# HOME RANGE, HABITAT USE, AND BEHAVIOR OF THE EASTERN DIAMONDBACK RATTLESNAKE (*CROTALUS ADAMANTEUS*) ON THE ORDWAY PRESERVE

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## ABSTRACT

The eastern diamondback rattlesnake (*Crotalus adamanteus* Beauvois) was studied by radio-telemetry from 3 September 1985 to 21 February 1989 at the Katharine Ordway Preserve/Carl S. Swisher Memorial Sanctuary, Putnam County, Florida. Five male and three female snakes were monitored for durations ranging from 33 days (11 observations) for a small female to 864 days (245 observations) for an adult male. Intervals between observations averaged 3.3 days. A total of 743 observations was used to determine home range, habitat use, movements and other behaviors for this species.

Diamondback home ranges were analyzed using the McPAAl computer program (Smithsonian Institution). Females (n=2) maintained smaller home ranges (mean = 46.5 ha) than males (n=4, mean = 84.3 ha). The ranges of both males and females overlapped, indicating that this species is not territorial. Diamondback activity patterns suggest that they occupy stable home ranges that remain similar from year to year.

Although rattlesnakes were recorded in all habitats available to them, the Swamp Forest/Mesic Hammocks and Xeric Hammocks were favored. They also utilized Wet Prairies during droughts. Eastern diamondbacks were almost entirely terrestrial, rarely climbing into trees (n=1) and infrequently going underground (n=35) during their activity season. During winter (Dec-Jan-Feb) rattlesnake movements decreased, but they remained on the surface 55.4% of the time. Burrows of armadillo (*Dasypus novemcinctus*, n=57) and gopher tortoise (*Gopherus polyphemus*, n=12), as well as root channels beneath stands of palmettos, were used as winter refugia.

Mean monthly distances traveled increased during fall (Sep-Oct-Nov), when snake movements averaged over 20 m per day. At this time males made longer moves, probably searching for breeding females, whereas females made shorter movements. Movements were always made during daylight hours.

The hunting strategy of *C. adamanteus* consisted of a sit-and-wait foraging behavior, with the main posture a tight coil from which it might ambush prey. Snakes spent anywhere from one day to almost a week coiled in the same hunting location. Necropsies of 14 rattlesnakes (from north-central Florida) that contained identifiable prey remains indicate that the cotton rat (*Sigmodon hispidus*, n=8) and the rabbit (probably *Sylvilagus floridanus*, n=5) are the numerically dominant prey; one sample included a white-footed mouse (probably *Peromyscus gossypinus*); other evidence identified the wood rat (*Neotoma floridana*) as prey for the eastern diamondback.

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## RESUMEN

Entre el 3 de septiembre de 1985 y el 21 de febrero de 1989, la serpiente de cascabel de espalda de diamante del este (*Crotalus adamanteus* Beauvois) fue estudiada usando radio telemetría en la Reserva Katharine Ordway/Carl S. Swisher Memorial Sanctuary, en el oeste del Condado de Putnam, Florida. Se monitorearon cinco serpientes machos y tres serpientes hembras por períodos que variaron entre 33 días (11 observaciones) para una serpiente hembra pequeña, hasta 864 días (245 observaciones) para un macho adulto. Los intervalos entre observaciones promediaron 3.3 días. Se utilizó un total de 743 observaciones para determinar el ámbito de hogar, uso de habitat, movimientos y otras conductas de esta especie.

Los ámbitos de hogar para esta serpiente cascabel fueron analizados usando el programa computacional McPAAL (Smithsonian Institution). Las hembras (n = 2), mantuvieron ámbitos de hogar más pequeños (promedio = 46.5 ha) que los machos (n = 4, promedio = 84.3 ha). Los rangos de serpientes machos y hembras se sobrepusieron, lo cual es indicativo de que esta especie no es territorial. Los patrones de actividad para esta serpiente cascabel sugieren que éstas ocupan ámbitos de hogar estables los cuales permanecen constantes año a año.

Aún cuando las serpientes de cascabel fueron registradas en todos los habitats disponibles para ellas, éstas prefirieron los habitats de Bosque Inundado/Bosques Altos Mésicos y Bosques Altos Xéricos. Durante sequías, también utilizaron Praderas Inundadas. Durante la temporada de actividad, estas serpientes fueron casi enteramente terrestres, rara vez subiendo a árboles (una observación), e infrequentemente sumergiéndose bajo tierra (n = 35 observaciones). Durante el invierno (dic-ene-feb), los movimientos de la serpiente cascabel disminuyeron, pero permanecieron en la superficie 55.4% del tiempo. Madrigueras de armadillo (*Dasypus novemcinctus*, n = 12), así como canales de raíces ubicados por debajo de agrupaciones de palmeras, fueron utilizados como refugios de invierno.

Las distancias promedio mensuales recorridas aumentaron durante el otoño (sep-oct-nov), cuando los movimientos de las serpientes promediaron sobre 20 m diarios. En este momento, los machos realizaron movimientos más largos probablemente en búsqueda de hembras reproductivas, mientras que las hembras realizaron movimientos más cortos. Los movimientos se realizaron sólo durante el día.

La estrategia de caza de *C. adamanteus* consistió en una conducta de sentarse a esperar, principalmente con una postura enrollada desde la cual podía sorprender a su presa. Las serpientes estuvieron entre un día hasta casi una semana enrolladas en la misma localidad de caza. Necropsias realizadas a 14 serpientes (provenientes del centro-norte de Florida), y que contenían restos de presa identificables, indican que el ratón cola de algodón (*Sigmodon hispidus*, n = 8), y el conejo ( probablemente *Sylvilagus floridanus*, n = 5) son las presas dominates numéricamente; una muestra contenía un ratón de patas blancas (probablemente *Peromyscus gossypinus*); también se identificó a la rata del bosque (*Neotoma floridana*) como presa para la serpiente cascabel.


## INTRODUCTION

The eastern diamondback rattlesnake, *Crotalus adamanteus*, is known to inhabit many Florida ecosystems, but is more often thought of as a denizen of xeric uplands (Carr 1940; Wright and Wright 1957; Klauber 1972). Here, it is often found as a burrow commensal of the gopher tortoise, *Gopherus polyphemus*. This large rattlesnake, along with other large snakes such as the eastern indigo (*Drymarchon corais couperi*), the Florida pine snake (*Pituophis melanoleucus mugitus*), and the rat snakes (*Elaphe guttata* and *Elaphe obsoleta*), probably exerts selective pressure on small mammal populations in these habitats. Little has been published about the life history of any of these reptiles or about the interactions and dynamics of this large-snake guild. Most of these species may be in need of conservation and management (Dodd 1987) yet have received little attention when wildlife-management policies are formulated.

Biological preserves may serve as last bastions for these snakes, but their home ranges are so large that small preserves are unlikely to meet the requirements

for stable populations through time (Dodd et al. 1988). The survival of these snakes will rest in the hands of preserve managers and government agencies that manage large tracts of land as wild areas become less common and as undeveloped tracts of land shrink in size. Resource managers will need information concerning home range, habitat use, movements, and denning activities in order to make effective management decisions. I conducted this study to collect information that will contribute to our knowledge of one of these important reptiles and will assist in developing management plans for conservation areas. This is the first study of free-ranging eastern diamondback rattlesnakes in Florida sandhills.

The main objectives of this study on *C. adamanteus* were: (1) to determine its home range; (2) to identify the habitats used by them in north-central Florida sandhills; (3) to delineate their overwintering and activity seasons; and (4) to determine whether unique sites are critical to them as overwintering refuges.

**Background.**– The eastern diamondback (Serpentes: Crotalidae) is the world's largest rattlesnake, averaging 130 cm in total length, with the largest reported at 244 cm (Conant and Collins 1991). It ranges along the coastal lowlands from southeastern North Carolina to eastern Louisiana, including all of Florida and its keys. Until recently, the diamondback was very common throughout most of Florida but, although it is still occasionally seen, does not appear to be as abundant. Herpetologists have noticed a decline in the numbers of large individuals (those attaining lengths of around 170 cm) over the past 20 years (S.R. Telford, Jr., and F.W. King, pers. comm.). The principal cause of their decline is habitat destruction, which results in fragmentation of populations, and highway mortality. In addition, there remains in the South, as elsewhere, a lingering prejudice against rattlesnakes which continues to lead to their destruction. This was made evident to me by the fact that a Putnam County, Florida, reptile-skin business was able to purchase over 8,000 eastern diamondback rattlesnakes that had been killed by north Florida and south Georgia residents in 1988 alone (J. A. Smith pers. comm.).

The little that has been published on the diamondback is largely anecdotal. Carr (1940) noted that the diamondback was "widely distributed; most abundant in palmetto flatwoods" and that they fed on "rats (*Sigmodon hispidus*) and mice (*Peromyscus* spp.)." Conant and Collins (1991) stated that they were "at home in the palmetto flatwoods and dry pinelands" and that they "frequently...take refuge in burrows of gopher tortoises, in holes beneath stumps, etc. Rabbits, rodents and birds are eaten." Klauber (1972) related that "it is said to live in almost any available type of habitat, except in especially wet places" and that "in most areas the Florida and eastern cottontails (*Sylvilagus f. floridanus* and *S. f. mallurus*) and the marsh rabbits (*S. p. palustris* and *S. p. paludicola)* are the mainstays of the adult diamondbacks." Allen (1961), a naturalist with probably more experience with this species than anyone, said that "it lives in all sorts of country: on the sandhills, in the "hammocks" (hardwood stands), in salt marsh, in flatwoods, and

many other situations. Favorite places include old fields, overgrown with weeds and broomsedge; the sandhills with plenty of scrubby oaks and longleaf pines; and stands of good hardwoods such as oaks, hickories, magnolia, and holly. In the hot summer it may move down into the cool, brushy tangles around the borders of ponds and lakes."

Although no field studies of this species have been published, Means (1985, 1986) outlined its natural history in two unpublished reports of his radio-telemetry study at Tall Timbers Research Station (33 km north of Tallahassee, Florida). He found that adult diamondbacks have large home ranges--up to 200 ha. Rattlesnakes at Tall Timbers are active from late March to early November and remain somewhat active on the surface throughout winter if not forced underground by cold weather. While Means observed eastern diamondbacks using gopher tortoise burrows as overwintering refuges, the snakes also used the stump holes of rotted trees or cavities in burned-out pines. Means also stated that "courtship and mating in the north-central portion of the geographic range of the eastern diamondback rattlesnake takes place between 15 August and 15 September." This also happens to be the time that female diamondbacks give birth to live young (Klauber 1972; Means 1986; Timmerman 1989).

