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Public information for solitary foragers: timber rattlesnakes use conspecific chemical cues to select ambush sites

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Many animals use public information (PI) gathered from conspecifics to assess the quality of potential foraging locations. To date, research on this phenomenon has focused almost exclusively on social foragers that live in groups and monitor nearby individuals. PI is potentially available to solitary foragers as well, in the form of cues (such as chemical cues) that persist in the environment after conspecifics are no longer present. In this study, I examined the response of a solitary sit-and-wait predator, the timber rattlesnake (*Crotalus horridus*), to chemical cues from conspecifics that had recently fed as opposed to those that had been deprived of food. Experiments with a T-maze indicated that timber rattlesnakes always follow conspecific chemical trails out of the maze, regardless of whether or not the individual leaving the trail had recently fed. However, an enclosure choice test found that individuals are more likely to select ambush sites in areas with chemical cues from conspecifics that had recently fed. These results indicate that snakes may use conspecific chemical cues not only to find mates, shelter sites, and hibernacula but also profitable food patches. Additionally, this study highlights the possibility that other solitary foragers may use PI to guide their foraging behavior. *Key words:* chemical cues, foraging behavior, inadvertent social information, public information, social foraging, timber rattlesnakes (*Crotalus horridus*). *[Behav Ecol 18:487–490 (2007)]*

INTRODUCTION

Animals generally acquire information about their environment from 3 sources: prior experience, personal information from current sampling, and social information from monitoring other animals (Valone and Templeton 2002). Social information garnered outside the context of signaling and communication has been referred to as inadvertent social information (ISI); public information (PI) is a form of ISI that allows for the assessment of resource quality (Valone and Templeton 2002; Danchin et al. 2004). Studies on a variety of taxa have shown that foragers often integrate experience, personal information, and ISI to locate and assess profitable foraging areas. However, most studies of ISI have focused on animals that live in groups, such as flocks of birds (Ward and Zahavi 1973; Templeton and Giraldeau 1995; Smith et al. 1999; Fernandez-Juricic et al. 2004), shoals of fish (Brown and Laland 2003; Coolen et al. 2003, 2005), and groups of mammals (Galef and Wigmore 1983; Templeton and Giraldeau 1995; Galef and Giraldeau 2001; Drapier et al. 2002; Chauvin and Thierry 2005). The possibility that solitary individuals may also use ISI to guide their foraging behavior has been overlooked. For more solitary foragers, cues that persist in the environment after conspecifics have vacated an area, such as chemical cues, are likely to be an important source of ISI—for example, female red-backed salamanders may use conspecific fecal pellets to assess local prey resources (Karuzas et al. 2004).

One group that may be particularly valuable for examining solitary foraging and ISI is snakes. Snakes are carnivorous, solitary foragers with well-developed chemosensory abilities (Mushinsky 1987; Schwenk 1995; Greene 1997), and recent studies indicate that they are more socially complex than previously realized (Greene et al. 2002; Clark 2004a; Shine et al. 2005). Many species are ambush predators that feed infrequently on patchily distributed prey (Duvall et al. 1990; Shine 1991; Greene 1992; Beck 1995; Clark 2004b). Although snakes have been found to use conspecific chemical cues to locate mates, communal shelters, and hibernacula (Gillingham 1987; Ford and Burghardt 1993), no studies have considered the importance of ISI for foraging behaviors. Conspecific chemical cues may contain a variety of information about an individual's status—garter snakes can use skin lipids from conspecifics to identify not only species and sex (Ford and Obleness 1986) but also mating status, body condition, and size (Shine et al. 2003; O'Donnell et al. 2004). Thus, snakes may also be able to use chemical cues to identify conspecifics that are successful foragers and use this information as ISI to guide their own foraging behavior.

