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BIOLOGY OF THE RINGNECK SNAKE, DIADOPHIS PUNCTATUS, IN FLORIDA

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BIOLOGY OF THE RINGNECK SNAKE, *DIADOPHIS PUNCTATUS*, IN FLORIDA

CHARLES W. MYERS [1]

SYNOPSIS: Two geographic color varieties of the ringneck snake, *Diadophis punctatus punctatus* (Linnaeus), occur in Florida. Snakes in the Peninsula are characterized by reddish subcaudal surfaces and by the curious trait of tail-coiling when disturbed; the snakes occupying extreme northern Florida have yellow subcaudal surfaces and do not tail-coil. In the intergrade zone the subcaudals vary from yellow through red and some yellow-tailed individuals will tail-coil. The color red and the associated tail-coil display are considered relict characters in Gulf Coastal ringneck snakes. Ways are enumerated whereby tail-coiling may serve an aposematic function. The almost universal occurrence of the color red in snakes that have tail-flash displays suggests the behavior may have been developed against birds; most other potential predators lack red vision.

Diadophis punctatus has been found in practically all the major terrestrial habitats in Florida, although most commonly in low, wet, pine flatwoods. Main factors determining the species' ecological distribution and population density seem to be food and degree of moisture in the microhabitat. Significant size differences in snakes of two different populations may be related to availability of food. Microhabitat associates in two different habitats are considered, and known and supposed coactions discussed. Other snakes are probably the most important predators and competitors for food and space.

The sex ratio in adults, at least, is 1:1. The gonads are bilaterally asymmetrical in position and usually in size. The testes are smallest in winter and spring. Spermatogenesis is initiated in the spring and cellular proliferation is greatest in summer. Spermatozoa released from the testis in late summer and fall are stored in the ductus deferens throughout most of the year. The largest ovarian eggs increased from approximately 3 mm in April to a near maximum of 24 mm in July when they were in the oviducts. Eggs are probably laid from late May or June into August; females probably lay each year; the time of mating is not known. Both sexes are thought to be sexually mature by their second spring. The male secondary sex characters—anal ridges and greatly enlarged kidney tubules—become apparent about when the spermatozoa are formed.

A series of prehatching stages is briefly described. Males carry the hemipenes in the functional (everted) position until at least 28 days before hatching. Ventral markings are not apparent until after the dorsum becomes lightly pigmented. The unpigmented dorsal scale pits are the last structures to become discernible.

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[1] The author is a research associate with the Museum of Natural History, University of Kansas, and a visiting scientist at Gorgas Memorial Laboratory, Panama City, Panamá. His current research includes a collaboration on a study of the herpetofauna of Panamá and revisions of certain Neotropical snake genera. The present study was conducted while he was a research assistant in the Florida State Museum (1958-1960) and an undergraduate student at the University of Florida. Manuscript received 9 December 1963.—ED.

Myers, Charles W. 1965. Biology of the Ringneck Snake, *Diadophis punctatus*, in Florida. Bull. Florida State Mus., vol. 10, no. 2, pp. 43-90.

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Introduction

Diadophis punctatus (Linnaeus, 1766) is one of the most abundant and widespread serpents in the United States, yet relatively little is known of its biology, especially in the South. Frank N. Blanchard, in a series of papers on reproductive behavior, eggs, and young in Michigan (1926, 1930, 1937a), and in a generic monograph (1942), contributed more than any other individual to our knowledge of this snake. Hugh Clark (1944) studied the anatomy and embryology of the hemipenis. Miscellaneous information is available in a number of scattered papers and notes by other authors. The present paper covers several facets of ringneck snake biology, certain aspects of which have not been previously investigated. More data gathered over a longer period of time would have been desirable, but a change in residence prevented it.

It is a pleasure to acknowledge the assistance of W. D. Klimstra at Southern Illinois University, and William E. Duellman and Henry S. Fitch at the University of Kansas in reading and criticizing the manuscript. The study benefitted greatly from discussions with James N. Layne and William J. Riemer at the University of Florida. Special thanks are due Sam R. Telford for a series of prehatching stages and other specimens and help. For supplying specimens, field notes, or other favors, I am indebted to Andy Beckenbach, Archie Carr, Howard Campbell, James Dobie, Richard Highton, Wayne King, Barry Mansell, Robert Mount, Wilfred Neill, Russell Pyke, Anne Meachem Rick, and Douglas Rossman. Robert Inger, Roger Conant, and Carl

Gans advised me in correspondence of snakes known to give caudal flash-displays of aposematic colors. Several persons made available their services as photographers, and the by-lines under their photographs do not express my gratitude adequately. Some of the field work was supported by National Science Foundation Grant No. B-4490, William J. Riemer, principal investigator.

Fig. 1. The tail-flash display in *Diadophis punctatus* is characteristic of red-tailed individuals. The specimen pictured (from Alachua County, Florida) had yellow subcaudals, but came from an intergrade zone between populations of red- and yellow-tailed snakes. *From a transparency by Sam R. Telford.*

Procedure

The parts of this study concerned with the species' foods, animal associates, sex ratios, and reproduction are based almost entirely on materials from two localities in north-central Florida: (1) A slash pine flatwoods with scattered cypress ponds just east of Hatchet Creek and south of state highway 26, 7 miles east, 2½ miles north of Gainesville, Alachua County (figs. 2 and 3), and (2) Hale's Siding[2], an abandoned railway embankment on the western edge of an extensive

[2] Sometimes rendered "Haile's Siding" in the literature; actually named after an early resident of the county and once a segment of the Gainesville and Gulf Railway Company (dissolved in 1943). Since its abandonment Hale's Siding has been a favorite collecting site for herpetologists.

Fig. 2. Slash pine flatwoods near Hatchet Creek, Alachua County, Florida. This is probably the optimum habitat for the ringneck snake in Florida. *Robert McFarlane.*

Fig. 3. The pine log microhabitat of *Diadophis punctatus* in the Hatchet Creek flatwoods. *Robert McFarlane.*

marsh (Payne's Prairie), 4¼ miles south, 3¼ miles west of Gainesville, Alachua County (figs. 4 and 5). The sections on systematics, habitats, behavior, prehatching development, and growth are based on specimen material and field observations from these and other places. Unless otherwise stated all specimens discussed were collected in Alachua County during 1958.

Specimens were killed by small injections of water-diluted nembutal (sodium pentabarbital) the day collected, and were weighed and measured before preserving. Measurements taken from preserved material are so indicated. The snakes were injected with and placed in 10 percent formalin; the internal organs were removed several days later and stored in the same preservative.

Greatest length and width measurements of eggs, testes, and kidneys were made to the nearest 0.5 mm with dividers and ruler; the width of the right ductus deferens (vas deferens) was taken at the posterior end of the right kidney with the aid of an ocular micrometer and dissecting microscope. Sperm smears were made by removing portions of the ductus deferens and spreading the contents on clean microscope slides. Testes were sectioned at 10 microns and stained with hematoxylin and eosin. Because of the difficulty in distinguishing between different size (year) groups of ova in some individuals, monthly trends in egg growth were based on individual averages of the two largest eggs, one from each ovary; this proved satisfactory for determining gross trends.

Sexual maturity in males was determined by the presence of sperm in the ductus deferens, in which male gametes are stored throughout most or all of the year, at least in Florida. Females were considered sexually mature after they became physiologically ready for mating and egg laying. This was subjectively determined in doubtful specimens by comparing ovarian egg and oviduct sizes with those of known adults (large specimens with ova measuring 2 mm or more, and oviducts 1 mm or more wide) and known juveniles (small specimens with ova less than 2 mm in diameter, and oviducts 0.5 mm or less in width).