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## METHODS AND MATERIALS

**Study Site.**– This study was conducted at the 3750 ha Katharine Ordway Preserve/Carl S. Swisher Memorial Sanctuary (hereafter referred to as the "Ordway") east of the town of Melrose in western Putnam County, Florida (lat. 29, 41'; long. 82, 00'). The Ordway consists of a series of sandy-soil habitats lying within the Trail Ridge and Interlachen Karstic Highlands geologic districts. Upland soils are coarse and well-drained, belonging to the Apopka, Candlier, and Tavares series, whereas the lower moister slopes and depressions consist of less well-drained sediments such as Myakka Fine Sand, Millhopper, and Lockloosa series (Franz unpubl. data). The elevation ranges from about 27 m to 55 m above sea level. The most common habitats include High Pine Forests and Old Fields; however, one-third of the tract is wetlands in the form of lakes, marshes, and swamps. The major connected wetland system is the Mill Creek system which flows easterly from Lake Melrose through the Ordway, filling dark-water lakes, swamps, and wet prairies before exiting the preserve near the town of Putnam Hall at the northeast corner of the property. These waters eventually make their way to the St. Johns River via Rice Creek. In addition, there are numerous isolated clear-water lakes lying in solution depressions between sand ridges. These lake basins support vegetative communities that differ from those of the connected dark-water wetland systems. The following are brief descriptions of the habitats referred to throughout the text: Lake Meadow, a grass-dominated habitat that surrounds most of the clear-water lakes; Xeric Hammock, a canopied dry forest of oaks, usually with a thick carpet of oak leaves on the forest floor; Old Fields, cleared openings, in various stages of succession, from former homesteads; High Pine Forest, better known as *sandhills*, these forests are dominated by longleaf pines and turkey oaks, with a ground cover of wiregrass; Mesic Hammock, a closed-canopied, moist forest dominated by hardwood trees such as laurel oak, pignut hickory, and sweet gum, often with a spotty understory of saw palmetto; Swamp Forest, a seasonally inundated forest of black gum, red maple, loblolly pine, and other flood-tolerant trees; and Wet Prairie, a freshwater marsh with maidencane and other grasses, and a few shrubs such as Virginia willow. For detailed descriptions of the habitats of the Ordway Preserve, consult Franz and Hall (1990).

**Radio-telemetry.**– Eastern diamondback rattlesnakes were studied by radio-telemetry from 3 September 1985 to 21 February 1989. Snakes were caught using the snake-hook and dip-net technique devised by Allen (1961). Snakes were captured as they crossed roads (n=7), in natural settings (n=4), and during controlled burns (n=2).

Miniature radio transmitters (AVM Instrument Co., LTD., Wildlife Materials, Custom Telemetry and Consulting, Inc.) broadcasting in the frequencies

of 164-166 MHz, were surgically implanted into the peritoneal cavity of the snake following the procedures outlined in Reinert and Cundall (1982). Transmitters weighed from 6 to 27 g and comprised up to 2% of the total body weight of the study animal. Transmitters measured from 30 to 70 mm and were attached to a flexible antenna measuring about 45 cm. Estimated life expectancies of these transmitters varied from 60 days to over a year.

Radio signals were received using a TR2 (Telonics) receiver. A truck with a mounted dipole antenna was driven over the roads in the area of the snake's last location. The search was continued until the transmission of the snake's radio was intercepted. The specific location was then determined by proceeding on foot with a hand-held, 2-element, H-antenna. Occasionally, snakes retreated to inaccessible areas of the preserve that necessitated search by canoe or airplane.

Snakes were located one to five times per week. Visits were restricted to less than five minutes during which time data were recorded. Care was taken to minimize disturbance to the area in order to insure that the reptile's behavior was unaffected. For each location, the following data were noted: date, time (eastern standard time), habitat type, whether snake was visible to observer, snake's position in vertical strata (in tree, on ground, below ground), snake's physical position or activity (coiled, loosely coiled, crawling), identity of burrows used (gopher tortoise, armadillo, or other), if snake rattled during visit, if snake's eyes appeared opaque (before shedding), if snake had recently shed, and if snake had recently fed (lump visible in body).

Each location was given a unique number and recorded on a blue survey flag placed as close as possible (within 1 m) to the snake's position. Attached to the flag wire was a small aluminum tag (Al Tag) bearing the location number and the snake's code name. The metal tags served as permanent markers in the event that snakes returned to these sites. Each location was marked on a Florida Department of Transportation aerial photograph (scale: 1"= 200'). These photographs are of such resolution that individual trees, roads, and other features could be used to establish the snake's location.

**Necropsies.**– To gain information on food habits, necropsies were performed on 22 *C. adamanteus*. These specimens were obtained as road kills from north-central Florida counties (Alachua, Bradford, Gilchrist, Marion, Putnam, and Union).

**Data Analysis.**– Home ranges were measured using the McPAAl (Smithsonian Institution) computer program. Minimum convex polygons, concave polygons, and 95% ellipses were calculated for snakes with a record of 50 or more observations. Movements between consecutive locations were measured as straight-line distances directly from the aerial photographs. Activity seasons and overwintering periods were subjectively assigned to each snake based on daily activities and general movement patterns.

Habitats were determined by a visual inspection of the environment and by reference to Ordway vegetation maps (Franz unpubl. data; Myers 1984). Since it was often difficult to distinguish between Mesic Hammocks and Swamp Forests on aerial photographs, these forests were combined for habitat analysis. Swamps were not inundated with water and looked superficially like extensions of the mesic forests for most of the study. Habitat utilization-availability analyses included a Pearson's Chi-square goodness-of-fit test and a Bonferroni simultaneous-confidence-intervals test. Both tests made comparisons between expected use and observed use for all habitats within each snake's range. The Pearson's Chi-square test was used to determine if snakes used the various habitats in proportion to their availability. Selection for or against certain habitats was evaluated using Bonferroni confidence intervals (Byers et al. 1984).

For the habitat analyses, the cumulative number of days that the snake was seen to occupy a certain area was used instead of the actual number of field observations. In other words, if the snake was visited on Monday, Wednesday, and Friday and had occupied the same site or a closely knit constellation of sites in a particular habitat, then five observation-days were scored for that particular habitat even though the snake had not been observed using it every day of that period. For an ambush hunter like the diamondback, the inclusion of these intermediate periods should more accurately reflect the proportions of time spent in various habitats. I decided on this procedure when preliminary 24-hour tracking bouts showed me that these snakes maintain their ambush positions hour after hour, and sometimes day after day. Additionally, for those times when snakes were not observed daily, the number of observation-days assigned to habitat-use were split evenly between two habitats when a snake moved from one habitat to another.

## RESULTS AND DISCUSSION

Eight eastern diamondback rattlesnakes (five males and three females) were radio-tracked for varying periods of time. An additional five snakes were implanted, but they did not contribute sufficient data, due mostly to transmitter failure. Home ranges were plotted for six snakes (four males and two females) tracked eight months or more. Ordway rattlesnakes were radio-tracked for durations ranging from 33 days (11 observations) for a small female, to 864 days (245 observations) for an adult male. Intervals between observations ranged from 1.5 hours to 20 days (mean = 3.3 days). The longer intervals were caused by snakes that retreated to inaccessible areas of the preserve.

**Home Range.**– Six snakes were radio-tracked for a minimum of eight months, including Male Number 3 (M3), who was followed for two consecutive

Table 1. Summary of radio-telemetry data for eight eastern diamondback rattlesnakes at the Ordway Preserve, Putnam County, Florida. SVL = snout-vent length.

| Snake | Sex | SVL (cm) | Period Observed | Duration (Days) | No. Obs. | No. Sites | Home Ranges (ha) | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Convex Polygon | Concave Polygon | 95% Ellipse |
| M1 | M | 132.5 | 09/03/85-06/03/86 | 273 | 82 | 28 | 53.80 | 31.73 | 165.62 |
| M2 | M | 75.8 | 09/18/85-05/11/86 | 234 | 71 | 28 | 100.19 | 67.95 | 259.16 |
| M3 | M | 126.5 | 09/06/86-01/16/89 | 864 | 245 | 131 | | | *** |
| | | | calendar yr 1987 | | | | 75.69 | 46.16 | 170.12 |
| | | | calendar yr 1988 | | | | 166.15 | 69.26 | 341.66 |
| M4 | M | 136.0 | 04/07/87-01/13/88 | 281 | 105 | 54 | 25.70 | 0.00 | 40.64 |
| F1 | F | 132.5 | 08/18/87-08/27/88 | 375 | 126 | 58 | 39.58 | 0.00 | 68.46 |
| F2 | F | 126.4 | 07/20/87-05/28/88 | 312 | 74 | 41 | 53.47 | 30.53 | 109.11 |
| F3 | F | 85.0 | 12/14/88-01/16/89 | 33 | 11 | 4 | ---- | ---- | ---- |
| M5 | M | 129.0 | 11/25/88-02/21/89 | 89 | 29 | 5 | ---- | ---- | ---- |

*** Yearly ranges are shown below.

years. The mean home range for these diamondbacks (minimum convex polygon) was 73.5 ha (Table 1). Females averaged 46.5 ha, while males averaged 84.3 ha. M3 exhibited a different-sized home range between years. In 1987 it used 75.7 ha and in 1988 it used 166.2 ha, encompassing much of the previous year's range. The smallest home range (25.7 ha) belonged to M4.

It has been suggested that seasonal changes in habitat productivity may result in changes in home range size (Harestad and Bunnell 1979). If this is true, it is likely that the home range of *C. adamanteus* changes over time, fluctuating as the home range of M3 did from 1987 to 1988. *Sigmodon hispidus*, one of the diamondback's principal prey, becomes exceedingly rare during droughts (J.F. Eisenberg unpubl. data), which are fairly common in north-central Florida.. Therefore, snakes may have to increase their home range size to find sufficient food. The Ordway has experienced reduced rainfall over the past several years (Franz and Dodd unpubl. data), but the historic rain patterns are unknown.

Average home ranges for Ordway diamondbacks are somewhat smaller than the ranges for Tall Timbers rattlesnakes (Means 1985). Tall Timbers females ranged over about 80 ha compared to about 50 ha for Ordway females and males used up to 200 ha compared to about 85 ha for Ordway males. However, we did not use identical home-range analytical techniques (Means pers. comm.), so it is not surprising that the values are somewhat different. Alternate methods of home-range estimation can provide different results, even in the same data set. As an example, using the minimum convex polygon method, which I have reported here, the home range of M1 is about 54 ha. However, using the 95% ellipse method, the same plotted coordinates yield a home range of 166 ha, an increase of 307% (see Table 1). Based on other radio-telemetry studies at the Ordway Preserve, Florida pine snakes (Franz 1984), eastern indigos, and eastern coachwhips (Dodd et al. 1988) have ranges that are similar in size to that of the eastern diamondback.

