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Pursuit-deterrent communication between prey animals and timber rattlesnakes (*Crotalus horridus*): the response of snakes to harassment displays

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Abstract A thorough understanding of communication requires an evaluation of both the signaler and receiver. Most analyses of prey–predator communication are incomplete because they examine only the behavior of the prey. Predators in these systems may be understudied because they are perceived as less tractable research subjects, due to their more cryptic hunting behaviors and secretive lifestyles. For example, research on interactions between rodents and rattlesnakes has focused on the behavior of rodent signalers, while responses of snakes have been virtually unexamined. Rattlesnakes are ambush predators, and capture rodents by waiting at foraging sites for long periods of time. In this study, I take advantage of the sedentary nature of this foraging strategy and use fixed videography to record natural encounters between timber rattlesnakes (*Crotalus horridus*) and their prey. Three different prey species were found to exhibit conspicuous visual displays to snakes, both when snakes were actively foraging, and when they were basking. After receiving displays, foraging snakes left their ambush sites and moved long distances before locating subsequent ambush sites, indicating that they responded to displays by abandoning attempts to ambush prey in the vicinity of signalers. This study represents the first quantitative analysis of the response of free-ranging snakes to signals from their prey, and elucidates a technique by which such quantitative data can be more easily obtained.

Keywords Timber rattlesnake (*Crotalus horridus*) · Pursuit-deterrent signal · Predator–prey communication · Anti-predator display · Eastern chipmunk (*Tamias striatus*) · Gray squirrel (*Sciurus carolinensis*)

Introduction

Interspecific communication between predators and prey has been described in a variety of systems. Several classic examples occur between rodents and crotalid snakes, including kangaroo rats and rattlesnakes (Bouskila 1995; Randall and Matocq 1997), California ground squirrels and rattlesnakes (Owings and Coss 1977; Swaisgood et al. 1999; Swaisgood et al. 2003), and Prairie dogs and rattlesnakes (Loughry 1987; Loughry 1989). In these systems, rodents deter snake predation both by physically harassing snakes, and by using visual or vibrational signals to indicate that snakes have been seen and subsequent predation attempts will be unlikely to succeed. Such pursuit-deterrent signals are unforced, honest communication wherein both parties benefit from the transfer of information (Hasson 1991). Predators avoid a costly pursuit that is likely to be futile, and prey benefit by reduced predation attempts.

As in any communication system, a complete understanding of the process involves studying the context in which the signal is given, the behavior of the signaler, and the response of the receiver (Bradbury and Vehrencamp 1998). However, many studies of pursuit-deterrent signaling do not take into account the response of the predator to the signal (Caro 1995). Indeed, previous research on snake–rodent interspecific communication focuses on the behavior of the signaler and nature of the signal. Although there have been some studies describing immediate responses of snakes to these displays (Rowe and Owings 1978; Hennessy and Owings 1988), none has examined how subsequent foraging efforts of snakes might have been altered; i.e., did they abandon their efforts to catch prey that had signaled.

Viperid snakes receiving such signals are sit-and-wait foragers, relying on cryptic behavior and patience to capture prey from the ambush (Klauber 1972; Greene 1997). Snakes foraging in this manner typically remain in one spot for hours, or even days at a time (Greene 1992). However, once a snake has been discovered, its probability of successfully capturing its prey decreases. If anti-snake displays are pursuit-deterrent signals, snakes should abandon foraging

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locations soon after receiving displays. If the snakes are not actively foraging when receiving this signal and are engaged in some other activity (i.e., thermoregulation), they would not be expected to abandon their site so long as the display provides no direct threat.

The behavior of snakes in these systems has been overlooked probably because snakes are generally secretive, cryptic, and difficult to study in a natural setting. In most of these studies, snakes have been artificially restrained or in captivity, nullifying the ability of snakes to exhibit a natural response. However, because many venomous snakes use a sedentary, sit-and-wait foraging tactic, it is possible to observe critical aspects of their foraging behavior in the wild by using fixed videography (Clark 2004). In this study, I use a combination of radio telemetry and video observation to record encounters between free-ranging timber rattlesnakes and several prey species that exhibit anti-snake displays. The resultant analysis is the first to examine how venomous snakes alter their foraging behavior in response to anti-snake displays under natural conditions.

Methods

Using radio telemetry, I tracked 17 individual timber rattlesnakes (11 females, 6 males, all adults) over the course of 2 years at a nature preserve in Chemung County, New York. Snakes were captured opportunistically throughout the study, and ranged in size from 650 g, 104 cm to 2100 g, 137 cm total length (mean = 1405 g, 121 cm). Radio transmitters (Holohil Systems, models AI-2T and SI-2T) were surgically implanted in peritoneal cavities of snakes under inhalation anesthesia, following methods of Reinert and Cundall (1982). Transmitters weighed less than 5% of the snake's body mass. Snakes were returned to their point of capture within 24 h of recovering from anesthesia, and radio tracking began immediately. Individuals were located on a daily basis.