Systematics

Diadophis punctatus ranges throughout most of the eastern United States; Florida is within the range of the nominate subspecies. Blanchard (1942) recognizes the following five races:

D. p. docilis Baird and Girard, 1853—western Texas.
D. p. arnyi Kennicott, 1859—central states.
D. p. stictogenys Cope, 1860—south-central states.

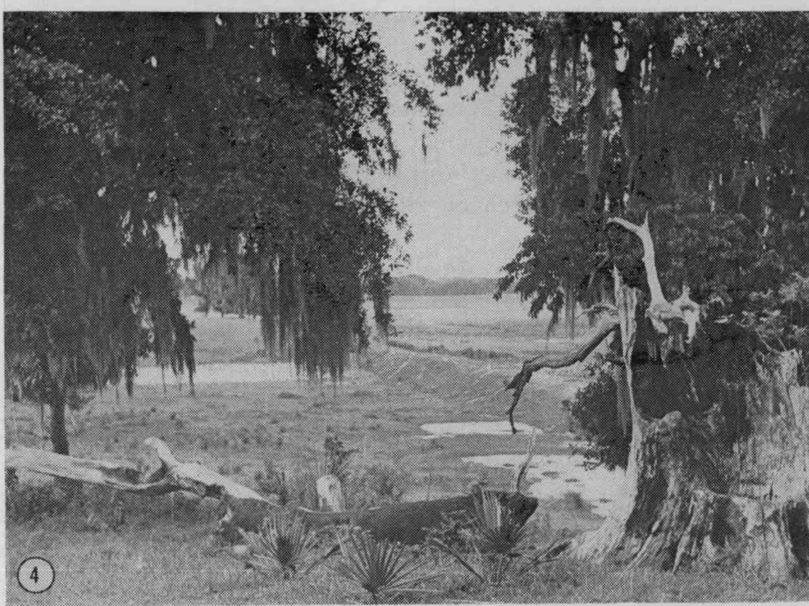

Fig. 4. View from xeric hammock, overlooking Payne's Prairie, Alachua County, Florida. The raised embankment in the center of the picture is Hale's Siding, an abandoned railway fill. *Andrew A. Arata.*

Fig. 5. Microhabitat of *Diadophis punctatus* on Hale's Siding. Ringneck snakes and other small vertebrates are found under such old railway ties. *Andrew A. Arata.*

D. p. punctatus (Linnaeus, 1766)—southeastern states.
D. p. edwardsii (Merrem, 1820)—northeastern states.

Mecham (1956) proposed that *Diadophis regalis* Baird and Girard is conspecific with *D. punctatus*, but made no attempt to clarify the controversial partition of what had been regarded as subspecies of *regalis* (see Schmidt, 1953: 182, footnote). I prefer not to upset established classification on slight evidence; more thorough studies of the western forms are needed to settle the question.[3]

Blanchard (1942) was hampered by lack of adequate living material and thus failed to note certain important color phenomena. It is not generally realized, for example, that the subspecies *D. p. stictogenys* and *D. p. punctatus* each contain two distinct color phases. Both races have geographically restricted populations characterized by reddish subcaudal surfaces and the curious trait of tail-coiling. Such populations occur in extreme southern Mississippi and possibly Louisiana according to James Dobie (*in litt.*, 1961), and in peninsular Florida (Neill, 1951). In their red tail color and tail-coiling, these populations of *stictogenys* and *punctatus* may prove to be contiguous on the southeastern Gulf Coastal Plain. Except for these and the subspecies *arnyi* (and probably *docilis*), all other populations of *D. punctatus* have yellow tails and seemingly do not practice tail-coiling. Blanchard (1942: 131) hypothesized a *D. p. docilis* → *arnyi* → *stictogenys* → *punctatus* → *edwardsii* line of evolution. Presumably, the red-tailed populations of *stictogenys* and *punctatus* are relict in their retention of the tail color and coiling mechanism of *docilis-arnyi* ancestry.

Alachua County, Florida, the focal point of the present study, lies in an apparent zone of intergradation between the peninsular red-tailed population of *D. p. punctatus* and a more northern yellow-tailed population of the same subspecies. Specimens I have examined indicate that an area of intergradation extends from the vicinity of Jacksonville on the East Coast, southwest through Alachua County, and then westward to the vicinity of the Appalachicola River Valley. Specimens south of this area have orange-red or coral-red tails; speciments north of it in the Coastal Plain of North Carolina and northern and southwestern Georgia have yellow subcaudals. Specimens with-

[3] In a publication recently received, Gehlbach (1965, Proc. U. S. Natl. Mus., vol. 116, pp. 300-307) clarifies variational aspects of *D. regalis*, which he places as a subspecies of *D. punctatus*. I cannot write with authority on the situation, but note that at least some individuals of *regalis* have very differently proportioned heads than *punctatus*, and suggest that hybridization (as opposed to intergradation) also be considered.

in the area of intergradation have yellow (a few specimens), orange-yellow, orange, or red subcaudals. Neill (1951) reports red-tailed ringnecks from "southern Georgia". The yellow-tailed "intergrades" coiled their tails as conspicuously (fig. 1) as red or orange-tailed individuals. I could not induce yellow-tailed specimens from southwestern Georgia to coil. *D. p. arnyi*, in populations far removed from yellow-tailed races, shows a range of variation from light orange to deep red.

Diadophis is believed to have originated in southwestern North America and probably to have reached Florida by way of the Gulf Coast (Blanchard, 1942: 129). This hypothesis is given further support by the relict distribution of tail color and coiling. Auffenberg (1963) described the fossil *D. elinorae* from the Middle Pliocene of Florida; Holman (1959) found *Diadophis* cf. *punctatus* present in the Florida Pleistocene.

Habitats

Ringneck snakes are primarily inhabitants of wooded regions. In the northern states *Diadophis punctatus* is usually found in hilly places with deciduous woods; on the southeastern Coastal Plain it occurs in a variety of habitats, but principally in flat, poorly drained pine lands. The following quotations from authors familiar with the species give a general idea of the habitats it occupies in various parts of its range:

Eastern Kansas: ". . . commonly found in more or less open woods, under stones, and in or under rotten logs and stumps. Ordinarily . . . on hillsides rather than on flat land. . . . " (Smith, 1950.) "Optimum habitat seems to be in open woodland with abundant flat rocks. Ring-necked snakes do not often bask in direct sunlight, but regulate their body temperatures by maintaining contact with the undersides of rocks warmed by sunshine. They are largely subterranean in habits. They are relatively scarce in woodland with a continuous leaf canopy shading the ground. In meadow habitat, where rocks are absent, the snakes are difficult to find, but have been seen on many occasions crawling through the grass or crossing roads. On several occasions they have been found in underground tunnels of the prairie vole. Several have been found in the humus and litter beneath the stick houses of woodrats." (Fitch, 1958.)

Western Missouri (Jackson County): ". . . usually limestone ledges on hillsides . . . always concealed under rocks, logs, or in decaying leaves." (Anderson, 1942.)

Michigan: "In the northern portions of the southern peninsula of Michigan more than 300 specimens have been collected within the past ten years. Here they are found under the loose rotted bark of fallen trees, chiefly hemlock, in old logs channeled by insects or decay, under boards or piles of boards that have long lain undisturbed and in old piles of hemlock bark. Many have been found in such places close to and at the edge of the Great Lakes beaches of Emmet and Cheboygan Counties. At the edges of unburned woods in such places they may be found in concealment absorbing the sun's heat." (Blanchard, 1942.)