Some rattlesnake home ranges overlapped (Fig. 1). In addition to the radio-tagged snakes whose ranges are outlined in this figure, eight other rattlesnakes were seen by field personnel in the areas used by telemetered snakes. This evidence suggests that diamondback rattlesnakes are not territorial.

**Density.**– No authoritative density estimates of *C. adamanteus* in native habitats has ever been made. Nevertheless, a crude density estimate is possible based on the observations of Ordway field personnel over the course of this study. A total of ten adult rattlesnakes were observed in the area just northeast of Ross Lake. Applying the average home range from this study, and drawing circular ranges around their locations, it can be estimated that this aggregation was occupying roughly 100 ha. We know that this sample does not represent 0% of the population in that 100 ha, nor does it likely represent 100% of the population. If we assume that it accounted for about 50%, we can derive a population of 20 adult snakes. This results in a crude density estimate of 1 rattlesnake per 5 ha. If we

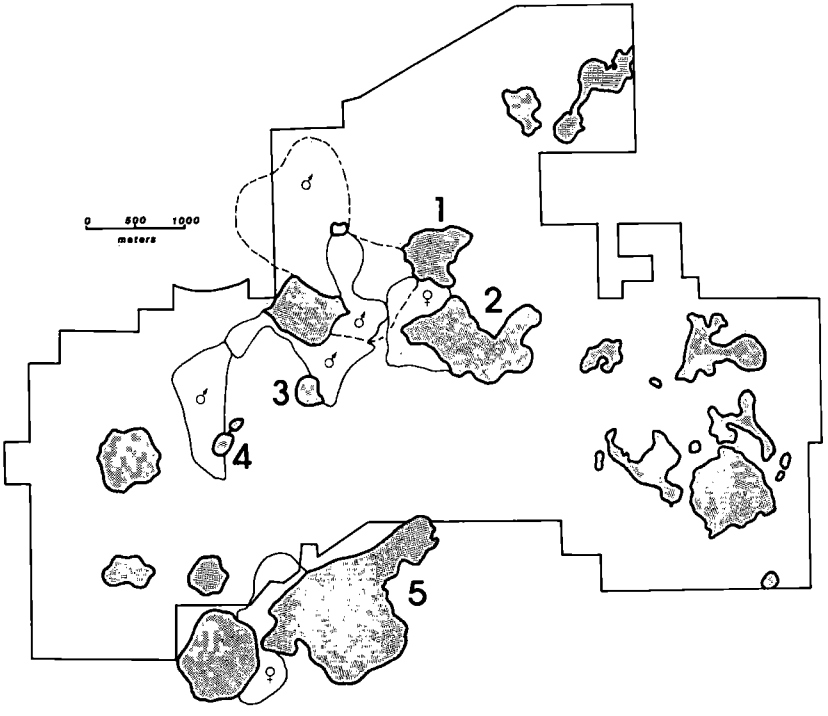


FIGURE 1.–Home ranges of six eastern diamondback rattlesnakes at the Ordway Preserve, Putnam Co., FL. The home range represented by the dashed line corresponds to M3, who was tracked for 864 days. The symbol within each range represents the sex of the snake. 1 = Ashley Lake; 2 = Goose Lake; 3 = McCloud Lake; 4 = Anderson Cue Lake; 5 = Long Pond.

continue with this line of reasoning, and make the bold assumption that all upland habitats (2500 ha) at the Ordway are similarly blessed with diamondbacks, there are approximately 500 adult *C. adamanteus* residing on the preserve. Means estimated that there were roughly 49 adult diamondbacks at the 400-ha Tall Timbers study area, or a density of 1 rattlesnake per 8 ha (Means 1986).

**Seasonal Activity Patterns.**– I have been able to identify, from the literature, four seasonal activity patterns for snakes. The first pattern consists of movements by temperate snakes to and from a hibernaculum. Most snakes of cold environs, including all the temperate species of rattlesnakes in the genera *Crotalus* and *Sistrurus*, aggregate in ancestral dens during the winter, either because reliable denning areas are a scarce resource or because the possibility of dehydration is lessened from the large mass of bodies in close proximity (Costanzo 1989). In the spring, snakes bask at the den; mating may take place there before they leave for their summer ranges. These ranges may be nearby or may lie several kilometers away (Landreth 1973). The snakes forage during the summer and return to the same, or a nearby, den in the fall. Home ranges of these snakes consist of denning

areas, summer ranges, and the corridors connecting them. They may be consistent from year to year (Parker and Brown 1980).

The second pattern involves movements by snakes that use shifting activity centers. These snakes continually move over new areas and do not return to familiar ones--at least not during the same season. Franz (1988) believes this to be the pattern shown by rat snakes (*Elaphe obsoleta quadrivittata* and *E. guttata*) in north-central Florida. He characterized the annual home range of these species as consisting of "winter use areas" and "summer use areas" connected by "migratory corridors," and never saw rat snakes returning to or from these two seasonal ranges. Several snakes made long distance moves (up to 17 km) along the migratory corridors. Franz reasons that the abundance of winter den sites available to the rat snakes in the mild Florida winter, and an inconsistent prey base (see previous *Sigmodon* discussion), may account for this pattern.

The same pattern of shifting activity centers has been reported for certain Wisconsin populations of the water snake (*Nerodia sipedon*) during their summer season (Tiebout and Carey 1987), but its pattern is different from that of Florida rat snakes. Every fall these temperate-zone water snakes find their way back to the same unique hibernaculum. Therefore, although they may forage in shifting ranges, their annual course describes a loop or a circle, since they return to the original starting point--the winter den site.

The fourth snake-movement pattern is the one exhibited by *C. adamanteus*. In this pattern, snakes have a fairly stable home range and use the same general area from year to year. There are no discernable migratory routes or summer and winter ranges. The snakes make somewhat circuitous routes through their environment often passing over the same terrain at different times of year.

Employing this movement strategy, the snake becomes thoroughly familiar with its environment, gaining knowledge through experience. Theoretically, the success of a sit-and-wait predator should depend on the identification of prime ambush sites. The diamondback knows its environment well enough to return to specific favorable locations within its home range. Rattlesnakes were observed returning to previously used sites on 35 occasions during the course of this study. For example, M3 used the hollow bottom of a large sweet gum (*Liquidambar styraciflua*) snag on the northeast shore of Ross Lake on three separate occasions--August 1987, September 1987, and May 1988.

The activity pattern shown by *C. adamanteus* is similar to that of Ordway populations of the Florida pine snake (Franz 1984), the eastern coachwhip and the eastern indigo (Dodd pers. comm.). These snakes have stable home ranges and may use certain locations more than once during the year.

**Food Habits.**– None of the snakes was observed capturing or consuming prey during the study. Several searches for snake scats at locations recently occupied by study animals were unsuccessful. Rattlesnakes were detected with stomach bulges (an indication of feeding) only twice (out of 490 observations), but because snakes

were hidden from view on 120 occasions during the summer, a few large meals probably went undetected. Food items consisting of anything smaller than rabbits and large squirrels are difficult to discern in a coiled diamondback.

Four species of mammals were identified as prey items in the gastro-intestinal tracts of 14 eastern diamondback rattlesnakes from north-central Florida (Table 2). The dominant prey were rabbits (*Sylvilagus* sp.) and cotton rats (*Sigmodon hispidus*). Three prey remains were of unidentified mammals. Two of the identifiable remains were taken from Ordway rattlesnakes; remains of a cotton mouse (*Peromyscus gossypinus*) were taken from the small intestine of M4. Cotton mice occur on the preserve in densities of 4-20/ha (Brand 1987) making it one of the more common prey available to *C. adamanteus*. A rabbit was taken from the stomach of a captured male that died during an October cold spell at the Ordway pole barn.

These two prey remains would be the extent of our knowledge of Ordway rattlesnake food habits if it had not been for the circumstances surrounding the disappearance of a radio-collared wood rat (*Neotoma floridana*) on 9 April 1989. An adult female, one of the subjects of a study on this species (HaySmith 1991), could not be located for several weeks. Then, a signal was discovered transmitting from a position near the prairie edge on the western side of Goose Lake. The radio collar was now in the stomach of an adult eastern diamondback rattlesnake coiled in a sawgrass (*Cladium jamaicense*) stand.

A radiograph was taken to locate the position of the wood rat's transmitter in the snake's GI tract when it was discovered that the snake was carrying two radio transmitters, one from the ingested wood rat, and one which I had implanted on 5 April 1986 (Fig. 2). This was M1, my first study subject, who I had lost in the Mill Creek Swamp when his radio failed in May 1986; he had been living in the wild for three years since last seen. His location in the saw grass was about 200 m from where the snake had originally been captured on 27 August 1985. Wood rats occur in densities of 1-3/ha on the preserve (Eisenberg unpubl. data) and represent a fairly large meal for a rattlesnake (about 130 g). A number of Ordway rattlesnake locations in mesic-hammock palmettos were very close to wood rat nests (HaySmith et al. in prep.). In addition to the rodents and rabbits reported here, diamondbacks also are known to occasionally feed on such birds as towhee, bobwhite, king rail, and wild turkey (Klauber 1972).

**Habitat Use.**– Locations of five Ordway rattlesnakes were used in the analysis of habitat selection. Female Number 2 (F2) did not have equal access to several of the habitats being considered and was eliminated from the analysis (Byers et al. 1984). Habitat-use data for one rattlesnake (M3) tracked for two consecutive years were treated separately, yielding a sample size of six.

