



Black Bear Reactions to Venomous and Non-venomous Snakes in Eastern North America

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Abstract

Bears are often considered ecological equivalents of large primates, but the latter often respond with fear, avoidance, and alarm calls to snakes, both venomous and non-venomous, there is sparse information on how bears respond to snakes. We videotaped or directly observed natural encounters between black bears (Ursus americanus) and snakes. Inside the range of venomous snakes in Arkansas and West Virginia, adolescent and adult black bears reacted fearfully in seven of seven encounters upon becoming aware of venomous and non-venomous snakes; but in northern Michigan and Minnesota where venomous snakes have been absent for millennia, black bears showed little or no fear in four encounters with non-venomous snakes of three species. The possible roles of experience and evolution in bear reactions to snakes and vice versa are discussed. In all areas studied, black bears had difficulty to recognize non-moving snakes by smell or sight. Bears did not react until snakes moved in 11 of 12 encounters with non-moving timber rattlesnakes (Crotalus horridus) and four species of harmless snakes. However, in additional tests in this study, bears were repulsed by garter snakes that had excreted pungent anal exudates, which may help explain the absence of snakes, both venomous and harmless, in bear diets reported to date.

Introduction

Several authors have presented evidence that snakes have influenced the evolution of vertebrates, especially mammals (Greene 1997). Venomous snakes and large constrictors have been significant sources of human mortality throughout history (Greene 1997; Isbell 2009; Headland & Greene 2011), and snake detection has been posited as a major driver in the evolution of keen binocular color vision in primates (Isbell 2009). Malagasy lemurs (*Lemur* sp.) that evolved in the absence of large boids or highly venomous viperids and elapids show little or no fear of snakes compared with most Old and New World monkeys (Mitchell & Pocock 1907; Burghardt et al. 2009). Vervet monkeys (*Cercopithecus aethiops*) give alarm calls to pythons (Struhsaker 1967; Cheney & Seyfarth 1990) but not to harmless snakes in East Africa (Burghardt et al. 2009) and we have seen similar reactions, including intraspecific alarm communication, in monkeys in West Africa (Starin & Burghardt 1992). New World white-faced capuchins (*Cebus capucinus*) alarm call more frequently to their major snake predator, the boa constrictor (*Boa constrictor*), than to a large, harmless snake (Meno et al. 2013).

Both experience-dependent and experience-independent factors may be involved. Rock squirrels (*Spermophilus variegatus*) distinguished rattlesnakes

641

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(*Crotalus* sp.) from gopher snakes (*Pituophis melanoleucus*) in a snake-abundant wilderness study area, but not in an urban area where all snakes are rare (Owings et al. 2001). When California ground squirrels (*Spermophilus beecheyi*) experienced relaxed selection from venomous, but not non-venomous, snakes, their venom resistance declined and their behavior toward snakes changed (Coss et al. 1993).

Snakes have killed black bears (Ursus americanus) by envenomation (Klenzendorf et al. 2004) and have killed sun bears (Helarctos malayanus) by constriction (Auliva & Abel 2000; Fredriksson 2005), although such deaths appear quite rare. However, the only published reports we found of bears' reactions to snakes are Bacon & Burghardt's (1976a) account of a captive black bear cub's reactions to a non-vemomous snake in Tennessee and Debruyn (1999) account of a wild adult black bear reacting to a non-venomous snake in the northern Great Lakes Region where venomous snakes have long been absent (Fig. 1) due to unfavorable temperatures since the Pleistocene (Richmond & Fullerton 1986; Oldfield & Moriarty 1994; Sattler & Dixon 1997; McDiarmed et al. 1999; Holman 2000). As unnecessary retreat from harmless snakes involves energy costs (Kats & Dill 1998), it is possible that unnecessary retreat by black bears from harmless snakes wanes where venomous snakes have long been absent, although this cost is probably minimal if only several meters, as likely in both bears and primates.

Although snakes are eaten by various mammals, birds, and other vertebrate predators (Fitch 1965: Oldfield & Moriarty 1994; Greene 1997), we found no report of snake remains in black bear scats. Detailed, long-term food habit studies have been conducted inside the range of venomous snakes in California (Grenfell & Brody 1983), Florida (Harlow 1961), Montana (Tisch 1961), North Carolina (Hardy 1974; Hamilton 1978; Landers et al. 1979), Pennsylvania (Bennett et al. 1943), Tennessee (Beeman & Pelton 1980), and Virginia (Cottam et al. 1939) as well as outside the range of venomous snakes in Alberta (Raine & Kansas 1990), New Brunswick (Zytaruk & Cartwright 1978), and northern Wisconsin (Norton 1981; Bertagnoli 1986). We further studied black bear diets outside the range of venomous snakes in Northern Michigan and Minnesota. While some animals that prey on snakes, including birds and primates, distinguish venomous from non-venomous snakes (e.g., Meno et al. 2013), bears may have no foragingrelated need to do so. Bears, however, are very capable of learning about cues associated with both food and foraging tactics (Bacon & Burghardt 1976a,b; Hopkins 2013).

Here, we documented black bear reactions to snakes inside and outside the range of venomous snakes. As



Fig. 1: Locations of reported bear-snake encounters (black dots) inside the range of venomous snakes (shaded area) and where only non-venomous snakes live (clear area south of the dashed line).

we accumulated observations from fortuitous observations, video cam recordings, and various published sources, our methods were not uniform and often are at the level of singular and anecdotal reports, even when video recorded. Observer effects were also not controlled when humans were present. While serious problems (Burghardt et al. 2012), we nonetheless feel that our observations raise important questions on the development and evolution of ursid behavior and should promote more systematic studies (Dukes 1965). The use of accumulated anecdotal and serendipitous reports on deception in non-human primates, for example, led to a now voluminous literature of systematic studies that have, in large part, supported the initial conclusions reached by the authors (Whiten & Byrne 1988) in spite of criticism based on reliance on tainted evidence (e.g., Burghardt 1988).