Ohio: " . . . rare in the heavily mined areas and especially in the hills which have been denuded of their timber for many years. . . . In practically every case, however, the hiding place was moist and in or near woods. Since most of the level and less rugged parts of Ohio were long since lumbered, the hilly, wooded areas were the most productive; the snakes were found as often on the tops of the hills as on the slopes or in the valleys between them." (Conant, 1951.)

Maryland: On the Coastal Plain, " . . . preferring moist situations near the edges of swamps and streams. It has been collected in such places beneath and within logs, under bark of decaying stumps and logs, and under loose bark and leaves on the forest floor. It can be found in very wet rotted logs during times when it is preparing to shed its skin."

West of the fall line, " . . . likely to be found in nearly any stretch of woodland beneath such cover as stones, logs, and the loose bark of rotting logs and stumps. . . . Usually this snake is found in a fairly damp locality. The largest specimens I have encountered were taken in Garrett County in narrow wooded valleys along mountain streams. It is often found in damp meadows and on hillsides beneath appropriate cover." (McCauley, 1945.)

Florida: "Usually in moist situations; often near water, under logs, bark, and in the less water-logged sphagnum beds." (Carr and Goin, 1955.)

The complexity and diversity of Florida habitats are rather remarkable. Carr (1940) recognizes 24 major ecological associations for the Florida herpetofauna and describes them according to vegetation, soil, topography, and drainage. The classification of habitats used here is basically that of Carr divided into primarily wet and dry potential situations for *Diadophis*. More recently Duellman and Schwartz (1958) classified amphibian and reptile habitats in southern Florida. One of several botanical works useful to the student of animal ecology in Florida is Laessle's (1942) fine treatment of plant communities in the Welaka area of northern Florida.

A. Moist Habitats

The following habitats differ greatly in type of soil, topography, and biota, but all offer surface microhabitats that remain moist for a good portion of the year. When the microclimates become excessively hot and nearly devoid of moisture during dry periods, ringneck snakes probably retire to subterranean retreats. The soil is usually firm enough for extensive tunneling by small fossorial animals, especially under rocks and logs.

1. Pine flatwoods. The several types of flatwoods (Carr, 1940; Laessle, 1942) are characterized by extreme seasonal changes in moisture. The slash pine-wire grass flatwoods appear to be the optimum habitat of the ringneck snake in northern Florida. Low, flat topography and the presence of an impermeable hardpan allows water to remain on the surface for considerable periods during winter and spring. Relatively arid conditions prevail during the early summer months.

The abundance of *Diadophis* and other small log-dwelling snakes (*Rhadinaea flavilata* and *Virginia striatula*) seems correlated with moisture, as they are more plentiful in the wetter flatwoods characterized by cypress ponds, slash pine (*Pinus elliottii*), wire grasses (*Aristida* spp.), pitcher plants (*Sarracenia* spp.), gallberry (*Ilex glabra*), saw-palmetto (*Serenoa repens*), Easter-lilies (*Atamosco* spp.), wild-honeysuckle (*Azalea* sp.), ground orchids (*e.g. Limodorum multiflorum*), polygalas (*Pilostaxis* spp.), and others. Small snakes can be found under bark and in deeper cavities of stumps and fallen logs during the winter and spring. When this microhabitat becomes too dry or hot during the warmer months, the reptiles move to the undersides of logs and then presumably into tunnels left by rotting root systems and the burrows of other animals. Some portions of the low flatwoods are saturated throughout the year, and in these a few snakes may be found at any season in damp, shaded logs. They prefer the loose-fitting bark of pine logs, but occasionally inhabit cypress logs. *Diadophis* has been found in sphagnum moss beds in some flatwoods (Carr, 1940; Carr and Goin, 1955).

2. Prairies and marshes. Both these words have special meanings in northern Florida; "prairie" in this area refers to a broad, flat, fresh-water marsh or wet meadow formed on the bed of an extinct lake; "marsh" denotes the true salt marsh and the open strip of grasses and sedges along river and lake margins.

Ringneck snakes are fairly abundant on the periphery of some prairies, such as Payne's Prairie south of Gainesville. Here they are commonly found on both the highway fill across the Prairie and at Hale's Siding, an old railway embankment on the western fringe of the Prairie (fig. 4). Along the highway specimens have been found under sod and debris as well as between the trunk and bases of the old fronds of cabbage palms. At Hale's Siding they are most often found under old railroad ties (fig. 5). Though *Diadophis* is not plentiful on the prairie proper, a few specimens have been found in mats of water-hyacinth on ponds peripheral to the main prairie. Duellman and Schwartz (1958) doubt that ringnecks live in the extensive sawgrass prairies of southern Florida, though they found specimens along roadways through these areas.

Only one specimen of *Diadophis punctatus* was taken in a salt-water marsh in Florida, a juvenile found under a rock in a *Juncus* marsh (fig. 7) near the mouth of the St. Marks River in Wakulla County. A low road embankment connects the marsh to a nearby pine flatwoods. The western *Diadophis amabilis* has also been reported from salt marsh (Van Denburgh, 1922; Stebbins, 1954).

3. Low HAMMOCK includes hydrophytic hammock and cabbage palm hammock. Carr (1940) lists the species as an occasional inhabitant of low hammock, which he defines as any hardwood forest growing on low, damp, wet, or flooded ground and including conditions intermediate between mesophytic hammock and cypress swamp. The low hardwood forests of northern Florida are probably a minor habitat of *Diadophis punctatus*. I took a few specimens in a sometimes flooded hardwood forest between Newnan's Lake[4] and the Hatchet Creek flatwoods in Alachua County (fig. 6). Richard Highton (*in litt.*, 1959) found a large *Diadophis* in a cabbage palm hammock on the flood plain of the Oklawaha River in Marion County.

4. MESOPHYTIC (MESIC) HAMMOCK. This is the magnolia-holly climax association of peninsular Florida. Of all ecological associations in the Peninsula, this seems to approach most closely the conditions *Diadophis* prefers in northern deciduous forests. Topography is usually gently rolling, the ground is damp but not saturated, rotting logs and a few rocks provide suitable microhabitats, and food is readily available in the earthworms, salamanders (*Plethodon glutinosus*), small frogs (*Hyla* spp., *Gastrophryne carolinensis*), and lizards (*Lygosoma laterale*) that commonly occur in or under the logs. In spite of these presumably ideal conditions, Carr (1940) lists *Diadophis* as only

[4] Often misspelled "Newman's Lake" on maps; named after Colonel Newnan, a participant in the Seminole wars.

Fig. 6. Low hammock near Hatchet Creek, Alachua County, Florida. *Diadophis punctatus* occurs in such forests, but not so abundantly as in low pine flatwoods. *Robert McFarlane.*

Fig. 7. *Juncus* saltmarsh with pine flatwoods in the background, near mouth of the St. Marks River, Wakulla County, Florida. A ringneck snake was collected at this locality. *Andrew A. Arata.*

an occasional inhabitant in these forests. Richard Highton (*in litt.*, 1959) found only one ringneck snake during his extensive work in the mesic hammock at O'Leno State Park, Columbia County. One specimen in the University of Florida collections (UF 176) is labeled as found in a "climax hammock under log" in Alachua County.

Why *Diadophis* and other reptiles fail to utilize this habitat more extensively is as yet inexplicable. As Carr notes (1940: 16), "Pure mesophytic hammock supports a surprisingly meager fauna in view of the apparently favorable physical conditions which obtain." Conditions associated with the rather complete leaf canopy may limit *Diadophis punctatus*. Fitch (1958) and others have noted the species as most abundant in open woodlands.

