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Interactions of diet and behavior in a death-feigning snake (*Heterodon nasicus*)

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INTERACTIONS OF DIET AND BEHAVIOR IN A DEATH-FEIGNING
SNAKE (*HETERODON NASICUS*)

BY

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THESIS

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ABSTRACT

Studies of animal behavior in captivity are limited in their ability to explain the influence of a natural environment on behavioral ecology. Defensive behaviors vary among individual animals, between sexes and with age, as well as with other less well-known factors. The toxin-rich diet of many toad-eating snakes might enable or cause their passive terminal defensive behavior of death-feigning. I videotaped death-feigning behavior in wild Plains Hog-Nosed Snakes (*Heterodon nasicus*) subjected to standardized harassment. Using stable isotopes, I also described the diet of the same individuals subjected to behavioral analysis (n = 40). *Heterodon* had broader diets than other snakes at the study site. Both diet and behavior differed between sexes and age classes. Male *H. nasicus* death-feigned for longer than females, but initiated death-feigning later. Female *H. nasicus* had more specialized diets than males; adults of both sexes consumed mostly turtle eggs during the study period, while juveniles fed on Six-lined Racerunners and their eggs. Residual individual variation in behavior might be attributable to diet or to other factors. Further research is necessary to elucidate the complex relationship between diet and behavior in toad-eating snakes.

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INTRODUCTION

When detected by a predator, individuals of a prey species employing anti-predator behaviors that increase their probability of survival should achieve greater fitness than those that do not. Natural selection should favor these behaviors, if heritable, along with some flexibility in when they are displayed. Some defensive behaviors are passive (*e.g.*, freezing, aposematism, crypsis) and usually effective in avoiding initial detection, while others are active (*e.g.*, fleeing, counter-attacking) and are typically employed after the predator has detected the prey. At least one class of passive behaviors, however, is used as a terminal defense by prey that have already been detected by a predator, and especially when direct contact is made (*i.e.*, an attack; Thompson et al. 1981).

Death-feigning

Death-feigning (also known as letisimulation, tonic immobility, or thanatosis) is known from a wide variety of animals from several phyla (Hoagland 1928), and has multiple independent evolutionary origins even within the vertebrates. The behavior involves immobility and often adopting a specific posture in response to an attack, despite the seeming increase in vulnerability. Death-feigning has been best studied in invertebrates. The behavior has been documented in crustaceans (Crozier & Federighi 1923, O'Brien & Dunlap 1975), arachnids (Bilde et al. 2006, Ebermann 1991, Hansen et al. 2008), and in insects from at least nine orders (Abbott 1926, Carlberg 1986, Cassill et al. 2008, Edmunds 1972, Larsen 1991, Moore & Williams 1990, Nishino et al. 1999, Villet 2006). Death-feigning has been especially well-studied in the coleopterans *Cylas formicarius* (Miyatake 2001), *Tribolium castaneum* (Miyatake et al. 2004, 2008b, 2009, Prohammer & Wade 1981), and species in the genus *Callosobruchus* (Hozumi & Miyatake 2005, Miyatake et al. 2008a, Nakayama &

Miyatake 2010, Ohno & Miyatake 2007). Death-feigning is also known from all five classes of vertebrates: fish (McKaye 1981, Tobler 2005, Wells et al. 2005), amphibians (Banta & Carl 1967, Brodie Jr et al. 1974, Lupo et al. 1991, Toledo et al. 2010), reptiles (Bertoluci et al. 2006, de Carvalho et al. 2011, Langkilde et al. 2003, Mori 1991, Prestrude & Crawford 1970), birds (Hohtola 1981, Sargeant & Eberhardt 1975, Thompson et al. 1977, 1981) and mammals (Fraser 1960, Kimble 1997). The predators against which death-feigning is effectively used are less well catalogued, but include both invertebrates (Miyatake et al. 2004) and vertebrates (Thompson et al. 1981).

Although death-feigning has been recorded from many species, little is known about the function of the behavior and the mechanism by which it deters predators and confers a survival advantage on its users. The diversity of prey species that employ death-feigning complicates the situation considerably, and any generalizations about the behavior are difficult to make. Additionally, predators of different species probably do not respond to a death-feigning display in the same manner. Within- and among-predator responses to the behavior are insufficiently characterized to be the subject of experimental testing, despite their potential for explaining the why and how of death-feigning.

The one exception to this lack of information is the death-feigning response described for Pygmy Grasshoppers (*Criotettix japonicus*). This species will assume a posture that maximizes their body's spread, preventing predators from being able to fit the grasshoppers into their mouths (Honma et al. 2006, Ruxton 2006). This probably represents a fairly specialized function of death-feigning, as many species are less rigid than grasshoppers when death-feigning, but it might have evolved from a more general ancestral form of death-feigning, the function of which was not exceeding predator gape size.

In most cases, the function of death-feigning is assumed to be a predator deterrent at the terminal stage of attack. In some species, this function has been experimentally demonstrated. For example, cats pursued active quail more often and for longer than immobilized quail (Thompson et al. 1981), and the majority of ducks that death-feigned when seized by a fox survived (Sargeant & Eberhardt 1975). Spiders were more likely to consume beetles that struggled following an initial attack than those remaining immobile (Miyatake et al. 2004). The exact mechanism by which death-feigning discourages predators from killing and eating their prey is uncertain, however, and there are likely as many different mechanisms as there are predator- prey pairs in which the prey species sometimes employs death-feigning. Would-be predators might lose interest in immobile prey (Gregory 2008, Heinen 1995, Herzog & Burghardt 1974), either because such predators require movement cues to trigger attack or because motionlessness relaxes the predator's attention and thus allows prey to escape. To date, no empirical evidence suggests that corpse mimicry is a mechanism of predator discouragement. Although it might be safer for predators to avoid eating dead prey (*e.g.*, the possibility of disease transmission), scavenging is common among vertebrate predators (DeVault & Krochmal 2002, DeVault et al. 2003) and is known from some invertebrates (Cramer 2008, Fellers & Fellers 1982). Furthermore, behavioral aspects of many death-feigning displays (*e.g.*, repeated body inversion in hog-nosed snakes) should signal that the prey item is not actually dead. Other potential explanations for the adaptive value of immobility are that remaining motionless may cause less harm to the prey than struggling within the predator's grip and may provide the prey with an opportunity to flee (Toledo et al. 2010), or that immobility may signal that fleeing is not necessary for the prey to defend itself, much in the same way that stotting in ungulates may advertise health and

speed to predators to deter them from wasting energy on an often-unsuccessful chase (Pitcher 1979).

Presentation to the predator of a particular visual stimulus might be an important component of the death-feigning behavior (Miyatake 2001). Because some predators are diurnal and others are nocturnal, this idea suggests that there might be a trade-off between death-feigning and other anti-predatory behaviors that are differentially successful against different types of predators or in different circumstances (Gregory 2008, King & Leaich 2006, Prohammer & Wade 1981). In a series of comparative experiments, Miyatake et al. (2004) found that death-feigning in beetles was the second of two sequential defenses, much as in snakes (Gregory 2008) and other vertebrates. In the case of the red flour beetle, *Tribolium castaneum*, having two sequential defenses is important to the effectiveness of both, suggesting that other chemically-defended animals are pre-adapted to evolve death-feigning or vice versa. There are many examples of death-feigning animals with chemical defenses (*e.g.*, Banta & Carl 1967, Hutchinson et al. 2007, Toledo et al. 2010, Williams & Brodie 2004). In a meta-analysis of anurans, Toledo et al. (2010) suggested that certain postures used while death-feigning may be exaptations of the behavior for minimizing injury to frogs while allowing their chemical defenses to act against predators attempting to ingest them. Gehlbach (1970) suggested that death-feigning behavior by species of *Diadophis*, *Heterodon*, *Natrix*, and *Naja* represented specialized function of the general form of death-feigning, and that, coupled with aposematic coloration, it may advertise presumed distastefulness or known toxicity to predators.

The frequency, intensity and duration of death-feigning vary with several intrinsic and extrinsic factors, including genotype and mating behavior (Nakayama & Miyatake

2010), and have been documented to be heritable (Miyatake et al. 2004). It is probable that death-feigning is used differentially by different individuals within a population, depending on their ability to use other mechanisms of defense. An increase in the duration or intensity of death-feigning with a concomitant decrease in locomotory ability has been observed in snakes (Gerald 2008, Gregory 2008, Gregory & Gregory 2006) and beetles (Ohno & Miyatake 2007), suggesting that death-feigning is displayed more often when escape is not an option or when escape ability is compromised (*e.g.*, at a young age, after feeding, or while gravid). Larval stoneflies can distinguish between different predator types and apply an appropriate defensive behavior to effectively avoid predation (Moore & Williams 1990), which suggests that stonefly death-feigning is not a generalized involuntary stress response but a flexible behavior capable of being employed only when appropriate. Gargaglioni et al. (2001) found that electrolytic lesions of two mesencephalic regions of the brains of death-feigning toads (*Bufo* spp.) promoted an increase in the duration of death-feigning, but did not affect the latency of the motor response to a thermal noxious stimulus. This study indicated that the brain is involved in recovery from death-feigning but not its initiation, and that the behavior is not entirely involuntary or reflexive. Lupo et al. (1991) found evidence for endocrine control of death-feigning in another species of toad – specifically, susceptibility to immobility was negatively correlated with plasma sex steroids and positively correlated with testosterone binding capacity. Evidence for involvement of the brain in modulation of death-feigning has also been documented in mammals (de Oliveira et al. 1997, Monassi et al. 1997). Differences in the utilization of death-feigning have been documented between sexes, and might be related to sexually dimorphic morphology (Gregory 2008,

Gregory & Gregory 2006), physiology (Hutchinson et al. 2008) or to other factors associated with sex, such as microhabitat or activity patterns (Miyatake 2001).

The idea that some variation in death-feigning behavior might be explained by diet originated with the observation that several snake species which commonly feign death are bufophagous (Gehlbach 1970, Hulme 1951, Ionides 1952, Mutoh 1983, Smith & White 1955, Wu 2004). The endogenous defensive steroids produced as a defense mechanism by many species in the Family Bufonidae, which are structurally similar to hormones responsible for regulating the body's response to stress, are ineffective poisons against several of these specialized snake predators (Huheey 1958, McDonald 1974, Wu 2004). Smith & White (1955) and McDonald (1974) suggested that death-feigning in *Heterodon* represented a nonadaptive physiological response to a diet high in bufotoxin, and was actually detrimental to the species' survival. Taken in context of other studies of death-feigning (*e.g.*, Gerald 2008, Gregory & Gregory 2006, Miyatake et al. 2004), this hypothesis is tenuous. Several anecdotal lines of evidence, however, suggest that there could be a link between toad-eating and death-feigning in snakes. McDonald (1974) concludes with the statement:

“Though highly speculative, the hypothesis proposed here is offered in the hope that more critical attention will be focused on both physiological and behavioral aspects of this interesting phenomenon.”

Natural History of the Plains Hog-nosed Snake

The North American hog-nosed snakes (*Heterodon*) are part of the crown group of derived snakes (Colubroidea) and are members of the subfamily Xenodontinae (within the Family Colubridae), where they appear to occupy a basal relationship to other members of

this clade (Pinou et al. 2004, Pyron et al. 2010, Vidal et al. 2010, Zaher et al. 2009).

Heterodon nasicus and *H. simus*, the Southern Hog-Nosed Snake, are sister species, with *H. platirhinos* (Eastern Hog-Nosed Snake) as the most basal member of the genus (Meylan 1982, Pinou et al. 2004).

A medium-sized snake (Table 1), *H. nasicus* is stout-bodied, with strongly keeled dorsal scales. Broadly defined, the species *H. nasicus* ranges from the high plains of south-central Canada to Mexico, with isolated populations in Manitoba, Wyoming, eastern Texas, eastern Missouri, Iowa, Minnesota, and Illinois. It occurs from near sea level to elevations over 2,400 m. Hog-nosed snakes prefer sandy, well-drained soils suitable for burrowing. In Illinois, *H. nasicus* is restricted to relictual populations in inland sand areas along the Mississippi and Illinois rivers (Phillips et al. 1999, Smith 1961). The species is listed as threatened in Illinois, owing mostly to the loss of sand prairie habitat (Phillips et al. 1999).

All species of *Heterodon* are diurnal or crepuscular (Ernst & Ernst 2003, Kroll 1973, Pendlebury 1976, Platt 1969), and spend nights in temporary burrows, which they dig. Individuals of *H. nasicus* are typically active between 27.0 and 35.0 °C (Platt 1969), but may be found at temperatures ranging from 21.4 to 36.2 °C. For an ectotherm, *Heterodon* appears to have a fairly high metabolism (Pough 1980), although all evidence for this claim is circumstantial – a short average lifespan (<20 years), young age of maturity (1-1.5 years for males, 2-3 years for females), and fast growth rate (0.5-3.0 cm/month; Marr 1944, Platt 1969, Sabath & Worthington 1959, Snider & Bowler 1992, Wright & Wright 1957).

Sexual dimorphism in overall body size is present in *Heterodon*, following the typical pattern for colubroid snakes lacking male-male combat (Shine 1993), with the largest females being up to 230% larger than the largest males (Ernst & Ernst 2003). Growth rates

for females are higher, but maturity is reached at a later age. Another well-quantified measure of sexual dimorphism in *Heterodon* is in the size of the adrenal glands, which are enlarged at birth in both sexes relative to other snakes (Mohammadi 2011, Smith & White 1955, Spaur & Smith 1971). The adrenal glands of snakes typically weigh $<1/5000^{\text{th}}$ of total body mass. Male *Heterodon* possess adrenal glands up to 3 times larger than those of females and up to 10 times larger than average for colubroid snakes (Smith & White 1955, Spaur & Smith 1971), while female *Heterodon* possess adrenal glands 2-2.5 times larger than average for colubroid snakes. The degree of dimorphism is slightly less in hatchlings than in adults, although the proportional size of the gland decreases in adults, to less than one-half that of hatchlings (Spaur & Smith 1971). The degree of adrenal gland enlargement also differs among species of *Heterodon*: *H. platirhinos* exhibits the greatest degree of enlargement (7.5-11 times larger than average), while *H. nasicus* exhibits more modest enlargement (only 2-3 times larger than average; Smith & White 1955).

Documented predators of *H. nasicus* include hawks, crows and coyotes (Blair & Schitoskey 1982, Platt 1969), but probably also include many mammalian mesocarnivores, predatory birds (*e.g.*, shrikes, corvids, flycatchers, icterids), and other snakes (*e.g.*, *Coluber constrictor*, *Lampropeltis* spp.). Juvenile hog-nosed snakes may fall prey to rodents, shrews, moles or other small mammals, or to large spiders (Edgren 1955), and hog-nosed snake eggs are probably depredated by a variety of vertebrates and invertebrates. Cannibalism of both the eggs and young has been documented (Hammack 1991, Iverson 1975, Mitchell & Groves 1993). No data exist on which predators are actually or potentially discouraged by any of the defensive behaviors in the repertoire of *Heterodon*, including the death-feigning display (Ernst & Ernst 2003, Munyer 1967).

