METROPOLITAN PITVIPERS

NOTES ON THE ECOLOGY, SYSTEMATICS AND HUSBANDRY OF TWO URBAN RATTLESNAKES

(Crotalus mitchelli pyrrhus and Crotalus tigris)

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With 2.3 million inhabitants and covering 266 square miles (688 sq. km), Phoenix, Arizona ranks as the ninth largest metropolitan area and largest desert city in the U.S. Phoenix lies at an elevation of 1205 feet (366 m) above sea level amidst the Lower Colorado subdivision of the Sonoran desert (Brown, 1982). This intermountain 'valley of the sun' is surrounded by low-elevation block-faulted mountain ranges that typify this region of the Basin and Range province (Dunbier, 1968).

Phoenix's climate is infamous, marked by extreme heat and low precipitation. Rainfall generally occurs in mid-winter and the summer monsoon season and averages just under 7 inches (171.2 mm) annually (Brown, 1994). Temperature extremes of 25 F (-4 C) on cold winter nights to 118 F (48 C) on hot summer days are not unusual. A unique aspect of this otherwise typical urban jungle is its natural features, and specifically its inhabitants. Rising 1500 ft (457 m) above the surrounding city, the Phoenix mountains are indisputably the most prominent feature of the city. Nearly 24000 acres (9713 ha) of desert mountains have remained largely undeveloped and are protected as part of the Phoenix Mountains Preserve, 8500 acres (3400 ha) of which are located in the centre of this sprawling metropolitan area. It is not surprising that three-quarters of a million humans every year traverse the fifty miles of established hiking trails on foot, horseback and mountain-bike. What may be surprising however, is despite this fervent human activity, the south-western speckled rattlesnake (*Crotalus mitchelli pyrrhus*) and tiger rattlesnake (*C. tigris*) are discretely going about their business, albeit a tenuous and delicate coexistence.

ECOLOGY

The south-western speckled rattlesnake (*Crotalus mitchelli pyrrhus*) and tiger rattlesnake (*Crotalus tigris*) occur sympatrically and syntopically (utilising near identical microhabitats) in the Phoenix Mountains Preserve and are likely to be the only Crotaline species still persisting in this geographically and genetically isolated range. Historically, the black tailed rattlesnake (*Crotalus molossus*) probably occurred within the preserve, with the western diamondback and Mojave rattlesnakes (*Crotalus atrox* and *Crotalus scutulatus*) inhabiting the surrounding outwash plains and intermountain valleys.

Superficially, *Crotalus mitchelli* and *Crotalus tigris* are morphologically similar in several ways, particularly in the Phoenix mountains. In the study area, these saxicolous (rock-dwelling) rattlesnakes are similar in size; a large Crotalus tigris is usually under 29.5 inches (750 mm) TL, while the slightly larger *Crotalus mitchelli* may reach 35.4 inches (900 mm) TL. Although in background colour and pattern, they are strikingly alike in the preserve, elsewhere throughout its range, *Crotalus mitchelli* is unrivalled in colour variation amongst the Crotalines. The typical background colour of speckled rattlesnakes in the Phoenix mountains is a rust or reddish brown, however barely five miles to the south, in the Salt River

Mountains, the very striking 'salt-and-pepper' morph is a slate to blue-grey snake with abundant snow-white flecking. In the White Tank Mountains west of Phoenix (where the tiger rattlesnake is not known to occur) *Crotalus mitchelli* is largely white with grey speckling and is frequently mistaken for an albino. Fire-red and carrot-orange *Crotalus mitchelli* can be found in the vicinity of Lake Pleasant and the Bradshaw Mountains just a few miles north west of Phoenix. Both species are considered largely desert-dwelling habitat specialists (Lowe et al., 1986), although they occur in a diverse array of biotic assemblages within their respective ranges.

Speckled and tiger rattlesnakes are almost entirely allopatric in distribution, existing sympatrically only in the Phoenix area and in the vicinity of Organ Pipe Cactus National Monument on the U.S.-Mexico border. The slightly more ecologically diverse *Crotalus mitchelli* can be found in five of the six subdivisions of Sonoran desert scrub, Mojave desert scrub, coastal scrub and chaparral, as well as the lower reaches of conifer woodlands, thorn forest and tropical deciduous forest in southern Baja.

To the east, *Crotalus tigris* occurs in four of the six Sonoran desert scrub subdivisions, as well as semidesert grassland, the lower fringes of Madrean evergreen woodland, Sinaloan thorn scrub, and possibly Sinaloan deciduous forest and Chihuahuan desert scrub. Although *Crotalus tigris* is generally considered a desert-dweller in the U.S., it has probably migrated northward from the more mesic grasslands and subtropical thorn scrub of Sonora, Mexico. Within all of these biotic communities, which are shared by several other Crotalus species, rocky micro-habitats are usually selected by the speckled and tiger rattlesnakes.