5. UPLAND HAMMOCK includes xerophytic hammock and oak-hickory association. Carr (1940) uses the term upland hammock to denote a variety of hardwood forests growing on rolling or hilly topography with good drainage, and states that *Diadophis* is an occasional inhabitant. These woods are rather dry, but moist conditions in logs, leaf litter, and subterranean retreats are usually available for small amphibians and reptiles. Specimens have been collected in oak-hickory forest in the Florida Panhandle and in xerophytic hammock (*Quercus virginiana* association) in Alachua County (fig. 4). The species probably occurs in other types of dry forest, but upland hammock generally does not support large ringneck snake populations.

6. TROPICAL HAMMOCK. Both Carr (1940) and Duellman and Schwartz (1958) report *Diadophis punctatus* from this habitat.

7. SEMI-AQUATIC SITUATIONS. Although the ringneck snake is not aquatic, Florida specimens are often found in places surrounded by water, and obviously they must occasionally swim. Specimens have been collected under the bark of pine stumps and logs standing or laying in flatwoods ponds. Carr (1940) mentions finding several among water-hyacinth roots in association with the mud snake (*Farancia*) and dwarf siren (*Pseudobranchus*). He told me these records were made on Payne's Prairie near Hale's Siding, and that subsequent observations led him to believe the ringneck snakes live in the hyacinths *above* the water level, where the plants form thick, floating mats out over the water surface from the shore in an extension of the terrestrial environment. Two University of Florida specimens are labelled as collected in hyacinths, UF 1362 from the south fork of the St. Lucie River in Martin County, and UF 4605 from 5 miles west of Daytona Beach in Volusia County.

B. Dry Habitats

The sand pine-rosemary scrub and long leaf pine-turkey oak (high pine) habitats are both developed on loose, porous, sandy soils. Drainage is good and evaporation rates high; consequently surface conditions are extremely dry and hot for long periods. Some animals living in these habitats have the ability to dig deep holes (*e.g. Gopherus polyphemus*) or to "swim" through the loose subsurface sands (*Neoseps reynoldsi*). All permanent residents of scrub and high pine may be presumed to have physiological adaptations or specialized habits that allow them to withstand desiccation and high temperatures.

To my knowledge *Diadophis* has never been found commonly in either of these habitats. Unfavorable physical conditions and a scarcity of its principal food items are probably the main limiting factors. Howard Campbell (verbal communication) collected a specimen under a log on a high pine ridge, and several more from an adjacent swampy ravine in Chattahoochee County, Georgia. During rainy weather on high-pine slopes in Walton County, I found *Pseudotriton ruber, Eurycea bislineata,* and *Plethodon glutinosus,* all species as unsuited as *Diadophis* to that environment, obviously taking advantage of the wet weather to disperse from their more normal habitat of wooded ravines with streams.

Behavior

Seasonal activity. In northern Florida ringneck snakes are found most easily during the spring and are hardest to find in the summer, when most individuals have retired to subterranean retreats. The seasonal distribution of the 123 specimens I collected was: January-February, 4; March-April, 77; May-June, 18; July-August, 6; September-October, 6; November-December, 12. Temperature and moisture are probably the major factors affecting seasonal variation in abundance at or near the ground surface.

Pine logs at the Hatchet Creek locality yielded over 100 ringneck snakes to various collectors in March and April, 1958. With the approach of warmer weather and drier conditions in May and June, all the small snakes normally found in rotting logs (*Diadophis, Virginia, Rhadinaea*) became progressively more difficult to find. The same general trend was noted at Hale's Siding. While the extensive collecting may have contributed to the seasonal decline in numbers, the wandering tendencies of *Diadophis* (Fitch, 1958; Ditmars, 1951: 276-277) probably permit it to fill unoccupied habitat fairly rapidly.

In Jackson County, Missouri, Anderson (1942), reports finding *punctatus* most often in April and May, and seldom in July and August. Brimley (1925) and Conant (1938) found May the peak month in North Carolina and Ohio, respectively. March, April, and May were the best months for *D. amabilis* in southern California (Klauber, 1928). Rossman (1960) reports that in Union County, Illinois, *D. punctatus* is found in greatest numbers during the fall when young of the year are present. In Florida's milder climate the peak of activity is somewhat earlier in spring than in more northern localities.

Blanchard (1937a) found evidence of seasonal differences between the sexes in microhabitat preference in Michigan; females were found in rotting logs more often than males during the egg-laying season. Similar reports have been made for *Storeria occipitomaculata* in Michigan (Blanchard, 1937b) and for *Tantilla gracilis* in Oklahoma (Force, 1935). Too few Florida *Diadophis* were collected during the late spring and summer to determine any possible sex differences in habitat preference.

HIBERNATION. In east-central Georgia *D. punctatus* hibernates gregariously in logs or insect burrows under moss (Neill, 1948). According to Carr (1940) it is one of the few Florida snakes to "hibernate" in groups. At least some individuals are active during periods of warm winter weather.

GREGARIOUSNESS. It is not unusual to find several *Diadophis* coiled together under some piece of cover, as a strip of bark on a pine log. Carr (1940) once found six in a short rotten pine stick not over an inch in diameter. This sociability, which has been documented in many parts of the range, probably facilitates breeding, and may possibly serve other purposes as well.

DAILY ACTIVITY. Ringneck snakes are often said to be nocturnal, but in the literature individuals are more often reported active in the daytime. The daily cycle probably varies according to weather, season, hunger, and breeding condition.

I have records for only three Florida specimens found outside of cover. One was found recently killed on the highway across Payne's Prairie the night of 26 September 1957. Douglas Rossman (verbal communication) found two individuals crawling in leaf litter within 100 feet of each other in a Levy County hammock about 3:30 P.M., 12 June 1960, on a warm day when the sky was becoming overcast.

CLIMBING. Ringneck snakes were found on the trunks of cabbage palms at the bases of old fronds, several inches from the ground, along the highway across Payne's Prairie. Specimens are often found under bark on the nearly vertical sides of pine stumps, and they have to climb steeply to reach their hiding places under the bark of large pine logs. They will sometimes travel under the bark of inclined logs to heights of several feet from the ground. McCauley (1945) mentions three Maryland specimens found 6 feet from the ground under the bark of a snag, which was leaning against a tree at an angle of about 45 degrees.

MOLT. Florida ringneck snakes were found shedding or about to shed (skin and eyes cloudy) in nearly every month from March to November. Ecdysis may also occur from December to February, but too few specimens were collected in these months.

COURTSHIP. Courtship and coition seem not to have been described for any species of *Diadophis*, although Storm's (1955) record of four *D. amabilis* coiled about each other at the base of a stump might have been a mating aggregation. Tubercles (anal ridges) on the dorsal scales of the cloacal region may possibly serve as tactile organs in courtship. These structures are characteristic of adult males, but are occasionally present in juveniles and females (fig. 18).

PTYALISM. When handled excessively, *Diadophis amabilis* and *D. regalis* are said to salivate copiously (Blanchard, 1942: 44; Stebbins, 1954: 360). I have not observed this trait in *D. punctatus*.

FEEDING. The enlarged, saber-like teeth at the posterior ends of the maxillary bones in *Diadophis*[5] are undoubtedly important in feeding. Many snakes with similar enlarged teeth have a weak venom with which they subdue their prey. Venom conduction can usually be surmised indirectly by the manner with which the jaws are manipulated over the prey, or the death of the food animal while it is still being held in the snake's mouth. Such behavior was not noted in *D. punctatus*, although I have received a few verbal reports of bites from this species causing a slight burning sensation.

Both visual and chemical cues are used for prey recognition. Constriction of prey has been reported for *D. amabilis* (Bogert, 1930; Ditmars, 1951), but has not been observed in *punctatus*.