Toads comprise a measurable proportion of the diet of all populations of *Heterodon* studied (13-57% in *H. nasicus*; Platt 1969). The life cycles of several trematode parasites include *Heterodon* as definitive hosts and amphibians as intermediate hosts (Goodman 1951, Parker 1941, Wright & Bishop 1915). In addition to the kinetic skull typically found in snakes, all species of *Heterodon* possess adaptations for bufophagy, including enlarged posterior maxillary teeth that deliver venom which can cause symptoms in ectotherms and, to a lesser extent, mammals (Averill-Murray 2006, Boulenger 1913, Bragg 1960, Grogan 1974, Kroll 1976, McAlister 1963, McKinstry 1978, Morris 1985, Platt 1969, Weaver 1965, Weinstein & Keyler 2009). Although *H. platirhinos* and *H. simus* are chiefly toad specialists, *H. nasicus* is known to feed on squamates and their eggs, turtle eggs, birds and their eggs, and small mammals in addition to amphibians (Barten 1980, Durso et al. 2011a, Ernst & Ernst 2003, Iverson 1975, Kolbe et al. 1999, Langford & Janovy 2011, Platt 1969).

A lesser known adaptation for bufophagy in *Heterodon* is an innate tolerance to bufonid toxins, which are a mixture of cardiotoxic compounds (*e.g.*, epinephrine, bufotenine, bufadienolides, digitaloids) of lethal potential to vertebrates, even at minute concentrations (Hayes et al. 2009, Licht & Low 1968, Rose & Valdes 1994, Smith & White 1955, Smith & Phillips 2006). Bufadienolides are cardiotoxic steroids that bind to, and inhibit, the ion transport ability of the sodium-potassium pump (Na^+K^+ -ATPase, hereinafter NKA; Dvela et al. 2007). Hormones produced in the adrenal glands of vertebrates maintain the NKA under normal circumstances (Besch et al. 1976, Dmitrieva et al. 2000, Graves 1986, Ikeda et al. 1991) and might play a role in counteracting the effects of bufadienolides in bufophagous snakes.

Connecting Adrenal Function to Diet

Reptilian adrenal glands consist of catecholamine-producing chromaffin tissue (homologous to the adrenal medulla in mammals), and corticosteroid-producing interrenal tissue (homologous to the mammalian adrenal cortex; Rupik 2002). Cells of the dorsal cap of the chromaffin tissue synthesize norepinephrine, and chromaffin islet cells synthesize epinephrine (Rupik 2002). The interrenal tissue synthesizes the corticosteroids aldosterone and corticosterone (Norris & Deviche 1997). Corticosterone and aldosterone maintain the normal balance of the NKA and promote NKA activity in cardiac cells (Ikeda et al. 1991, Lyoussi & Crabbé 1996, Therien & Blostein 2000). Norepinephrine and epinephrine modulate NKA activity (Svoboda et al. 1986), but do not directly counteract corticosteroids or bufadienolides (Cook et al. 1983). The role that adrenergic agents play in counteracting bufadienolides is not well understood, but they might stimulate corticosteroid release (Axelrod & Reisine 1984).

Spaur & Smith (1971) proposed several hypotheses to explain the sexual dimorphism in the adrenal glands of *Heterodon*, including: (a) a dietary correlation that reduces intersexual competition for toads, or (b) a defensive correlation, where males are more inclined to exhibit death-feigning. Sexual differences in metabolic rates, gonadal pleiotropic effects, or genetic sex linkage of the traits are also suggested. Because the adrenal glands produce hormones that help maintain the function of the NKA, it is reasonable to expect that selection pressure to counteract the potentially lethal effects of bufadienolides could result in the evolution of adrenal enlargement (Mohammadi 2011).

The extent of bufophagy is directly correlated to adrenal size in some xenodontine snakes (Ernst & Ernst 2003, Smith & White 1955). McDonald (1974) speculated that *Heterodon* and other death-feigning snakes compensated for toxins associated with

bufophagy by reducing production of similar endogenous hormones, comprising relatively high, but balanced, levels of sympathetic and parasympathetic activity. Furthermore, transient endogenous catecholamines could trigger the compensatory mechanism under stress and lead to wide-spread parasympathetic effects that include death-feigning. Smith and White (1955) suggested that resistance to sympathomimetic agents present in toad toxins required the production of endogenous catecholamines that promote parasympathetic effects (Malmejac 1964). Skin secretions of *Xenopus laevis* differentially alter climbing and tongue-flicking behavior in snake species having different diets and physiologies (Temple & Barthalmus 1994). Mohammadi (2011) found a positive allometric relationship between adrenal mass and body size in 3 of 4 species of phylogenetically-independent bufophagous snakes relative to closely related non-bufophagous species. She also reported sexual dimorphism in adrenal gland size was present in 3 of the 4 bufophagous species examined (*Heterodon platirhinos*, *Rhabdophis tigrinus* and *Waglerophis merremii*, but not *Natrix natrix*).

Death-feigning in Hog-nosed Snakes

Anecdotal reports suggest that *H. nasicus* and *H. simus* death-feign less frequently and for a shorter duration than *H. platirhinos* (Carr & Goin 1955, Edgren 1955, Hudson 1942, Myers & Arata 1961). For example, Kroll (1977) reported that 13 of 25 *H. nasicus* (52%) captured in Texas feigned death. The individual and interspecific variation in the expression of this behavior (Hemken 1974, Myers & Arata 1961) are poorly understood. To date, the only examinations of individual variance in death-feigning behavior have either been hindered by a habituation response in captivity, small sample sizes, or both (Durham

1980, Edgren & Edgren 1955, Hemken 1974, Raun 1962). Only one study has investigated sexual dimorphism in behavioral traits (Durham 1980).

Death-feigning is an innate behavior in *Heterodon*, occurring as early as the hatchling stage (Raun 1962). The display is often described as stereotyped because it follows a predictable sequence, although some stages may be skipped. Following crypsis, escape is usually the next option pursued to avoid predatory attack. If escape is not feasible, many hog-nosed snakes laterally flare the head, spread the anterior ribs (Edgren 1955, Hardaway & Williams 1976, Young et al. 1999), emit an audible hiss (Young & Lalor 1998), and occasionally strike with a closed mouth. These behaviors are the most-frequently omitted, and the snake either follows one or more of them with a death-feint or goes directly to it. The body is contorted and inverted to present the ventral surface, and the mouth is opened and the tongue extended. Often defecation and regurgitation accompany this final stage of the behavior. Maximum reported durations for death-feigning range from >10 (Burghardt & Greene 1989) to >45 (Haltom 1931) minutes. If an attempt is made to re-orient a death-feigning hog-nosed snake, the snake will immediately resume the inverted body posture. Tactile stimulus is usually required for death-feigning in *Heterodon* (Durham 1980), although *H. platirhinos* can enter the death-feint without being touched (pers. obs.). Sometimes during death-feigning, blood hemorrhages from the mouth (Edgren 1955, Kroll 1977), another defensive mechanism employed by several other reptiles (e.g., *Phrynosoma*, *Rhinocheilus*, *Tropidophis*, *Lampropeltis*; Kroll 1977). Eventually, the mouth closes and the head is brought upright as the snake examines its surroundings. The death-feint might then resume, especially following tactile stimulation, or the body could re-orient, concluding the display.

Heterodon are capable of assessing their surroundings throughout the death-feint and can ascertain the presence or absence of a predator and the direction of its gaze (Burghardt & Greene 1989), a phenomenon also reported in lizards (Gallup 1972, Hennig 1979, Santos et al. 2010) and birds (Arduino & Gould 1984, Gallup 1974, Hennig & Dunlap 1978). McDonald (1974) reported abrupt onset of bradycardia concomitant with body inversion during death-feigning in *H. platirhinos*, followed by gradual recovery. Curiously, Kroll (1977) reported self-wounding while death-feigning in 7 of 25 Texas *H. nasicus* (28%), entailing 1-3 bites to their own dorsal midbody, of sufficient depth to expose muscle tissue and cause scarring.

Reports of similar death-feigning behavior in snakes other than *Heterodon* have been sporadic. The behavior has been reported from several other bufophagous species within the suborder Serpentes (*e.g.*, *Rhabdophis tigrinus*, Hirai 2004, Mutoh 1983; *Waglerophis* [= *Xenodon*] *merremi*, Amaral 1934, Vitt 1983; *Hemachatus haemachatus*, Branch 1988, Shine et al. 2007; *Natrix natrix*, Gregory & Isaac 2004, Madsen 1983), and might be found in other toad specialists (*e.g.*, the viperid *Causus*, Greene 1997; the elapid *Naja*, Luiselli et al. 2002). Most of these reports probably represent independent, convergent evolution of the same behavior, rather than an ancestral behavior that has been lost by the many species that do not regularly display when attacked by a predator. Several reports from non-bufophagous species (Gehlbach 1970, Gregory & Gregory 2006, Rugiero 1999, Stevenson 2010, Visser 1966) suggest that infrequent use of the behavior may be fairly widespread, however, and has been overlooked in several well-studied species because it is rarely expressed (Gregory et al. 2007, Vogel & Han-Yuen 2010). Nevertheless, death-feigning in *Heterodon* is more completely

characterized and has been the subject of more experimentation than in any other snake genus (Mori & Burghardt 2000).

The idea that death-feigning is a reflexive behavior was proposed by Edgren & Edgren (1955) and Gehlbach (1970). Because of the simplicity, sudden onset and rapid recovery of death-feigning in snakes, Gehlbach (1970) thought it might represent an involuntary reflex and contrasted death-feigning with the erratic displays that often precede it in many snake species, which he thought must be under endocrine control. Burghardt & Greene (1989) reported that *Heterodon* can use sophisticated visual abilities to adaptively modify their anti-predator behavior, however, despite their seemingly unconscious condition. Their experiment demonstrated that death-feigning in *Heterodon* is not an involuntary reflex.

Because most captive *Heterodon* habituate to human contact and eventually cease to death-feign, performing replicated, controlled examinations of the behavior presents a challenge. The situation is further complicated by the difficulty of obtaining adequate numbers of wild-caught individuals, as *Heterodon*, like many snakes, are difficult to detect (Durso et al. 2011b) and typically occur at low population densities at all but a few sites throughout their range. Obtaining gravid females and experimenting on their offspring potentially constitutes pseudoreplication, especially if genetic or maternal effects influence the death-feigning behavior.

The purpose of my study was to compare both diet (especially, the contribution of toads) and behavior (frequency and intensity of death-feigning) between sexes and among size classes and individuals from a wild population of Plains Hog-nosed Snakes. This approach allowed me to circumvent the common problems associated with studies of

Heterodon behavior in the lab. My null hypotheses were that differences in diet and behavior would not exist between sexes and size classes.

Use of Stable Isotope Method for Quantifying Vertebrate Diets

Most ecologically important elements have at least two stable isotopes, one of which is usually much more abundant than the others. For example, average relative abundances of ^{12}C and ^{13}C atoms in terrestrial ecosystems are 98.89% and 1.11%, respectively. Organisms are made up of a mix of isotopes representing each of their constituent elements, the ratios of which can be measured for a particular element by stable isotope analyses. The standard for carbon isotopes is PeeDee cretaceous belemnite (PDB), while nitrogen isotopes are measured against atmospheric air (Griffiths 1991). Differential notation is used to express the difference in isotopic ratios between a sample and a standard. Delta units (δI), used to represent the isotopic ratio, are derived by dividing the absolute isotopic composition of a sample (A_{sample}) by that of the standard (A_{standard}) and subtracting one (Ehleringer & Osmond 1989, Ehleringer & Rundel 1989):

$$\delta\text{I}_{\text{standard}} = \left(\frac{A_{\text{sample}}}{A_{\text{standard}}} - 1 \right) 1000$$

Multiplication by 1000 allows the isotopic ratio to be expressed on a “per mil (‰)” or “parts per thousand” basis.

In most ecological studies, δC is typically negative, while δN is typically positive. For any isotope, a sample is enriched when its δI is more positive than that of another sample, whereas the sample is depleted when its δI is more negative than that of another sample. Consumer tissues often become enriched in heavier isotopes, because metabolic reactions favor incorporation of one isotope over the other (*e.g.*, lighter isotopes react faster, and thus make up a larger portion of an organism’s waste products). Relative to their prey,

predator isotopic values are, on average, 1‰ enriched in carbon and 3‰ enriched in nitrogen (Peterson & Fry 1987). These values are generalizations, however, and may vary widely among species, populations, communities and ecosystems (Pilgrim 2005, 2007). Carbon isotope ratios provide information about the carbon fixation pathway at the base of the food chain (*e.g.*, C3 vs. C4 photosynthesis), whereas nitrogen isotope ratios provide information about the trophic level (Peterson & Fry 1987).

Pilgrim (2005) has shown that inter-individual isotopic variation exists within a population of predators that are eating the same prey species. This phenomenon can extend over multiple trophic levels. Additionally, the diet of most species probably changes throughout the year, and may be different for individuals of different sexes, ages or phenotypes. These additional sources of variation considerably complicate the use of isotopes as a tool to directly study animal diets. Griffiths (1991) asserted that natural variation in isotopic composition of biological materials is mostly caused by source variation rather than variation occurring during assimilation of materials into an organism. Both source and process information should be addressed when interpreting results of stable isotope analyses, however, as overall isotopic composition of biological materials is impacted by ecological, physiological and biochemical factors (Gannes et al. 1997, Pilgrim 2005).

A strength of stable isotope analyses is that they can provide a quantitative measure of trophic niche width along continuous axes common to all species (Bearhop et al. 2004). Stable isotope ratios can offer insight into the range of prey species consumed, the evenness of prey components in the diet over time, the range of trophic levels from which prey are consumed, foraging location, and variability in individual physiology and in diet-tissue fractionation (Criss 1999, Olive et al. 2003, Peterson & Fry 1987). The technique offers a

powerful approach for distinguishing between population and individual level generalism in diet over time, and can be accomplished non-lethally.

The stable isotope method is superior to gut content surveys for studies of animal diets because it is not biased towards slowly-digested prey items, integrates dietary information over multiple timescales, and allows for collection of data from all individuals in a population, instead of just those which have fed recently. This last point is especially relevant for studies of ectotherms, such as snakes, which feed relatively infrequently (Dorcas et al. 2004, Rodríguez-Robles 1998, Rodríguez-Robles & Greene 1999, Rodríguez-Robles & Jesús-Escobar 1999). Stable isotope analyses are also well suited to studies of snake diets because snakes always consume their prey whole, so the issue of tissue fractionation is minimized when compared to predators that only eat part of their prey.

METHODS

Study Site

Thomson Sand Prairie (TSP) is a 103.5 ha elongate unit of the Upper Mississippi River National Wildlife & Fish Refuge, located in Carroll County, Illinois (739790 E 4647614 N UTM Zone 15N; Fig. 1) along the eastern border of the Mississippi River. Inland sand areas in Illinois are restricted to the shores of water bodies, most extensively along the Mississippi, Illinois and Green Rivers, as a result of outwash from the Wisconsin glaciers about 10,000 years ago. Although TSP lies in an unglaciated region, meltwater streams from glaciers carried sand down river valleys and deposited it along their banks.

The TSP occurs at 180 to 190 m above sea level, and is elevated 2 to 10 m above the river basin. The western part of TSP has a 12 to 20% slope with a westerly aspect. The soils are fine-grained, yellowish-brown Sparta and Ade loamy sands virtually free from organic matter except in the uppermost layer. It is exceptionally well-drained (>200 cm to the water table) and acts as a dune to the Mississippi River, isolating the floodplain from the river. Each of the several inland sand areas along the Mississippi has probably been isolated by water in the recent past, and there is probably little gene flow between populations of their flora and fauna.