To collect data on encounters between snakes and rodents, I trained video cameras on snakes that were either basking (loose coils, exposed to sunlight), or foraging (compact coils, head held in front of coil perpendicular to runways used by small mammals) (Reinert et al. 1984). Cameras were set up as soon as the snake was observed to assume a hunting or basking posture. Three different video units were used concurrently in the field. Each unit consisted of a security camera coupled to a time-lapse videocassette recorder (Mobile 12 V Time Lapse Recorder Model NCL3300) powered by a 12 V sealed lead-acid battery. Cameras (High Resolution Color CCD IR, model BC 1035) recorded in color when ambient light was available, and under low light conditions automatically switched to black and white recording with infrared LEDs. Time-lapse VCRs were set to record continuously at 6.67 recording frames per second, with the date and time to the nearest second displayed on the tape. Tapes were then reviewed and data was extracted on snake residence times and encounters with its potential prey. Anti-snake displays were defined as any encounter in which a potential prey

item repeatedly moved towards and away from a snake, coming within 50 cm and then retreating.

Cox proportional hazards regression analysis was used to analyze the effect of harassment displays on time to subsequent abandonment of hunting or basking sites by snakes. The PHREG procedure in SAS was used to analyze time at which snakes abandon their sites, with harassment displays as a time-dependent covariate (Allison 1995; SAS 2003). This procedure compares the effect of a variable (anti-snake display) on the survival or termination event (in this case, the abandonment of a site by a snake) in order to determine if the variable increases or decreases the probability of survival or termination. Statistical comparisons of mean distance traveled by snakes after abandoning sites were made with a resampling procedure, using the software package Resampling Stats. Resampling procedures avoid any assumptions about normality or variance, and were used in this case because the sample size of snakes receiving displays was small compared to snakes not receiving displays. All values are given as mean \pm SE.

Results

Over the course of the study, I recorded snakes for a total of 1840 h. Details on snake foraging behavior and predatory encounters are reported elsewhere (Clark 2004). On 12 different occasions, rodents or birds that are natural prey items of timber rattlesnakes were observed to exhibit anti-snake displays. I observed snake harassment displays seven times by chipmunks (*Tamias striatus*), four times by eastern gray squirrels (*Sciurus carolinensis*), and once by a wood thrush (*Hylocichla mustelina*) (Table 1). On average, snakes received displays from prey once every 6.4 days.

Anti-snake displays consisted of repeated approaches by the signaler within 50 cm of the snakes, followed by rapid retreats (mean number of approaches to within 50 cm = 6 ± 1). Displays were given for various durations, from 2 to 31 min (mean duration = 15 ± 3 min). Sciurid rodent displays (chipmunks and gray squirrels) included characteristic tail-flagging behavior described by Owings and Coss (1977). These displays may have included an audio component as well, but video cameras used in this study were not equipped with microphones. Snakes that had been harassed were never observed to subsequently encounter prey at that location. Snakes showed no immediate, overt response to any displays (no rattling, striking, or other defensive behaviors). The only snake movements seen during and immediately after displays were small shifts in position of the head and the body.

Six of these displays were given when snakes were basking, and six were given to actively foraging snakes. After displays ended, the mean time to site abandonment for the six actively foraging snakes received was 4.6 ± 1.7 h. Cox regression analysis shows that harassment displays had a highly significant effect on abandonment times of snakes (hazard ratio = 4.3, $\chi^2 = 11.1$, $P < 0.001$); foraging snakes receiving displays were 4.3 times as likely to abandon sites after harassment than foraging snakes that did not receive

Table 1 Characteristics of anti-snake displays and responses of snakes

Species displaying	Behavior of snake ^a	Duration of display (min)	No. of Approaches ^b	Time to abandonment (h) ^c	Distance snake moved (m) ^d
Chipmunk	Hunt	10	6	2	50
Chipmunk	Hunt	2	3	4	5
Thrush	Hunt	19	6	1	275
Squirrel	Hunt	11	5	6	106
Squirrel	Hunt	12	13	1	150
Squirrel	Hunt	14	5	11	3
Chipmunk	Bask	13	3	10	3
Chipmunk	Bask	20	7	28	6
Chipmunk	Bask	6	4	12	4
Chipmunk	Bask	25	8	11	13
Chipmunk	Bask	12	5	20	3
Squirrel	Bask	31	8	10	4

^a“Behavior of snake” is the behavior in which the snake was engaging while the displays were given, either hunting or basking

^b“Approaches” are instances in which the displayer comes to within 0.5 m of snake, and then retreats

^c“Time to abandonment” is the time from which the display ended to which the snake moved out of the frame of the camera

^d“Distance snake moved” is the distance between the site of the display and then next site at which the snake was found not moving

displays. For basking snakes, mean time to site abandonment after receiving displays was 14.5 ± 3.0 h. Displays did not significantly effect abandonment times of basking snakes (hazard ratio = 0.67, $\chi^2 = 0.6$, $P = 0.45$).

