (Shine *et al.*, 2000). Snakes have adapted to various ecological niches with tremendous physiological, morphological, and behavioural specialization (Greene, 1997), and show varied antipredator responses even among closely related species (Bowers *et al.*, 1993; Herzog & Burghardt, 1986) or among populations of the same species (Burghardt & Schwartz, 1999; Mori & Burghardt, 2000). Thus, it is likely that closely related species have evolved different adaptive responses to changes of temperature. The absence of temperature effects may simply reflect the low tendency in performing the focused responses (e.g. strike in *Rhabdophis tigrinus*: Mori & Burghardt, 2001). In addition, when interspecific comparisons are made, we should keep in mind the fact that snake species have different preferred body temperatures (Lillywhite 1987; Mori *et al.*, 2002, and the references therein), and thus, "low" body temperature for a given species may not be necessarily "low" for another species. In some species (e.g. *T. ordinoides* and *R. tigrinus*) consistent individual differences in response to temperature can also occur (Brodie & Russell, 1999; Mori & Burghardt, 2001).

(4) DIFFERENCES IN EXPERIMENTAL DESIGN

The most important problem underlying inconsistent results may arise from differences in experimental design. This is not a minor problem, because it underlies an important issue in understanding the behavioural mechanisms of animals. In most studies, flight responses are observed or enhanced at higher temperatures (Table 1). Among the eight studies using *Thamnophis*, however, this trend was observed only in five (Brodie & Russell, 1999; Fitch, 1965; Heckrotte, 1967; Passek & Gillingham, 1997; Shine *et al.*, 2000). This does not necessarily imply that the remaining three studies (Arnold & Bennett, 1984; Schieffelin & de Queiroz, 1991; Scribner & Weatherhead, 1995) showed the absence of an increased flight response at higher temperature. Rather, this difference in results is clearly related to differences in experimental protocols. In the latter studies they had no opportunity to show flight responses because the snakes were continuously followed by the stimulus (human hand) (Scribner & Weatherhead, 1995) or were scored after they became exhausted (Arnold & Bennett, 1984) or motionless (Schieffelin & de Queiroz, 1991). These authors did not include "flight" in the available options of behavioural variables.

Another potentially confounding factor is the effect of test order of stimulus and thermal condition (Burghardt & Schwartz, 1999). As pointed out by various authors (Arnold & Bennett, 1984; Schieffelin & de Queiroz,

1991), the temperature effects observed by Arnold & Bennett (1984) may have been confounded with order effects, which resulted in thermal effects different from those obtained by Schieffelin & de Queiroz (1991). Balancing testing order of different conditions is typically the most effective means of dealing with the test order problem (but see Burghardt & Schwartz, 1999, for problems that might still exist even with balanced test orders, such as differential habituation effects).

The inconsistencies in results noted above may also reflect differences in the internal conditions of the animals. Snakes often shift antipredator responses sequentially (Bowers *et al.*, 1993; Duvall *et al.*, 1985; Schieffelin & de Queiroz, 1991). This behavioural sequence may reflect motivational and/or physiological changes of snakes throughout the interaction between the prey and the predator. The snakes tested by Arnold & Bennett (1984) were undoubtedly in the final stage of the sequence because behaviours were recorded when the snakes were exhausted after being chased down a track, whereas the snakes tested by Schieffelin & de Queiroz (1991) were in earlier stages of the sequence. Passek & Gillingham (1997) quickly uncovered common garter snakes in retreats, and the flight response they observed represented the initial stage of the antipredator behavioural sequence. It is also possible that captive-induced motivational and/or physiological modification, such as recent feeding (Ford & Shuttlesworth, 1986; Herzog & Bailey, 1987) and other unintentional treatments, could affect the responses of snakes (Shine *et al.*, 2000).

PROPOSED TERMINOLOGY

The above four factors can be divided into two categories. Differences in results due to interspecific differences and differences in experimental design potentially reflect biologically significant phenomena, whereas inconsistency of wording and erroneous citations represent artificial “noise” that can create confusion and hinder understanding. To remove confusion caused by semantic differences attached to words used to characterize the responses we have attempted to integrate the terminology and provide new definitions applicable to antipredator responses of snakes. Defining behaviour patterns from multiple viewpoints would be useful to understand the nature of those behaviours (Drummond, 1981). We begin by showing that antipredator responses can be characterized in at least three dimensions.