Sand prairie vegetation consists mostly of bunch-grasses (*e.g.*, *Dicanthelium* spp., *Panicum* spp., *Stypa* spp.) and herbaceous plants (*e.g.*, *Tradescantia* spp., *Penstemon* spp., *Ionactis* spp.), but also includes the abundant cactus *Opuntia humifusa*, mosses, lichens, and a few woody shrubs and small trees. Of particular interest are the sand ‘blowouts’ present in the southwest portion of the prairie (Hart & Gleason 1907; Fig. 1). These features are bowl-shaped, elliptical depressions of bare sand 260 – 1,400 m² in area. The blowouts are mostly

oriented along a west-east axis (parallel to the prevailing wind), and aligned along the same longitude. They are formed by wind action when a disturbance (*e.g.*, borrow pit, ungulate grazing) interrupts a bunch-grass stand and allows the wind to carry sand away to the east (Gleason 1910). Due to characteristics of their roots and seeds, a few species are able to colonize the bare sand in the blowout basin (*e.g.*, *Acerates* spp., *Lespedeza* spp., *Tephrosia virginiana*), and these constitute an important microhabitat for *H. nasicus* (Thol 2008, Reedy, unpubl. data). The majority of *H. nasicus* captures (especially young-of-year individuals) occur in blowouts (Thol 2008, pers. obs.).

Field Methods

Snake Collection

Over a two year period, I walked a 1.85 km U-shaped transect through the Thomson Sand Prairie (19 and 20 September 2009, 28 days between 18 May and 18 September 2010, and 30 days between 23 May and 26 June 2011). I was typically accompanied by 4-8 experienced assistants. People walking the transect began heading north at the prairie's southern border (739577 E 4646385 N UTM Zone 15N; Fig. 1) between 0715 and 1015 h, turned around between 0740 and 1040 h (739596 E 4647295 N UTM Zone 15N) and finished to the east of the starting location at the same latitude (739656 E 4646385 N UTM Zone 15N) between 0830 and 1145 h. This period corresponds with the daily maximum activity period for *Heterodon nasicus* (Platt 1969).

As part of a larger effort to document activity patterns, detectability and life history of herpetofauna on TSP, we recorded the time and location of all reptile and amphibian encounters on transects. In particular, we obtained measurements (sex, tail and snout-vent length [SVL; ± 1 mm] and mass [± 1 g]) and tissue samples from all snakes encountered.

During May and June 2010, I collected scale tissue from Western Foxsnakes (*Pantherophis vulpinus*; n = 14), Eastern Gartersnakes (*Thamnophis sirtalis*; n = 7) and North American Racers (*Coluber constrictor*; n = 4), and scale and blood tissue from *H. nasicus* (n = 44). I palpated guts of all snakes for food items, and examined the buccal lining of *H. nasicus* for trematode parasites.

I modeled *H. nasicus* detection probability as a function of temperature, wind speed, transect duration and number of observers using program PRESENCE (Version 3.1, Proteus Research and Consulting Ltd., Dunedin, New Zealand). I subdivided each transect into fifteen-minute segments, so that 15 min of walking on the sand prairie constituted one sampling unit (“visit”). The estimates of detectability therefore correspond to the probability of finding at least one *H. nasicus* during a 15-min search by 5-9 experienced observers. I made the assumption that snakes are equally likely to be found on any part of the transect, because the entire route covers suitable habitat (Kolbe 1999, Thol 2008). Site occupancy (ψ) was held constant at 1, because TSP was continuously occupied by *H. nasicus* throughout the sampling period. Detectability (p) was either held constant (in the null model) or allowed to vary with temperature, wind speed, duration of transect or number of observers. I tested the fit of the global model using 10,000 parametric bootstraps, and ranked models using Akaike information criteria adjusted for small sample sizes (AIC_c) because the goodness-of-fit parameter \hat{c} did not show evidence of under- or over-dispersion (White et al. 2001).

Prey Collection

To collect small vertebrates, I constructed a circular (200 m circumference) drift fence-pitfall trap array, to the north of the transect route (739560 E 4647635 N UTM Zone 15N; Fig. 1) between 20 May and 24 June 2010. The fence was constructed of 45-cm tall

aluminum flashing and buried to a depth of ~15 cm, so that the resulting barrier was ~30 cm in height. Along the inside I buried 40 evenly-spaced 4.5-L plastic jars of 20 cm depth with 8.4 cm diameter openings. Along the outside I buried 12 evenly-spaced 18.9-L plastic buckets of 38 cm depth with 30 cm diameter openings.

I checked all pitfalls twice a day for 35 days, at approximately 0800 and 2000 h, and removed all vertebrates. Rodents (*Microtus ochrogaster*, n = 7), anurans (*Lithobates pipiens*, n = 7; *Anaxyrus americanus*, n = 6) and Six-lined Racerunners (*Aspidozelis sexlineata*, n = 9) were weighed, euthanized (by decapitation for anurans and lizards and by cervical dislocation for mammals), wrapped in aluminum foil and frozen. Additionally, I opportunistically captured anurans and racerunners from TSP during the study period. These were weighed, euthanized, and stored in the same way as those captured in the pitfalls.

On 10 nights between 3 June and 24 June 2010, I set 44 small mammal traps (Wilson et al. 1996) in a line between the drift fence and the transect route (739578 E 4647473 N UTM Zone 15N; Fig. 1). I baited the traps with oats and peanut butter and checked the traps the following morning, removing all mammals captured.

I opportunistically collected eggs from freshly-laid turtle nests (n = 20 *Chelydra serpentina* eggs and 8 *Chrysemys picta* eggs) throughout TSP. Eggs were weighed, wrapped in foil and frozen. Eggs of racerunners (n = 5) were obtained from the guts of *H. nasicus* on 24 - 26 June 2010.

I grouped prey into six categories for analysis based on similarities between their carbon and nitrogen isotopic signatures. These were (a) toads (*Anaxyrus americanus*, n = 6), (b) racerunners and their eggs (*Aspidozelis sexlineata*, n = 14), (c) painted turtle eggs (*Chrysemys picta*, n = 8), (d) snapping turtle eggs (*Chelydra serpentina*, n = 20), (e) leopard

frogs (*Lithobates pipiens*, $n = 7$), and (f) voles (*Microtus ochrogaster*, $n = 7$). I did not include prey species that were represented by <4 individuals in my analyses.

Behavioral Analyses

Upon detection of an individual *H. nasicus* by one of the transect walkers, I immediately started recording snake behavior using a Canon G10 digital camera. I recorded the reaction of each snake to standardized harassment, which consisted of me tapping the snake twice per second on the head with my fingers to simulate attack by a predator. If a snake inverted its body, I ceased tapping to simulate the putative effect of the behavior on a startled or disinterested predator. If a snake subsequently ceased feigning death, I resumed tapping. Because *H. nasicus* are known to adjust the duration of their bodily inversions based on predator eye contact (Burghardt & Greene 1989), I kept my gaze on the screen of my camera throughout the duration of the filming. I filmed each snake for 120 seconds. Any trials that were interrupted by unusual circumstances (*e.g.*, the arrival of additional observers) were omitted.

I transferred digital video files to a computer and scored each recording for the number of seconds to body inversion and the duration of inversion (Gallup 1974). I compared these two dependent variables between sexes using an ANCOVA, using the covariates of time of capture and body size (mass or SVL, but not both because they are autocorrelated; Kolbe 1999). I also tested for interactions among these three variables. I omitted non-significant interactions from my final analyses. I examined probability of death-feigning as a function of sex using a chi-squared test. I modeled latency to inversion and duration of inversion as a function of body size (mass or SVL) and time of capture using a multiple logistic regression.

Tissue Sampling, Preparation, and Analysis

As *H. nasicus* is threatened in Illinois, and because I wished to sample individuals multiple times per year and in subsequent years, I non-lethally sampled three tissue types from each specimen collected. I clipped two to four ventral scales from each snake and wrapped them in aluminum foil before freezing them. I also drew blood from each snake's subcaudal vein and centrifuged the blood immediately to separate the red blood cells (RBCs) from the plasma. I drew off the plasma and deposited it in a tin capsule. I transferred the RBC pellet to a second tin capsule using forceps and placed the two closed capsules together into a microcentrifuge tube, which was subsequently frozen.

While frozen, whole prey items and tissue samples from snakes were freeze-dried for 24-48 h to remove water. Turtle eggs were punctured to facilitate complete drying. Once whole prey items were sufficiently brittle, each was placed in a steel canister with two ball bearings and agitated in a roll-grinding machine until the sample was homogenized. A small amount (~2 µg) of the resulting powder was weighed into tin capsules in preparation for mass spectroscopy. Snake blood and scale tissue samples were small enough to place directly into tin capsules without grinding. Each sample was weighed to standardize output as a function of sample mass in mass spectroscopy.

Isotope samples were processed by the University of Georgia Analytical Chemistry Laboratory using a Carlo Erba CHN Elemental Analyzer (Model NA1500) coupled to a Thermo Finnigan Delta V Isotope Ratio Mass Spectrometer via a Thermo Finnigan Conflo III Interface. The output provided measures of total C, δC vs. PDB, percent ^{13}C , total N, δN vs. air and percent ^{15}N for each sample. I plotted δC vs. δN for all samples to visually depict trophic relationships in the TSP vertebrate community. I compared differences among tissue

types and between sexes. I estimated correlation coefficients among tissue and isotope values within individuals, and correlated these values with continuous metrics of snake SVL and mass, as well as the day that the sample was obtained.

I used the Bayesian mixing model software MixSIR (Moore & Semmens 2008, Semmens et al. 2009) for MATLAB to analyze the relationship between the predator (*H. nasicus*) and its potential prey. A Bayesian approach to stable isotope mixing models is advantageous because it allows the inclusion of prior knowledge about diet (*e.g.*, gut contents) in the analysis and explicitly accounts for, and characterizes, any uncertainty in isotope values when estimating the contribution of sources to a mixture (*i.e.*, individuals in a predator population). I analyzed males and females, adults and young-of-year, and the three tissue types separately. I used average fractionation coefficients for N and C from the literature (Peterson & Fry 1987). I set the number of iterations to one million for all models.

Synthesis of Dietary and Behavioral Data

To assess whether relationships existed between either carbon or nitrogen isotopic ratios and death-feigning latency or duration, I used a multiple regression to estimate parameters describing the explanatory value of each isotope value for each tissue type for predicting the SVL, mass, death-feigning latency and death-feigning duration. Because toads were enriched in C¹³, I expected snakes that were enriched in carbon to be feeding more heavily on toads, with potential implications for their defensive behavior.

I used the software IndSpec1 (Bolnick et al. 2002) to calculate the degree of individual specialization of *H. nasicus* in the TSP population. I used the ratio of the within-individual component (WIC) of niche width to the total niche width (TNW), expressed along a single continuous dimension (WIC/TNW; Ebenman & Nilsson 1982, Roughgarden 1972),

to quantify inter-individual variation in resource use. I used only individual *H. nasicus* for which I had stable isotope values of carbon and nitrogen for the three tissue types (scale, RBC and plasma; $n = 30$). I adjusted these values using the average among-tissue variance within each individual. By analyzing sexes and age classes separately, as well as together, I isolated these components of inter-individual variation from other sources of variation (*e.g.*, ecomorph; Matthews & Mazumder 2004, behavioral syndrome; Sih et al. 2004).

RESULTS

Snake Collection

I made a total of 125 captures of 75 individual snakes. An average of 1.83 snakes were caught per day during the survey periods, at a rate of 0.194 snakes per person-hour. The maximum number of snakes caught in a single day was 8 (on 10 June 2010) and the minimum was 0 (on 8 days). Larger snakes were captured later in the morning ($R^2 = 0.45$, $p = 0.01$ for SVL; $R^2 = 0.40$, $p = 0.04$ for mass).

The sex ratio of the 75 *H. nasicus* captured on TSP was slightly male-biased, with males representing 52% of captures. Young-of-year snakes comprised 19 (52.7%) of the 36 female and 29 (74.4%) of the 39 male snakes. Adult male SVL was smaller than in adult female snakes ($F_{1,26} = 1.45$, $p = 0.24$; Table 1). Male and female young-of-year snakes were of similar SVL ($F_{1,47} = 0.42$, $p = 0.52$). Tail lengths were longer in adult males than in adult females ($F_{1,26} = 4.16$, $p = 0.05$) and in young-of-year males than in young-of-year females ($F_{1,47} = 47.68$, $p < 0.0001$). Adult male snakes tended to weigh less than adult females ($F_{1,26} = 3.55$, $p = 0.07$). Male and female young-of-year snakes were of similar mass ($F_{1,47} = 0.28$, $p = 0.6$). Mass and snout-vent length were correlated ($R^2 = 0.93$, $p < 0.0001$).

Gut contents were obtained from 14 (11%) of 125 *H. nasicus* captures. These included 8 adult *H. nasicus*, all of which had consumed between 1 and 10 *C. serpentina* or *C. picta* eggs, and 6 juvenile *H. nasicus*, three of which had consumed *A. sexlineata* and three of which had consumed 1 to 2 *A. sexlineata* eggs. One juvenile *H. nasicus* was captured on two subsequent days and its gut contained 2 *A. sexlineata* eggs on each day. No trematode parasites were observed in the buccal lining of any *H. nasicus* at TSP.

No single model of detection probability had unequivocal support over the others (Table 2). The estimates of detection probability were similar among all models, suggesting that none of the covariates chosen (air temperature, wind speed, duration of transect, and number of people) had an important effect on the probability of detecting *H. nasicus* at TSP. The naïve estimate for detection probability given by the null model was $24.78 \pm 0.05 \%$, meaning that *H. nasicus* could be expected to be found about once per hour when surveying the transect.

Behavioral Analyses

From the 40 subjects encountered in May and June, 2010, I obtained 29 video recordings of *H. nasicus* behavior, of which 23 snakes feigned death within the first two minutes (six snakes, four females and two males, never did). The overall incidence of death-feigning was 79.3%. There was no relationship between snake gender and the probability of death-feigning ($\chi^2 = 0.10$, $p = 0.76$). Excluding subjects which never death feigned, the average latency to death-feigning was 23 sec, and the average duration of a death-feint was 39 sec. Mean latencies for males (33 sec) and females (16 sec) were similar ($F_{1,27} = 1.70$, $p = 0.21$; Fig. 2). The duration of inversion for female *H. nasicus* (49 sec) was similar to that for males (29 sec; $F_{1,21} = 1.77$, $p = 0.20$; Fig. 2). Including subjects which never death-feigned (*i.e.*, latency = 120 sec, duration = 0 sec) produced mean latencies to inversion for males and females that were different ($F_{1,27} = 4.11$, $p = 0.05$).

Large snakes death-feigned for longer durations than small ones ($F_{1,21} = 21.82$, $p = 0.0002$ for mass; $F_{1,21} = 32.55$, $p < 0.0001$ for SVL), and a SVL-by-sex interaction ($F_{1,21} = 8.63$, $p = 0.009$, Fig. 3) indicated that this trend was driven by females. Large female snakes death-feigned for longer than small females ($R^2 = 0.82$), while male snakes did not follow

this relationship as strongly ($R^2 = 0.51$). The time of capture did not influence the latency to inversion ($F_{1,21} = 1.60$, $p = 0.22$) or the duration of death-feigning ($F_{1,21} = 0.11$, $p = 0.75$), nor were there any interactions with time of capture and the morphometric variables ($F_{1,21} \leq 2.44$, $p \geq 0.15$). Mass ($p = 0.06$), time of capture ($p = 0.055$), and SVL ($p = 0.11$) were good, but non-significant, predictors of the probability that a subject would feign death. The model including time of capture and mass had a lower AIC (28.461) and a greater Δ AIC (2.636) than that including time of capture and SVL (AIC = 30.014, Δ AIC = 1.086). The model including time of capture and mass correctly predicted whether an individual subject would death-feign 77.3% of the time.