DEFENSE. Though I have never seen a ringneck snake try to bite when handled, McCauley (1945: 62) states that occasional individuals will attempt to chew. A much more effective defense mechanism is the discharge of the very unpleasant-smelling contents of the anal sacs, which probably makes them unpalatable to some predators.

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[5] Zweifel's (1954) illustration for *Diadophis amabilis* is of a mandible and not a maxilla as stated.

Klauber (1931: 68) noted a captive *D. amabilis* "which would lie on its back and play dead."

A curious behavioral trait thought to have protective value is that of tail-coiling. When captured and first handled, ringneck snakes often elevate and spiral the tail in such a manner that the brightly colored ventral side is uppermost. A splendid colored illustration of the tail display of *Diadophis amabilis* is on pl. 90 of Schmidt and Inger's "Living Reptiles of the World" (1957); the tail-coil of *D. punctatus* (fig. 1) is usually not so tightly spiraled nor so conspicuously elevated as in *D. amabilis*.

Tail-coiling in *Diadophis* probably has an aposematic function because the reaction is seemingly evoked only when the individual is molested. The red subcaudal coloring is probably an integral constituent of the display, for tail-coiling in *D. punctatus* is associated closely with populations of red-tailed individuals. This is not coincidence, for nearly all other snakes with caudal flash behavior have red as one of the colors displayed. Red caudal displays have been observed in the following families and species of snakes:

Aniliidae
- *Anilius scytale,* (Carl Gans, *in litt.*, 1961)
- *Cylindrophis rufus,* (De Sola., 1939; Tweedie, 1957)

Colubridae
- *Calamaria* spp., (Davis, 1948; Loveridge, 1945)
- *Farancia abacura,* (Davis, 1948)
- *Diadophis amabilis,* (various sources)
- *Diadophis punctatus,* (various sources)
- *Diadophis regalis,* (various sources)

Elapidae
- *Callophis trimaculatus,* (Mertens, 1946)
- *Maticora bivirgata,* (Robert Inger, *in litt.*, 1961)
- *Maticora intestinalis,* (Tweedie, 1957)
- *Micrurus affinis,* (Roger Conant, *in litt.*, 1961)
- *Micrurus frontalis,* (Schmidt and Inger, 1957)
- *Micrurus mipartitus,* (personal observation)

At least two species of colubrids display caudal areas that lack red. *Drymarchon corais corais* elevates a yellow tail as a threatening gesture (Neill, 1960), and individuals in some populations of *Thamnophis eques megalops* display a coil in which a light greenish-yellow ventral surface is contrasted against a dark dorsum (Roger Conant, *in litt.*, 1961). At least one boid, *Charina bottae,* has a tail-display, but the tail is not colored differently from the rest of the body (see Carr *et al.*, 1963).

Of the principal colors or color combinations used for "advertisement" in the animal kingdom (Cott, 1957), perhaps most interesting in snakes is the emphasis on red, usually red and black, in widely separated and unrelated species. Red is conspicuous on the bodies of various venemous elapids. One possibility is that certain important predators have strongly developed red vision. Investigations of color vision in vertebrates[6] are limited to relatively few species, but among possible predators of snakes, only birds and the higher primates seem to show a highly developed sensitivity to red. In birds red is both a color of warning and attraction (see Cott, 1957: 191-192, and Walls, 1942, and their citations); a similar parallel can be drawn for man (Kenyon, 1925).

In elapid snakes the bright-colored tail is probably used as a true warning display—an advertisement of the owner's venomous capabilities. In some elapids the tail imitates a raised head while the snake retreats from danger. Some harmless snakes mimic elapids in both coloration and behavior. Ringneck snakes, however, neither mimic other animals nor possess a dangerous venom apparatus. Tail-coiling behavior may offer survival value to *Diadophis* in the following ways:

1. False Warning Display.—Cott (1957: 305-307) cites cases in which harmless animals successfully warded off the attack of would-be predators by sudden displays of color or by increase in size.

2. True Warning Display.—Some predators might associate the caudal display with an undesirable taste or odor, as of the anal sac secretions.

3. Diverting Display.—Stebbins (1954: 358) suggests that the tail-coil might serve to distract attention from more vulnerable parts of the body. If the display caused a predator to hesitate or to focus its attack on the tail, it might improve chances of survival.

A combination of the above might give protection from a variety of predators, but little can be added toward our knowledge of the phenomenon without experimentation and more detailed observation. While an aposematic or predator-diverting function of tail-flash displays in snakes can be logically postulated, it needs verification. Following are some relevant problems especially in need of attention:

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[6] It is generally agreed (*e.g.* Portman, 1959; Stephenson and Stewart, 1956) that only vertebrates can be considered (at least on present evidence) as reactants of selective importance toward warning and cryptic colorations.

1. Kinds of stimuli that will illicite the tail-flash display.

2. Reactions of predators when confronted by the display.

3. The exact nature of inter- and intraspecific variation in tail-flash behavior and caudal coloration in *Diadophis.*

4. Functions of the anal sac secretions.

Foods

Earthworms, amphibians, and reptiles constitute the main foods of *D. punctatus.* Some authors state that it eats insects. Ernst (1962) "observed ringnecks capturing winged insects that have fluttered to the ground . . . [at] a night light." Insects were found in Florida ringnecks only when amphibian remains were also present and apparently were secondarily ingested. Reports of insects, bird eggs, and young mice (Blanchard, 1942) need clarification, as does a record by Barbour (1950) of salamander eggs (*Aneides aeneus*) in the stomach of a Kentucky specimen. The eggs could have been secondarily ingested, though some snakes (*e.g. Leptodeira*) do feed on amphibian eggs.

All but 2 of 68 Alachua County ringneck snakes contained some material in the intestines, but only 15 had food in the stomach (table 1). This high incidence of matter in the intestines does not necessarily indicate frequent feeding, for indigestible residues can remain in the colon at least 2 weeks and probably much longer. Intestinal matter was generally not identifiable, except in some flatwoods specimens whose lower guts contained protozoan parasites (gregarines?) of earthworms, and quantities of sand that might have been derived from earthworm crops. The protozoans occurred only in the encysted state (see section on parasites) and usually in association with sand grains; the same cysts were found in several earthworms in *Diadophis* stomachs.

The diet of *D. punctatus* varies with the local availability of prey species. Earthworms constituted the principal food at Hatchet Creek; a few ground skinks (*Lygosoma laterale*) were also eaten. Only one specimen from Hale's Siding contained an earthworm, but six had small frogs (*Gastrophryne carolinensis* and *Rana pipiens*) in their stomachs. Judging from the relative numbers of individuals with food in their stomachs (table 1), food is more readily available at Hale's Siding than at Hatchet Creek. These differences may be seasonal, as most of the Hatchet Creek specimens were collected from March to May and the Hale's Siding specimens from July to September.

Mean and maximum size of specimens from both localities also suggest a better food supply at Hale's Siding: 15 adults from Hale's Siding ranged from 212-355 mm in length, with a mean of 292.6 ± 10.23 mm; 51 Hatchet Creek adults ranged from 212 to 352 mm, mean 263.2 ± 3.59 mm; these differences are significant ($T' = 2.72$; $P < .02 > .01$). Eight (53%) of 15 individuals from Hale's Siding were more than 300 mm in total length, whereas only three (6%) of 51 Hatchet Creek specimens were larger than 300 mm. It is highly unlikely that these differences are due to chance ($X^2 = 15.52$; $P < .001$), though they could, of course, be attributed to genetic or age-class composition factors in the populations. As the proportions of males to females are similar in both samples, sex is not a factor.