Methods

We directly observed interactions of free-ranging wild black bears and snakes in West Virginia, Minnesota, and Michigan using methods described by Rogers and Wilker (1990) and Debruyn (1999). In those studies, we observed habituated, wild, free-ranging individuals that foraged, napped, nursed, etc., without obvious attention to us.

In Arkansas and New York, we used remote trail cams to record rare high definition video of fortuitous interactions between non-habituated, wild, free-ranging black bears and snakes. These video observations were obtained from over 20:00 hours of video in Arkansas and 18:40 hours of video from New York.

Our observations and video recordings inside the range of venomous snakes were in Northern Arkansas, southern New York, Tennessee, and West Virginia; observations outside the range of venomous snakes were in northeastern Minnesota and the Upper Peninsula of Michigan (Fig. 1).

While viewing encounters or videos, we noted bears' reactions to the sight, scent, sound, and movements of snakes as well as the behavior of the snakes. When bears showed awareness of snakes, we classified their reactions as fearful if they hastily retreated or exhibited agonistic behaviors (blowing, slapping the ground, narrowing the muzzle, and/or clacking the teeth); or as non-fearful if bears displayed no agonistic behavior or made no hasty retreat. We also noted if the snake was ignored as well as curious or exploratory responses. We compared reactions inside and outside the range of venomous snakes using a two-tailed Fisher's exact test, pooling reactions to venomous and non-venomous snakes inside the range of venomous snakes due to the small total sample size.

To further assess relations between black bears and snakes, we recorded any bear behavior that might suggest predatory interest and also looked for snake remains in 1552 scats collected for us by 147 state and federal workers outside the range of venomous snakes in northern portions of Michigan, Wisconsin, and Minnesota. Although originally part of a study by Bacon & Burghardt (1976a), we reviewed the reactions of captive black bear cubs to a water snake (*Nerodia sipedon*) in Tennessee and present additional details.

Finally, we captured common garter snakes (*Thamnophis sirtalis*) and presented them by hand to wild, habituated, free-ranging black bears to observe reactions to snakes that had defensively excreted cloacal exudate that would undoubtedly be present if bears attempted to prey on these snakes. Natricine snakes (including *Nerodia* and *Thamnophis*) are well known for their ready deployment of this tactic, and they are among the most common snakes in the areas of this study.

This work was conducted under permits from the Minnesota Department of Natural Resources and the Michigan Department of Natural Resources in compliance with guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011). No bears or snakes were harmed in this study.

Results

We observed or remotely videotaped 15 encounters in which wild, free-ranging black bears were <1 m from five species of snakes under natural conditions (Table 1). We also observed reactions of five human habituated black bears as we presented snakes to them by hand or released a snake where one was foraging. Encounters are individually identified in Table 1 and below using a combination of numbers and the initials of the co-authors who observed them.

Encounters Inside the Range of Venomous Snakes

On June 16, 2009, a free-ranging adolescent male was remotely video recorded as it paused with its head nearly over a coiled 1.8-m timber rattlesnake (*Crotalus horridus*) in Arkansas (1MM). The bear looked past the snake, sniffing the air for 14 s. When the bear continued, the bear gave no sign of recognition as its nose passed 10 cm above the snake and its paw lightly brushed it, causing the snake to move slightly (but unseen).

Table 1: Behaviors of black bears (Ursus americanus) during encounters with snakes (Serpentes) inside and outside the range of venomous snakes in North America

Codea ID Code ^a	Location State	Snake			Black Bear	
		Range ^b	Species ^c	Behavior	Age and Sex	Reaction
Natural enc	ounters					
1MM	AR	Inside	Timber rattlesnake	Coiled, non-moving	Juvenile male	Unaware
2MM	AR	Inside	Timber rattlesnake	Coiled, non-moving, then moved	Juvenile male	Reared back, avoided
ЗКН	WV	Inside	Timber rattlesnake	Unknown	Adult female with cubs	Reared back, avoided, agonistic displays
4RC	NY	Inside	Timber rattlesnake	Coiled, non-moving	Juvenile	Unaware
5MM	AR	Inside	Timber rattlesnake	Non-moving, then moved	Adult	Reared back, avoided
6MM	AR	Inside	Timber rattlesnake	Coiled, non-moving	5-month-old cub	Repeatedly sniffed, then walked on
7SH	WV	Inside	Timber rattlesnake	Non-moving, then moved and rattled	Adult male	Reared back, avoided
8SH	WV	Inside	Black ratsnake	Non-moving, then moved	Adult male	Reared back, avoided
9SH	WV	Inside	Black ratsnake	Non-moving, then moved	Adult male	Reared back, avoided
10SH	WV	Inside	Black ratsnake	Non-moving, then moved	Adult male	Reared back, avoided
11TD	MI	Outside	Western fox snake	Non-moving	Adult female	Unaware
12TD	MI	Outside	Western fox snake	Non-moving, then moved	Adult female	Sat down and watched
13LR	MN	Outside	Garter snake	Crawling to and from hibernaculum	Adult female	Raked grass for bed next to hibernaculum and spent winter there
14LR	MN	Outside	Redbelly snake	Moving	Adult female	Sniffed, then ignored
15LR	MN	Outside	Redbelly snake	Non-moving, then moved	7-mo cub	Reared back, then ignored
Encounters	with handheld	or released si	nakes			
16LR	MN	Outside	Garter snake	Moving in hand	Adult male	Sniffed, drew back
17LR	MN	Outside	Garter snake	Moving in hand	Adult male	Sniffed, drew back
18LR	MN	Outside	Garter snake	Moving in hand	Adult female	Sniffed, drew back
19LR	MN	Outside	Garter snake	Moving in hand	Yearling female	Sniffed, ignored
20LR	MN	Outside	Garter snake	Moving on ground	Adult male	Ignored

^aID Code: the number of the encounter and the initials of the author of this paper who contributed it.