Stable Isotope Analyses

Stable isotope readings were successfully obtained for scale samples from 31, RBC from 34, and plasma samples from 32 *H. nasicus*. Isotopic signature varied among tissue types ($F_{2,64} \geq 9.59$, $p < 0.001$ for carbon, $p = 0.008$ for nitrogen; Fig. 4) and among individuals ($F_{21,64} \geq 78.1$, $p < 0.001$ for both isotopes; carbon $R^2 = 0.93$, nitrogen $R^2 = 0.90$), as well as between sexes ($F_{1,64} \geq 12.30$, $p = 0.002$ for carbon; Fig. 5, $p = 0.02$ for nitrogen; Fig. 6). Females (mean carbon signature = -23.8 ± 0.04) were enriched in carbon relative to males (mean carbon signature = -24.0 ± 0.08 ; Fig. 7). Both SVL and mass were correlated with plasma and scale carbon and nitrogen isotopic composition ($p < 0.001$ for both tissues and size measures), but not with RBC isotope signature. There was a sex-by-mass interaction for nitrogen for the same two tissue types ($p < 0.052$ for plasma, $p < 0.057$ for scale).

Hatchling *H. nasicus* isotope values reflected those of adult females (Fig. 8). As size increased, plasma isotopic content became enriched in carbon and depleted in nitrogen. This

trend reversed between 285 and 330 mm snout-vent length. Above this range, plasma from larger snakes was more enriched in nitrogen and depleted in carbon. Nitrogen was about twice as variable as carbon for all three tissue types (Table 3). Mean within-individual, among-tissue variance (standard deviation was ± 1.03 for carbon, ± 2.06 for nitrogen) was about twice as wide as mean among-individual variance (standard deviation was ± 0.61 for carbon, ± 0.96 for nitrogen).

Heterodon nasicus had the broadest range of carbon and nitrogen isotope values of the four snake species at TSP. Other snake species, as well as other vertebrates, were depleted in nitrogen relative to *H. nasicus* (Table 4, Fig. 9). Isotope values for *P. vulpinus* scales comprised two distinct groups, while values for *C. constrictor* and *T. sirtalis* clustered tightly together. *Chelydra serpentina* eggs were the prey type most enriched in nitrogen (Fig. 10), whereas voles and *A. sexlineata* were the most depleted in nitrogen. Voles were the prey type most enriched in carbon, while *A. americanus* were the most depleted in carbon. Adult *A. sexlineata* had similar isotopic values to their eggs. Small *L. pipiens* showed some overlap with large voles; otherwise, all prey types occupied distinct regions within the trophic space (Fig. 10).

The mixing model predicted that *H. nasicus* fed on *C. serpentina* eggs with a posterior probability of 44.9-75.7% (Fig. 11). This prediction was substantiated by gut content analyses of adult *H. nasicus* at TSP. Although the guts of several juvenile *H. nasicus* contained *A. sexlineata* or their eggs, the mixing model did not predict that racerunners made up a substantial fraction of the diet of *H. nasicus* (posterior probability $< 17.7\%$). Additionally, the model predicted that *A. americanus* comprised 5.8-24.4% of the diet, although no *A. americanus* were recovered from guts of *H. nasicus* at TSP. The proportion of

diet made up of *A. americanus*, *A. sexlineata*, and especially *C. serpentina* eggs, increased for RBCs over plasma and for scale tissue over RBCs (Fig. 11). Concomitantly, the proportion of diet made up of voles decreased from 30.1-38.3% for plasma to < 8.1% for scale tissue. Leopard frogs and *C. picta* eggs were not predicted to comprise a substantial fraction of the diet (posterior probability < 3.6% in both cases). Adult *H. nasicus* of both sexes were predicted to have a specialized diet of *C. serpentina* eggs (Fig. 12), whereas juvenile snakes were predicted to feed more broadly on voles, toads and racerunners, with a substantial maternal signature from turtle eggs (Fig. 13). Juvenile plasma showed the smallest contribution from turtle eggs of any tissue type.

Plasma nitrogen content was the best predictor of the duration of death-feigning in the regression model ($p = 0.04$, $R^2 = 0.95$). A quadratic term for plasma nitrogen was also a good predictor ($p = 0.04$). The nitrogen ratio of RBCs was a good predictor of snake body mass ($p = 0.03$, $R^2 = 0.79$). All other nitrogen terms and all carbon terms were not significant contributors to the model.

The absolute values of niche width are relatively unimportant compared to the ratio of between-individual to within-individual resource use. Total niche width was similar for carbon and nitrogen. Female *H. nasicus* had more specialized diets than males (Table 5). Adult *H. nasicus* had more specialized diets than juveniles.

DISCUSSION

Natural History

Heterodon nasicus at TSP are morphologically within the range of known phenotypic variation for the species (Kolbe 1999, Platt 1969). The population appears to be stable, with many gravid females contributing to annual reproduction in 2010. Although this population has been isolated from conspecifics for several thousand years (Smith 1961), the ecosystem at TSP is similar to that ancestrally inhabited by *H. nasicus*.

Heterodon nasicus at TSP appear to use sandy blowouts disproportionately to their availability, but whether this is due to higher snake abundance or higher detection probability in blowouts is unclear. For a snake, *H. nasicus* has a relatively high detection probability (Durso et al. 2011b, Steen et al. in press). The ecosystem at TSP appears to be conducive to studies of *H. nasicus* due to their catchability and relatively high abundance (Kroll 1973, Platt 1969).

Behavioral Analyses

Studies of animals in the wild are critical to understanding the adaptive value of behavior in relation to the environment in which it evolved. Measures of behavior obtained from subjects in a natural setting are more reliable indicators of behavioral utility than those obtained in captive trials. By keeping constant the few controllable factors known to influence the dynamics of death-feigning in *Heterodon* (*i.e.*, threat presence and eye contact; Burghardt & Greene 1989), I was able to investigate natural variation in anti-predator response in wild *H. nasicus*. Whether human stimuli are appropriate proxies of snake predators is difficult to assess, but humans have been used to stimulate defensive behavior in many other studies of squamates (*e.g.*, Burger et al. 1991, Burghardt & Greene 1989,

Hemken 1974, Scudder & Chiszar 1977). My results indicate differences in latency to initiation and duration of death-feigning with sex and body size, and an interaction of sex and body size, which was driven mainly by females. Sexual dimorphism in behavior has rarely been documented in snakes, and has not been reported for *Heterodon*. Loss of death-feigning behavior in *Heterodon* in captivity has probably prevented researchers from detecting this effect.

Individuals of *H. nasicus* death-feigned for a relatively short time, compared to records for other members of the genus (Carr & Goin 1955, Edgren 1955, Hudson 1942, Myers & Arata 1961). My results are consistent with what is known about changes in adrenal gland morphology and concomitant physiological changes in endocrine system function throughout life and between sexes in *Heterodon* (McDonald 1974, Smith & White 1955). Mohammadi (2011) has shown that the effects of adrenal mass cannot be explained simply on the basis of one adrenal tissue type (chromaffin or interrenal) being larger than the other, meaning that a single hormone (and the adrenal tissue that produces it) can not be responsible for bufadienolide resistance. Alternatively, adrenal hormones might not play a role in bufadienolide resistance, in which case adrenal enlargement may be a response to stresses induced by ingestion of bufadienolides (*sensu* McDonald 1974).

That male *H. nasicus* did not show as strong an ontogenetic change in behavior despite approximately equal sample sizes between the two sexes indicates that behavior of female hog-nosed snakes is more variable. Any influence of gravidity could not be isolated because all adult female *H. nasicus* in my study were gravid at the time of testing. Female *H. nasicus* typically reproduce in alternate years (Ernst & Ernst 2003); as such, in a given year I would expect that gravid females are most likely to be detected in visual encounter surveys,

due to their increased frequency of movement and basking to provide an optimal thermal environment for embryo development (Gregory et al. 1987, Lillywhite 1987, Peterson et al. 1993). Future work should target non-reproductive adult females for comparison with gravid females. Immobility is used most often by gravid female Terrestrial Gartersnakes (*Thamnophis elegans*; Gregory & Gregory 2006), and by European Grass Snakes (*Natrix natrix*) of intermediate size, likely as a result of their limited locomotory ability (Gregory et al. 2007). Shine et al. (2003) observed shifts in anti-predator behavior of reproductive Red-sided Gartersnakes (*Thamnophis sirtalis parietalis*) as a result of both changes in physiology and habitat use. Platt (1969) speculated that the relatively limited locomotory ability of *Heterodon* was partially responsible for the evolution of passive terminal defense behavior in the genus.

Stable Isotope Analyses

Stable isotope analysis is an ideal tool for examining long-term diets of wild animals. Isotopic signatures provide information from all individuals captured instead of just those which have fed recently, greatly improving the inferential power available to answer questions about dietary composition. Sexual dimorphism in the carbon isotope ratio of male and female *H. nasicus* might be indicative of different diets, or it could represent physiological differences in food processing. The mass-by-sex interaction is expected, because hatchling animals of both sexes carry the isotopic signature of their mothers, from whose diet all of the hatchling carbon and nitrogen is derived (Pilgrim 2007).

Isotope analyses indicated that *H. nasicus* at TSP feed extensively on the eggs of *C. serpentina*, as reported by Kolbe et al. (1999). Although I also documented *C. picta* eggs in the guts of *H. nasicus*, eggs of this turtle were not predicted to make up a large proportion of

diet. The presence of *A. sexlineata* in the diet of small *H. nasicus* is masked by the maternal isotope signature. Although voles were not found in the guts of *H. nasicus* at TSP, the mixing model predicted that they make up a substantial fraction of the diet. Vole reproduction occurs in the spring and fall in the Midwest (Fitch 1957, Rose & Gaines 1978) and so young voles might not be abundant in May and June. Turtle eggs are in high abundance in late spring and early summer, and *H. nasicus* might feed almost exclusively upon them during this time. Eggs represent low-risk sources of energy with low handling time and high temporal and spatial predictability. *Anaxyrus americanus* probably represent only a small proportion of the diet of *H. nasicus* at TSP. That the *H. nasicus* in my study harbored no trematode parasites also indicates a low contribution of amphibians to their diet. Other potential food sources available to *H. nasicus* on TSP that were not sampled include eggs of birds and other turtle species (*Terrapene ornata*, *Emydoidea blandingii*, *Graptemys* spp.), gray treefrogs (*Hyla chrysoscelis* x *versicolor*), mice (*Peromyscus* sp.), ground squirrels (*Spermophilus tridecemlineatus*), moles (*Scalopus aquaticus* and *Condylura cristata*) and shrews (*Blarina* and *Sorex* spp.). Opportunistic surveys, drift fence captures and mammal trapping yielded fewer than 3 individuals of any of these prey species during my study.

Although scale tissue is replaced at a slower rate than blood, estimation of this turnover rate will require multiple years of isotope data. The apparent lack of influence of body size on RBC isotopic composition could be due to lower inter-individual variation in diet at the intermediate time scale. However, RBC samples were also more easily contaminated than either plasma or scale tissue samples, because small amounts of plasma might have remained in the centrifuge tube.

Plains Hog-nosed Snakes had a greater niche breadth than the other three snake species at TSP. Inter-individual variation in diet was broadest for *H. nasicus*, which contributed to the overall wide niche breadth for the species. However, such variation between conspecifics has potentially important ecological, evolutionary, and conservation implications. Such variation challenges the traditional view taken by ecologists who consider the niche as a property of the species or population as a whole. Individual variation also facilitates frequency-dependent interactions that can affect population stability, the amount of intraspecific competition, fitness-function shapes, and a population's capacity to diversify and speciate rapidly (Bolnick et al. 2003). Some of the variation in *H. nasicus* isotopic composition is due to the greater variety of sizes sampled. Even among adult snakes, however, *H. nasicus* exceeded other species' niche breadth.

Foxsnakes and gartersnakes are generalists on endotherms and ectotherms respectively (Rodríguez-Robles & Jesús-Escobar 1999, Ernst & Ernst 2003), whereas racers are broad generalists, consuming a variety of vertebrate prey. At TSP, previous knowledge about the diets of these species is supported by stable isotope data (Fig. 14). All three species overlap somewhat with *H. nasicus* and with one another. The relatively poor diversity of the snake community at TSP might indicate weak interspecific competition, so that a specialized diet would provide little benefit to a species (Luiselli 2006, Mushinsky & Hebrard 1977). The high phylogenetic dispersion of the TSP snake community (4 genera in 3 subfamilies) might indicate that competition played a role in structuring the local assemblage (Colston et al. 2010), to the exclusion of closely related species that occur in Carroll County (*e.g.*, *P. obsoletus*, *H. platirhinos* and *T. radix*).

Plains Hog-nosed Snakes probably have a more generalized diet than either of their congeners. The diet of *H. nasicus* shifts as they age, and adults consume a wide variety of vertebrate prey, whereas small (<250 mm SVL) juveniles are restricted to a single prey type (*A. sexlineata* and their eggs). As these snakes grow (to 250-400 mm SVL), their dietary breadth increases, with a corresponding increase in growth rate until sexual maturity is attained (Platt 1969). These smaller snakes probably target different prey than large (>400 mm SVL) adults, but this is difficult to verify because smaller adults are rarely encountered. Large adults, especially females, probably feed almost exclusively on turtle eggs during the late spring and early summer.

The index of individual specialization proposed by Bolnick et al. (2002) uses a population's total diet to define resource availability so that individuals are compared to their population rather than to the whole environment. When sex and size variation were taken into account, individual isotopic compositions were still specialized, consistent with results from dietary studies of other ectotherms (Araújo et al. 2007, Svanback & Bolnick 2005, Svanback & Persson 2004). Such variation could also be an artifact of differences in physiology among individuals, however, or it could represent the combined effect of both dietary and physiological differences among individuals.

Synthesis

Because toads were the most enriched in carbon of any vertebrate prey sampled, I expected that *H. nasicus* whose tissues were also more enriched in carbon might death-feign more readily or for the longest durations, when compared to subjects with more depleted carbon ratios. This relationship was not supported by my data – female *H. nasicus*, which death-feigned for shorter durations, were depleted in carbon. Among adult snakes, however,

females death-feigned for longer and initiated death-feigning sooner, which could be attributed to diet, reduced locomotory ability as a consequence of gravidity (Gregory & Gregory 2006), or both. Any explanation of the seemingly-contrary measures of death-feigning intensity (latency and duration) between sexes is precluded by a lack of understanding of how bufadienolides influence the stress response of snakes. The *a priori* expectation that males should show a more intense response due to their larger adrenal glands is also subject to revision as biologists improve their understanding of the physiology of toad-eating snakes.