TABLE 1. OCCURRENCE OF FOOD IN *Diadophis punctatus* FROM TWO LOCALITIES IN ALACHUA COUNTY, FLORIDA

Locality	Number with food in stomach	Number with matter only in intestines	Number with empty digestive tracts	Totals
Hatchet Creek flatwoods	7	43	2	52
Hale's Siding	8	8	0	16
Totals	15	51	2	68

The variety of prey Alachua County ringnecks eat must certainly be greater than indicated by table 2, because the total sample is rather small and several types of habitat are not represented. Known and probable prey species in the Hatchet Creek flatwoods are the pine log associates of *Diadophis* shown in table 3. Potential prey not normally found in the pine logs includes *Ambystoma cingulatum, Acris gryllus, Hyla* spp., and *Rana* spp. Known and probable prey species at Hale's Siding are shown in table 4. One exception is the red-tailed skink (*Eumeces egregius*) which I found in *Geomys* mounds at this locality and which I suspect falls prey to *Diadophis* on occasion. No evidence was found that *Diadophis* eats other snakes, but this is a matter of record (Blanchard, 1942: 110) for other parts of the range, and I have been told of a captive Florida individual that ate a *Rhadinaea flavilata*. Barbour (1950: 104) showed that salamanders are a major dietary item when available. No salamanders were present in specimens from either the Hatchet Creek or Hale's Siding localities. However, a ringneck collected at the edge of a small hammock stream in Alachua County contained the salamander *Manculus quadridigitatus*, and one collected in a bed of sphagnum moss in Leon County contained a *Eurycea bislineata*. A specimen from Liberty County was found under the same log as a *Plethodon glutinosus*, a species which might form an important part of the diet in hammock habitats where they occur together. Predation on *P. glutinosus* by ringneck snakes has been reported by McCauley and East (1940: 122) in Maryland and by Barbour (1950: 104) in Kentucky.

TABLE 2. FOOD OF 71 *Diadophis punctatus*, ALACHUA COUNTY, FLORIDA

Food item	Number of specimens containing food item	Per cent frequency of occurrence
EARTHWORMS	26*	36.6
AMPHIBIANS	8	11.3
Manculus quadridigitatus	1	1.4
Gastrophryne carolinensis	4	5.6
Rana pipiens (juveniles)	2	2.8
Unidentified frog	1	1.4
REPTILES	3	4.2
Lygosoma laterale	2	2.8
Unidentified reptile scales	1	1.4
UNIDENTIFIED MATTER ONLY	34	47.9

*Based on indirect evidence of protozoan cysts in intestines in 19 cases (see text). Two individuals with empty guts excluded.

Evidence of geographic variation in food preferences of *Diadophis punctatus* is slight. Blanchard (1942: 77, 110) states that captive midwestern snakes (*D. p. arnyi*) readily accepted earthworms, whereas northern individuals (*D. p. edwardsii*) could be induced to eat them only rarely.

ANIMAL ASSOCIATES

The following account of animal associates of *D. punctatus* and their real or supposed coactions is limited mainly to the Hatchet Creek and Hale's Siding localities in Alachua County, for which fairly complete lists were compiled of vertebrates and the more conspicuous invertebrates sharing the ringneck snakes' microhabitats (tables 3 and 4).

PREDATORS. Certain predaceous invertebrates, such as large spiders and centipedes, probably feed on young ringneck snakes occasionally. Large centipedes are commonly found in pine logs. An attack on a ringneck snake by the "larva of a caryatid [carabid?] beetle" has been reported (Barber, 1906).

TABLE 3. MICROHABITAT (PINE LOGS) ASSOCIATES AND THEIR COACTIONS WITH *Diadophis punctatus* IN PINE FLATWOODS NEAR HATCHET CREEK, ALACHUA COUNTY, FLORIDA

Species	Prey	Predator	Food competitor	Space competitor	Neutral
COMMON INVERTEBRATES					
Earthworms	X				
Centipedes		?	?	?	
Termites				X	
Ants				X	
AMPHIBIANS					
Bufo terrestris	?		?	?	
Hyla femoralis (juveniles)	?				
Gastrophryne carolinensis	X				
REPTILES					
Emeces inexpectatus	?			?	
Lygosoma laterale	X				
*Thamnophis sauritus**			X		
Virginia striatula	?		X	?	
Rhadinaea flavilata	?	?	X	?	
Lampropeltis doliata	?	?	X	?	
*Coluber constrictor**		X	X		
Elaphe spp.*		?	X		
*Micrurus fulvivus**		X	X		

* Not a common inhabitant of fallen pine logs at this locality; record based on a single specimen. The *Elaphe* record is based on a fragment of shed skin; both *E. guttata* and *E. obsoleta* undoubtedly occur.

The most important predators on *Diadophis punctatus* are probably other snakes. Coral snakes (*Micrurus fulvius*) have been known to eat *Diadophis*, as well as many other species of small reptiles (Schmidt, 1932); a ringneck was found in the stomach of a *Micrurus* found under a pine log in the Hatchet Creek flatwoods. Blacksnakes (*Coluber constrictor*) eat many other species of serpents and are often abundant in *Diadophis* habitats in Florida, although different habits reduce the chances of predation. Only one ringneck (from Hatchet Creek) was found in more than 100 blacksnake stomachs examined from Florida. Uhler *et al.* (1939) examined 34 Virginia *C. constrictor;* of 16 with food, 2 had fed on ringnecks. Other possible snake predators in the Hatchet Creek flatwoods are *Lampropeltis doliata* and *Rhadinaea flavilata*, both typical microhabitat associates of the ringneck snake. Ophiophagous tendencies in *Rhadinaea* have not been documented, but it feeds readily on frogs and lizards and perhaps small snakes as well. The ratsnakes, *Elaphe obsoleta* and *E. guttata*, are found in pine flatwoods and possibly take an occasional ringneck. The rattlesnake *Sistrurus miliarius* has been found in Alachua County flatwoods; one of 12 specimens with food from Georgia contained a *Diadophis* (Hamilton and Pollack, 1955). At Hale's Siding, *Coluber constrictor* and *Lampropeltis getulus* were found under the same type of cover (railroad ties) as *Diadophis* and are probable predators. *Lampropeltis getulus* has ac-

TABLE 4. MICROHABITAT (OLD RAILROAD TIES) ASSOCIATES AND THEIR COACTIONS WITH *Diadophis punctatus* AT HALE'S SIDING, PAYNE'S PRAIRIE, ALACHUA COUNTY, FLORIDA

Species	Prey	Predator	Food competitor	Space competitor	Neutral
COMMON INVERTEBRATES					
Earthworms	X				
Leeches, crickets, roaches, bombardier beetles (Carabidae)				?	?
AMPHIBIANS					
*Pseudacris nigrita**	?				
Gastrophryne carolinensis	X				
Rana pipiens	X			?	
Rana catesbeiana	?	?		?	
REPTILES					
Sceloporus undulatus				?	?
Ophisauris ventralis				?	?
*Seminatrix pygaea**					?
Thamnophis sirtalis			X	?	
Thamnophis sauritus			X	?	
*Heterodon platyrhinos**				?	?
Lampropeltis getulus		X	X		
*Farancia abacura**				?	?
Coluber constrictor		X	X		
MAMMALS					
Blarina brevicauda		?	X	?	
*Cryptotis parva**		?	X	?	

* Not typically found in this microhabitat; record based on a single specimen.

cepted the ringneck snake in captivity (Wilson and Friddle, 1946). Because of cover type, *Diadophis* is probably less secure from predation by large snakes at Hale's Siding than it is in the flatwoods where it can take refuge under bark and in small tunnels in rotting pine logs.