First, they can be viewed from changes in the distance between predators and prey. If a behaviour involves prey movement that reduces this distance, it can be called an “approach” response. Conversely, if a behaviour involves prey movement that increases this distance, it can be called a “withdrawal” response. All responses that do not involve active movement by the prey that decreases or lengthens the distance between the prey and the predator we term “neutral” responses.

In this perspective, strike and neck-butting are considered approach responses, body-flatten, tail-vibration, and immobilization are categorized as neutral responses, and flight is considered a withdrawal response.

Second, antipredator responses can be categorized from the viewpoint of how much movement is involved in the behaviour. From this viewpoint, the flight response is considered the most “locomotive” reaction, whereas immobilization or freezing is characterized as the most “static” response. Several common responses such as strike and tail-vibration would be considered “active-in-place” responses because they involve movement of body parts without any locomotion. This categorization partially reflects the amount of energy required for performing various antipredator responses. This strictly behavioural typology in terms of movement does not rule out the possibility that different responses have varying energetic consequences for different snakes. We envision that phylogenetic analyses of antipredator repertoires and their contextual deployment could be useful adjuncts to studies of metabolism, muscle physiology, and foraging mode.

Third, antipredator responses can be viewed in terms of their apparent function. If a response involves any behavioural element apparently designed to deter the intruding predator from attempting predation, the response can be called “threatening”. Representative threatening responses are strike, bluff, hissing, rattling, and body-flatten. In this system, antipredator responses such as immobilization and head-hide are considered “cryptic” because these behaviours rely on reducing the probability that the predator will recognize the animal as prey. Snakes that are aposematically coloured or marked may be immobile, as are cryptic prey, but may engage in some behaviour to enhance the antipredator display (e.g. Greene, 1973; Mori & Hikida 1991). Functional interpretations are more difficult to confirm than the mere description used in the other two perspectives but are also a key aspect of biological inquiry. Flight is considered a protective response labeled as “escape”: although the snake may reveal its presence, it acts to reduce the probability of capture not by actual deterrence, but by removing itself from the situation. Other examples of “escape” responses are evasive movements such as reversal of direction during flight (e.g. Brodie, 1993). We do not use the word “defensive” as the antonym of “threatening” in order to avoid confusion (see above).

APPLICATION

It is useful to characterize antipredator responses from all three perspectives. As an example, we did this for the antipredator behaviours of *R. tigrinus* recorded in Mori & Burghardt (2000, 2001). One of the most characteristic behaviours is the neck arch, in which the snake raises the head slightly and strongly bends the anterior part of the neck region ventrally so that the snout is directed to, and makes contact with, the substrate. We would label this a neutral, static, threatening response

Table 1 continued...

