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Canid Elicitation of Blood-Squirting in a Horned Lizard (*Phrynosoma cornutum*)

GEORGE A. MIDDENDORF III AND WADE C. SHERBROOKE

In staged, predator-prey encounters between Texas horned lizards, *Phrynosoma cornutum*, and a canid, *Canis familiaris*, 47 of 55 lizards (85%) squirted blood from orbital sinuses. The probability of blood-squirting was not significantly affected by either (1) lizard body temperature (low, 85% vs high, 100%) or (2) time of day (diurnal, 70% vs nocturnal, 70%). A canid was more likely to elicit blood-squirting (100%) than a canid-mimicking human (20%). When the canid was restrained from direct contact, blood-squirting did not occur, but when lizards were simultaneously subjected to human tactile stimulation, 20% squirted blood. Lizards responded similarly to canid saliva and distilled water, implying that saliva does not provide cues used in the discrimination of canids. Overall, tactile cues appear to play a significant role in the elicitation of blood-squirting. Because roadrunners and grasshopper mice are known to not elicit blood-squirting in predator-prey encounters, these data support the canid antipredator defense hypothesis as an explanation of this unique behavior. Blood-squirting appears to be a context-dependent reptilian antipredator display in which elicitation of the squirting response is determined by predator type.

MANY reptiles use cloacal discharges and external glandular secretions in encounters with predators, presumably as antipredator devices. In a few rare cases, the putative defensive substance is, or includes, blood of the displaying, prey animal, e.g., cloacal autohemorrhage, cephalic autohemorrhage, and blood-squirting (Greene, 1988). The specific role of blood in these situations remains unknown, but if it is to serve an antipredator function, it must (1) be employed in the presence of an appropriate predator, and (2) reduce the likelihood of predation.

In the last century, Wallace (1871) and others (Hay, 1892; Stejneger, 1893; Van Denburgh, 1897) reported horned lizards (*Phrynosoma*) to have the unique ability to squirt blood "from the eye." The first years of this century saw reports of this phenomenon by Cope (1900) and others (Holder, 1901; Bryant, 1911; Hurter, 1911), beginning a tradition (Van Denburgh, 1912; Winton, 1914; Ruthling, 1919) that has moved into the popular literature (Ditmars, 1949; Morris, 1974; Carr, 1977). Yet, despite all these reports, the specific context, mechanism, and function of the behavior remain poorly understood. Except for Lambert and Ferguson (1985) who reported blood ejection in 5.9% of 118 *P. cornutum* encounters on a highway and Parker (1971) who noted blood-squirting in 4.6% of 65 captures of *P. solare*, most past

reports of blood-squirting have been limited to anecdotal observations.

Studies of the mechanism of blood-squirting are limited. Bruner (1907) in his detailed study of reptilian mechanisms of raising venous blood pressure in the head, suggested that increased blood pressure in the orbital sinus leads to blood-squirting from a rupture of the nictitating membrane. In contrast, Burleson (1942) reported that blood escaping from the orbital sinus passes into the lower eyelid (conjunctival sac), without rupturing the nictitating membrane. Both noted that blood passed through the conjunctival sac to the exterior. Burleson (1942), Heath (1966), and Cowles (1977) hypothesized that a fluid from the lacrimal or Harderian glands may be added to the blood before ejection from the eye. Although Heath's (1964, 1966) studies of thermoregulation and cephalic-shunting in *Phrynosoma* provide a mechanistic explanation for increasing blood pressure levels in the orbital sinus, many details of blood release and discharge remain unclear. Few studies exist of the ejected blood, and although Schmidt et al. (1989) established that the blood of *P. cornutum* contains a factor enabling it to detoxify antivenom of *Pogonomyrmex maricopa*, other aspects of *Phrynosoma* blood chemistry are unknown.