Altitudinal distribution ranges from sea level to 8000 ft (2440 m) for *Crotalus mitchelli,* and sea level to 4800 ft (1465 m) for *Crotalus tigris* (Campbell and Lamar, 1989). Speckled rattlesnakes have been observed on the highest peaks of the Phoenix mountains at 2704 ft (824 m) above sea level. Recently, a few Crotalus tigris have been observed on the western slopes of the Peloncillo mountains in extreme south eastern Arizona at the New Mexico border representing a significant range extension for the species in the U.S.

How successfully these ecologically equivalent, almost entirely allopatric rock-dwellers coexist in the Phoenix mountains is unclear and, in part, the focus of this inquiry. Niche differences between ecologically similar species are often difficult to define. Such differences are linked to the principle of competitive exclusion regarding the inability of ecological equivalents to stably coexist (Gause, 1934). Despite many similarities, it is difficult to determine to what extent Crotalus mitchelli and Crotalus tigris compete for resources, or if competition occurs at all. Although habitat, food and time are traditionally the three resource dimensions partitioned by coexisting species (Pianka, 1975), habitat has been found to be the most common form of sympatric species separation (Schoener, 1974).

Despite their physical similarities, obvious structural differences exist between these species which may allow exploitation of differing resources. The head of Crotalus tigris is small, particularly when compared to Crotalus mitchelli, however the evolution and function

of this feature is unknown. Crotalus tigris is the only rattlesnake in which the maximum head width is less than twice the size of the rattle basal segment width (Lowe, et al. 1986). Lowe et al. (1986) observed the difficult withdrawal of a dead rodent from a narrow rock crevice by Crotalus tigris and suggested that such "mouth tongs" might come in handy for a lizard eating rock-dweller.

A variety of rodent and lizard species occur in the Phoenix mountains, all of which are probably consumed by Crotalus mitchelli and Crotalus tigris. Pocket mice(Perognathus spp.), wood rats (Neotoma albigula), Harris' antelope squirrel (Ammospermophilus harrisii) and kangaroo rats (Dipodomys spp.) are all found in the preserve. The tree lizard (Urosaurus ornatus), side-blotched lizard (Uta stansburiana), zebra-tailed lizard (Callisaurus draconoides), desert spiny lizard (Sceloporus magister), western whiptail (Cnemidophorus tigris) and western chuckwalla (Sauromalus obesus) are the most frequently observed lizard species. All but adult chuckwallas are likely eaten by speckled and tiger rattlesnakes.

Within the syntopic association of Crotalus mitchelli and Crotalus tigris in the preserve, subtle micro-habitat preferences may yet be revealed. Partitioning of food resources and seasonal activity variation could enable these potential competitors to avoid direct competition and successfully coexist. Given the larger size of Crotalus mitchelli, the larger rodent species such as ground squirrels, wood rats and kangaroo rats may comprise the bulk of their diet whereas Crotalus tigris are more likely to be restricted to smaller prey items such as pocket and deer mice as well as the aforementioned lizard species.

Differences in seasonal activity between the species have been observed. Crotalus mitchelli are prominently active during the dry spring months of April and May, and are generally observed diurnally. While hiking the many arroyos and canyon trails in the early evening of these months, it would not be unusual to see three or four speckled rattlesnakes, usually active males. Whilst Crotalus tigris can be observed during this time, their activity peaks in the mid and latter part of the monsoon season, and they have even been referred to as the "September rattlesnake" (Lowe et al., 1986). At sundown after an August or September monsoon rain, you are most likely to find tiger rattlesnakes. The majority of foraging by the tiger rattlesnake occurs in late summer and fall, and may represent a subtle seasonal shift in habitat use. Prey densities are typically higher in the open, flat alluvial areas and arroyos below the steep, rocky reaches inhabited by both rattlesnake species. Foraging success may be greater as Crotalus mitchelli and Crotalus tigris seasonally shift their habitat use and move out to the flats. Both species are crepuscular or nocturnal in the hot summer months. During a recent radio-telemetry study in the Squaw Peak area of the preserve, both Crotalus mitchelli and Crotalus tigris were frequently observed resting discretely amongst the rocks and vegetation only a few feet from the trail bustling with unwary hikers.

The stability of their coexistence can, in part, be measured by evidence of recruitment. Yearling juveniles, sub-adults and young sexually mature adults (< 4 yr.) have been observed, with an approximately equal percentage of both species. Generally neonates and juveniles are exceedingly difficult to locate and quantify

in the field, however most of these observations were made as the snakes unwittingly found themselves in the backyards of humans residing along the perimeter of the preserve. If only a single species was represented by recruitment, then competition and the exclusion of a subordinate form may be indicated.