Until a systematic method for observing the natural reactions of predators to death-feigning is devised, any study of this phenomenon will be hampered by a lack of direct evidence of its effectiveness and mechanism (Munyer 1967). However, inter-individual variation in behavior might be correlated with adrenal gland size in individuals of the same sex and similar body size. Enlarged adrenal glands might be a functional requirement for bufophagy and bufadienolide resistance. Alternatively, adrenal enlargement might be a secondary consequence of bufophagy, either as a response to stress invoked by bufadienolide metabolism or a developmental response to the presence of the steroidal toxins of toads (Mohammadi 2011). If variation in adrenal gland size has any influence on the expression of defensive behavior, this would provide strong evidence for a link between diet and behavior. Because variation between individuals of the same size and sex might be slight, an ideal method to investigate this phenomenon might be to identify multiple geographically isolated populations that show differences in adrenal gland size across all sexes and age classes. The variation in defensive behavior among individuals within such populations could then be assessed.

Experiments that attempt to isolate the ways in which a predator perceives either a death-feigning snake or a non-death-feigning one would help elucidate the mechanism of death-feigning. Aspects of the behavior that could be important include immobility or stereotyped movement, body inversion, ventral coloration or pattern, the presence of blood, the smell of fecal matter or other exudates, or other as yet unconsidered components. The sensory systems of relevant predators should be assessed and tested for their response to each aspect of death-feigning in isolation to best understand the mechanism.

CONCLUSIONS

The adaptive significance, if any, of death-feigning is difficult to understand. In reptiles, death-feigning is not unconscious behavior but is instead cognitive in function (Burghardt & Greene 1989, Gregory et al. 2007). Gregory et al. (2007) called for “a new taxonomy of this class of antipredator behaviors,” suggesting that corpse mimicry is not the purpose of death-feigning. Individual and intersexual variation in death-feigning behavior has been documented in many species, including several snakes.

Limitations of the stable isotope method include the complications introduced by fractionation, ontogenetic and temporal variation in sources, and isotopic routing (Gannes et al. 1997, Pilgrim 2005). Mixing models are predictive but are limited in their ability to meet assumptions by the quality and quantity of laboratory data available, especially for fractionation coefficients. Other avenues for measuring diet could be pursued, such as amplifying and identifying prey DNA from predator feces or examining the parasite community of predators and prey so that the host-specific life cycles of certain trematode parasites might be used to track food chains (Pizzatto & Shine 2011). The application of isotopes to research involving parasites and their hosts might also be advantageous for studies of trophic and behavioral ecology (*e.g.*, Doucett et al. 1999, Pinnegar et al. 2001, Press et al. 1987, Trudell et al. 2003).

Because populations of *H. nasicus* have decreased in size and number over much of its range (Phillips et al. 1999, Tennant 1985, Wright & Didiuk 1998), further study of this species is warranted. Conservation efforts can be aided by a better understanding of interactions of *Heterodon* with both their predators and prey. Hog-nosed snakes are good candidates for reintroduction programs, because of their lack of site fidelity to overwintering

sites (Platt 1969, Plummer & Mills 2000). The Southern Hog-nosed Snake is the most endangered of the three species, having suffered almost complete extirpation over the western half of its range (Tuberville et al. 2000), and even the widespread Eastern Hog-nosed Snake is not immune to habitat degradation (*e.g.*, Lagory et al. 2009). A thorough understanding of the biology of all *Heterodon* will help inform conservation decisions and elucidate the relationship between diet and behavior in toad-eating snakes.

TABLES

Table 1: Morphological characteristics (means \pm one standard error) of 75 Plains Hog-nosed Snakes (*Heterodon nasicus*) from Thomson Sand Prairie (Carroll Co., Illinois) in 2010 and 2011.

		n	Snout-vent length (mm)	Tail length (mm)	Mass (g)
Male	Young-of-year	29	178 \pm 0.7	33 \pm 0.2	6.70 \pm 0.06
	Adult	10	451 \pm 14.4	84 \pm 2.8	111 \pm 8
Female	Young-of-year	19	182 \pm 0.9	25 \pm 0.1	6.44 \pm 0.09
	Adult	17	498 \pm 6.6	68 \pm 0.8	162 \pm 5

Table 2: Model selection results for PRESENCE model of Plains Hog-nosed Snake (*Heterodon nasicus*) detection probability (p).

The dispersion parameter, \hat{c} , is estimated at 0.90, indicating no overdispersion.

Model	AIC _c	Δ AIC _c	Model Likelihood	AIC _c weight	number of parameters	(-2*LogLikelihood)
$\psi(\cdot), p(\cdot)$	153.46	0.00	1.00	0.40	2	149.23
$\psi(\cdot), p(\# \text{ people})$	154.91	1.45	0.49	0.19	3	148.16
$\psi(\cdot), p(\text{duration})$	155.32	1.86	0.40	0.16	3	148.57
$\psi(\cdot), p(\text{wind})$	155.84	2.38	0.30	0.12	3	149.09
$\psi(\cdot), p(\text{airtemp})$	155.85	2.39	0.30	0.12	3	149.10
$\psi(\cdot), p(\text{all})$	164.16	10.70	0.00	0.00	6	147.55

Table 3: Mean (\pm one standard error) stable isotope ratios for blood plasma, red blood cell and scale carbon (δC^{13}) and nitrogen (δN^{15}) of 40 Plains Hog-nosed Snakes (*Heterodon nasicus*) from the Thomson Sand Prairie (Carroll Co., Illinois), as measured from samples collected in May and June, 2010.

		Carbon			Nitrogen		
		Plasma	Red blood cells	Scale	Plasma	Red blood cells	Scale
Male	Young-of-year	-24.315 \pm .058	-23.512 \pm .083	-23.147 \pm 0.233	8.745 \pm 0.276	10.989 \pm 0.253	9.267 \pm 0.457
	Adult	-23.658 \pm 0.200	-23.431 \pm 0.048	-22.822 \pm 0.117	11.351 \pm 0.284	11.592 \pm 0.200	12.260 \pm 0.196
Female	Young-of-year	-24.082 \pm .085	-23.197 \pm .067	-22.515 \pm .152	8.804 \pm 0.140	10.178 \pm 0.153	9.496 \pm 0.336
	Adult	-23.519 \pm .108	-22.954 \pm .134	-22.700 \pm .145	11.099 \pm 0.122	10.646 \pm 0.155	11.182 \pm 0.192

Table 4: Mean (\pm one standard error) stable isotope measurements of scale content for four species of terrestrial snake at the Thomson Sand Prairie (Carroll Co., Illinois) as measured from samples collected in May and June, 2010.

Species	Carbon	Nitrogen
<i>Coluber constrictor</i>	-22.670 ± 0.141	6.91 ± 0.268
<i>Heterodon nasicus</i>	-22.789 ± 0.024	10.257 ± 0.079
<i>Pantherophis vulpinus</i>	-23.307 ± 0.137	7.381 ± 0.320
<i>Thamnophis sirtalis</i>	-23.942 ± 0.076	9.108 ± 0.162

Table 5: Results of IndSpec estimation of degree of individual specialization for 30 Plains Hog-nosed Snakes (*Heterodon nasicus*) at the Thomson Sand Prairie (Carroll Co., Illinois) in 2010.

Carbon				
Model	Within-individual variation (WIC)	Between-individual variation (BIC)	Total niche width (TNW)	Relative degree of individual specialization (W/T)
All individuals	0.25	0.9511	1.201	0.2081
Males	0.2917	0.3422	0.6339	0.4602
Females	0.2374	1.219	1.456	0.163
Young-of-year	0.2732	0.5591	0.8323	0.3282
Adults	0.226	1.428	1.653	0.1367
Nitrogen				
Model	Within-individual variation (WIC)	Between-individual variation (BIC)	Total niche width (TNW)	Relative degree of individual specialization (W/T)
All individuals	0.2698	0.8164	1.086	0.2484
Males	0.4188	1.084	1.503	0.2786
Females	0.1453	0.6435	0.7888	0.1842
Young-of-year	0.455	0.4897	0.9447	0.4816
Adults	0.06738	0.6676	0.735	0.09168

FIGURES

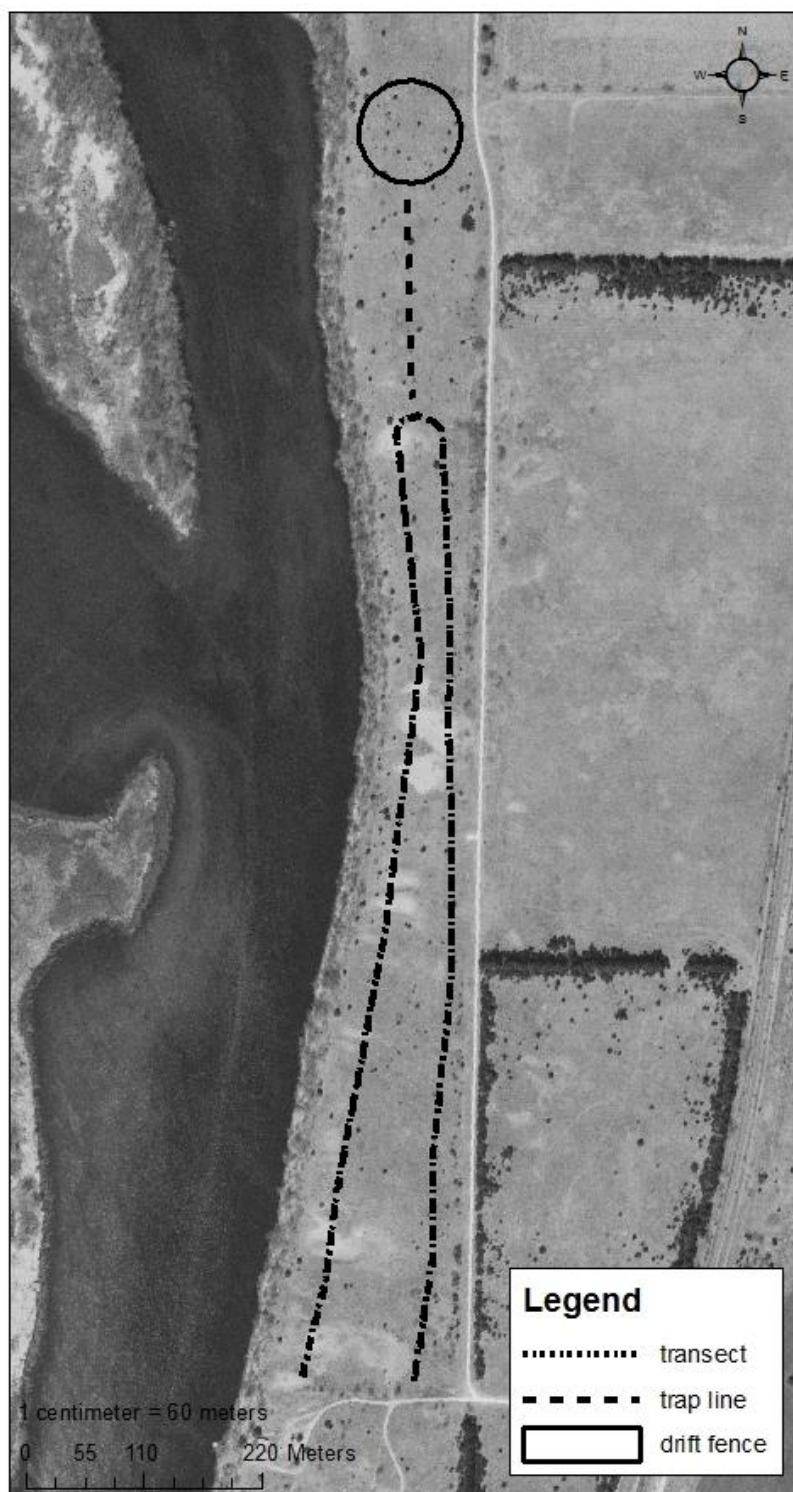


Figure 1: Map of Thomson Sand Prairie unit, Upper Mississippi National Wildlife & Fish Refuge, Carroll County, Illinois.

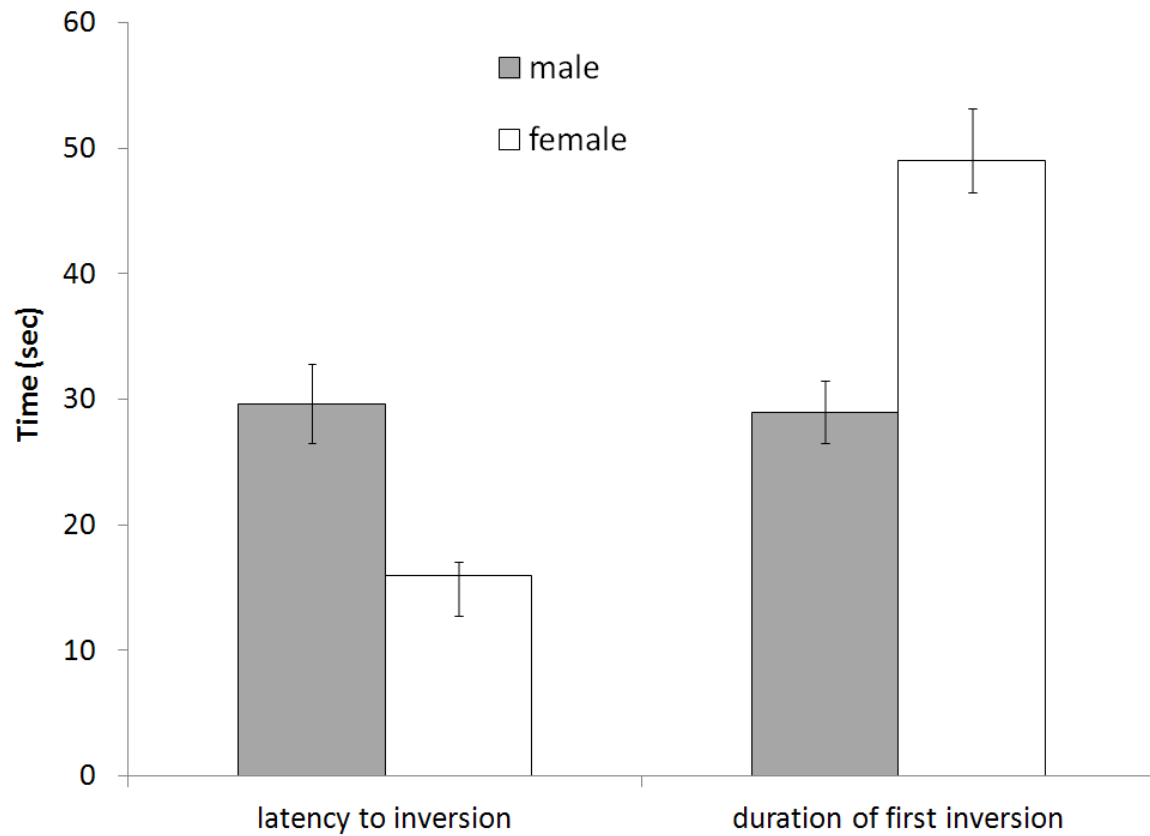


Figure 2: Differences in mean values for death-feigning behavior as a function of sex in Plains Hog-nosed Snakes (*Heterodon nasicus*) at Thomson Sand Prairie (Carroll Co., Illinois) in May and June, 2010. Bars represent ± 1 standard error.