Hypotheses of the function of blood-squirting abound in the literature, but most authors (Holder, 1901; Oliver, 1955; Schmidt and In-

ger, 1957) have suggested that the discharge of blood by *Phrynosoma* may serve a defensive function by irritating potential predators. Hay (1892) reported two cases of inflammation in human eyes that received discharges of *P. cornutum* blood. However, he, Cowles (1977), and we experienced no particular adverse effect when blood was tasted. Even so, Hay hypothesized that the discharge may act as a distraction, allowing the lizards time to escape. Pope (1955) and Miller (1948) suggested that the blood is essentially harmless. Further, Schmidt and Inger (1957) and Morris (1974) questioned the potential efficacy of blood-squirting in reducing predation.

Although most hypotheses have focused on predation, other explanations have been suggested or investigated, including ones relating to thermoregulation (Collins, 1974, 1982), sexual dimorphism (Lambert and Ferguson, 1985), breeding season (Bryant, 1911; Van Denburgh, 1922), molting cycle (Winton, 1916; Milne and Milne, 1950; Reeve, 1952), parasitism (Winton, 1914), hibernation (Pequegnat, 1945), and various environmental variables (Pequegnat, 1945; Lambert and Ferguson, 1985). Some authors have suggested that squirting is secondarily acquired by only a few individuals (Winton, 1914; Tate, 1971) or is a polymorphic trait (Lambert and Ferguson, 1985).

Holder (1901), Burleson (1942), and Cowles (1977) hypothesized that canids may be effective elicitors of blood-squirting, as well as responding adversely to the squirted blood (see also Van Denburgh, 1922; Klauber, 1939; Reeve, 1952). In the 1960s, R. Cowles and C. Shaw, in predator-prey trials at the San Diego Zoo, apparently found that canids both elicit blood-squirting and react negatively to the blood (C. Gans, pers. comm.; see also Cowles, 1977, p. 163). Yet, Milne and Milne (1950) did not observe blood-squirting by *P. cornutum* subjected to attack ("gnawing") by young dogs. Furthermore, Snow (1973, Bureau of Land Management, Habitat Management Series 6, T-N-238, unpubl.) reported horned lizards in the stomach contents of the kit fox, *Vulpes macrotis*, and Collins (1982, 1985) observed coyotes, *Canis latrans*, eating *P. cornutum* without ill effects. Thus, considerable doubt remains concerning (1) the ability of canids or other potential predators to elicit blood-squirting, (2) whether the blood serves an antipredator function, and (3) if so, how?—be it due to negative olfactory or

gustatory cues, to visual impairment or ocular irritation, or to distraction for escape.

Previous observers have been frustrated by the rarity of blood-squirting and an inability to elicit the behavior. In this paper we explore some of the potential cues responsible for eliciting the behavior and determine the ability of the lizards to use this putative antipredator mechanism at various temperatures and in diurnal and nocturnal settings. Our evidence supports the hypothesis that blood-squirting in *Phrynosoma* is an antipredator behavior used against canids and that this response is not seen in all predator-prey interactions.

METHODS

Adult Texas horned lizards, *P. cornutum* (Harlan), were collected in Cochise County, Arizona, and Hildago County, New Mexico. Twenty-six adult animals (SVL 78–100 mm) were used in 1989 and 20 animals (SVL 76–96 mm) in 1990. Each lizard was measured, weighed, sexed, and individually numbered on the ventrum. Animals were housed in a $5.5 \times 4.6 \times 2.2$ m screened, retaining cage at the Southwestern Research Station in the Chiricahua Mountains near Portal, Arizona. *Pogonomymex* ants were provided ad libitum, and water was supplied by natural rainfall and sprinkler for "rain-harvesting" (Sherbrooke, 1990a).