^bInside or Outside the range of venomous snakes

^cSpecies: timber rattlesnakes (*Crotalus horridus*), black ratsnakes (*Pantherophis obsoleta*), western fox snakes (*Pantherophis vulpinus*), common garter snakes (*Thamnophis sirtalis*), redbelly snakes (*Storeria occipitomaculata*).

On that same date, the same bear retraced its steps and again stopped just short of the coiled, non-moving snake (2MM). Again, the bear sniffed the air for 14 s while looking past the snake with its head nearly over it. That time, the bear stepped toward the center of the coil, reared back looking down at the snake, and hastily retreated. The bear's body prevented us from seeing whether the startled reaction was due to the bear stepping on the snake or the snake possibly moving. The differences in the two reactions certainly indicate that the bear did not just ignore the snake in the initial encounter, but was unaware of its presence.

On July 23, 2011, a 6-year-old mother with three cubs was directly observed as she encountered a 60cm timber rattlesnake in West Virginia (3KH). The bear blew, reared back, and followed her cubs up a nearby tree where the mother directed agonistic displays toward the snake blowing, clacking her teeth, and slapping the trunk. After a minute, the bear descended from the tree and ran toward the snake, briefly blowing and slapping the ground <1 m from the snake, She then rejoined her cubs in the tree. For the next 1.5 h, the bear intermittently directed agonistic displays toward the encounter location before descending to resume foraging.

On August 4, 2002, an adolescent bear in southern New York (4RC) was remotely video recorded as it passed <1 m from a coiled timber rattlesnake without hesitating or looking toward the snake.

After sunset on June 10, 2009, a remote trail cam in Arkansas recorded an adult black bear whose foot was descending toward a timber rattlesnake when the snake moved, causing the bear to rear back and retreat (5MM).

On July 2, 2009, a remote trail cam in Arkansas recorded a five-month-old cub that repeatedly

approached and sniffed a large motionless timber rattlesnake mostly hidden under vegetation. After 11 s of hesitant investigation, the cub walked on (6MM).

In West Virginia, a mature, wild, free-ranging, male bear was observed to spring back and circumvent a timber rattlesnake that had rattled and moved (7SH). In the same area, in three separate observations, three other mature wild, free-ranging black bears leaped back when non-venomous black ratsnakes (*Pantherophis obsoleta*) moved at close range (8SH, 9SH, 10SH).

In summary, of the six timber rattlesnake responses observed in detail, two remained coiled and nonmoving (4RC, 6MM), three moved just enough to avoid being contacted by the bears (1MM, 2MM, 5MM), and one rattled (7SH). None assumed defensive postures or struck at the bears. Bears reared back and avoided all the black ratsnakes encountered. However, the only prolonged and extreme response (blowing, clacking, tree slapping) took place by a mother with cubs toward a rattlesnake.

Encounters Outside the Range of Venomous Snakes

Outside the range of venomous snakes, we documented five encounters between wild, free-ranging black bears and three species of non-venomous snakes.

On June22, 1992, a 5-year-old female was observed as it passed <1 m from a coiled 1.8-m western fox snake (*Pantherophis vulpinus*), apparently unaware, in Michigan's Upper Peninsula (as mentioned in the introduction) (11TD).

Later that day, the same bear encountered the snake again and sniffed food immediately adjacent to it (12TD). Again, the bear appeared not to notice the non-moving snake. When the snake moved, the bear sat down and watched it. When the snake quartered past the bear, the bear moved off a few feet without exhibiting agonistic behavior.

During September 13 to October 13, 2002, a 15year-old female black bear created an overwinter bed 4 m from a garter snake hibernaculum in Minnesota (13LR). During that month, the bear frequently raked bedding (leaves and grass) from the area around the hibernaculum as dozens of snakes gathered to hibernate. The bear produced three cubs in the bed in January 2003. During April 9–12, 2003, the bears and snakes became active as temperatures reached 12–20°C daily. The bear family left the area on April 12–13 as is typical for bears in that region (Rogers 1987). On April 13, 26 snakes (including a mating ball of 13 snakes) were active between the hibernaculum and the bears' bed. Scats near the bed contained no snake remains. On August 23, 2011 in Minnesota, a 6-year-old mother sniffed and ignored a moving 28-cm redbelly snake (*Storeria occipitomaculata*) (14LR). When her seven-month-old cubs arrived a few minutes later, one foraged to within 7 cm of the non-moving snake. When the snake moved, the cub leaped back, looked briefly toward it, and resumed foraging within 3 cm of it (15LR). Unlike the mother with cubs encountering the rattlesnake, the mother in this case did not intervene or respond in any way toward the snake.