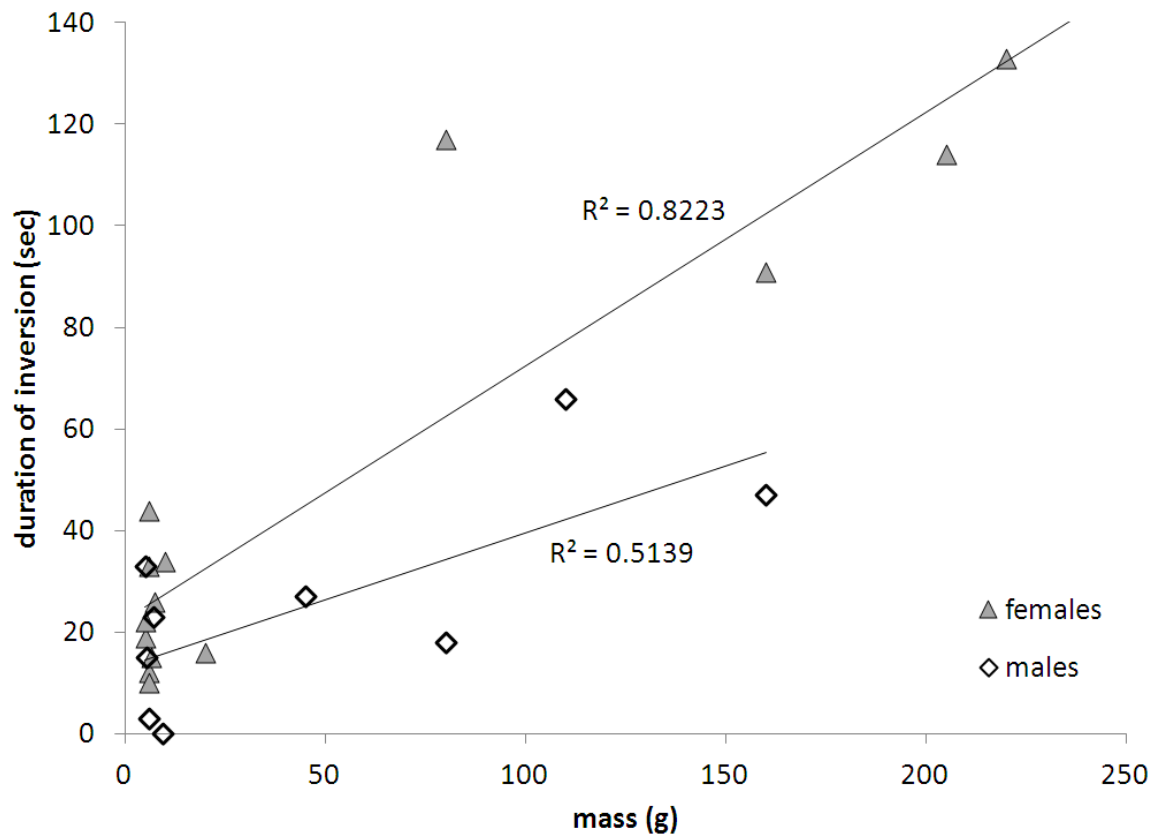


Figure 3: Relationship between intensity of death-feigning behavior and body mass for male (open diamonds) and female (shaded triangles) in Plains Hog-nosed Snakes (*Heterodon nasicus*) at Thomson Sand Prairie (Carroll Co., Illinois) in May and June, 2010.

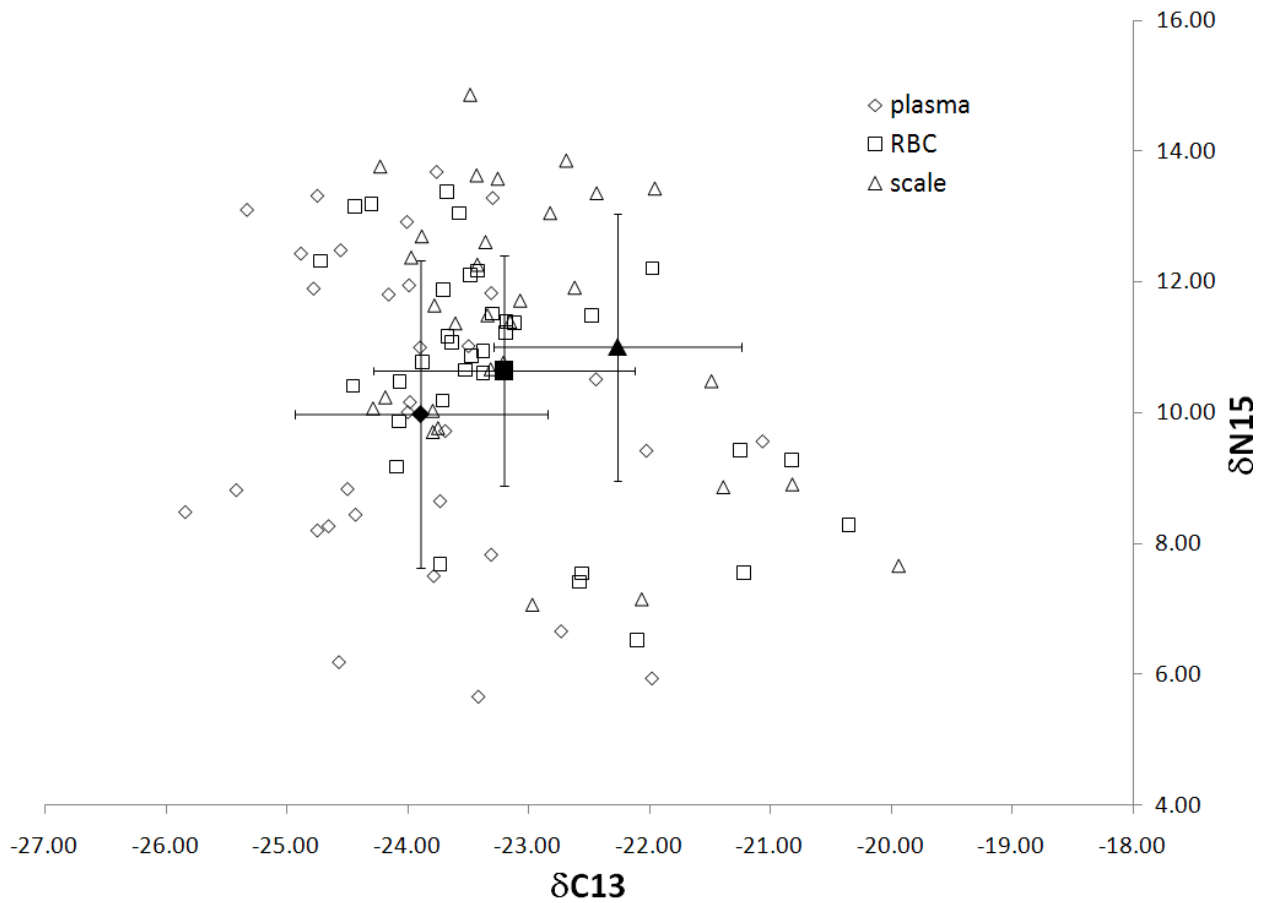


Figure 4: Mean stable isotope values for C^{13} and N^{15} in three tissue types of Plains Hognosed Snakes (*Heterodon nasicus*) at Thomson Sand Prairie (Carroll Co., Illinois) in 2010. Hollow symbols represent individual data points. Solid symbols represent means, bars represent ± 1 standard deviation. RBC = red blood cells.

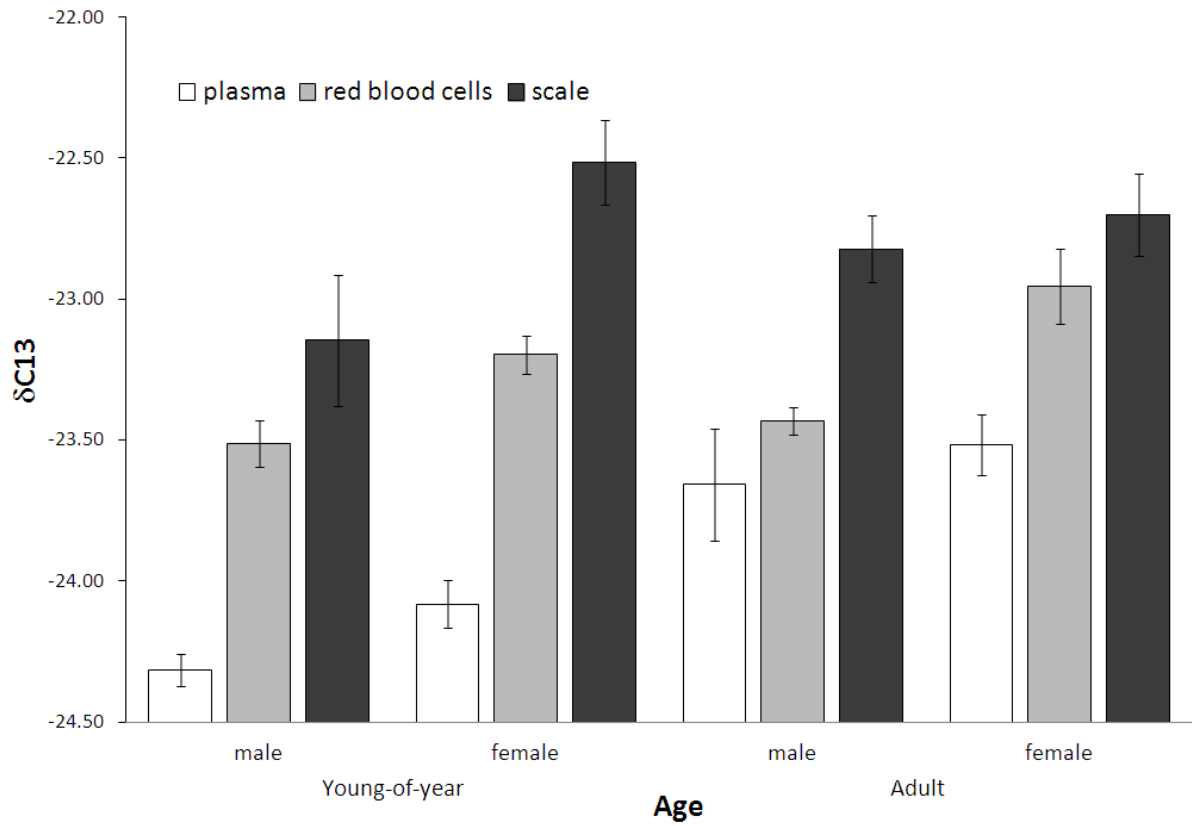


Figure 5: Stable isotope values for C^{13} in three tissue types of Plains Hog-nosed Snakes (*Heterodon nasicus*) at Thomson Sand Prairie (Carroll Co., Illinois) in 2010, as a function of age and sex. Bars represent ± 1 standard error.

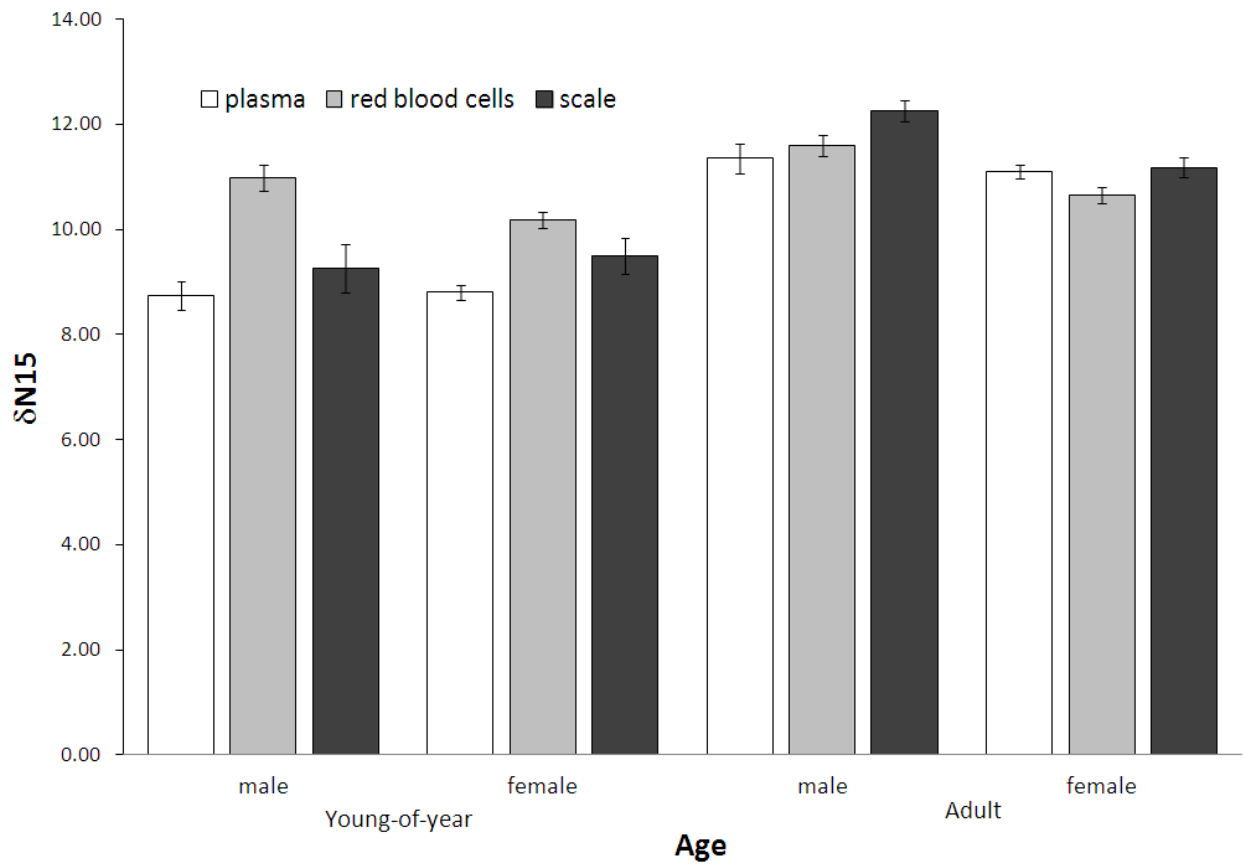


Figure 6: Stable isotope values for N^{15} in three tissue types of Plains Hog-nosed Snakes (*Heterodon nasicus*) at Thomson Sand Prairie (Carroll Co., Illinois) in 2010, as a function of age and sex. Bars represent ± 1 standard error.