Wild hogs roam through Hatchet Creek flatwoods and probably take an occasional ringneck snake during their rooting. Opossums (*Didelphis marsupialis*) occur in flatwoods and eat a variety of foods; Reynolds (1945: 367) found *Diadophis punctatus* remains in 2.7 percent of 259 opossum scats in Missouri. Two shrews, *Blarina brevicauda* and *Cryptotis parva*, are potential mammalian predators. A Kansas *Blarina* accepted many *D. p. arnyi* in captivity; *Diadophis* anal sac secretions spread over other types of foods did not deter this shew from feeding. The introduced armadillo (*Dasypus novemcinctus*) is also a likely predator.

Ernst (1962) lists several predators of *D. punctatus* in Maryland: " . . . brown trout (snake swimming across a pool), bullfrog, American toad, skunk, Black snake, and Screech Owl." The bullfrog (*Rana catesbeiana*) is a recorded predator of *Diadophis amabilis* also (Graf *et al.*, 1939).

FOOD COMPETITORS. The following account is limited to inhabitants of major *Diadophis* microhabitats (tables 3 and 4). Considered are those species known or suspected of eating one or more kinds of animals also preyed upon by *Diadophis*.

In the Hatchet Creek flatwoods, toads (*Bufo terrestris*) probably eat some earthworms in the vicinity of pine logs, but other snakes are doubtless more important as food competitors. *Virginia striatula* feeds primarily, if not exclusively, on earthworms at this locality. *Rhadinaea flavilata* and *Coluber constrictor* take small amphibians and the lizard *Lygosoma laterale*. *Lampropeltis doliata* and *Micrurus fulvius* are also known to eat *Lygosoma*. Young ratsnakes (*Elaphe* spp.) are known to feed on a variety of small amphibians and lizards. *Thamnophis sauritus* feeds upon small amphibians. Because of their abundance and habitat preference, *Virginia* and *Rhadinaea* are probably the two most important competitors.

At Hale's Siding certain of the frogs may feed on earthworms but, as in the flatwoods, snakes seem to be the most important competitors. *Coluber constrictor* and *Thamnophis sauritus* are known to eat frogs. *Thamnophis sirtalis* was found to utilize the leopard frog (*Rana pipiens*), and probably takes earthworms and narrow-mouthed toads (*Gastrophryne*) as it is known to do in other parts of its range. *Lampropeltis getulus* feeds on a wide variety of vertebrates. *Seminatrix* *pygaea* has taken earthworms in captivity (Rossman, 1956), but is not likely an important food competitor because of its highly aquatic habits. Two species of shrews (*Blarina brevicauda* and *Cryptotis parva*) found under railroad ties probably compete with *Diadophis* for earthworms and small frogs.

SPACE COMPETITORS. Though ringneck snakes were sometimes found in pine logs and stumps infested with ant and termite colonies, they were never in direct contact. Blanchard (1942: 108) believes that northern *Diadophis punctatus* avoids those logs with the most ants, but Ditmars (1951: 277) observes that, "In the South . . . Ring-necked snakes were most frequently found under the bark of trees infested by ants; often the working streams of these insects would pass but a fraction of an inch from the spot where the reptile was coiled." In some areas of the South nearly every fallen log contains ants, so it is not surprising that ringnecks are found "most frequently" in such logs. Ditmars (*loc. cit.*) continues: "In one instance . . . during the early spring, I exhumed one of these snakes while digging through a large and thickly populated anthill." Possibly the weather was cool and the ants inactive or less pugnacious.

I have often found other species of vertebrates in the same log or under the same cover with *D. punctatus*, but never in close proximity. This seems to indicate that some kind of displacement occurs. Snakes can perhaps detect some animals by smell and avoid places where they are concealed; some displacement might be brought about by size differences. Judging from assemblages of hibernating animals, some interspecific avoidance in *Diadophis* may break down during hibernation (*vide* Burt, 1935; Lachner, 1942); more details are needed.

NEUTRALS. Whether two species associated in space and time can each exist without affecting the other is debatable. Certainly some effects can be too slight for detection; "neutralism" is at least a convenient term under which to consider species of only subtle interactions at best.

None of the microhabitat associates in the Hatchet Creek flatwoods are regarded as neutrals (table 3), but several species are hesitantly listed as such for the Hale's Siding locality (table 4). These "neutral" species are chance wanderers from the adjoining marshy prairie or xeric hammock. There might be space competition between these and *Diadophis*, but any overall effects on the latter are probably very slight. Hale's Siding is a man-made extension of an ecotone between a fresh-water marsh and a well drained hammock; the siding runs adjacent to the hammock and then juts out into the prairie (fig. 4).

Some strictly terrestrial species follow the siding onto the prairie; species of greatly diverse habits thus associate more often than they would normally. Such out-of-place species are apt to produce but little effect on one another.

PARASITES

No detailed study was made of parasites, but it was evident that the *Diadophis* populations sampled were not heavily parasitized. Occasional unidentified worms were found in or on the digestive tract, and microscopic nematodes were observed during examination of the lower gut contents. Small, fluid-filled sacs, probably representing an early stage of some parasite, were attached to the outside of the gut in a few specimens.

Formalin preserved digestive tracts of 73 Alachua County specimens were examined for protozoan parasites. Gregarine(?) cysts (Sporozoa) were present in 24 of 46 snakes from the Hatchet Creek flatwoods, but were absent in all 16 specimens from Hale's Siding. The cysts were elliptic in shape, with pointed ends, and ranged in length from 11.5 to 30.0 microns. Each cyst held six sporozoites and a centrally located intra-residual body. These sporozoans were ingested with the earthworms eaten by *Diadophis* (see section on foods).

SEX RATIOS

The sex ratio is one to one in adult ringneck snakes collected at Hatchet Creek and Hale's Siding in 1958 (31 males, 30 females). However, 22 juveniles from various Florida counties shows a preponderance of males (14 males, 8 females). The deviation from an expected 1:1 ratio is not significant, but further information on sex ratios in juveniles is desirable (see also page 81).

REPRODUCTION

The following account of reproduction is based on a series of 68 *Diadophis* collected in Alachua County in 1958, 55 from the Hatchet Creek flatwoods, and 13 from Hale's Siding. Where specimens supplementary to these are discussed, they are so indicated by the date (a year other than 1958) or locality.

GENERAL MORPHOLOGY OF THE UROGENITAL ORGANS

MALE. The gross anatomy of the male system is essentially the same as that Fox (1952) described for *Thamnophis sirtalis* and *T. ele-*

gans. The right gonad is usually longer than the left, but this is less frequently so for the right kidney (table 5). The organs on the right side lie anterior to those on the left.