There appears to be no consensus as to how these comparable snakes came to occupy the same basin mountain ranges in the Sonoran desert. Fowlie (1965) theorised that during the latter part of the Pleistocene Crotalus tigris dispersed northward from northern Mexico to occupy the Arizona Development, partially displacing Crotalus molossus in the process. Fowlie (1965) further suggested Crotalus mitchelli migrated from the west occupying the homologous adjacent region, exerting counter pressure against further Crotalus tigris expansion. This may suggest that these morphologically similar and ecologically equivalent rattlesnakes are derived from distinctly separate lineage, and not sister species as proposed by Brattstrom (1964) and Klauber (1972). Analysis of venom proteins (Foote and MacMahon, 1977) and micro-dermatoglyphic structures (Stille, 1987) further support the likelihood of separate lineage. Finally, Fowlie (1965) proposed that, due to the "displacement principle" the more primitive forms, such as Crotalus mitchelli and Crotalus tigris were in turn displaced by invading "highly developed forms" such as Crotalus cerastes, Crotalus atrox and Crotalus scutulatus, and thus restricted to fragmented, disjunct rocky-foothill regions of the desert.

CAPTIVE MANAGEMENT

Recently, issues concerning contrasting approaches to the accommodation of captive reptiles, specifically the physical environment, were addressed (Warwick and Steedman, 1995). The virtues of naturalistic versus clinical captive environments were comparatively accessed, with a general recommendation for naturalistic environments when appropriate. Crotalus mitchelli and Crotalus tigris were housed in naturalistic environments at the Phoenix Zoo for public exhibition and interpretation, and in clinical environments for quarantine and off-exhibit holding purposes. These are common techniques employed by most zoological and academic institutions. As a result of the burgeoning herpetocultural industry in North America, clinical environments for captive reptiles are increasingly advocated, generally to maximise utility. As inherently sedentary, energy conserving creatures, rattlesnakes seem to tolerate and even thrive in a clinical environment. Providing that fundamental physiological and psychological requirements are met, (e.g. heat source for thermoregulation, adequate nutrition and cleanliness, control of stress inducing stimuli and appropriate behavioral enrichment), reproductive success and longevity can be achieved. Crotalus mitchelli has reproduced prolifically in both a naturalistically furnished public exhibit adorned with native plants, full spectrum lighting, and numerous retreats amongst granite slabs, as well as the austere confines of a 10 gallon aquarium and aspen bedding.

In the wild, speckled and tiger rattlesnakes may exhibit a moderately nervous to extremely irascible temperament, the speckled rattlesnake to a greater extent. However they differ regarding their ability to acclimate to captivity. Wild-caught Crotalus mitchelli, particularly adults, frequently (ca. 50%) adjust poorly to captive conditions and retain an

excitable, agitated demeanour. Such captives rarely feed well, or at all, even when offered a wide variety of natural prey items, and if retained in captivity, usually languish. Similarly, some captive bred offspring (even second or third generation) have difficulty recognizing and accepting food. In this author's experience, two or three neonates of each litter produced are "poor-doers", (refusing all prey items, live or pre-killed, regardless of presentation - maladaptation syndrome), and often languish despite the most tenacious efforts. This ratio may approximate numbers of behaviorally unfit wild-born snakes. A technique for inducing wild-caught rattlesnakes to feed has been employed with moderate success. Offering a dead mouse (in a secure environment) envenomated and killed by a conspecific may entice the anorectic captive to eat. Occasionally, confining a stubborn feeder in a small, dark container in close proximity to the prey item (live pinkies or fuzzies for neonates) is effective. Tiger rattlesnakes however, adapt surprisingly well to captivity. Of 18 wild-caught Crotalus tigris (neonates, sub-adults, adults), all readily accepted live or pre-killed laboratory mice within one week of capture.

Murphy and Armstrong (1978) recommended that inordinately high levels of relative humidity be avoided for captive arid-dwelling rattlesnakes, i.e. Crotalus mitchelli stephensi. Offering water once weekly overnight to both species has proven to be sufficient. Tiger rattlesnakes do however seem to respond favorably to a heavy weekly misting during the summer monsoon season (a stimulus for feeding and breeding behaviour).

Courtship and copulation has been observed from April to July for captive Crotalus mitchelli with parturition occurring in October and November (6 litters, 3 generations). Courtship for captive Crotalus tigris occurred sporadically in July and August with a single observation of copulation on 1 August. Speckled rattlesnake brood size ranged from six to eight offspring, weights ranged from 17-22 g. Details concerning reproductive strategies for Crotalus tigris remain obscure. Young may be born as early as June or as late as September. Tryon (1992) reports a single occurrence of captive reproduction at the Knoxville Zoological Gardens in 1992, and refers to a previous incident at St. Louis Zoological Park in the mid-1 970s. These appear to be the only records of the captive breeding of the tiger rattlesnake in a zoological institution.

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