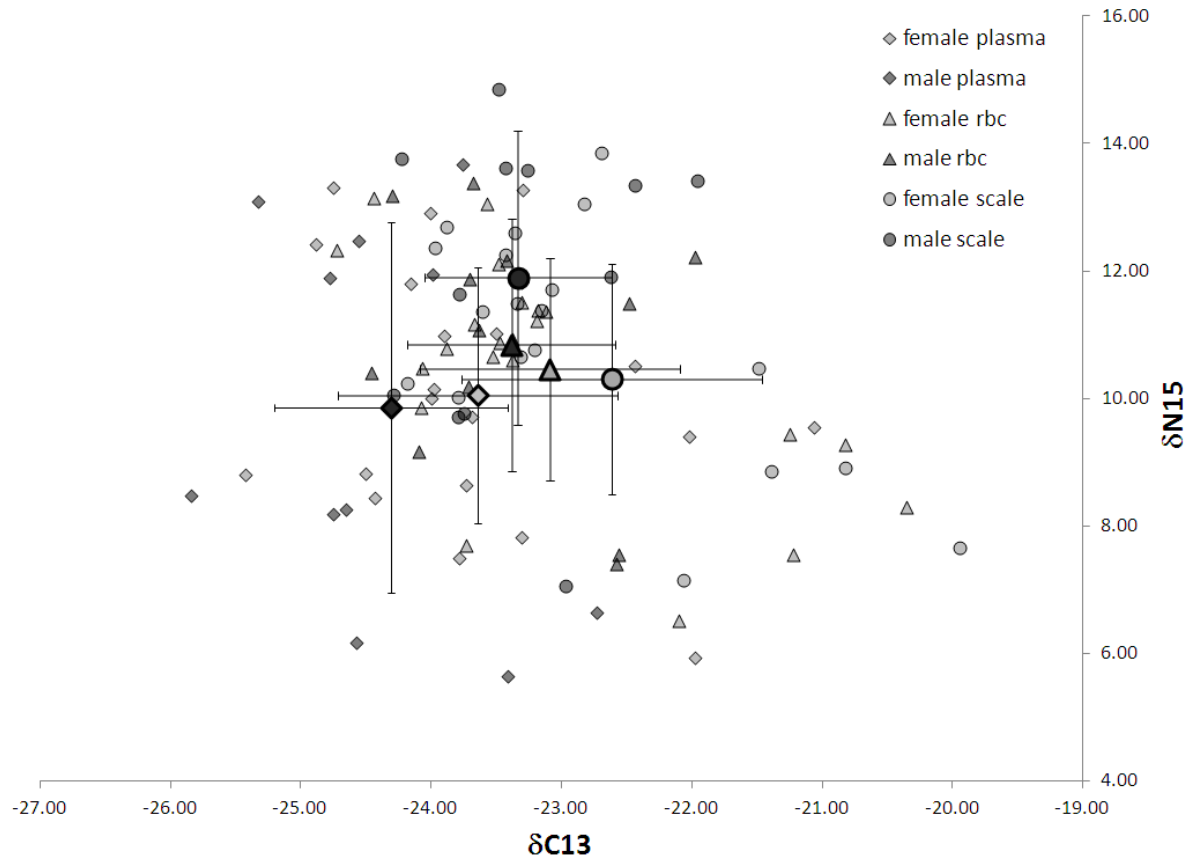
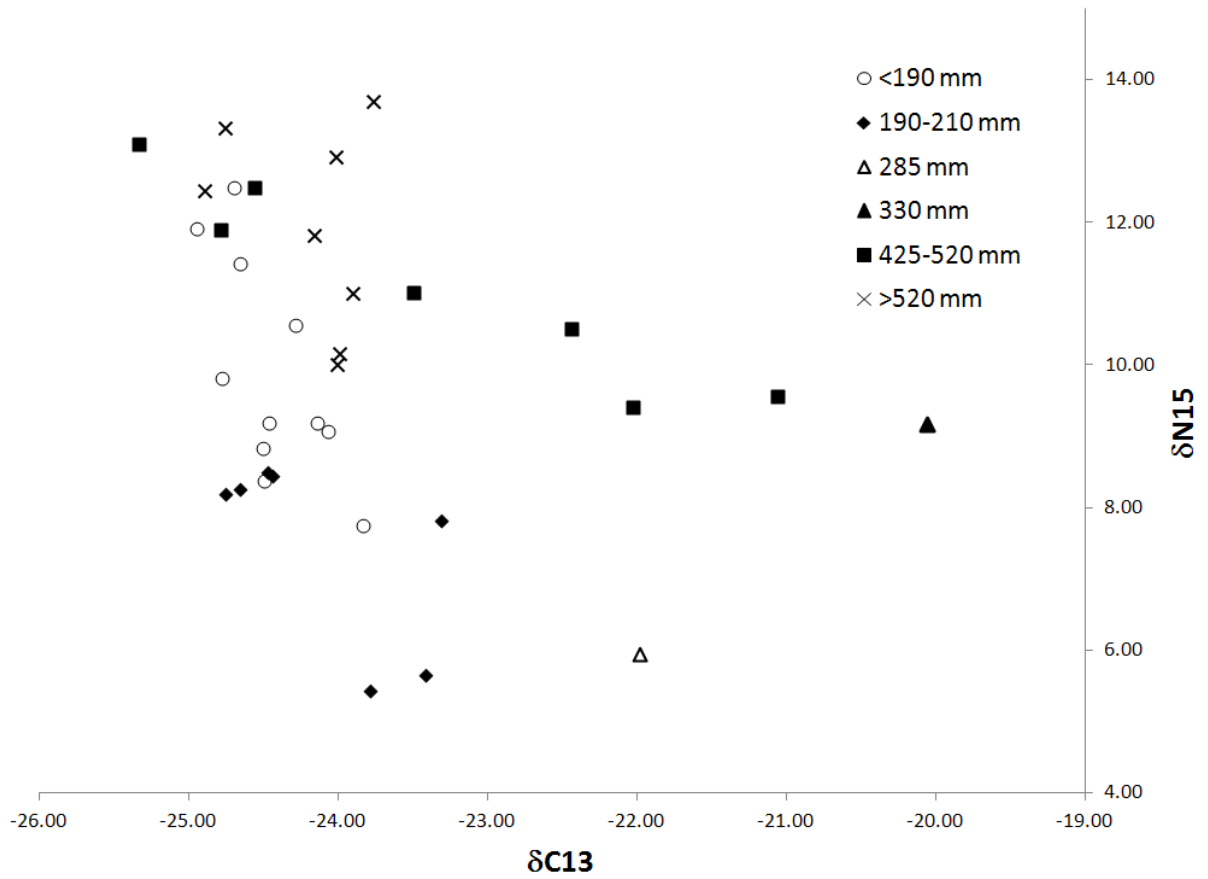


Figure 7: Stable isotope values for C^{13} and N^{15} in three tissue types from male and female Plains Hog-nosed Snakes (*Heterodon nasicus*) at Thomson Sand Prairie (Carroll Co., Illinois) in 2010. Larger symbols represent means, bars represent ± 1 standard deviation. RBC = red blood cells.



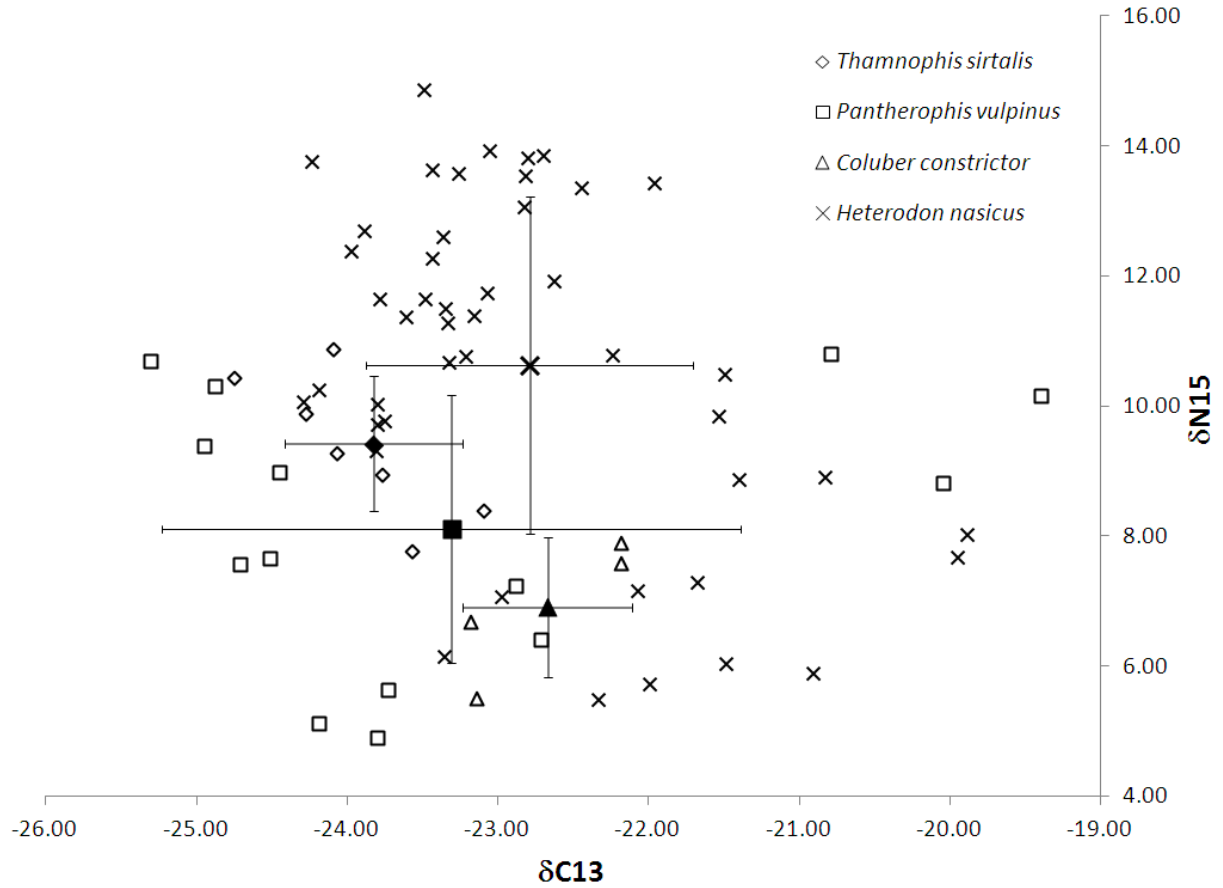


Figure 9: Mean stable isotope values for C^{13} and N^{15} in scale tissue of four species of terrestrial snake at Thomson Sand Prairie (Carroll Co., Illinois) in 2010. Symbols without error bars represent individual data points. Symbols with error bars represent means, bars represent ± 1 standard deviation.

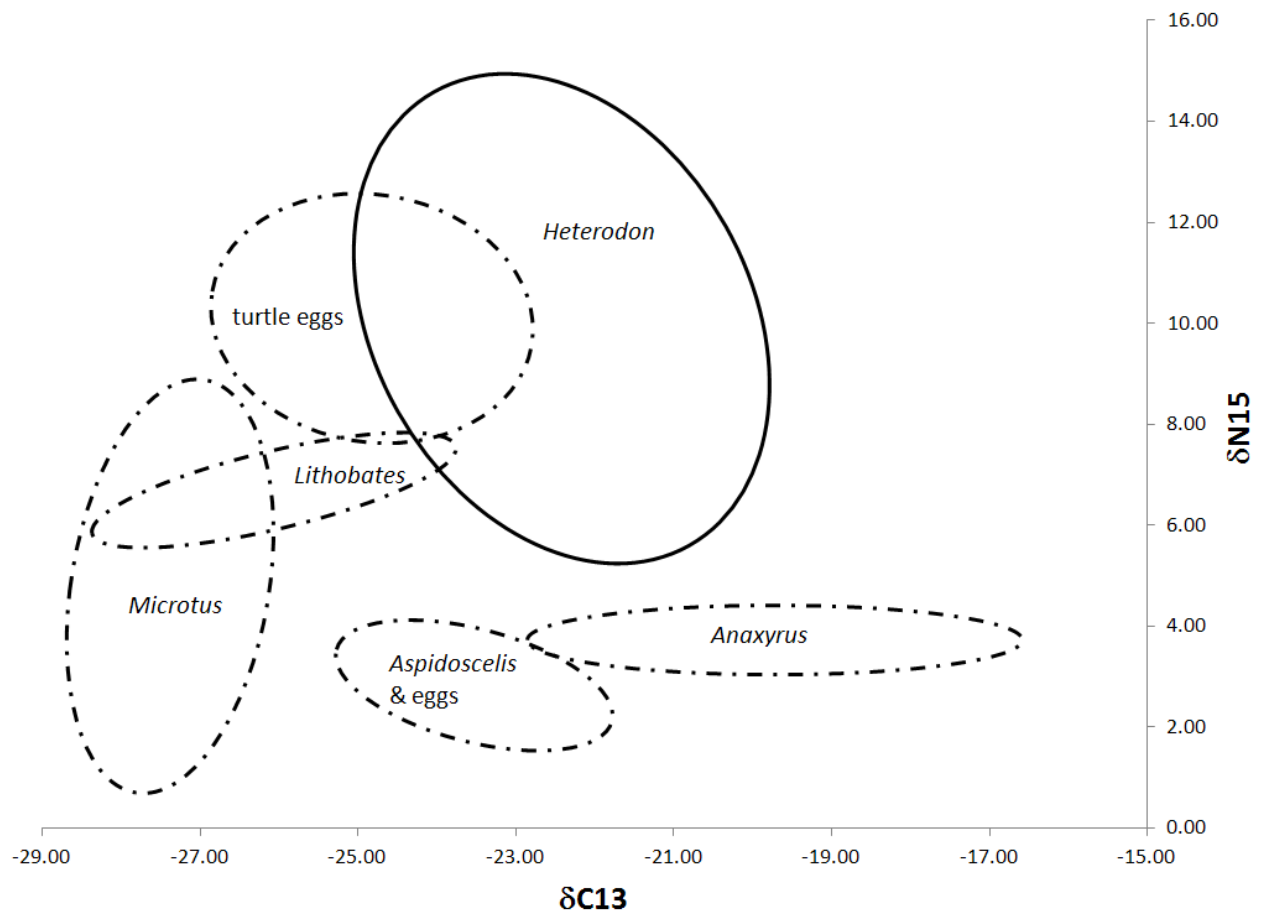


Figure 10: Structure of the predator-prey community of Thomson Sand Prairie (Carroll Co., Illinois) in 2010 as depicted in trophic space. Stable isotope values for C^{13} and N^{15} are presented for whole organisms (dotted circles) or Plains Hog-nosed Snake scale tissue (solid lines).