Reactions to Harmless Snakes Presented to Human Habituated Free-Ranging Black Bears

In five independent tests in Minnesota on August 23, 2011 and May 12, 2012, the senior author (LR) presented wild-caught garter snakes to five wild, freeranging black bears accustomed to hand-feeding. The snakes had excreted anal exudate upon capture moments before. Two mature males (16LR, 17LR) and a mature female (18LR) sniffed the handheld snakes and immediately drew back, tucking their noses toward their chests as if repulsed. None exhibited agonistic or fear responses. A yearling female looked and sniffed toward a handheld snake from 13 cm and moved on without expressing repulsion or further interest (19LR). In the fifth test, we released a garter snake where a mature male was foraging for berries. The bear foraged to within 8 cm, ignoring the snake (20LR).

In a sixth test, recorded (and buried in) a description of ingestive behavior in black bears (Bacon & Burghardt 1976a), two captive black bear cubs reacted to a water snake (Nerodia sipedon) in their large outdoor enclosure in the Great Smoky Mountain National Park in Tennessee. They had likely never experienced venomous snakes even though such are present, though rare, in the park. Accustomed to slapping and eating mice and insects in their enclosure, the bears approached the snake but did not slap it. The snake went into antipredator, defensive mode, making its head and body appear larger (e.g., flattening) and performing mouth open strikes. Instead of showing fearful responses, one of the bears slowly approached closer and used a raking motion with her forepaws to draw the snake closer for investigation, but did not attempt to eat it.

Snakes as Food

Although a four-month-old female cub ate the shed skin of a western fox snake in Michigan's Upper Peninsula on June 8, 1993, we found no snake remains in black bear scats collected by state and federal workers in northeastern Minnesota (1288 scats), northern Wisconsin (148 scats), and Northern Michigan (116 scats) or in hundreds of scats we examined grossly or systematically in northeastern Minnesota during 1969–2013. We observed no predation or predatory attention to snakes during approx. 25:00 hours of foraging in Michigan in 1990-1999 (TD) or during approx. 45:00 hours of foraging in northeastern Minnesota in 1986–2013 (LR, SM).

Failures to Detect Non-Moving Snakes

Bears did not react until snakes moved or were stepped on in 11 of 12 encounters with non-moving timber rattlesnakes (1MM, 2MM, 4RC, 5MM, 7SH), black ratsnakes (8SH, 9SH, 10SH), a fox snake (11TD, 12TD), and a redbelly snake (15LR) (Table 1). The exception was a five-month-old cub that sniffed a timber rattlesnake in Arkansas (6MM). In three of the 12 encounters, the snakes did not move and went unnoticed (1MM, 4RC, 11TD).

Differences in Reactions of Bears Inside and Outside the Range of Venomous Snakes

Inside the range of venomous snakes, of those encounters where bears were aware of the snake's presence, seven adolescent and adult bears reared back and avoided snakes (2MM, 3KH, 5MM, 7SH, 8SH, 9SH, 10SH), but a five-mo-old cub repeatedly sniffed a large, coiled, non-moving timber rattlesnake (6MM). The captive bears in the enclosure in Tennessee responded cautiously, but not fearfully to a harmless snake. In contrast, outside the range of venomous snakes, no bear that detected snakes reacted fearfully in four natural encounters (12TD, 13LR, 14LR, 15LR) and five human-induced encounters (16LR, 17LR, 18LR, 19LR and 20LR). Including all 17 reactions, eight inside and nine outside the range of venomous snakes, reactions differed significantly (Fisher's exact test, p < 0.01).

Discussion

Assuming that our results can be generalized, is the difference in adult black bear reactions to snakes inside vs. outside the range of venomous snakes due to natural selection or behavioral plasticity due to experience? Had those bears acting fearfully previously encountered and/or been bitten by venomous snakes? Garter snakes that currently live in areas glaciated 10 000 yr ago show rapid behavioral genetic

and experience based plasticity (Placyk & Burghardt 2011) and similar rapid changes could be expected in bears as well.

The only known death of a black bear from a venomous bite was a four-month-old cub that weighed 3.3 kg in Virginia in early June 2000 (Klenzendorf et al. 2004). The position of the bite on the inner thigh of that cub suggests that the cub had reared back on its hind legs, as was typical of adolescent and adult bears that encountered snakes within the range of venomous snakes in this study. However, calm reactions by many cubs to snakes, even within the range of venomous snakes, suggests that experience is also a factor. In fact, as with humans and nonhuman primates, individual differences in fearful responses to snakes are the norm. For example, the only bear to repeatedly approach and sniff a rattlesnake in this study was a five-month-old cub in Arkansas (6MM). Additional evidence comes from hand-reared cubs known not to have experience with venomous snakes. In West Virginia, within the range of venomous snakes, a hand-reared three-month-old black bear cub showed no fear of a pair of mating black ratsnakes on April 31, 2010, nor of a single black ratsnakes on May 2, 2010 (J. Rosenthal, pers. comm.). In west central New Hampshire, at the edge of the range of venomous snakes, hand-reared cubs, five-month old, ignored snakes (B. Kilham, pers. comm.). In his field notes from June 25, 1993, Kilham wrote: 'There was a large 20-inch garter snake on my boundary line that had recently eaten a mouse. It moved about six feet and disappeared into a rock pile in front of us. The cubs detected no odor and no interest when walking right over the spot.' Kilham also wrote that he 'also caught and offered snakes to cubs, and they would react to the snakes' movement with surprise and show curiosity, they had no real interest.' Rosenthal and Kilham recall only benign responses to snakes by their hand-reared cubs over their years of observation and note taking. Similarly, the two young bears studied by Bacon & Burghardt (1976a) showed no fearful responses to a harmless, but dramatically defensive, water snake.