All experimental trials in 1989 were conducted between 0700–0930 MST in an open, sand arena near Rodeo, New Mexico, between 7–14 June. Fully shaded air temperatures (2 cm above substrate) ranged between 19.9 C and 29.0 C. Trials for effects of time of day, conducted 23–24 August 1990, were performed in the retaining cage. The canid used for both years was a 2–3-year-old female, yellow Labrador retriever (*Canis familiaris*). Lizards were randomly assigned to treatments with the restriction that animals used in previous tests were divided equally between groups; experiments were run in the sequence presented in this paper. A verbal record was made of observed responses of the dog and lizard interactions during the trials. To limit exposure of the dog to blood and thereby minimize any potentially inhibiting effects, all trials were halted at the first sign of blood-squirting (one or both eyes) or, if the behavior was not elicited, at the end of the predetermined trial period. Trial durations were 10 min, except for the low/high temperature

TABLE 1. ELICITATION OF BLOOD-SQUIRTING BY *Phrynosoma cornutum* IN RESPONSE TO CANID OR NONCANID ATTACKS UNDER VARIOUS EXPERIMENTAL CONDITIONS. Means and one standard deviation are shown for time to initiation of blood-squirting.

	Trial duration (min)	Sample size (n)	Number of lizards squirting	Time to squirting (sec)
Canid attack	10	10	10	72.5 ± 76.2
Simulated canid attack (human)	10	10	2	579.0 ± 14.1
Canid saliva	10	10	4	85.5 ± 74.8
Distilled water	10	10	4	70.8 ± 107.6
Restrained canid attack				
With tactile	10	10	2	76.0 ± 4.2
Without tactile	10	10	0	—
Canid attack				
Low temperature	3	13	11	24.6 ± 16.8
High temperature	3	12	12	33.3 ± 22.2
Canid attack				
Diurnal	3	10	7	42.2 ± 25.2
Nocturnal	3	10	7	29.0 ± 23.2

and diurnal/nocturnal trials which were run for 3 min. In all trials, the dog attacked the lizard repeatedly and continuously. Attacks involved barking, pawing, gentle biting, nibbling, and picking up and tossing of the lizard.

Statistical analyses of numbers of lizards squirting blood in the different treatments employed chi-square tests ($df = 1$ for all tests). Response time differences were analyzed using Wilcoxon tests. Significance levels for all tests were $P = 0.05$. Because all or none of the animals responded in one of the treatments in three experiments, the results for these are reported without chi-square analysis.

RESULTS

Canid vs human stimulation.—Responses to two potential predators, a canid and a human mimicking the dog's behavior, were assessed in 20 trials on two subsequent days. Lizards were selected randomly and placed in the center of the arena. In alternating trials, either the canid or one of us on all fours, barked at, approached, chased, and physically manipulated the lizard (WCS touched, stroked, tapped, picked up, and tossed but did not bite).

Blood-squirting behavior was elicited in all 10 canid trials, whereas it was seen in only two human (simulated canid) trials (Table 1). Re-

sponse time to blood-squirting was significantly faster to the canid ($U = 20$, $P < 0.05$; Table 1).

Canid saliva vs distilled water.—The potential role of canid saliva as a cue for eliciting blood-squirting was assessed in 20 trials on two subsequent days. Saliva was obtained from the canid used in all trials. Distilled water was used as a control in alternating trials. Lizards were hand restrained, and physically manipulated by the experimenter until some degree of eye puffing (see below) was observed. At this point a cotton swab applicator was used to apply either saliva or water to the nasal and ocular region by tapping and stroking.

In both treatments, the same proportion of animals, four of 10, squirted blood ($\chi^2 = 0$, $P > 0.05$; Table 1). Differences in time to blood-squirting between the two treatments were not significant ($U = 11$, $P > 0.05$; Table 1).

Restrained canid attack (with and without human tactile manipulation).—In this experiment, we attempted to isolate the tactile component of an attack from other predator stimuli. In all 20 trials, lizards were protected from the attacking dog by an encircling enclosure of welded wire (2.5×5 cm grating; 37 cm diameter; 58 cm high) stabilized by the experimenter. The enclosed lizards were exposed to canid visual, au-

ditory, and olfactory cues (as the dog attacked outside the enclosure) but not to tactile components of the attack. In alternating trials, the lizards were either left unmolested or hand stimulated (touching, poking, scratching) by the experimenter randomly on the head and body.

When exposed to an attack by a restrained canid in the absence of tactile stimulation, no lizards squirted blood. Only two of 10 lizards responded when subjected to the additional factor of human tactile stimulation (Table 1).