Field studies of timber rattlesnakes (*Crotalus horridus*) have indicated that the possibility of ISI is particularly strong for this species: individuals trail conspecifics to important environmental features, such as hibernacula (Brown and Maclean 1983; Reinert and Zappalorti 1988; Cobb et al. 2005), and correlated movements between individuals moving through foraging habitat are common (Clark RW, personal observation). To examine the possibility that timber rattlesnakes use ISI while foraging, I conducted a series of laboratory experiments exposing food-deprived timber rattlesnakes to chemical cues from conspecifics that had or had not recently fed.

METHODS

Test subjects

Snakes consisted of 16 individuals (8 males, 8 females) from 3 litters of *C. horridus*, born in the laboratory to wild-caught females. Gravid females were caught on 15 August 1999 in Wyoming, Clinton, and Lycoming Counties, Pennsylvania and released after giving birth in captivity. Experiments were

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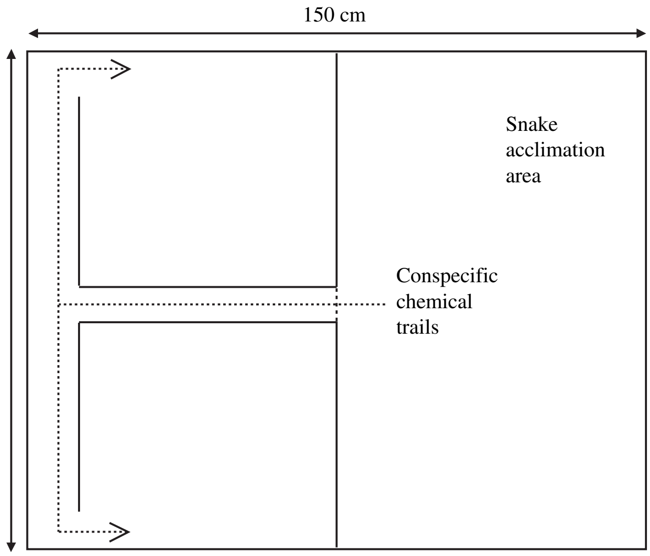

Figure 1
T-maze enclosure design used in experiments 1 and 2.

conducted with captive-born snakes between November 2002 and December 2003, during which the snakes ranged from 85 to 101 cm total length and 438 to 635 g in body mass. Snakes were housed individually in 75-l aquaria equipped with a water dish and heating pad at one end and reared on a diet of prekilled laboratory mice. Snakes were maintained in a Cornell University animal holding facility at 22–26 °C under a 12:12 h light:dark light cycle.

T-maze design

To test conspecific use of ISI, trailing behaviors were observed in a T-maze constructed inside a testing enclosure. The testing enclosure was a wooden, open-topped enclosure (150 × 75 × 120 cm), which was divided into equal halves (75 × 75 × 120 cm) with a removable wooden partition. The T-maze was constructed in one half of the testing enclosure using bricks for the maze walls and a clear piece of Plexiglas for the ceiling. The base of the "T" was 75 cm in length and ran down the middle of the testing arena; the top was also 75 cm in length and ran across one end of the arena (Figure 1). The maze was 6 cm tall and 6 cm wide and had a removable door for the opening and each arm. The wooden enclosure and T-maze apparatus were cleaned thoroughly with detergent between trials to reduce contamination with residual chemical cues.

Conspecific chemical cues

In all trials, conspecific chemical cues came from donors that had recently fed (F) or had not recently fed (NF). F snakes ate one mouse a week for 3 weeks and then 4 mice in the week prior to the experiment, whereas NF snakes had not eaten for 4 weeks prior to the experiment. This range of feeding frequency is similar to that found in natural populations of this species, which contain some individuals who have not fed in months and others with multiple large food items in their stomach at once (Brown 1993; Clark 2002, 2006). Individuals were always tested with chemical cues from unrelated, same-sex conspecifics to avoid any chemosensory behavior related to courtship or kin aggregation. Test subjects were always tested in an NF condition to increase their probability of exhibiting foraging behaviors.