As cubs are probably at more risk from snakebites than are adults (the levels and development of venom resistance in black bears is unknown), one might expect more fear responses from cubs than have been found. On the other hand, the adaptive value of curiosity and exploration of myriad food resources in an omnivorous species may be a constraint on the evolution of such innate responses.

If there is a genetic predisposition to fear snakes inside the range of venomous snakes, as has been suggested for primates (Isbell 2009), the agonistic displays of mothers, as were observed in this study, could facilitate fear of snakes by juveniles (Burghardt et al. 2009: Isbell 2009). Although there is experimental evidence that juvenile monkeys observing adults act fearfully in the presence of snakes results in their acquiring similar fears (citations in Burghardt et al. 2009), these experiments were actually not able to eliminate innate reactions to snakes, which in fact exist in adult Japanese macaques (Macaca fuscata) raised without any prior experience with snakes (Burghardt, unpubl. obs.; Shibasaki & Kawai 2009). Recent neurophysiological studies (Van Le et al. 2013) have documented that the pulvinar area in the thalamus plays a crucial role in visual snake recognition in this species of primate. The amygdala and superior colliculus have also been implicated in the neural snake recognition pathway (Pessoa & Adolphs 2010; Maior et al. 2011). The pulvinar is most developed in primates and seems absent in many mammals (Pessoa & Adolphs 2010). If it is also less prominent in bears and canids, this may explain why many mammals, including carnivores, do not have extreme and rapid recognition of snakes as dangerous stimuli. Dogs, for example, are frequent victims of venomous snakebites that may be triggered more by curiosity and approach by the dogs rather than accidentally disturbing a resting snake. On the other hand, even venomous snakes may pose far less a threat than they do for rodents, such as ground squirrels that are preyed upon by rattlesnakes and that need to respond rapidly to avoid near fatal envenomation (e.g., Ennis & Coss 2006). More research on the responses of other carnivores to snakes would be most valuable.

It is important to also note that startle responses to unexpectedly spotting a snake at close range can occur even in seasoned herpetologists, as the two herpetological authors of this paper (GMB and RC) can attest (see also Coss 2003). This behavior can occur to both harmless and venomous snakes and does not indicate a fearful response, as noted in some bears here and in primates in the previously mentioned studies (see also Burghardt et al. 2009).

Although most species of bears, including black bears, eat a wide range of vertebrate and invertebrate animals, snakes are notably absent in reported bear diets. Black bear reactions to pungent cloacal ('anal') exudates in this study may help explain the absence. Defensive use of cloacal scent is widespread among snakes (Greene 1997); and natricine snakes, such as water snakes and garter snakes, are noted for the pungency and repulsiveness of the odor produced, which is often rubbed on the putative predator. These snakes may also have a distinctive odor even when not actively producing the cloacal secretion.

Unlike rock squirrels that discriminate between gopher snakes and rattlesnakes (Owings et al. 2001). black bears avoided both ratsnakes and rattlesnakes within the range of venomous snakes. The difficulty black bears demonstrated in recognizing non-moving snakes suggests that it may be difficult for them to discriminate between harmless and dangerous snake species. In humans, detecting and indiscriminately avoiding all snakes has probably been favored by natural selection, as in Africa where it is difficult to discriminate between harmless and dangerous snake species (Burghardt et al. 2009). Despite the black bear's sense of smell and sophisticated ability to distinguish color and form from stationary stimuli (Burghardt 1975; Bacon & Burghardt 1976b). Debruyn (1999) reported that the black bear he observed twice failed to detect a non-moving, plainly visible, 1.8-m fox snake at close range. During a second encounter, the bear sniffed food adjacent to the snake, causing the snake to move. The bear sat down and watched. As the snake moved past the bear, the bear quickly moved a meter or so away, displaying no agonistic behavior. As with primates, including humans, bears may have a certain fascination in observing such alien looking animals, as Darwin recorded during his informal zoo experiments with monkeys (Darwin 1871, 1872).

A factor that may help explain the lack of response to non-moving snakes is that bears evolved from canid ancestors that relied on hunting almost exclusively, often in low light conditions, and were dichromats rather than trichromats such as primates that generally have excellent color (wavelength) discrimination (Neitz et al. 1989). In fact, although black bears do have good color vision and can readily discriminate ripe from unripe berries, for example (Bacon & Burghardt 1976b), whether related canids such as dogs have color vision was not documented until later, and then, the function it serves in nature is still unknown (Neitz et al. 1989). Many predatory species are especially attuned to movement, and nonmoving stimuli cease to 'exist.' For example, racers, diurnal snakes are active and visual hunters that had to have crickets move, even if a motionless one was very close by (Herzog & Burghardt 1974), in spite of having excellent chemosensory abilities which they can use to detect prey and predators (Cooper et al. 2000). Non-human primates, on the other hand, often had to recognize nonmoving fruits and other vegetation similarly to bears. Thus, movement perception of both prey and predators may be constrained by the evolutionary foraging ecology of lineages.

The repulsed reactions of five bears to recently captured garter snakes, which readily exude obnoxious secretions, may help explain the lack of snakes in bear diets. Defensive use of anal scent is widespread among snakes (Greene 1997). On the other hand, repeated failures by black bears to locate rattlesnakes, fox snakes, and ratsnakes by scent suggest that scent may be reduced in those species of snake that specialize in ambushing small mammals. Alternatively, bears may have reduced their reliance on certain kinds of chemosensory information. While bears certainly are highly chemosensory oriented, we are not aware of any detailed studies of the sensitivity of bears to different kinds of chemical odorants. We suggest that this is a promising area for research using some of the more powerful experimental methods now available.