After harassment, foraging snakes moved a distance of 98 ± 104 m to a new site ($n = 6$), whereas foraging snakes that were not harassed moved an average of 29 ± 7 m ($n = 82$), a difference that was non-significant ($P = 0.08$). Basking snakes moved an average of 6 ± 4 m after harassment ($n = 6$), whereas basking snakes that were not harassed moved 16 ± 7 m ($n = 16$); also a non-significant difference ($P = 0.7$).

Discussion

Snakes exhibited differential responses to displays given by prey, depending on if they were actively foraging or not. Foraging snakes responded to displays by decreasing their time to site abandonment, and tending to move farther before resuming foraging. Snakes that were not actively foraging showed no increased tendency to abandon their site, and when they did move, moved no farther than snakes that were not harassed. These results indicate that the anti-snake displays serve as effective pursuit-deterrent signals, causing snakes to abandon efforts to prey on individuals in areas in which displays are given. The relatively long delay (mean = 4.6 h) between anti-snake displays and abandonment by hunting snakes is somewhat puzzling. However, other variables also have strong effects on snake movement, such as thermoregulation and diel activity cycles. In general, snake behaviors occur over a longer temporal scale than we are used to, and what may seem like a long delay to a human observer may not be so for a foraging snake.

Prey animals would not be expected to exhibit pursuit-deterrent signals towards predators that are not actively hunting. However, because the hunting method used by snakes is sedentary and opportunistic, it could be difficult for prey to distinguish between snakes that are foraging and snakes that are basking. Additionally, basking snakes may soon begin hunting in nearby areas after reaching a thermal optima. Therefore, displays may be given to any snake that is discovered within their home range.

Displays given to snakes in this context may be signals not only to snakes, but also to other potential prey individuals within the immediate vicinity. The caller may benefit from this behavior by either warning nearby kin, or by alerting all potential prey in the area to the presence of an ambush predator, thus lowering the probable foraging success of the snakes (the ‘perception advertisement’ function of signaling to predators) (Frankenberg 1981). Such a function is partially supported by the long distances snakes move after displays are given, relocating to areas containing prey that have not been alarmed.

Because ambush foraging snakes generally do not pursue fast, active mammals, the nature of alarm or pursuit-deterrent signals directed toward them is often different from signals given to more active predators. Several systems have been described where signalers respond to snakes with snake-specific calls, designed to alert conspecifics but not cause them to flee (reviewed in Hauser 1996). These alarm calls and the behaviors they induce may also serve as pursuit-deterrent signals, but none of these studies quantitatively evaluate the behavior of the snakes under natural conditions. A recent analysis of alarm calling in rodents found that alarm signals most likely evolved to communicate with predators, indicating that the pursuit-deterrent function of alarm calling may be under appreciated in many systems (Shelley and Blumstein 2005).

Although snake harassment behavior is well documented in other sciurid rodents (Owings and Coss 1977; Loughry 1987; Towers and Coss 1991), it has not previously been reported in eastern chipmunks or gray squirrels. Alarm calls have been studied in both species, but only in the context of alarms given toward active predators (Lishak 1984; da Silva et al. 1994). The anti-snake displays recorded in this study are much less confrontational than those reported for other sciurids. It would be worthwhile to undertake a systematic comparison of anti-snake behaviors in a range of sciurids to elucidate life-history traits that correlate with display aggressiveness. Gray squirrels and chipmunks form much looser social groups than other sciurids (Loughry 1987; Koprowski 1996; da Silva et al. 2002; Swaisgood et al. 2003), perhaps eliminating most of the kin selection benefits derived from confronting venomous snakes.

Although wood thrushes have not been previously reported of harassing snakes, this behavior is similar to predator 'mobbing', which occurs frequently in passerine birds (reviewed in Ficken and Popp 1996). A recent study shows that mobbing by Arabian babblers may primarily be a form of prey-predator communication, although no data are presented on the snake responses to the signals (Ostreiher 2003). Pursuit-deterrent signals may be common in many passerine species, and ambush-foraging snakes may be ideal predators to examine predator responses to such signals. Such studies can help fill a broad gap in our knowledge of predator-prey communication systems by collecting quantitative data on the responses of predators to prey signals.

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