Responses of lizards at low and high body temperatures to canid attack.—Because of its potential significance in predator-prey encounters, we assessed whether blood-squirting might be influenced by body temperature (T_b). Twenty-five lizards were tested in canid attack trials lasting three minutes. Alternating trials were conducted for the lizards which, prior to testing, had been either held on ice ($\bar{x}$ $T_b \pm 1$ SD: 10.9 ± 0.8 C, start of trial; 16.0 ± 2.1 C, end) or placed in the sun (30.3 ± 4.4 C, start; 30.1 ± 3.4 C, end).

Body temperature did not affect blood-squirting; almost all lizards in both groups squirted blood when exposed to the canid (Table 1). Body temperature also did not significantly affect response time ($U = 81.5$, $P > 0.05$; Table 1).

Response of lizards to diurnal and nocturnal canid attack.—Because many canids are active nocturnally, as well as diurnally, and may encounter buried, surface sleeping, or active *Phrynosoma* at night (Harris, 1958; Williams, 1959; Sherbrooke, 1991), we examined whether the response to canids would vary as a function of time of day. We conducted canid attack trials on lizards at either 1030–1130 MST (diurnal) or 2230–2330 MST (nocturnal). Temperatures for day trials ranged between 31–32 C and for night trials between 20–22 C. Ten animals were selected randomly for each period. Nocturnal trials were conducted under ambient light (no moon was visible), and a dim red light was used intermittently to facilitate observations.

Blood-squirting was not significantly affected by time of day; seven of 10 lizards squirted blood in both diurnal and nocturnal treatments ($\chi^2 = 0$; Table 1). Response times to blood-squirting did not differ between trials ($U = 33.5$, $P > 0.05$; Table 1).

Additional behavioral observations.—Several stereotypic behaviors by *P. cornutum* were noted repeatedly throughout the staged predator-prey

encounters. Initial signs indicating a likelihood of blood-squirting included puffiness of the ocular area. The tissue swelling is due to an increase in blood pressure in portions of the cephalic veins and an infusion of the circumocular blood sinus (Bruner, 1907; Heath, 1964). The visible features of blood-squirting can be divided into four stages: (1) slight puffiness, following initial closure of the eyelids; (2) inflation and protrusion of the eyelids and ocular area; (3) the appearance of a slight opening near the center of the appressed edges of the eyelids, usually just prior to blood-squirting; and (4) ejection of a stream of blood (Fig. 1). Although eye puffiness was often observed in response to the canid, its appearance did not guarantee blood-squirting. In fact, if the canid ceased harassing the lizard, the tissues surrounding the eyes quickly deflated and the eyelids opened. Inflation of the ocular region prior to squirting could proceed slowly, move back and forth between stages 1 and 2, or take place rapidly. In many trials, progression through the stages to blood-squirting took less than 15 sec.

Hurter (1911) commented on the apparent directionality with which ejected blood is released, implying that lizards aim at an attacking predator's mouth or eyes. We were impressed by the frequency with which the dog was struck by blood on the muzzle and near the eyes. Nevertheless, we obtained no clear evidence that horned lizards direct the discharge of blood from the opening between the eyelids. During our efforts to obtain photographs of blood-squirting, we observed that the trajectory of blood leaving the eye was vertical to the frontal plane of the head (Fig. 1). Perhaps orientation of the head during blood-squirting permits some aiming at the predator's mouth or eyes. This might be a purposeful directing of the blood at a target or an incidentally associated result of the use of horns in defense. It is also possible that the vertical trajectory was due to our tactile stimulation of the eyelids.