There are, however, some experimental studies of the reactions of both felids and canids to snake scent gland secretions. An informal experiment by Price and LaPointe (1981) suggested that several North American carnivore species are hesitant to approach or eat food tainted with kingsnake (Lampropeltis getulus splendida) cloacal secretions. To provide more controlled and systematic experiments, domestic cats were tested with both secretions and extracts from secretions along with controls and a shed snake skin derived from a gray ratsnake (Pantherophis sp.) (Wright & Weldon 1990). Cats were not repulsed by the secretions and in fact salivated and/or rubbed on them more than on controls stimuli. Less food was eaten when it was treated with secretions, however. In other experiments, domestic dogs (Canis familiaris) and coyotes (Canis latrans) were presented with western diamondback rattlesnake (Crotalus atrox) scent gland secretions and extractions in kennel (dog) and field (coyote) tests (Weldon & Fagre 1989). The coyotes were actually attracted to the stations with the snake secretions more than to control stations and rubbed and rolled on them. Dogs presented with filter paper containing snake chemicals licked, bit, and even ate them as compared to controls. In another experiment with terriers comparing the rattlesnake with alligator paracloacal gland secretions, no significant differences were found. The authors conclude that there 'was no indication that canids are repelled by scent gland secretions' (Weldon & Fagre 1989:1589). They also cite a paper published in Japan on a brown bear (Ursus arctos) that salivated when presented with snake carcasses or a rope previously housed with snakes. Salivation has been reported in both canids

and felids to snake gland secretions. Unfortunately, these tests did not use the highly pungent and aversive, to humans, natricine gland secretions, although the lack of response to the highly toxic rattlesnake is telling. None the less, such minimal responses to snake secretions and snake odors generally by all carnivores tested suggest that there is little exaptation to either avoid or prey upon snakes in the carnivore lineage going back very far in its evolutionary origins.

From the snake's perspective, reduced scent might enhance success in ambushing small prey that are chemically sensitive while at the same time increasing chances of being stepped on by large mammals, as nearly happened repeatedly in this study. Greene (1997) hypothesized that rattlesnakes evolved the motion and sound of rattling in part to alert bears and procyonids. Rattling is within the range of hearing of most mammals, including bears (Fay & Popper 1994; Nachtigall et al. 2007). By using movement and sound to alert large mammals, rattlesnakes may (1) avoid being injured, (2) save the costs of expending venom defensively, as well as (3) avoid the need to defensively exude anal scent that could linger and reduce subsequent hunting success. Sharp-hooved ungulates that have roamed North America for millions of years (Kurten 1971) may pose a special threat to snakes, but rattling by a 0.5-m rattlesnake (Crotalus sp.) caused collared peccaries (Pecari tejacu sonoriensis) to immediately retreat (Neal 1959). Studying the reactions of bears to the rattles of rattlesnakes would be a most useful area.

These results also pose a larger question: Why do bears generally, even in venomous snake areas, respond quite less vigorously and intensely than monkeys and apes to snakes? While this is a large topic that also involves consideration of other families in the Order Carnivora, especially canids, a few observations may be useful in encouraging more detailed analyses. While great ape and human evolution seem to be centered in Africa, where there evolved many venomous snakes, bears are conspicuously absent from that continent. Furthermore, we know that while large and dangerous constricting snakes were around at the beginnings of placental mammalian radiations, venomous snakes did not really begin to evolve until about the time of the major anthropoid (new and old world monkeys, apes) radiations about 50 mya (Isbell 2009). By that time, bears had been around a long time and thus did not evolve in settings where venomous snakes were that common. However, Asia has sloth (Melursus ursinus), Asian black (Ursus thibetanus), and sun bears (Helarctos malayanus). It would be most useful to gather data on the behavior

of these bears to snakes found in their habitats, including large constrictors such as pythons (Pythonidae). We encourage those able to study natural populations of all bears to collect and publish serendipitous observations as well as those gained through systematic studies (Dukes 1965). Bear ecology, evolution, and cognitive abilities (e.g., Bacon & Burghardt 1976a,b; Vonk et al. 2012) parallel the apes in several important ways, and thus bear cognition and behavior may illuminate aspects of primate and hominid evolution generally as well as in differing ways of dealing with dangerous snakes.

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Literature Cited

- Auliya, M. & Abel, F. 2000: Zur Taxonomie, geographischen Verbreitung und Nahrungsokilogie des Netzpythons (*Python reticulates*) – Teil 1 (geographische Verbreitung). Herpetofauna **22**, 5—18.
- Bacon, E. S. & Burghardt, G. M. 1976a: Ingestive behaviors of the American black bear. Ursus **3**, 13–25.
- Bacon, E. S. & Burghardt, G. M. 1976b: Learning and color discrimination in the American black bear. Ursus 3, 27—36.
- Beeman, L. E. & Pelton, M. R. 1980: Seasonal foods and feeding ecology of black bears in the Smoky Mountains. Ursus 4, 21–24.
- Bennett, L. J., English, P. F. & Watts, R. L. 1943: The food habits of the black bear in Pennsylvania. J. Mammal. 24, 25—31.

Bertagnoli, G. G. 1986: Availability and use of foods by black bears in Wisconsin. M.S. Thesis. Univ. of Wisconsin-Stevens Point, Stevens Point, WI.