Rattlesnakes preferred the Swamp Forest/Mesic Hammocks, Xeric Hammocks, and Wet Prairies to other habitats within the Ordway (Table 3). Based on utilization-availability analysis, rattlesnakes used these habitats, which

Table 2. Prey identified from scat and stomach samples of eastern diamondback rattlesnakes from north-central Florida, showing sex and SVL (=snout-vent length; in cm) of snake and location in GI tract[a].

| Prey | County | Sex | SVL | Date | Location | Notes on prey |
|---|---|---|---|---|---|---|
| *Sylvilagus* sp. | Alachua | F | 136.5 | 04 Oct 1987 | 3 | ----- |
| *Sylvilagus* sp. | Putnam[b] | M | 146.0 | 26 Sep 1987 | 1,2,3 | ----- |
| *Sylvilagus* sp. | Alachua | M | 108.0 | 10 Sep 1987 | 1,2 | Teeth present, probably a juvenile |
| *Sylvilagus* sp. | Alachua | M | 129.0 | Aug-Sep 1987 | 1,2;3 | Infant |
| *Sylvilagus* sp. | Alachua | M | 102.0 | Nov 1988 | 1,2,3 | ----- |
| *Neotoma floridana*[c] | Putnam[b] | M | 132.5 | 09 Apr 1989 | --- | Adult female, 218g |
| *Sigmodon hispidus* | Gilchrist | M | 132.0 | 20 Oct 1987 | --- | Sample included a tooth |
| *Sigmodon hispidus* | ----- | -- | ---- | ----- | --- | ----- |
| *Sigmodon hispidus* | Bradford | M | 110.0 | 29 Aug 1988 | 3 | Sample incuded a tooth |
| *Sigmodon hispidus* | Alachua | M | 120.0 | 29 Sep 1986 | 1,2 | Sample contained a jaw |
| *Sigmodon hispidus* | Alachua | M | 135.0 | Sep 1986 | 3 | ----- |
| *Sigmodon hispidus** | Marion | F | 104.0 | Sep 1987 | 3 | Foot bones in sample |
| *Sigmodon hispidus** | Alachua | M | 102.5 | 07 Oct 1987 | 3 | Foot bones in sample |
| *Sigmodon hispidus** | Union | M | 78.5 | 29 Aug 1988 | 1,2,3 | ----- |
| *Peromyscus* sp.** | Putnam[d] | M | 135.0 | 13 Jan 1988 | 2 | ----- |
| Cricetid rodent | Putnam | F | 116.0 | 09 Oct 1987 | --- | Hair sample degraded |
| Unidentified mammal | ------ | M | ----- | ----- | --- | No diagnostic hairs |
| Unidentified mammal | Putnam | M | 48.0 | 06 Oct 1987 | 3 | No diagnostic hairs |
| Unidentified mammal | Putnam[b] | M | 56.2 | Jun 1988 | Scat | No diagnostic hairs |

[a] 1=Stomach, 2=Small intestine, 3=Large intestine
[b] From Ordway Preserve
[c] Radio-collared woodrat from Ordway Preserve
[d] M4 from this study; dissected after found dead
* Indicates "probable" prey identification
** This is almost certainly *P. gossypinus* based on habitat

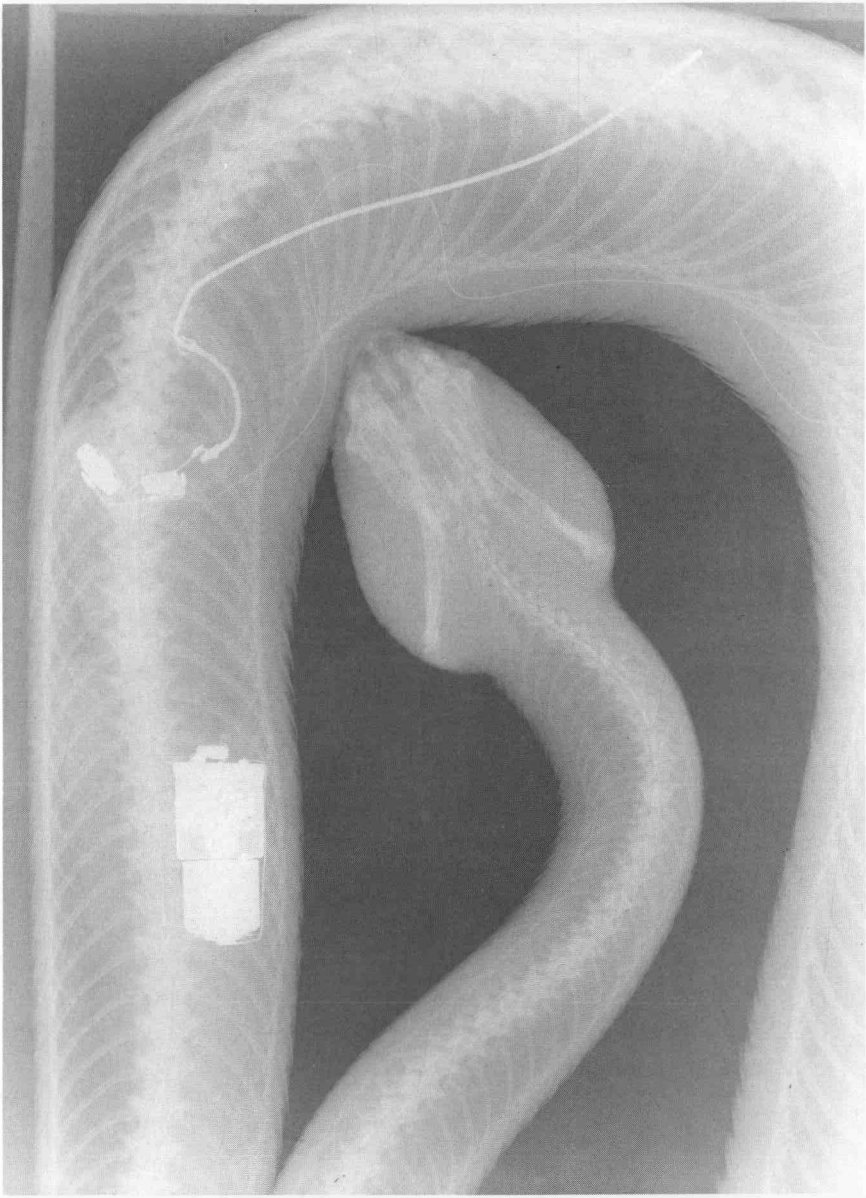

FIGURE 2.--Radiograph of an eastern diamondback rattlesnake (M1) that has ingested a radio-collared wood rat. The uppermost transmitter is the wood rat's radio collar. The lower transmitter (cylindrical) was implanted into the snake during this study.

Table 3. Habitat use by eastern diamondback rattlesnakes at the Ordway Preserve, Putnam County, Florida.

| Habitat[1] | Total Area (ha) | Proportion Available | Observed use (No. Sites) | No. Observation-Days[2] | Actual Proportion Used | Bonferroni Intervals | Selection[3] |
|---|---|---|---|---|---|---|---|
| OF | 71 | 0.170 | 6 | 7 | 0.004 | $0 \leq p \leq 0.009$ | – |
| XH | 52 | 0.125 | 56 | 299 | 0.203 | $0.176 \leq p \leq 0.231$ | + |
| HP | 186 | 0.446 | 33 | 174 | 0.118 | $0.096 \leq p \leq 0.140$ | – |
| S/MH | 73 | 0.175 | 164 | 742 | 0.572 | $0.539 \leq p \leq 0.606$ | + |
| WP | 30 | 0.072 | 22 | 148 | 0.100 | $0.080 \leq p \leq 0.121$ | + |
| LM | 5 | 0.012 | 0 | 0 | 0.000 | ———— | –[4] |

[1]Habitats are Old Field (OF), High Pine (HP), Xeric Hammock (XH), Swamp Forest-Mesic Hammock (S/MH), Wet Prairie (WP) and Lake Meadow (LM).
[2]See section on data analysis for explanation of "observation-days."
[3]Selection indicates whether the expected use fell within (0), below (–), or above (+) the confidence interval (alpha= 0.10) of the observed use derived from the Bonferonni z statistic (Byers et al. 1984).
[4]Confidence interval could not be calculated but avoidance indicated.

constituted about 37% of the total area available, more than would be expected if movements within habitats were completely random (1189 observation-days, 242 sites). Snakes used the Old Fields and High Pine Forests, which constituted more than 60% of the area available, less than would be expected (181 observation-days, 39 sites). The Lake Meadow, which constituted less than 1% of the area available, also was used less than would be expected (0 observations).

The Wet Prairie, a habitat with a wide array of possible prey species, was used by two radio-tagged rattlesnakes during drought periods in 1988. On 20 April, F1 entered the prairie on the west side of Goose Lake and remained in that habitat until about 25 August. During this period she used over 15 locations and traveled over an area approximately 20 ha in size. On about 1 August, M3 entered the same prairie and remained until about 26 August. At this time rain caused a rise in water levels, which presumably drove the snakes from the marshes. The use of the Wet Prairie by these snakes demonstrate the diamondback's ability to exploit an ephemeral resource. Except under drought conditions, the wet prairie is inundated by water and is unsuitable to diamondback foraging since these snakes do not hunt in watery or wet conditions. They are adept swimmers, however (Carr 1940).

Of other large Ordway snakes, only the two rat snakes are reported to use the mesic forests to the same extent that *C. adamanteus* used such habitats. However, these species use the habitat in a somewhat different fashion. The yellow rat snake is decidedly arboreal, favoring the holes of live oak trees in which to hide. The corn snake is more terrestrial and semi-fossorial, choosing mole (*Scalopus aquaticus*) runways and other mammal burrows (Franz 1988). Since the three species of snakes feed on similar prey (small mammals and birds) and use similar habitats, it is interesting to note that their niches do not greatly overlap. This apparent resource partitioning would tend to reduce competition among the snakes for food.

**Activity Seasons.**-- Unlike some snakes we studied at the Ordway, *C. adamanteus* did not seek refuge for long periods during the winter. It may seek shelter in some burrow for a few days or, rarely, a few weeks, but will remain on the surface as long as the weather is not too inclement. For this reason, it is often difficult to say exactly when winter begins and ends for the eastern diamondback rattlesnake. Means (1985) characterized the winter behavior of *C. adamanteus* as a "picture of restless inactivity." It appears that this species takes advantage of every opportunity to remain on the surface.

The earliest date I believe snakes began overwintering at the Ordway was 27 November, and the latest was 30 December; both animals were adult females. The earliest date for the resumption of summer activity patterns was 11 March, and the latest was 10 April; both were adult males. The winter season for eastern diamondbacks at the Ordway is thus roughly December through February. Snakes move very little, if any, during this period, but are quite vagile during the

"summer," from March to November. Means (1985) recorded the activity seasons of Tall Timbers diamondbacks as late March to early November, which is just slightly shorter than the activity period on the Ordway Preserve.

**Movements.**– Diamondbacks traveled farther during the months of September, October and November than any other period, averaging over 20 m per day (Table 4). During winter (December, January, and February) they moved less than 10 m per day. Snakes were included in the sample pool for a particular month only if they had been tracked for at least 20 days during that month. Although a small sample size precludes statistical analysis of intrasexual movement patterns, it appears that females may move nearly as far as some males, but use their home ranges more intensely, making more localized moves (Table 5). The movements of five Ordway rattlesnakes are depicted in Figures 3-7.

Means (1985) believes that increased snake movements in the fall, observed in both our studies, relate to three separate diamondback behaviors. The first is the fall mating behavior, during which time males make long moves searching for prospective mates. Next, an increase in movements related to foraging efforts is noticed, Means reasons, because of high mammal and bird populations due to recruitment by young of the year. Finally, the onset of cold weather stimulates snakes to search for suitable wintering grounds. We must await further studies to discover whether his interpretation of these seasonal movements is correct.