In response to attacks, horned lizards often thrust their heads back at the canid, using the horns to deter biting. The canid usually responded by dropping the lizard and then, in further bites, avoided the head. In several cases, the head-tilted-backward response (Sherbrooke, 1987a) was associated with an incident of blood-squirting. Frequently, the lizards under canid attack raised their tails into a vertical position, promoting bites to the tail and often leading to subsequent lifting and tossing of the lizard. Seemingly, tail-raising served to direct

Fig. 1. Adult Texas horned lizard, *Phrynosoma cornutum*, squirting blood from the right ocular sinus following exposure to a canid, *Canis familiaris*, and human tactile stimulation of the eyelid. Note the strong stream of blood (diameter ~ 1 mm) leaving the parted eyelids and breaking into droplets. Blood on the head resulted from a previous squirt. Photo copyright by Raymond A. Mendez.

attention away from the head. After tossing the lizard, the canid often experienced difficulty relocating it. In addition, we noted that lizards frequently opened their mouths and protruded the tongue during attacks. The function, if any, of this behavior is not clear. In contrast to some earlier reports (Ditmars, 1949; Cutter, 1959),

we did not note a loud popping sound when blood-squirting was initiated.

DISCUSSION

Our study shows that Texas horned lizards, *P. cornutum*, squirt blood in response to staged

attacks with a canid. Furthermore, the lizards discriminate between a canid and a human mimicking a canid, being less inclined to squirt blood in response to noncanid attacks. Specific visual, olfactory, auditory, and tactile cues associated with presumptive predators may allow such discrimination by the lizards.

Elicitation of blood-squirting.—Visual cues, particularly those associated with size and motion, have been shown as important determinants of defensive behavior in rattlesnakes (Scudder and Chiszar, 1977). However, our preliminary attempts to understand the cues associated with blood-squirting suggest that, although visual cues may play some role, they do not, by themselves, provide sufficient stimulation to elicit blood-squirting. Lizards subjected to restrained canid attack (without human tactile stimulation) did not squirt blood in spite of clear visual cues (both static and moving), even in combination with other cues. During nocturnal canid attacks (when visual cues presumably are diminished), lizards squirted blood with the same frequency as during diurnal canid attacks (when visual cues are more readily obvious).

Seemingly, canid saliva did not provide sufficient olfactory cues for the lizards to discriminate between it and distilled water. But application of these fluids to the head and eyelids in some instances may have provided a tactile stimulus for blood-squirting. We did not specifically evaluate other potential olfactory cues. Although not specifically investigated, we believe that auditory cues are unlikely to elicit blood-squirting. In the diurnal/nocturnal trials, little barking occurred at night, yet the lizards' responses were similar to those seen during the day.

Tactile cues from an attacking dog are important in eliciting blood-squirting. In restrained canid attack experiments, blood-squirting only occurred when human tactile cues were supplied. In the canid saliva/distilled water trials, blood-squirting was seen in 40% of the trials, possibly in response to physical stimulation of the head and eyelids. However, using a coyote skull with lower jaw, simulated canid attacks focused on the abdominal region of the lizards were unsuccessful in eliciting blood-squirting (0%, $n = 3$).

Hay (1892) first noted that blood-squirting could be elicited by mechanical stimulation of the horns. As reported later by Holder (1901), Ruthling (1919), and Cutter (1959), we found

that we could elicit the behavior in the absence of a dog by tapping and stroking the head, particularly the region anterior to the occipital horns. However, if lizards were exposed to a canid until eye swelling (stage 2) was initiated and then subjected to human tactile manipulation of the head and eyelids, the rate of blood-squirting approached that of canid stimulation alone (69% squirted, $n = 13$; data collected while obtaining Fig. 1). This was achieved through the physical stimulation of the eyelids, the edges of which, like the head and dorsal surface, are abundantly provided with mechanoreceptors (Sherbrooke, 1988).

Temperature, time, and predators.—The behavior of ectothermic lizards may be influenced by temperature, resulting in different antipredator defenses (Hertz et al., 1982; Crowley and Pietruszka, 1983; Greene, 1988). However, we found no difference in blood-squirting response for lizards at low and high body temperatures. Similarly, lizards attacked by a canid during diurnal and nocturnal trials were equally likely to squirt blood. Although *Phrynosoma* are primarily diurnally active, they may be crepuscularly active, as well as remaining inactive on the surface at night (Sherbrooke, 1988, 1991). Thus, blood-squirting in *Phrynosoma* has the potential of being an effective defense against diurnal, crepuscular, or nocturnal predators. This broad, temporal response is compatible with the canid antipredator hypothesis, because canids are active day and night.