- Burghardt, G. M. 1975: Behavioral research on common animals in small zoos. In: Research in Zoos and Aquariums (Anon., ed.). National Academy of Sciences, Washington, DC, pp. 103—133.
- Burghardt, G. M. 1988: Anecdotes and critical anthropomorphism. Behav. Brain Sci. 11, 248—249.

- Burghardt, G. M., Murphy, J. B., Chiszar, D. & Hutchins, M. 2009: Combating Ohpiophobia. In: Snakes: Ecology and Conservation (Mullin, S. J., Seigel, R. A., eds). Comstock Publishing Associates, Ithaca, NY, pp. 262—290.
- Burghardt, G. M., Bartmess-LeVasseur, J. N., Browning, S. A., Morrison, K. E., Stec, C. L., Zachau, C. E. & Freeberg, T. M. 2012: Minimizing observer bias in behavioral studies: a review and recommendations. Ethology 118, 511—517.
- Cheney, D. L. & Seyfarth, R. M. 1990: How Monkeys see the World. Univ. of Chicago Press, Chicago, IL.
- Cooper, W. E. Jr, Burghardt, G. M. & Brown, W. S. 2000: Chemical stimuli from potential prey and predators: behavioural responses by hatchling racers (*Coluber constrictor*) from two geographically distinct populations. Amphibia-Reptilia **21**, 103—115.
- Coss, R. G. 2003: The role of evolved perceptual cues in art and design. In: Evolutionary Aesthetics (Voland, E., Grammer, K., eds). Springer-Verlag, Heidelberg, pp. 69—130.
- Coss, R. G., Guse, K. L., Poran, N. S. & Smith, D. G. 1993: Development of antisnake defenses in California ground squirrels (*Spermophilus beecheyi*): II. Microevolutionary effects of relaxed selection from rattlesnakes. Behaviour **124**, 137—164.
- Cottam, C., Nelson, A. L. & Clarke, T. E. 1939: Notes on early winter food habits of the black bear in George Washington National Forest. J. Mammal. **20**, 310–314.
- Darwin, C. 1871: The Descent of Man and Selection in Relation to Sex. Murray, London.
- Darwin, C. 1872: The Expression of Emotions in Man and Animals. Murray, London.
- Debruyn, T. D. 1999: Walking With Bears. The Lyons Press, New York.

Dukes, W. F. 1965: N = 1. Psychol. Bull. **64**, 74–79.

Ennis, M. & Coss, R. G. 2006: Orbital frontal cortex ablations of rock squirrels (*Spermophilus variegatus*) disinhibit innate antisnake behavior. Behav. Neurosci. **120**, 1299—1307.

Fay, R. R. & Popper, A. N., eds. 1994: Comparative Hearing: Mammals. Springer Handbook of Auditory Research Series. Springer-Verlag, New York.

Fitch, H. S. 1965: An ecological study of the garter snake, *Thamnophis sirtalis*. Univ. Kans. publ., Mus. Nat. Hist. 15, 493—564.

Fredriksson, G. M. 2005: Predation on sun bears by reticulated python in East Kalimantan, Indonesian Borneo. Raffles Bull. Zool. **53**, 165–168.

Greene, H. W. 1997: Snakes: The Evolution of Mystery in Nature. Univ. of California Press, Berkeley, CA.

Grenfell, W. E. Jr & Brody, A. J. 1983: Seasonal foods of black bears in Tahoe National Forest, California. Calif. Fish and Game 69, 132—150.

Hamilton, R. J. 1978: Ecology of the black bear in southeastern North Carolina. M.S. Thesis, Univ. of Georgia, Athens, GA.

Hardy, D. M. 1974: Habitat requirements of the black bear in Dare County, North Carolina. M.S. Thesis, Virginia Polytechnic Institute, Blacksburg, Virginia.

Harlow, R. F. 1961: Characteristics and status of Florida black bear. Trans. North American Wildlife and Natural Resources Conference **26**, 481–495.

Headland, T. N. & Greene, H. W. 2011: Hunter-gatherers and other primates as prey, predators, and competitors of snakes. PNAS **108**, E1470—E1474.

Herzog, H. A. Jr & Burghardt, G. M. 1974: Prey movement and predatory behavior of juvenile western yellow-bellied racers, *Coluber constrictor mormon*. Herpetologica **30**, 285–289.

Holman, J. A. 2000: Fossil Snakes of North America: Origin, Evolution, Distribution, and Paleoecology. Indiana Univ. Press, Bloomington, IN.

Hopkins, J. B. I. I. I. 2013: Use of genetics to investigate socially learned foraging behavior in free-ranging black bears. J. Mammal. **94**, 1214—1222.

Isbell, L. A. 2009: The Fruit, the Tree, and the Serpent: Why We See so Well. Harvard Univ. Press, Cambridge, MA.

Kats, L. B. & Dill, L. M. 1998: The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5, 361—394.

Klenzendorf, S. A., Lee, D. J., Vaughan, M. R. & Duncan, R. B. Jr 2004: *Crotalus horridus* (Timber Rattlesnake).
Defense and black bear death. Herpetological Rev. 35, 61—62.

Kurten, B. 1971: The Age of Mammals. Columbia Univ. Press, New York.

Landers, J. L., Hamilton, R. J., Johnson, A. S. & Marchinton, R. L. 1979: Foods and habitat of black bears in southeastern North Carolina. J. Wildl. Manage. 43, 143 —153.