Snakes were observed crawling on 40 occasions. The majority of these observations were made between 0600 and 1800 hours (Table 6). Eastern diamondbacks move during the day and are only rarely seen traveling at night. Nevertheless, Ditmars (1936) believed that in South Carolina, "their tracks across

Table 4. Mean monthly distances traveled by eastern diamondback rattlesnakes at the Ordway Preserve, Putnam County, Florida. Samples include only those individuals tracked 20+ days during the month.

| Month | Sample Size | Range (m) | Average Distance Moved Per Day (m) |
|---|---|---|---|
| January | 5 | 0.0 - 15.4 | 4.5 |
| February | 7 | 0.0 - 4.5 | 4.2 |
| March | 5 | 1.1 - 32.6 | 17.5 |
| April | 6 | 3.9 - 26.7 | 12.3 |
| May | 6 | 0.6 - 52.3 | 21.4 |
| June | 4 | 8.7 - 19.5 | 13.1 |
| July | 4 | 10.5 - 26.9 | 18.6 |
| August | 4 | 8.8 - 23.1 | 15.2 |
| September | 6 | 12.0 - 36.7 | 24.9 |
| October | 7 | 2.9 - 45.5 | 22.2 |
| November | 7 | 4.4 - 34.2 | 28.3 |
| December | 7 | 0.06 - 19.5 | 9.1 |

Table 5. Distances traveled by eastern diamondback rattlesnakes at the Ordway Preserve, Putnam County, Florida.

| Total Distance (m) | Snake | Duration Tracked (days) | No. Obs. | Interval Between Obs. (days) | Distance Per Obs. (m) | Distance Per Day (m) |
|---|---|---|---|---|---|---|
| 3,409 | M1 | 273 | 82 | 3.3 | 41.6 | 12.5 |
| 5,697 | M2 | 234 | 71 | 3.3 | 80.2 | 24.3 |
| 22,420 | M3 | 864 | 245 | 3.5 | 91.5 | 25.9 |
| 3,816 | M4 | 281 | 105 | 2.7 | 36.3 | 13.6 |
| 5,664 | F1 | 375 | 126 | 2.9 | 45.0 | 15.1 |
| 5,184 | F2 | 312 | 74 | 4.2 | 70.1 | 16.6 |
| 554 | F3 | 33 | 11 | 3.0 | 50.4 | 16.8 |
| 649 | M5 | 89 | 29 | 3.1 | 22.4 | 7.3 |

Table 6. Activities of eight eastern diamondback rattlesnakes at the Ordway Preserve, Putnam County, Florida. Numbers in parentheses represent percentages of observations for that particular time interval.

| Hours | No. Obs. | Coiled | Loose | Crawling | Snake Not Visible |
|---|---|---|---|---|---|
| 0600-1200 | 449 | 217 (75.1) | 47 (16.3) | 25 (8.6) | 160 |
| 1201-1800 | 240 | 129 (75.9) | 27 (15.9) | 14 (8.2) | 70 |
| 1801-2400 | 44 | 21 (84.0) | 3 (12.0) | 1 (4.0) | 19 |
| 2401-0559 | 10 | 6 (100.0) | 0 (0.0) | 0 (0.0) | 4 |
| Totals | 743 | 373 (76.1) | 77 (15.7) | 40 (8.2) | 253 |

the sandy roads were frequently seen, and always demonstrating their prowlings to be at night," and Ernst (1992) reported that "many are run over by autos at night." I can find no evidence in my study, or elsewhere, to support these claims; no rattlesnakes in the present study were observed traveling after sundown. However, one diamondback rattlesnake was seen crawling at the Ordway in September 1983 at about 2200 hrs at the Smith Lake house (Franz pers. comm.).

Because of their diurnal movement pattern, and because diamondbacks eat diurnal mammals such as rabbits and squirrels, Means (1985) classifies the

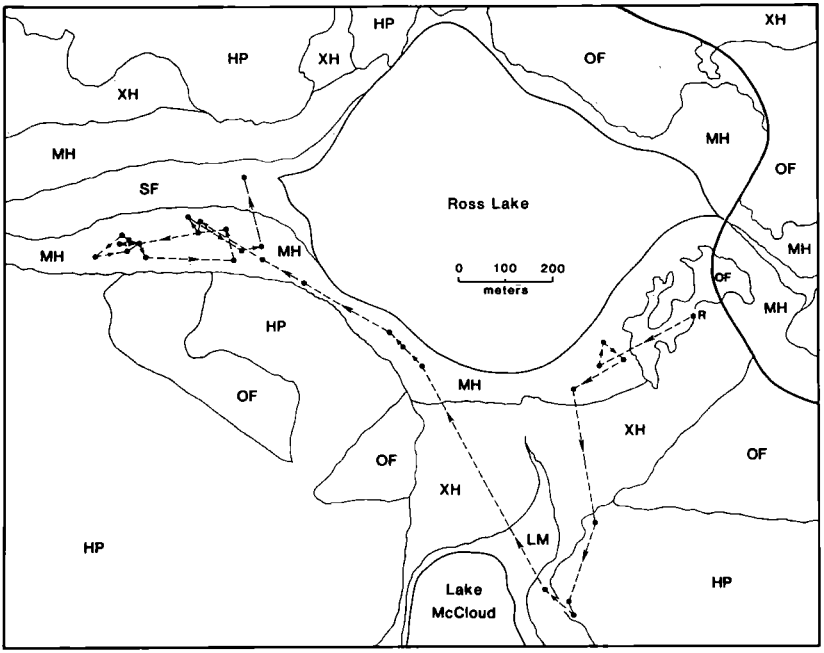


FIGURE 3.--Movements of a male eastern diamondback rattlesnake (M1) at the Ordway Preserve, Putnam Co., FL. R indicates point of capture and release. OF=old field. XH=xeric hammock. HP=high pine forest (sandhill). MH=mesic hammock. SF=swamp forest. WP=wet prairie. LM=lake meadow. Bold lines denote sand roads.

diamondback as a diurnal predator. I prefer to think of this rattlesnake as holotemporal. This is a term originated by Means and used by Cook (1983) to describe the activity patterns of the cottonmouth (*Agkistrodon piscivorous*) another Florida crotalid. Although eastern diamondbacks eat diurnal prey, they also takes nocturnal animals, such as wood rats and cotton mice. When located at night, diamondbacks were always noted in the same hunting postures as they were during daylight hours, indicating that they are ready to catch prey both day and night. Because they move between ambush sites mostly during the daylight hours, I suggest that they are more commonly nocturnal feeders.

Theoretically, a predator relying on crypsis to capture crepuscular and nocturnal prey must be in position long before it hopes to ambush its victim, therefore it should change to a new location only during the time of day when these prey would be less likely to move--during the morning hours. A predator that feeds solely on active diurnal prey should change ambush positions more often at night, before the next sunrise.

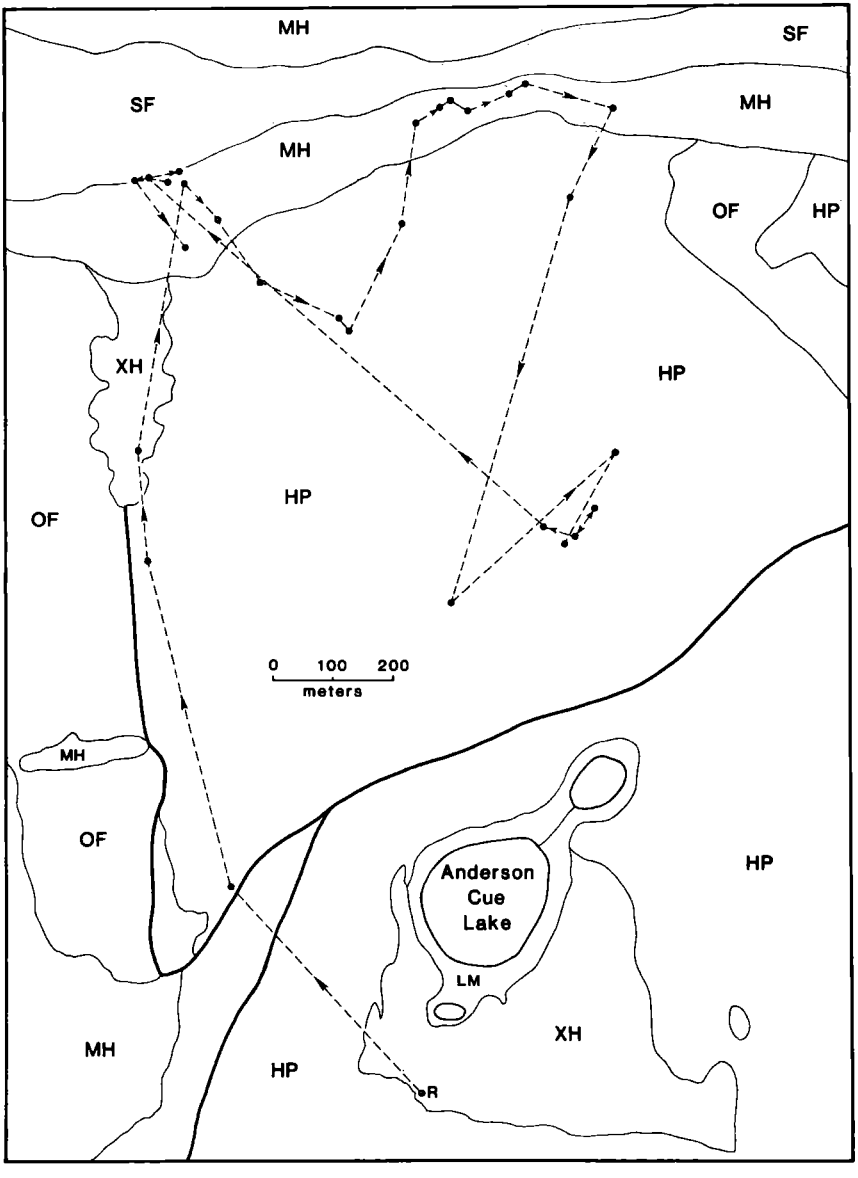


FIGURE 4. Movements of a male eastern diamondback rattlesnake (M2) at the Ordway Preserve, Putnam Co., FL. R indicates point of capture and release. OF=old field. XH=xeric hammock. HP=high pine forest (sandhill). MH=mesic hammock. SF=swamp forest. WP=wet prairie. LM=lake meadow. Bold lines denote sand roads.