Experiment 1: T-maze, conspecific chemical trails versus no trail
In the first experiment, individuals were tested for their preference of either F or NF conspecific chemical trails versus the unused arm of the T-maze. Eight individuals (4 males, 4 females) were randomly tested with F conspecific chemical trails and the other 8 with NF. To create chemical trails, a conspecific was allowed to crawl once through the base of the T-maze and either the left or the right (randomly chosen) arm. The other arm was left untreated. The test snake was then placed in the empty half of the enclosure and allowed to acclimate for 24 h, after which the entrance to the T-maze was opened. Trials ended after 24 h, and the choice of the test snake was recorded as right arm, left arm, or no choice (snake did not enter maze). All trials were video recorded and coded for blind observation and data recording.

Experiment 2: T-maze, F versus NF conspecific chemical trails
Following the results of experiment 1, a second experiment was designed using the same T-maze apparatus to offer test snakes the simultaneous choice between chemical cues from F and NF conspecifics. Conspecific chemical trails were created in the same fashion as in experiment 1, except that one arm of the T-maze contained F conspecific chemical trails and the other NF. The order in which F and NF trails were laid down was chosen randomly, as was the arm of the maze containing the trail. The testing procedure and data recording were the same as in experiment 1.

Experiment 3: arena trial, F versus NF conspecific chemical cues
After analyzing the results of experiment 2, a third experiment was designed to examine the choice of test snakes for F or NF conspecific chemical cues in the context of ambush site selection. To create conspecific chemical cues, the wooden enclosure was partitioned into equal halves and a water dish and hide box (25 × 25 × 4 cm) were placed in each half along with either an F or an NF conspecific. The snakes were left in the enclosures for 3 days, after which they were removed, along with the partition, thus creating a single arena with conspecific chemical cues from an F snake on one half and an NF snake on the other half. A test snake was then placed in the middle of the enclosure to begin the trial. Trials lasted for 72 h, and the amount of time the test snake spent outside the hide boxes in an ambush coil (sensu Reinert et al. 1984; Clark 2004b) was recorded, along with the location of the ambush coil (F or NF side of enclosure). Trials were videotaped, and tapes were coded for blind observation and data recording.

Statistical analysis

Statistical significance in the T-maze trials was determined using the binomial test (Sokal and Rolf 1995). For experiment 3, after testing to ensure normality, a t-test was used to determine if the difference in time spent on the F side of the enclosure versus the NF side was significantly different from zero.

RESULTS

In all trials of experiment 1 where a choice was made, the test snake chose the arm of the T-maze with conspecific chemical cues. Thus, test snakes chose both F and NF conspecific chemical cues over the blank path ($P < 0.01$). In 1 of 16 trials in experiment 2, the test snake did not enter the T-maze and so no choice was made. In 9 of the trials, the test snake chose the F trail, whereas in the 6 remaining trials, the test snake chose the NF trail. There was no significant difference in the choice of F trails over NF trails ($P = 0.15$). In experiment 3, the 16

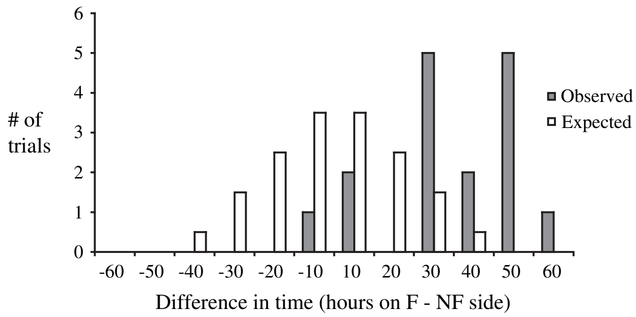

Figure 2
The observed difference in time snakes spent in ambush coils on the F versus NF side of the enclosures. Open bars show the normal distribution of difference in time centered on 0, which would be expected if snakes exhibited no preference.

snakes spent an average of 48 ± 17 h in an ambush coil outside the hide box. Fifteen of the 16 snakes spent more time in an ambush coil on the F side of the enclosure than the NF side. Overall, test snakes spent 28 ± 19 more hours on the F side than the NF side of the enclosure, a difference significantly greater than zero, zero being expected if there were no preference ($T = 6.0$, degrees of freedom = 15, $P < 0.001$) (Figure 2).