<i>Sistrurus catenatus</i>	adult (?)	negative, no reaction remain stationary	positive, rattle rattle while flee	field	step closely	Prior & Weatherhead (1994)
<i>N. sipedon</i> ^c	various	more refuge-seeking more predator-disorienting	n.a.	laboratory	chase while swimming in water	Scribner & Weatherhead (1995)
<i>T. sirtalis</i> ^c	ditto	more predator-disorienting	n.a.	ditto	ditto	ditto
<i>T. sauritus</i> ^c	ditto	ditto	n.a.	ditto	ditto	ditto
<i>S. miliarius</i> ^d	various	n.a.	strike	field	approach or tap on head	May <i>et al.</i> (1996)
<i>Rhabdophis tigrinus</i>	adult & neonate	body-flatten, neck-flatten neck-arch, immobilize	flee	laboratory	pin by hook or tap by hand	Mori <i>et al.</i> (1996)
<i>Crotalus v. viridis</i> ^a	adult	closer distance before rattling	longer distance before rattling	field	approach	Kissner <i>et al.</i> (1997)
<i>T. sirtalis</i> ^c	adult (?)	body-flatten	flee, bite (?) ^f	field	approach or grab by hand	Passek & Gillingham (1997)
<i>T. ordinoides</i>	neonate	fewer reversals crawled short distance	more reversals crawled long distance	laboratory	tap by hand	Brodie & Russell (1999)
<i>Pseudonaja textilis</i>	various	shorter flight distance remain stationary	longer flight distance flee	field	approach	Whitaker & Shine (1999)
<i>T. sirtalis</i>	adult	remain still, strike body flatten	flee	field	peck by finger	Shine <i>et al.</i> (2000)
<i>P. textilis</i> ^{a, b}	adult	n.a.	n.a.	laboratory	wave or touch with stimuli	Whitaker <i>et al.</i> (2000)
<i>R. tigrinus</i>	adult	body-flatten, neck-flatten neck-arch, immobilize dorsal facing posture	flee	laboratory	pin by hook	Mori & Burghardt (2001)
<i>Gloydius shedaoensis</i>	adult & juvenile	no overt response	flee, strike, tail-twitching	field	approach and tap by stick	Shine <i>et al.</i> (2002)
<i>Agkistrodon piscivorus</i> ⁱ	various	n.a.	n.a.	field	stand beside, step on, and pick up	Gibbons & Dorcas (2002)

TABLE 2. Characterization of antipredator responses of *Rhabdophis tigrinus tigrinus* (after Mori & Burghardt, 2001) and other common antipredator responses of snakes from three independent viewpoints. Definitions of terminology are presented in text.

BEHAVIOUR	CHANGE OF DISTANCE:		AMOUNT OF MOVEMENT:		APPARENT FUNCTION:	
	Withdrawal (W)	Neutral (N)	Static (S)	Active-in-place (Ac)	Escape (E)	Cryptic (C)
	Approach (Ap)		Locomotive (L)		Threatening (T)	
Strike		Ap		Ac		T
Neck-flatten		N		S		T
Body-flatten		N		S		T
Neck-arch		N		S		T
Neck-butting		Ap		Ac		T
Jerk		N		Ac		T
Immobile		N		S		C
Flee		W		L		E
Reversals		N/W		L		E
Head hide		N		S		C
Tail vibration		N		Ac		T
Rattling		N		Ac		T
Feign death		N		S		C
Hissing		N		S		T
Cloacal discharge		N		S		T
Body thrash		N		L		T

TABLE 3. Characterization of antipredator responses of snakes observed in temperature-effect studies listed in Table 1. Responses in parentheses indicate the increased tendency of the responses at the temperature. Ac, active-in-place; Ap, approach; C, cryptic; E, escape; High, higher temperature; L, locomotive; Low, lower temperature; N, neutral; S, static; T, threatening; W, withdrawal. Definitions of terminology are presented in text. *Only in pregnant females.

Authority	CHANGE OF DISTANCE		AMOUNT OF MOVEMENT		APPARENT FUNCTION	
	Low	High	Low	High	Low	High
Fukada (1961)	N	W	S	L	T	E
Fitch (1965)	N, Ap	W	S, Ac	L	T	E
Heckrotte (1967)	Ap	W	Ac	L	T	E
Mutoh (1983)	N	—	S	—	C	—
Arnold & Bennett (1984)	N, Ap	N	S, Ac	S	T	C
Layne & Ford (1984)	—	(W)	—	(L)	—	—
Hailey & Davies (1986)	N	W	S	L	C	E
Goode & Duvall (1989) ^a	Ap	W	Ac	L	T	E
Schieffelin & de Queiroz (1991)	N	N, Ap	S	Ac	C	T
Weatherhead & Robertson (1992)	—	—	—	—	—	—
Keogh & DeSerto (1994)	N	Ap	S	Ac	C	T
Prior & Weatherhead (1994)	N	N, W	S	Ac, L	C	T, E
Scribner & Weatherhead (1995)	—	—	—	—	—	—
May <i>et al.</i> (1996)	—	Ap	—	Ac	—	T
Mori <i>et al.</i> (1996)	N	W	S	L	T, C	E
Kissner <i>et al.</i> (1997) ^a	—	—	—	—	(C)	(T)
Passek & Gillingham (1997)	N	W	S	L	T	E
Brodie & Russell (1999)	—	(W)	—	(L)	—	—
Whitaker & Shine (1999)	N	W	S	L	C	E
Shine <i>et al.</i> (2000)	N, Ap	W	S, Ac	L	T, C	E
Whitaker <i>et al.</i> (2000)	—	—	—	—	—	—
Mori & Burghardt (2001)	N	W	S	L	T, C	E
Shine <i>et al.</i> (2002)	N	Ap, N, W	S	Ac, L	C	T, E
Gibbons & Dorcas (2002)	—	—	—	—	—	—