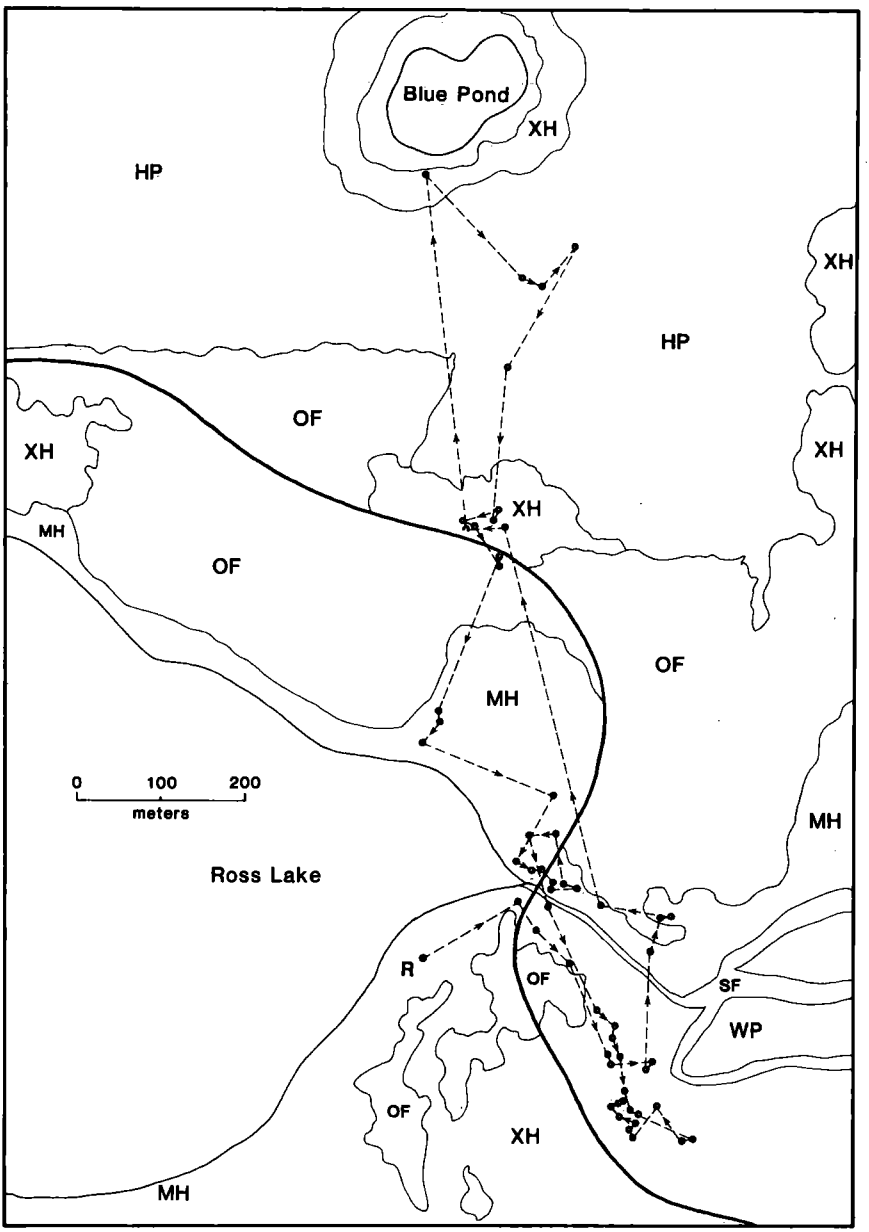


FIGURE 5.--Movements of a male eastern diamondback rattlesnake (M4) at the Ordway Preserve, Putnam Co., FL. R indicates point of capture and release. OF=old field. XH=xeric hammock. HP=high pine forest (sandhill). MH=mesic hammock. SF=swamp forest. WP=wet prairie. LM=lake meadow. Bold lines denote sand roads.

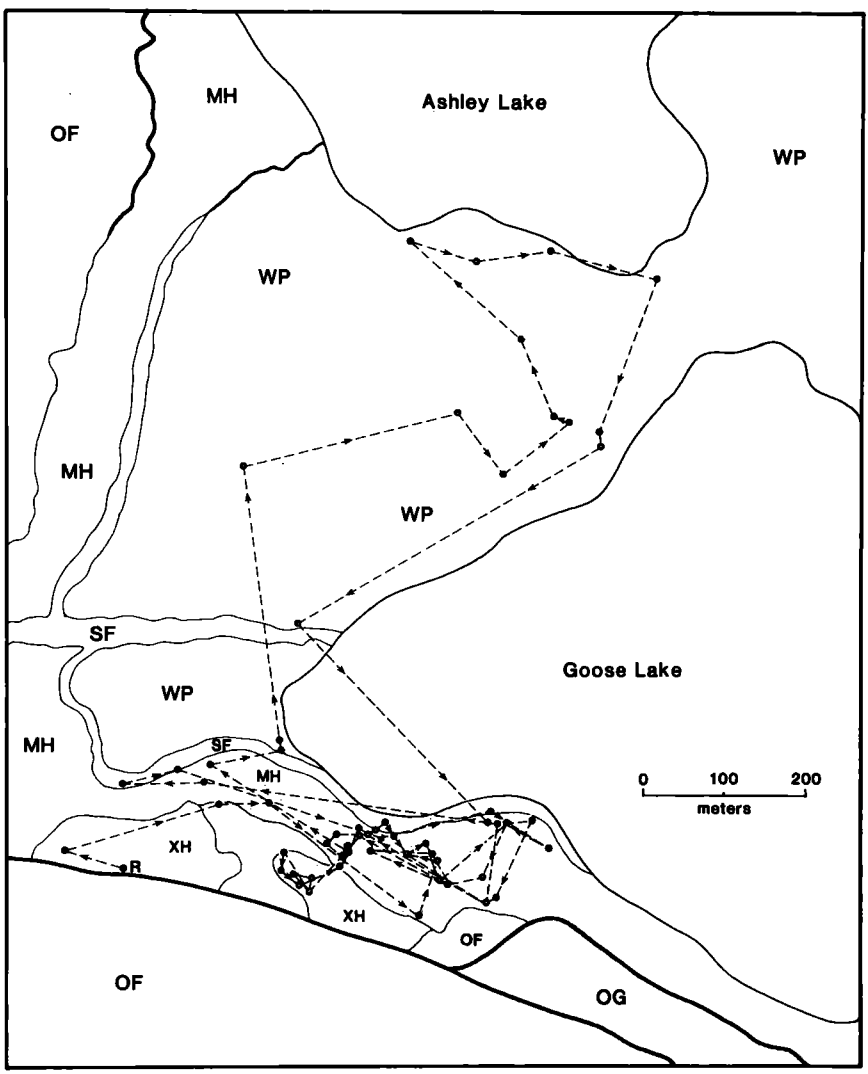


FIGURE 6.--Movements of a female eastern diamondback rattlesnake (F1) at the Ordway Preserve, Putnam Co., FL. R indicates point of capture and release. OF=old field. XH=xeric hammock. HP=high pine forest (sandhill). MH=mesic hammock. SF=swamp forest. WP=wet prairie. LM=lake meadow. Bold lines denote sand roads.

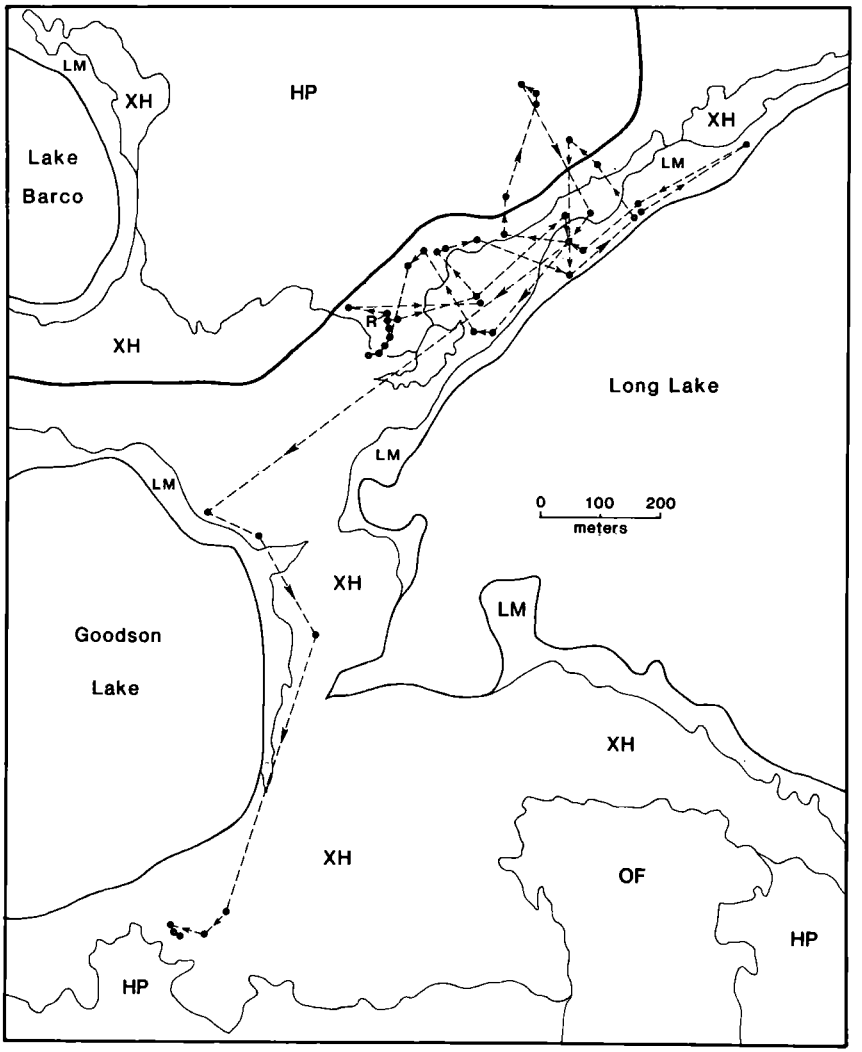


FIGURE 7.–Movements of a female eastern diamondback rattlesnake (F2) at the Ordway Preserve, Putnam Co., FL. R indicates point of capture and release. OF=old field. XH=xeric hammock. HP=high pine forest (sandhill). MH=mesic hammock. SF=swamp forest. WP=wet prairie. LM=lake meadow. Bold lines denote sand roads.

**Behavior.**– Eastern diamondbacks were usually seen tightly coiled (373 obs., 76.1% of obs.) in a position from which they could ambush prey. They spent anywhere from one day to a week coiled in the same position. The snakes were seen in a loosely coiled position in 77 cases (15.7% of obs., Table 6). The function of this "loose" position is unknown, although Martin (1987) thought that these configurations were related to thermoregulatory behavior. Outside of the winter season, Ordway diamondbacks seem to spend little or no effort at thermoregulating as far as I can determine. In this respect, the species also is similar to the cottonmouth (Cook 1983).

Snakes were almost entirely terrestrial, spending almost no time above the surface of the ground, and spending little time below the surface (Table 7). The only observation of the diamondback's climbing ability was made on 6 Oct 1985 at 0913 hrs when M2 was seen about 1 m off the ground, coiled in a leaning turkey oak tree in High Pine Forest. The ambient air temperature was 19° C and the snake's core body temperature was 16° C. Perhaps the snake was attempting to thermoregulate by positioning itself in the direct sun. In general, the eastern diamondback rattlesnake is a very poor climber, rarely getting off the ground more than a meter. This is borne out by this study and by the observations of numerous colleagues. It is difficult to accept the observation of Rutledge (1936), who claimed to have seen an adult diamondback 15 feet high in a tree, and another in the nest of a woodpecker after it had eaten the resident bird and several eggs. In addition, although we know that any rattlesnake may occasionally climb into a low tree or bush, the statement by Ernst (1992) that the diamondback's "activity is not restricted to ground level" is too strong. *C. adamanteus* rarely climbs for any reason.