DISCUSSION

The T-maze trials show that timber rattlesnakes will preferentially follow the chemical trails of conspecifics over a blank substrate. This choice is apparently unaffected by whether or not the chemical trails are from conspecifics that have recently fed or not. However, the enclosure experiment showed that timber rattlesnakes spent more time in ambush coils on substrate marked with chemical cues from F conspecifics versus NF conspecifics.

Whereas the enclosure experiment supports the hypothesis that timber rattlesnakes use a form of PI to guide their foraging behaviors, the T-maze experiments are more ambiguous. Although the results indicate that ISI is important for navigating unknown terrain, the feeding history of the conspecific providing the chemical trails does not seem to matter. This may be because test subjects in these trials were not foraging, but rather attempting to safely navigate new territory. The snakes in these experiments were left in an enclosed area for 24 h, and may have entered the T-maze primarily in order to escape the enclosure. If so, following the trail of a conspecific may be a successful strategy for finding an exit. In this context, the feeding history of the conspecific would be irrelevant. This use of ISI may be present in other snake species as well. For example, research on brown tree snakes (*Boiga irregularis*) using a Y-maze found that males followed chemical cues from other males as often as females (Greene et al. 2001) and preferred both to the unmarked arm. For this reason, research attempting to isolate mating or courtship trailing behaviors from more general conspecific trailing should include adequate controls to make sure snakes are behaving in a courtship context and not simply attempting to navigate the maze using ISI.

This study raises the possibility that PI and ISI may be used by a wider variety of animals than previously realized—particularly among low-energy ambush predators. These predators often exhibit a 2-stage foraging strategy, with a short search stage while they move through the environment looking for appropriate ambush sites and a prolonged wait stage where they hide and attempt to attack prey that come within range (Clark 2006). They may assess the presence and success of conspecifics during the search stage, while attempting to locate good ambush sites.

Many of these species feed very infrequently on prey that is patchily distributed. If ISI exists in a patch in the form of chemical cues left by previous foragers, this information is likely to be used in assessing the patch. A large body of theory already exists on the costs and benefits individual foragers accrue when deciding whether or not to join a group that is exploiting a patch (Giraldeau and Caraco 2000; Beauchamp and Ruxton 2005; Ruxton et al. 2005). These models could also be adapted to find the optimal decisions faced by solitary foragers who have ISI or PI about other foragers that have already exploited a patch. The way in which foragers respond to ISI should depend on the way in which prey resources in a patch are depleted by other foragers: if a single forager cannot readily deplete a patch, then PI indicating a high-quality patch may increase the probability that a second forager will select that patch. Alternatively, if resources in a patch are quickly depleted after a forager has visited, then ISI indicating the presence of previous foragers in a patch may increase the probability that a forager will reject the patch. Given that timber rattlesnakes feed on average less than once a week (Clark 2006), it is unlikely that a single forager could rapidly deplete local prey resources in an area of abundant woodland rodents. Therefore, PI indicating a high-quality patch should increase the likelihood that they will stay in that patch.

Skin lipids present on the integument of snakes have long been known to function as sex pheromones (Mason et al. 1989), and they may mediate conspecific attraction in other contexts as well (Graves and Duvall 1995). These skin lipids have low volatility and are likely to persist in the environment for a relatively long time (Graves et al. 1991). Recent studies on garter snakes have shown that skin lipid pheromones are also used to assess a suite of characteristics about the donor, including body condition and size (Shine et al. 2003; O'Donnell et al. 2004). Future experiments should determine whether or not these same skin lipids encode ISI, indicating feeding history to other conspecifics.

Recent research has revealed that some snake species may live in cryptic social groups (Shine et al. 2005), exhibit kin recognition (Clark 2004a), and have parental care (Greene et al. 2002). Along with the experiments described here, these studies indicate that complex sociality, although not obvious to nonchemically oriented observers like humans, may be an important aspect of the life history of many snakes.

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