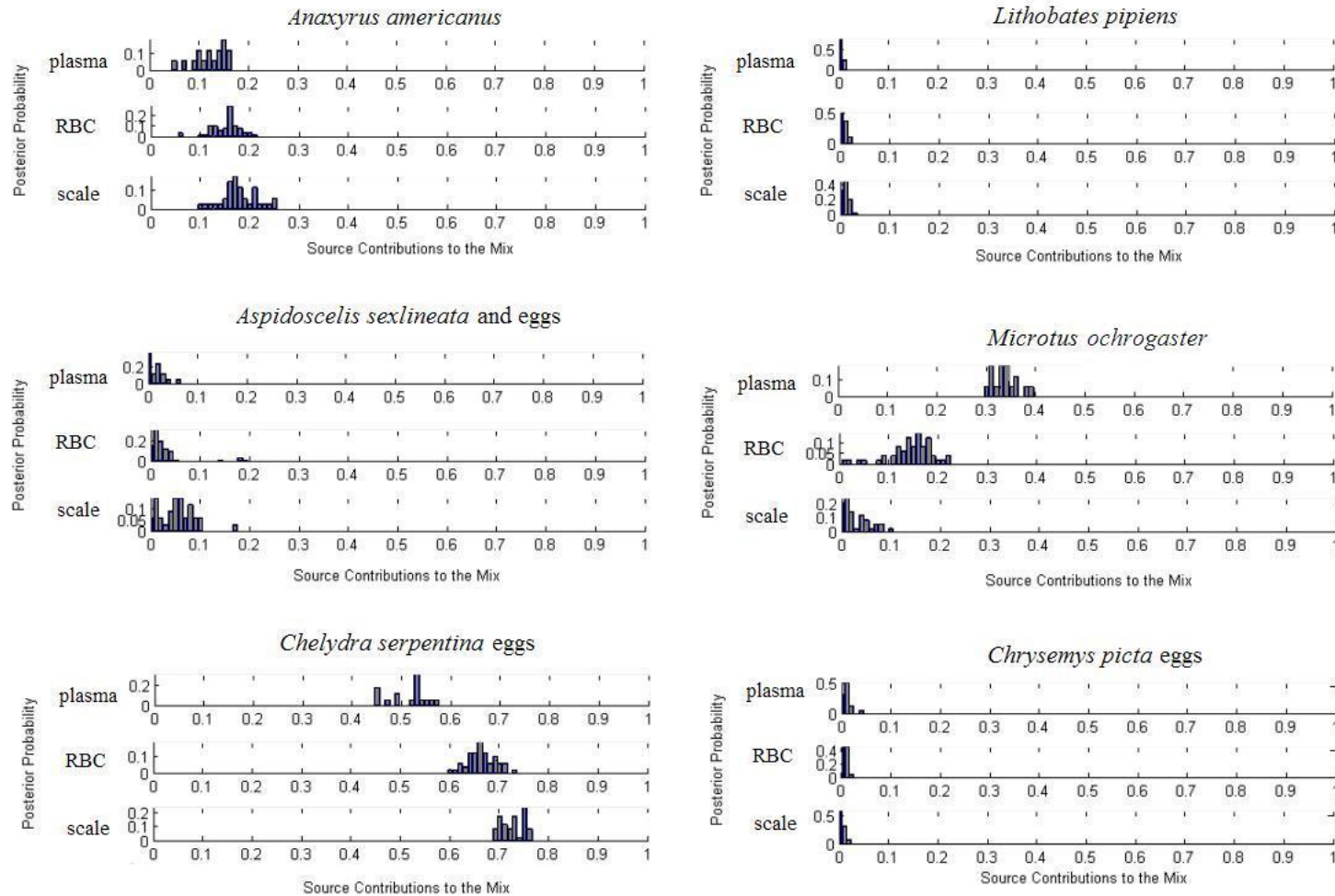


Figure 11: Posterior probability that six prey types contribute to the diets of *Heterodon nasicus* at the Thomson Sand Prairie (Carroll Co., Illinois), estimated by MixSIR using uninformative priors. Scale tissue represents the longest time scale, plasma tissue represents the shortest time scale. All individuals are included in this analysis. RBC = red blood cells.

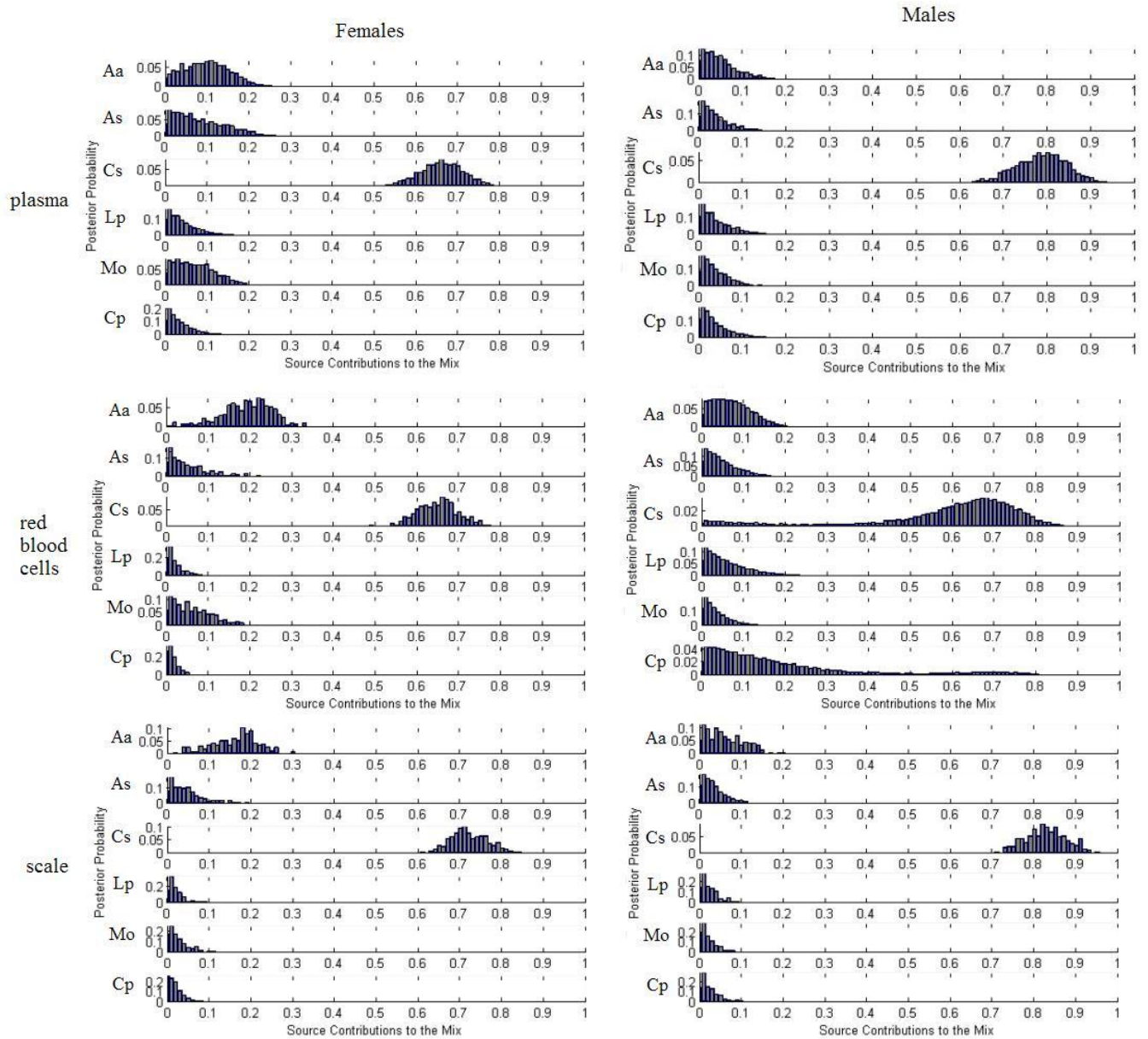


Figure 12: Posterior probability that six prey types contribute to the diets of adult *Heterodon nasicus* at the Thomson Sand Prairie (Carroll Co., Illinois), as a function of snake gender.

Probabilities were estimated by MixSIR using uninformative priors. Aa = *Anaxyrus americanus*; As = *Aspidoscelis sexlineata* + eggs; Cp = *Chrysemys picta* eggs; Cs = *Chelydra serpentina* eggs; Lp = *Lithobates pipiens*; Mo = *Microtus ochrogaster*.

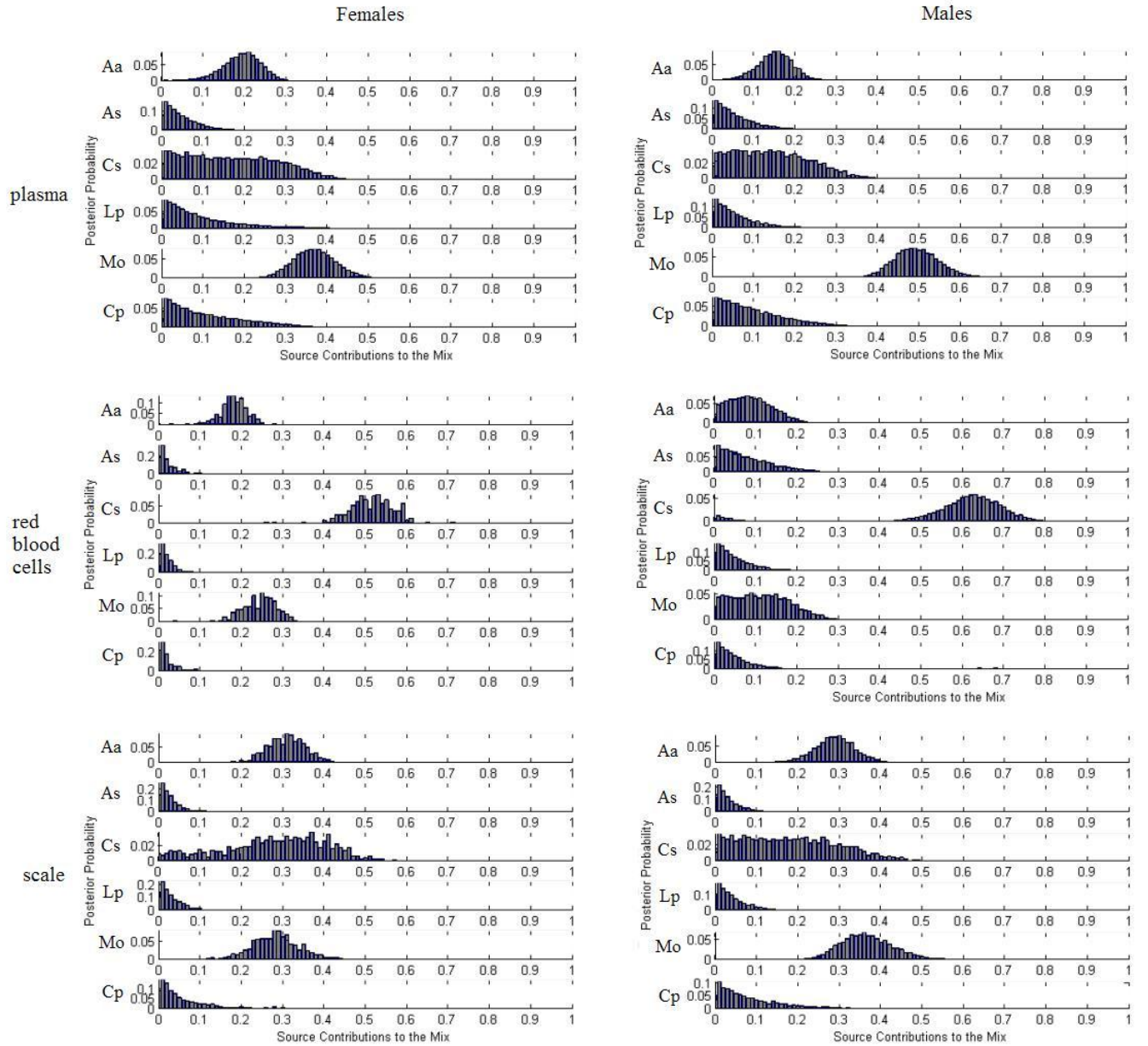


Figure 13: Posterior probability that six prey types contribute to the diets of young-of-year *Heterodon nasicus* at the Thomson Sand Prairie (Carroll Co., Illinois), as a function of snake gender. Probabilities were estimated by MixSIR using uninformative priors. Aa = *Anaxyrus americanus*; As = *Aspidoscelis sexlineata* + eggs; Cp = *Chrysemys picta* eggs; Cs = *Chelydra serpentina* eggs; Lp = *Lithobates pipiens*; Mo = *Microtus ochrogaster*.

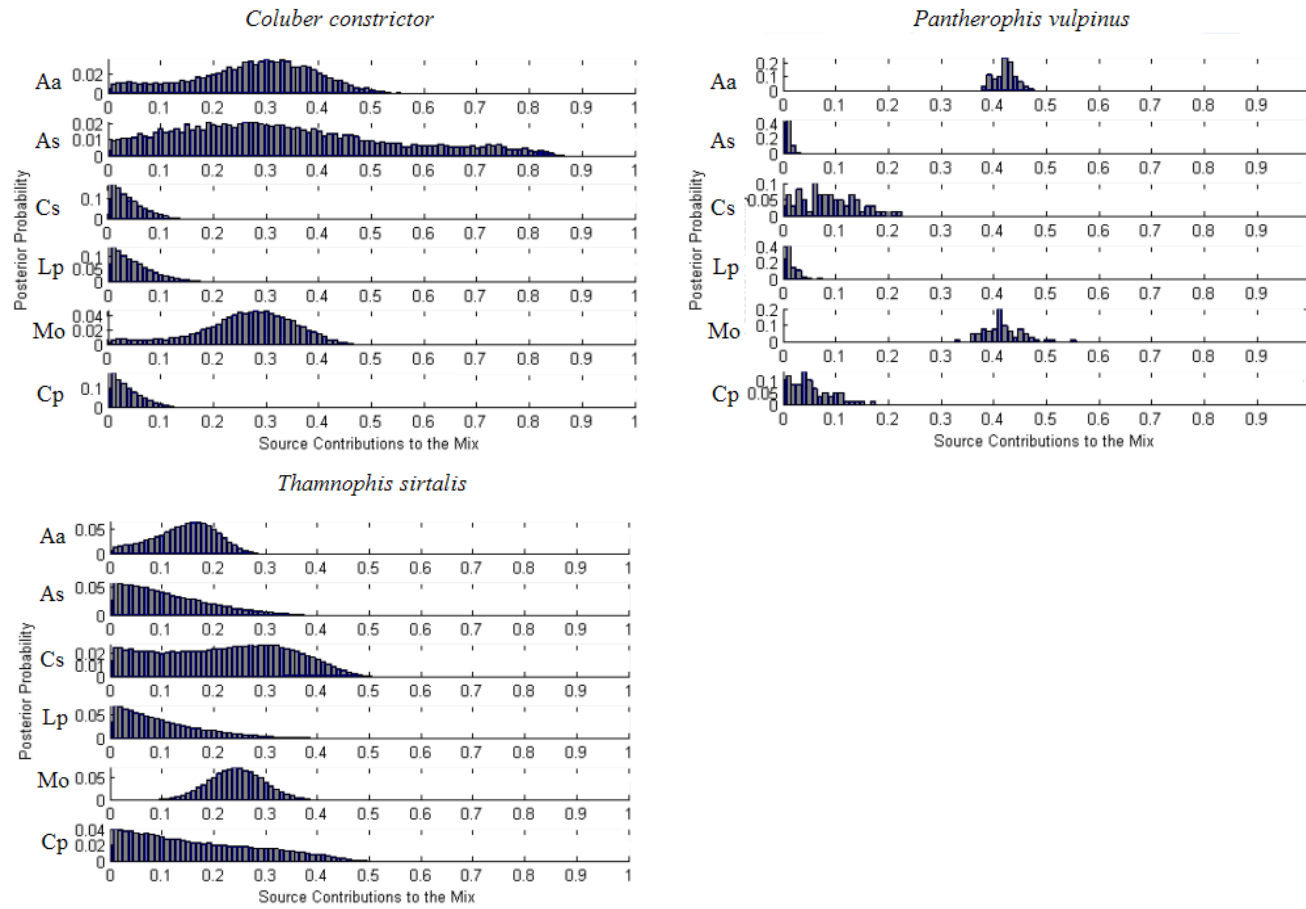


Figure 14: Posterior probability that six prey types contribute to the diets of *Coluber constrictor*, *Pantherophis vulpinus* and *Thamnophis sirtalis* at the Thomson Sand Prairie (Carroll Co., Illinois), based on scale tissue, estimated by MixSIR using uninformative priors. Aa = *Anaxyrus americanus*; As = *Aspidoscelis sexlineata* + eggs; Cp = *Chrysemys picta* eggs; Cs = *Chelydra serpentina* eggs; Lp = *Lithobates pipiens*; Mo = *Microtus ochrogaster*.

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