During the summer, snakes were seen on the surface 91.8% of the time (403 obs.). They were observed using burrows or other refuges below the surface on only 35 occasions (8.0 %). In winter, burrow use was more common, yet diamondbacks sought refuge below ground only 44.6 % of the time (95 obs.). In addition, they were occasionally seen above ground during weather so cool that it was uncomfortable to the human researchers accustomed to Ordway summers.

As an extreme example of this behavior, F1 spent the night of 26 January 1988 coiled on the forest floor in a mesic hammock near Goose Lake when the minimum temperature recorded in a xeric hammock 1.5 km away was -2° C. Although it is likely that the vegetation of a mesic hammock would ameliorate conditions by a degree or two, this would still be one of the lowest reported voluntary temperatures tolerated by any species of snake, including *Vipera berus*, a snake that ranges slightly above the Arctic circle (Lillywhite 1987).

Means (1985) observed the same behavior by Tall Timbers rattlesnakes in the winter. He reported that rattlesnakes there became so frost-bitten by rapidly moving cold fronts that they were forced to retreat to an underground refugium for

Table 7. Arboreal, terrestrial, and fossorial habitat use by eight eastern diamondback rattlesnakes at the Ordway Preserve, Putnam County, Florida. Numbers in parentheses represent percentages of the observations in that season.

| | Arboreal[1] | Terrestrial[2] | Fossorial[3] | Unknown[4] |
|---|---|---|---|---|
| "Winter" | | | | |
| December-February | 0 | 112 | 95 | 11 |
| | (0.0) | (55.4) | (44.6) | |
| "Summer" | | | | |
| March-November | 1 | 403 | 35 | 85 |
| | (0.2) | (91.8) | (8.0) | |

[1] In tree or bush
[2] On surface of ground
[3] In burrow or hole below the ground
[4] Snake was not visible due to thick vegetation--it could not be determined whether snake was on surface or below ground.

2 to 4 weeks. Klauber (1972) reported several instances when temperate-zone rattlesnakes were killed by early cold snaps as the snakes tried to make their way to dens.

**Winter Habitats and Den Sites.**– Snakes used Mesic Hammocks, Xeric Hammocks, High Pine forests, and Lake Meadows as overwintering habitats. Old Fields, Swamp Forests, and Wet Prairies were not used. Of the 76 observations of burrow use, 94% of which were made in the winter (December through February), only 12 were gopher tortoise burrows. Four records were of unidentified holes, and 57 were identified as dens of the nine-banded armadillo (*Dasypus novemcinctus*) although it should be noted that this animal often commandeers and reshapes old *Gopherus* holes. Means observed that his study animals used gopher tortoise burrows, stump holes, or some other reliable shelter during winter. Ordway rattlesnakes often used dilapidated holes as a base of operations and were often visible within a meter of the burrow mouth. The cooler weather at Tall Timbers probably dictates that rattlesnakes choose good den sites that will be reliable during a frost. Ordway diamondbacks should be able to use less-protected den sites because of the slightly milder winters here.

Snakes always used more than one winter site during this study. In a few cases, movements between these winter locations included changes in habitat. For example, M3 began the winter of 1986-87 in a Mesic Hammock. But, on 7 January he moved to a Xeric Hammock, and used four different sites within this vegetation zone. Then, on 21 January, he moved back to a Mesic Hammock and disappeared into a palmetto thicket, probably taking refuge in channels among the root systems. He did not reappear above-ground until 16 March. This same snake

was the only individual observed over three winters. M3 used the same overwintering areas in 1987-88 and 1988-89, which was different from the habitat he had used in the winter of 1986-87.

**Ecdysis.**– Ten sloughing events were recorded during the course of the study. If all sloughings were successfully recorded, which is not certain since rattle segments were not color-coded during this study, the interval between events averaged 246.1 days (1.5 sloughings per snake per year). Klauber (1972) reported that a captive *C. adamanteus* at the San Diego Zoo shed an average of 2.1 times per year over a nine-year period, however, he was uncertain as to how captivity affects shedding frequency in snakes. Diamondbacks were observed in the "opaque" stage of ecdysis an average of 18.2 days (n=9).

**Defensive Behavior.**– Much has been written about the impressive defensive display of the eastern diamondback rattlesnake. Ditmars (1936) had this to say: "Most formidable of the North American poisonous snakes and ranking in size with the largest of the tropical venomous serpents of both the New and the Old World, this huge rattlesnake with its bright and symmetrical markings is a beautiful and a terrible creature. Ever bold and alert, retaining its wild nature when captive, there is awe-inspiring grandeur about the coil of this reptile: the glittering black eyes, the slowly waving tongue, and the incessant rasping note of the rattle. All dignity, the diamond-back scorns to flee when surprised. His neighbor, the cane-brake rattler, may retreat in good order, rattling as he goes, but retreating nevertheless; with this reptile of the hummocks it is different. The vibration of a step throws the creature upon guard. Taking a deep inhalation, the snake inflates the rough, scaly body to the tune of a low, rushing sound of air. Shifting the coils to uncover the rattle, this is 'sprung' with the abruptness of an electric bell. There is no hysterical striking, but careful watching, and if the opportunity to effect a blow is presented, the result may be mortal."

Conant and Collins (1991) wrote that the diamondback was "an ominously impressive snake to meet in the field; suddenly finding yourself in close proximity to the compact coils, broad head, and loud buzzing rattle is almost certain to raise the hair on the nape of your neck."

In fact, the defensive behavior and subsequent reactions of *C. adamanteus* to an immediate threat vary widely, from a seemingly unconcerned immobility to an impressive, animated display, such as has been described above. Carr (1940) noted that "there seems to be great individual variation in disposition; on a few occasions I have heard diamond-backs rattle in apparent rage at my presence when they were concealed in palmettos twenty or thirty feet away. Much more often, however, they permit one to approach within two or three feet before becoming agitated. I have stepped directly over two which showed no signs of resentment, and I once had the unsettling experience of placing my foot squarely upon a six-foot individual coiled neatly at the mouth of a gopher hole in thick broom-sedge, mashing its head into

the sand. Apparently the only annoyance which this indignity caused the snake accrued from the mouth-full of sand which it got, for it never sounded its rattle and made no attempt to strike, but merely gaped and twisted its jaws."

As long ago as the late 1700's, Bartram recognized that, more often than not, the diamondback was a "wonderful creature" that is "never known to strike until he is first assaulted or fears himself in danger" (Bartram 1928). In only 9 of my 743 visits to diamondback locations was the rattling behavior elicited. In 6 cases the snake was in open terrain, crawling or stretched out, and in 2 cases the snake was in the opaque stage of ecdysis, a situation which tends to make many species nervous (pers. observ.). In no case did any of the snakes make an attempt to strike or bite me while I was tracking them to their locations. Occasionally, due to carelessness on my part, I stepped very close to, or over the top of, coiled diamondbacks, affording them ample provocation to strike in self-defense.

Such passive behavior seems to be typical today, but it should be recognized that intense selection has probably been at work on the rattlesnake's more aggressive nature by humans. An easily agitated diamondback, quick to sound its rattle, may be perfectly adapted for living peacefully with some of the large, slow-moving, hoofed mammals of the Pleistocene age, but it is not adapted for living in harmony with humans in the 20th century.

**Mortality.**-- Two radio-tagged snakes died during the study. At 1050 on 13 Jan 1988 I tracked M4 to his winter den site at an armadillo burrow in a small palmetto thicket near Goose Lake. The snake was found dead, about 3 m from the burrow, lying on its back. The anterior portion of the head was battered and both functional fangs were missing. One small hole had been made through the dorsum of the head--the rest of the body was not damaged. The right fang, with part of the maxillary bone, lay close to the head. After an investigation of the corpse and its vicinity, I concluded that the snake had been killed by an enemy that does not eat snakes, a white-tailed deer (*Odocoileus virginianus*). Deer tracks were commonly seen leading down from the main clay road to this area, and a fresh set of tracks were discovered that day.

Deer have been reported to kill snakes since at least 150 B.C. (Nicander 1953); this behavior is not restricted to Old World deer species (Klauber 1972). Klauber corresponded with various outdoorsmen across the United States who personally witnessed the killing of rattlesnakes by native deer, some as far south as Mississippi and Louisiana. To my knowledge, this behavior has never been witnessed in Florida.

On 28 May 1988 I tracked F2 to a xeric hammock on the property of Dr. D. A. Sanders. I discovered that the snake had been killed and eaten. The snake had last been seen alive 6 days earlier. The carcass, consisting of the skeleton with a little dried tissue adhering to it, was approximately 10 m from the snake's last location. The head and tail were missing, otherwise the carcass was intact and the skeleton was articulated. The transmitter, connected to the carcass by its antenna

wire, was still functioning. Because the skeleton had not been crushed or scattered in the manner characteristic of our local mammals, I concluded that this snake had been killed and eaten by a raptor, probably a red-tailed hawk, *Buteo jamaicensis*.

Although many species of hawks may feed on snakes, the red-tailed is probably the most notorious (Knight and Erickson 1976). Klauber (1972) cited many instances of red-tailed hawks making away with adult rattlesnakes, mostly in the western states. If the intended prey is small enough, the hawk may fly to several hundred feet and drop the snake to the ground in an effort to incapacitate it.

On 17 July 1986 a radio-tagged, male indigo (*Drymarchon corais*) approximately 133 cm in total length, was seen consuming a diamondback rattlesnake (approx. 65 cm in total length) in the Brantley Lake area of the preserve (Charest pers. comm.). Indigos, along with king snakes (*Lampropeltis getulus*), are known to be long-standing enemies of rattlesnakes (Klauber 1972). King snakes have not been reported from the Ordway, and indigos appear to be quite rare (Franz and Dodd pers. comm.).

## CONCLUSIONS

**Summary.**– The eastern diamondback rattlesnake (*Crotalus adamanteus*) is an ambush predator, feeding on small mammals, mainly *Sylvilagus* and *Sigmodon*, and some birds. It hunts from a tight coil, remaining motionless, waiting to ambush prey. Diamondbacks may spend from one day to as much as a week coiled in the same position and move between selected hunting locations mainly during the daylight hours.