Maior, R. S., Hori, H., Barros, M., Teixeira, D. S., Tavares, M. C. H., Ono, T., Nishijo, H. & Tomaz, C. 2011: Superior colliculus lesions impair threat responsiveness in infant capuchin monkeys. Neurosci. Lett. **504**, 257—260.

McDiarmid, R. W., Campbell, J. A. & Touré, T. 1999: Snake Species of the World: A Taxonomic and Geographic Reference, Vol. 1. Herpetologists' League, Washington, DC.

Meno, W., Coss, R. G. & Perry, S. 2013: Development of snake directed antipredator behavior by wild Whitefaced Capuchin monkeys: I Snake-species discrimination. Am. J. Primatol. **75**, 281—291.

Mitchell, P. C. & Pocock, R. I. 1907: On the feeding of reptiles in captivity with observations on the fear of snakes by other vertebrates. Proc. Zool. Soc. Lond. 1907, 785—794. Nachtigall, P. E., Supin, A. Y., Amundin, M., Roken, B., Meller, T., Mooney, T. A., Taylor, K. A. & Yuen, M.
2007: Polar bear *Ursus maritimus* hearing measured with auditory evoked potentials. J. Exp. Biol. 210, 1116— 1122.

Neal, B. J. 1959: A contribution on the life history of the collared peccary in Arizona. Am. Midl. Nat. **61**, 177–190.

Neitz, J., Geist, T. & Jacobs, G. H. 1989: Color vision in the dog. Vis. Neurosci. **3**, 119–125.

Norton, N. C. 1981: Food habits, growth, and cover types used by northern Wisconsin black bears. M.S. Thesis, Univ. of Wisconsin-Stevens Point, Stevens Point, WI.

Oldfield, B. & Moriarty, J. J. 1994: Amphibians and Reptiles Native to Minnesota. Univ. of Minnesota Press, Minneapolis, MN.

Owings, D. H., Coss, R. G., McKernon, D., Rowe, M. P. & Arrowood, P. C. 2001: Snake-directed antipredator behavior of rock squirrels (*Spermophilus variegatus*): population differences and snake-species discrimination. Behaviour **138**, 575–595.

Pessoa, L. & Adolphs, R. 2010: Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. Nat. Rev. Neurosci. 11, 773— 782.

Placyk, J. S. & Burghardt, G. M. 2011: Evolutionary persistence of chemically elicited ophiophagous antipredator responses in gartersnakes, *Thamnophis sirtalis*. J. Comp. Psychol. **125**, 134—142.

Price, A. H. & LaPointe, J. L. 1981: Structure-functional aspects of the scent gland in *Lampropeltis getula spendida*. Copeia **1981**, 138—146.

Raine, R. M. & Kansas, J. L. 1990: Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. Ursus **8**, 297—304.

Richmond, G. M. & Fullerton, D. S. 1986: Summation of quaternary glaciations in the United States of America. Quat. Sci. Rev. **5**, 183—196.

Rogers, L. L. 1987: Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monograph No. 97. 72 pages.

Rogers, L. L. & Wilker, G. W. 1990: How to obtain behavioral and ecological information from free-ranging, researcher-habituated black bears. Ursus **8**, 321—328.

Sattler, R. A. & Dixon, E. J. 1997: Timing the post-glacial arrival of black bears (*Ursus americanus*) in southeast Alaska and eastern Beringia. Curr. Res. Pleistocene **14**, 155–157.

Shibasaki, M. & Kawai, N. 2009: Rapid detection of snakes by Japanese Monkeys (*Macaca fuscata*): An evolutionarily predisposed visual system. J. Comp. Psychol. **127**, 131—135.

Sikes, R. S., Gannon, W. L., & the animal care and use committee of the American Society of Mammalogists

2011: Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J. Mammal. **92**, 235—253.

Starin, E. D. & Burghardt, G. M. 1992: African rock pythons (*Python sebae*) in The Gambia: Observations on natural history and interactions with primates. The Snake **24**, 50—62.

Struhsaker, T. T. 1967: Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In: Social Communication Among Primates (Altmann, S. A., ed.). Univ. of Chicago Press. Chicago, IL, pp. 281–324.

Tisch, E. L. 1961: Seasonal food habits of the black bear in the Whitefish Range of northwestern Montana. M. S. Thesis, Montana State Univ., Bozeman, MT.

Van Le, Q., Isbell, L. A., Matsumoto, J., Nguyen, M., Hori, E., Maior, R. S., Tomaz, C., Tran, A. H., Ono, T. & Nishijo, H. 2013: Pulvinar neurons reveal neurobiological evidence of past selection for rapid detection of snakes. PNAS **110**, 19000—19005.

Vonk, J., Jett, S. E. & Mosteller, K. W. 2012: Concept formation in American black bears (*Ursus americanus*). Anim. Behav. 84, 953—964.

Weldon, P. J. & Fagre, D. B. 1989: Responses by canids to scent gland secretions of the western diamondback rattlesnake (*Crotalus atrox*). J. Chem. Ecol. **15**, 1589— 1604.

- Whiten, A. & Byrne, R. W. 1988: Tactical deception in primates. Behav. Brain Sci. **11**, 233–244.
- Wright, J. & Weldon, P. J. 1990: Responses by domestic cats (*Felis catus*) to snake scent gland secretions.J. Chem. Ecol. 16, 2947—2953.
- Zytaruk, B. & Cartwright, D. 1978: Black bear movements and food habits in New Brunswick. Proc. 4th Eastern Black Bear Workshop **4**, 227–239.