(Table 2). Although neck-arch may not deter predation by itself, it may attract the attention of the predator to the nuchal glands, and the secretions from the glands may act as a predator deterrent (Mori *et al.*, 1996; Mori & Burghardt, 2000, 2001). Thus, functionally, neck-arch can be regarded as a threatening response. Another characteristic behaviour of *R. tigrinus* is neck butting, in which the snake swings its head backwards with erratic movements so that the dorsal part of the neck region is butted against the stimulus object. This behaviour is labeled as an approach, active-in-place, threatening response. These three perspectives also help characterize the nature of components revealed by principal components analysis of behaviour at different temperatures (see Mori & Burghardt, 2001).

Using this terminology, some of the antipredator responses listed in Table 1 are characterized as follows. Head hide: neutral, static, cryptic response; tail vibration: neutral, active-in-place, threatening response; rattling: neutral, active-in-place, threatening response (Table 2). Death feigning is one of the most dramatic and complex antipredator responses in snakes. Because such immobility may induce predators to divert their attention from the dead prey or make them not recognize it as "food" (Burghardt & Greene, 1988), this behaviour is considered neutral, static, and cryptic. Other common antipredator responses in snakes (Greene, 1988) can be effectively characterized (Table 2).

As an overview of the temperature effects on antipredator responses of snakes, all the antipredator responses listed in Table 1 are characterized from the three viewpoints and summarized in Table 3. General tendencies, as well as the similarities and discrepancies, in antipredator responses among the previous studies are easily understood using this table. In the change of distance dimension, withdrawal is a predominant response at higher temperature and never observed at lower temperatures. Obviously, all studies except for one (Arnold & Bennett, 1984), which did not include flight as a response variable, show the same tendency in the amount of movement: as temperature increases, snakes change their responses from static to locomotive ones. In the apparent function dimension, escape is a predominant response at higher temperature followed by threatening response. No studies show escape response at lower temperatures. Different results among the studies revealed in Table 3 are not due to the artifact caused by confusing terminology but, in most cases, attributable to biologically significant factors described above. The similarities and discrepancies in the three dimensions among the studies are important sources of information that would help interpret and understand adaptive and functional significances of temperature-dependent antipredator tactics in snakes.

CONCLUSION

The use of varying experimental designs is needed to uncover novel aspects of a phenomenon. However, there

needs to be more recognition and careful consideration of the various factors that can affect behavioural responses, especially when the animal has several behavioural options that change sequentially. These factors can include changes in internal factors such as motivation and physiological condition (stress level, recent feeding, reproductive state, ecdysis). Most behavioural responses are the results of an interaction between external and internal factors (Mook, 1996). Although it may not be possible to control all the internal factors during an experiment, such internal factors should be considered when comparing studies. As with any complex behaviour that varies within and across species, it is important to eliminate any artificial confusion and precisely focus our attention on the real sources of differences. The aim of the present paper is not only to review the literature on the thermal effects on antipredator responses in snakes, but also to call researchers' attention to the existing confusion of terminology and propose a resolution. We have to admit that our proposed terminological categorization partially relies on a subjective judgment of the adaptive function of the snake's behaviour (e.g. threat, escape) and thereby infer the animal's "intention". Such judgments are actually at the heart of much behavioural research, but such testable inferences can be usefully derived through a judicious application of critical anthropomorphism (Rivas & Burghardt, 2002). We hope that our attempt to remove terminological confusion will help to clarify biologically relevant mechanisms that cause different behavioural responses of snakes under different thermal conditions, and in other contexts as well.

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