Predator specificity.—The data documenting a high incidence of blood-squirting by *P. cornutum* in response to attacks by a dog are particularly interesting when compared to responses by the lizards to other potential predators. Sherbrooke (1988, 1991) conducted predator-prey trials with *P. cornutum* and the nocturnally active, carnivorous grasshopper mouse, *Onychomys torridus*. During attacks, which were focused on the ocular region, the lizards exhibited a number of presumably antipredator behaviors, but neither exhibited swelling of the orbital region (eyelids) nor squirted blood. Sherbrooke (1990b) also examined predator-prey interactions between *P. cornutum* and the diurnally active, greater roadrunner, *Geococcyx californianus*. During vigorous attacks by these birds, several presumably antipredator behaviors were observed, but in only two trials were the lizards seen to briefly engorge their orbital sinuses with blood, and

blood-squirting was never observed. Yet another presumptive defensive behavior, the horns-raised response (Sherbrooke, 1987a), was not observed in any canid, roadrunner, or grasshopper mouse trials.

In our study, only 20% ($n = 10$) of *P. cornutum* squirted at a human (on all fours) that continuously harassed the lizards (simulated canid attack). The rate of blood-squirting to upright humans appears to be even less; Parker (1971) reported that only 4.6% of *P. solare* squirted when captured, whereas Lambert and Ferguson (1985) noted a similar rate for *P. cornutum* (5.9%). In contrast, 85% of all canid interactions ($n = 55$) resulted in blood-squirting.

For *Phrynosoma*, movement and size are known to play a role in prey recognition (Weese, 1917, 1919; Sherbrooke, 1987b); they may also be important in the recognition and categorization of potential predators, as has been suggested for both frogs (Lettvin et al., 1959; Maturana et al., 1960) and rattlesnakes (Scudder and Chiszar, 1977). The failure of humans to elicit blood-squirting may not be due to a lack of recognition of a potential predator by *Phrynosoma*, but rather, the lizards may not deem blood-squirting to be an appropriate response to this particular predator. We routinely observed other antipredatory responses to a human (on all fours), including escape attempts, dorsal-shield displays, and open-mouthed charges. Other cases of open-mouthed charges at (presumably bipedal) humans have also been documented (Dodge, 1938; Lowe and Woodin, 1954; Tanner and Krogh, 1973). Perhaps humans, particularly when upright, are too large to normally be categorized as predators. Alternatively, humans, based on size and behavior, may be assigned a position within a hierarchy of antipredator responses (Duvall et al., 1985; Greene, 1988) that does not normally include blood-squirting as a response.

The variations in presumed antipredator behaviors by *P. cornutum* suggest that distinct, stereotyped responses may be utilized for particular predators (Sherbrooke, 1981). Thus, different contexts (predator types) may elicit different, specific antipredator behaviors (Greene, 1988). Blood-squirting (if it is a canid antipredator defense) may only be effective in certain types of predator-prey interactions. Indeed, the absence of blood-squirting as a response to rodent and avian attacks, in contrast to that displayed to a canid attack, supports the canid-defense hypothesis for *Phrynosoma* blood-squir-

ing. However, blood-squirting also may be defensive against other medium-sized mammalian carnivores, such as felids, procyonids, and mustelids—as well as other canids.

These initial findings leave many questions unresolved. Until we know the full range of potential predators (Sherbrooke and Montanucci, 1988) that can elicit blood-squirting and until we can conduct experiments on factors associated with each, it will be difficult to determine the importance of specific stimuli, or combinations of stimuli, in predator recognition and response by horned lizards. Nonetheless, we have shown that blood-squirting can be readily elicited in interactions with a presumptive canid predator, as well as demonstrated that the behavior is not elicited in interactions with two other, noncanid predators. These results fulfill one of the major criteria of an antipredator defense, specifically that reptilian secretions or discharges serving an antipredator function should be elicited by the presence of or attack by a predator for which the defense has evolved. We are presently investigating the other criterion—whether the elicited discharge reduces the probability of predation.

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