Belying this sedentary foraging behavior is the fact that these snakes possess large home ranges. Females use about 40 ha, whereas males maintain ranges that may reach 170 ha. During the fall, snakes travel farther than other times of year, and at least one researcher feels that these long-distance movements are made in search of breeding females. Although females may move nearly as far, in total distances, as some males, their movements are more localized, suggesting that they use their home range more intensely. This reptile maintains a rather stable home range from year to year. It makes somewhat circuitous routes through its environment, passing over some of the same terrains at different times. It may return to certain locations more than once during the year.

At the Ordway, their preferred habitats include the Swamp Forests/Mesic Hammocks and Xeric Hammocks, areas that Ordway field studies have shown probably contain the highest prey diversity, but they also make opportunistic forays into Wet Prairies when water levels recede during droughts. Rattlesnakes use armadillo and gopher tortoise burrows in which to overwinter, as well as the root channels underneath palmetto thickets, and may or may not return to the same winter dens yearly.

The eastern diamondback, which is an important predator on rodents and lagamorphs, is declining in numbers, and like other snakes that possess large home ranges, will continue to face threats from human development that fragments their environment. Although the diamondback's real threat to public safety is very low (more people are killed every year by lightning strikes and bee stings), the perceived threat by the public is still quite high. Given this situation, the probability for future diamondback survival anywhere but on wildlife preserves and other large tracts of land is probably low unless conservation measures are taken. It would indeed be a tragic turn of events if this magnificent reptile, which figures prominently in southern legend and literature, should disappear from our landscape.

**Management Implications.**– *C. adamanteus* is native to many of Florida's vegetative communities. These natural areas, and the wildlife in them, have evolved in the presence of natural fires (Dye 1989). Management practices for areas containing eastern diamondback rattlesnakes should be consistent with an *ecosystem* or *natural-resource management* approach, similar to the kind advocated by the Florida Park Service (Glisson and Perry 1994). The control of exotic plants that invade and threaten ecosystems (Doren 1991) and the use of prescribed fire (Dye 1989) should be implemented. In addition, the natural maturation of riparian areas containing mesic and swamp habitats should be allowed, since these are often high-use foraging areas for these rattlesnakes. The gopher tortoise, a keystone species to many sandhill creatures (Eisenberg 1983), is also important to rattlesnakes at various times. During the winter, snakes may use the tortoise den as a refugium. During the fall, it is known that gravid females sometimes use "gopher holes" as parturition sites. Various animals relying on the gopher tortoise for survival, such as the Florida mouse (*Podomys floridanus*), may also be important components in the diet of baby rattlesnakes. Any management plans under consideration for *C. adamanteus* should include *G. polyphemus* whenever present.

All rattlesnake-prey species expected to be found at the Katharine Ordway Preserve occur there, but population levels are often lower than would be expected (Eisenberg pers. comm.). Under this situation, rattlesnakes cannot focus their foraging efforts on *Sylvilagus* and *Sigmodon*, abundant prey over most of the southeast. Here, management schemes must insure the health of small mammal communities in the mesic and xeric forests, areas shown to be used preferentially by Ordway diamondbacks.

If unnaturally high numbers of *C. adamanteus* are wished for, managers should consider artificially raising the numbers of the snake's prey base, particularly rabbits and cotton rats. I believe food to be the prime limiting factor for these snakes. Considering the number of winter observations that identified *Dasypus* burrows as refugia for Ordway diamondbacks, management plans that may adversely affect populations of the armadillo should be studied carefully. The

types and locations of burrows in an area may also be a limiting factor to this species.

**Conservation.**-- No demographic study of the eastern diamondback has ever been published, therefore the extent of its decline is difficult to determine. As early as 1976, Ross Allen (pers. comm.) cautioned me that eastern diamondback rattlesnake numbers had declined drastically over the preceding 20 years in Florida, due mostly to habitat destruction. One thing is certain--biologists record fewer and fewer local sightings of this species every year (W. Auffenberg, F.W. King, R. H. Mount, S.R. Telford, Jr., pers. comm.), yet malicious killing and the harvest for their skins and curios continues unabated. Enge (1991) felt that this snake is "the most likely candidate for some form of protection from human harvest" considering the relatively high scores that it received from a biological vulnerability ranking system (Millsap et al. 1990). Ernst (1992) felt that ecological studies of the eastern diamondback should be conducted soon, "as much of its habitat is disappearing, particularly in Florida, or it may be too late to assure the survivorship of this magnificent beast." Indeed, between 1936 and 1980, Florida's total forest cover declined by 29% (Bechtold and Knight 1982); an educated guess of the extant original forest would put the figure at no more than 50% today. Where once forests were often replaced by agriculture, which can provide at least marginal habitat for snakes, now most land clearing is linked to housing and commercial development. The continued destruction and fragmentation of native habitats can only lead to still greater declines for all of Florida's snakes.

In 1993, the Gopher Tortoise Council formed the Rattlesnake Conservation Committee. The purpose of the committee is to investigate the biological status of *C. adamanteus* and promote its conservation throughout the southeast. It has become evident to the committee members that this species warrants conservation and management--in some states, perhaps, as a harvestable species, in other states as an endangered species. In fact, I believe most Florida herpetologists would agree that there is sufficient evidence to warrant listing the eastern diamondback rattlesnake as a Species of Special Concern in the state of Florida. According to the Florida Game and Fresh Water Fish Commission's Wildlife Code, a Species of Special Concern is a species "which warrants special protection, recognition, or consideration because it has inherent significant vulnerability to habitat modification...or substantial human exploitation which, in the foreseeable future may result in its becoming a threatened species...[and]...may occupy such an unusually vital niche that should it decline significantly in numbers or distribution other species would be adversely affected..."

The State of Florida has made great strides in conservation in the last 10 years. The Preservation 2000 program for conservation land acquisition places Florida at the forefront of such activities (Calleson et al. 1993). At the same time, however, about 1,000 people move to Florida every day--people who know little, or nothing, about the fragile nature of the Florida environment or of the struggles that

Florida citizens have made over the last several decades to save some of it. The State could provide critical insurance for future conservation by establishing mandatory state educational curricula for schools, colleges, and universities. Such curricula should stress why the preservation of biological diversity is so important in our own efforts to survive into the 21st century. The stewardship of our natural resources, including those creatures that are potentially dangerous and often misunderstood, such as the alligator (*Alligator mississippiensis*), the Florida panther (*Felis concolor coryi*) and the eastern diamondback rattlesnake, will be passed on to future generations. Without the critical information needed to form unbiased opinions, these citizens of an ever-more complicated world will be unable to make the proper decisions affecting Florida's quality of life.

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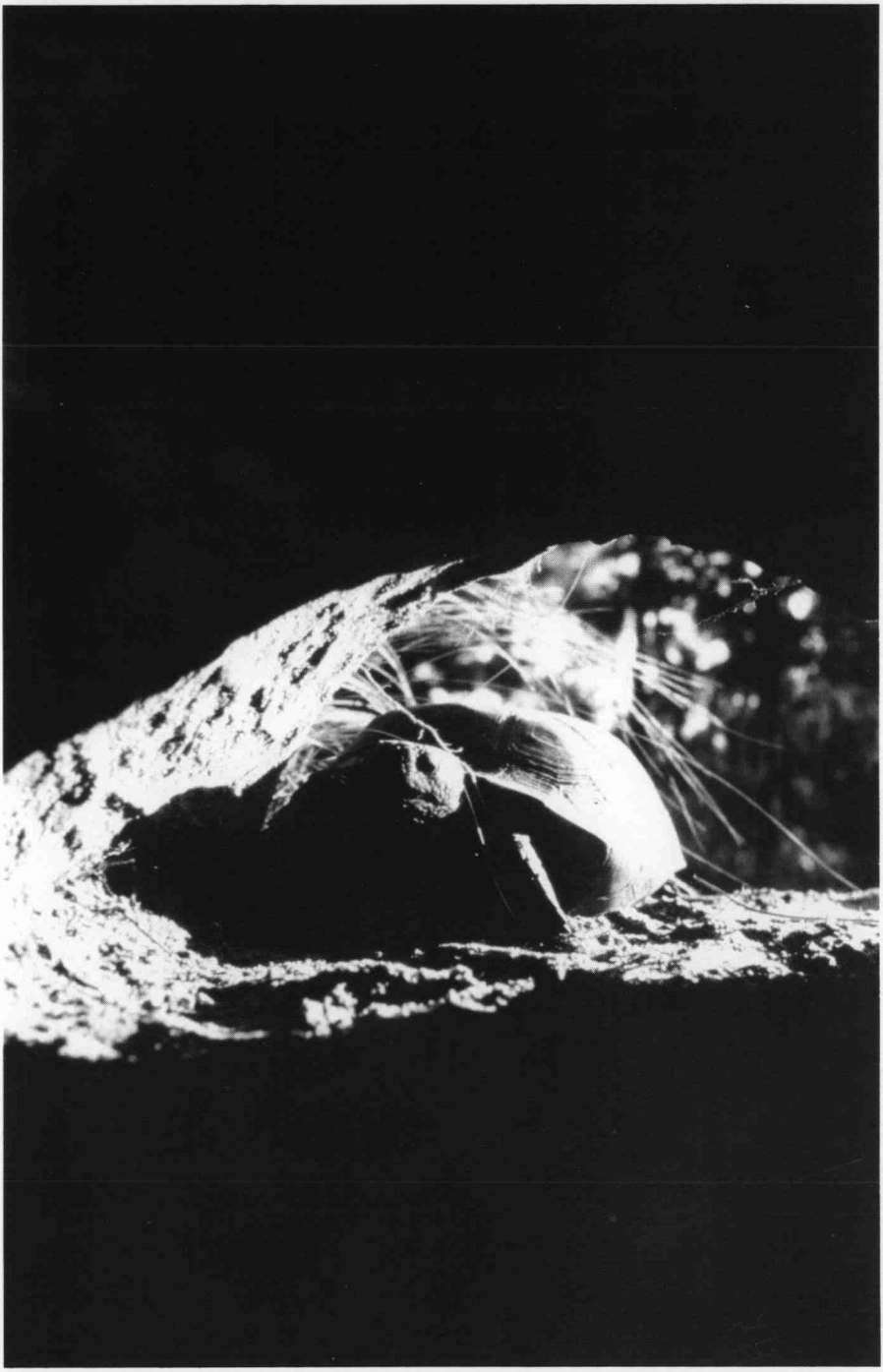

Gopher tortoise (*Gopherus polyphemus*) entering burrow. Photo by Fiona Sunquist.

Florida mouse (*Podomys floridanus*) meets gopher frog (*Rana capito areolata*). Photo by Fiona Sunquist.

Gopher tortoise (*Gopherus polyphemus*) meets Florida mouse (*Podomys floridanus*). Photo by Fiona Sunquist.

Eastern diamondback rattlesnake (*Crotalus adamanteus*) in typical posture for ambushing prey. Photo by Walter Timmerman.