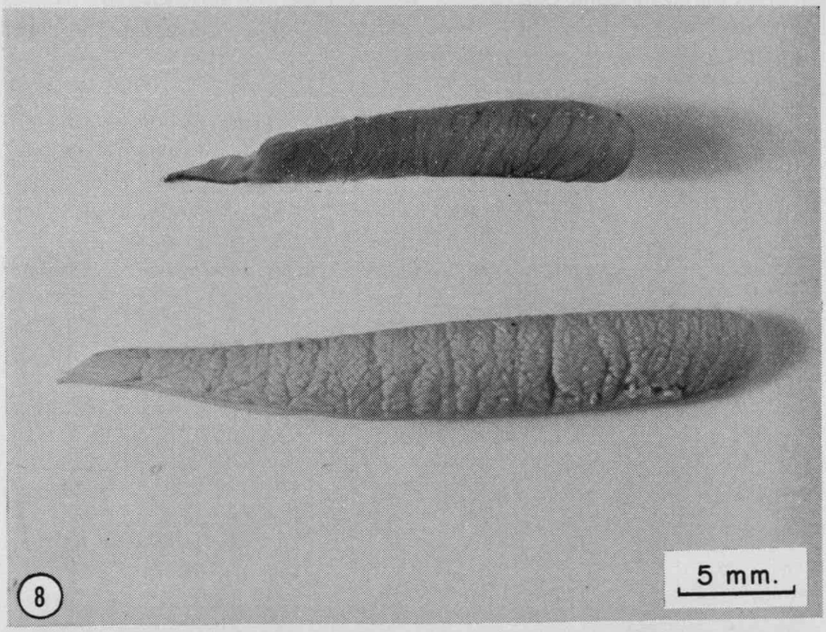
TABLE 5. LENGTH AND WIDTH RELATIONSHIP IN TESTES AND KIDNEYS OF *Diadophis punctatus* (JUVENILES INCLUDED) FROM ALACHUA COUNTY, FLORIDA

Structure	Right larger*	Both the same*	Left larger*	Mean and range in mm. (right organ above)	Number
TESTES					
Length	22	5	4	7.7 (3.5-13.0) 6.8 (3.0-11.0)	31 pairs
Width	7	19	5	2.5 (1.0-4.0) 2.5 (1.0-4.5)	31 pairs
KIDNEYS					
Length (males)	15	9	10	18.3 (9.0-30.0) 17.6 (9.0-25.0)	34 pairs
Length (females)	16	6	11	16.0 (7.0-21.5) 13.5 (7.0-21.0)	33 pairs
Width (males)	7	21	6	3.5 (2.0-5.0) 3.4 (2.0-4.5)	34 pairs
Width (females)	5	24	4	2.8 (2.0-3.5) 2.8 (2.0-4.0)	33 pairs

* Relative size differences in given pairs of organs.

An enlarged segment of the urinary tubule of the male kidney has been described for several snakes and lizards (*vide* Fox, 1952). These "sexual segments" of the kidney tubules are remarkably enlarged in adult male *Diadophis punctatus* (figs. 8 and 9), and become visible to the naked eye at about the same time that the external anal ridges are developed (fig. 18). The adult male kidney is large, white, and convoluted on the surface. Certain other species of snakes (*e.g. Virginia striatula, Rhadinaea flavilata,* and *Sibon nebulatus*) show kidney tubules that are as enlarged as in *Diadophis*. Other species (*e.g. Farancia abacura, Heterodon simus, Natrix sipedon,* and *Thamnophis sirtalis*) have relatively smaller tubules that are often hardly noticeable to the naked eye.

FEMALE. The female reproductive organs lie in the same position as those of the male, the ovary and oviduct replacing the testis and ductus deferens. A marked bilateral asymmetry is evident not only in position of the urogenital organs, but also in the number of mat-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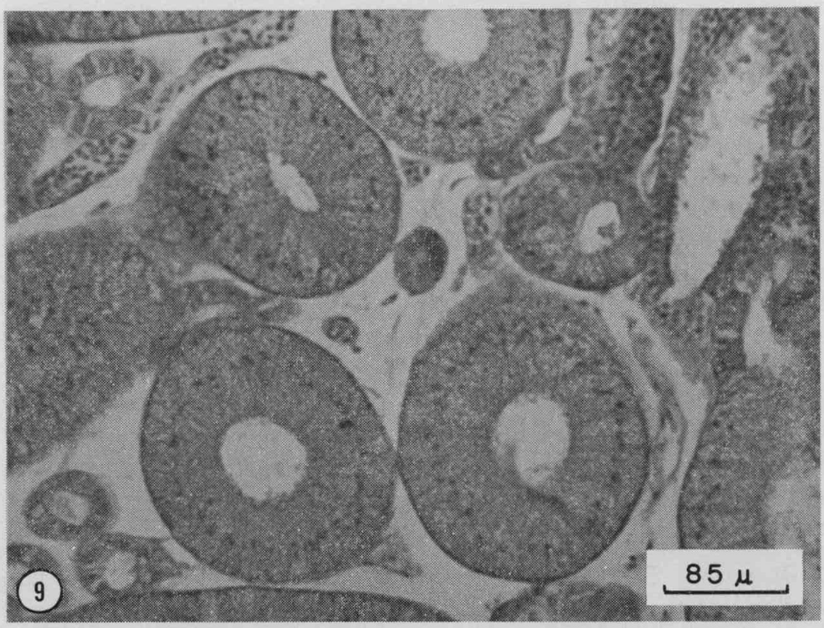
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urating ova distinguishable from the smaller ova that would have matured in later seasons. In 13 specimens the right ovary contained the greater number of ova, the left contained more in only 2; 8 individuals had the same number in each ovary.

The kidney in the adult female (fig. 8) is smaller than that of males of equivalent or even shorter body length and lacks the convoluted appearance caused by the enlarged tubules of the male organ. The female kidney is also darker; in juveniles of both sexes the kidney resembles that of the adult female in color and texture.

ANOMALIES. Aberrations and diseases of the urogenital system are not rare: 5 (7%) of 68 specimens showed defects of some sort. One male had a hard, black, greatly reduced right testis. A single male and female each had a single shriveled, hard, black kidney. Two females had a small posterior lobe of one kidney completely separate from the main organ, and attached only by a clear membrane.

SEASONAL CHANGES IN THE MALE GENITAL TRACT

SPERMATOGENESIS. That the gonads of the male serpent undergo seasonal fluctuations in size and weight is well known, but in few cases have the cyclic changes been plotted and the underlying cellular causes studied. Following is a generalized description of spermatogenesis in the right testis. Inadequate seasonal sampling and certain difficulties in interpretation preclude a more detailed description.

In the four late March specimens spermatogonia seem to be the only germinal elements present. These are clustered around small but distinct lumina of the seminiferous tubules. (fig. 10)

In 13 specimens taken the first half of April, spermatogonia are generally abundant and spermatocytes are appearing. One specimen has few spermatogonia and abundant spermatocytes. Early spermatids are present in a few, and one specimen collected 5 April has small clusters of late spermatids. The lumina of the tubules are fairly distinct but are starting to be invaded by spermatocytes and a few spermatogonia.

Fig. 8. The kidneys of male and female *Diadophis punctatus* differ in both size and texture. Top: kidney removed from an adult female, 285 mm total length. Bottom: kidney from an adult male, 254 mm total length. *Robert McFarlane.*

Fig. 9. Cross section of the male kidney of *Diadophis punctatus*. The thick-walled urinary tubules give the male kidney its convoluted appearance (fig. 8). The reason for this sexual dimorphism in kidney structure is unknown. *Photomicrograph* by *Sam R. Telford.*

In the first half of May (5 specimens) spermatogonia and spermatocytes are abundant and spermatids present. The lumina are now large but poorly defined because of invasion by loose bundles of spermatocytes and spermatogonia (fig. 11).

No June and July material is available, but in four August specimens spermatocytes and spermatids are abundant and spermatogonia scarce. Mature sperm are conspicuous in one individual collected 21 August, but scarce in three others taken in the first week of the month. The diameters of the seminiferous tubules are now much greater than in specimens killed in March and the lumina are not sharply defined (fig. 12).

Spermatogonia are scarce in an individual collected 22 November, but other germinal elements are common. The seminiferous tubules resemble those in August specimens.

TESTICULAR SIZE AND WEIGHT. The cell poliferation described above is the direct cause of seasonal variation in testicular size and weight. Testes are smallest in the March and April samples and largest in August specimens. Increases in gonadal length and weight show similar curves when plotted, but weight increase (fig. 14) is the more striking.

DUCTUS DEFERENS. Spermatozoa produced in the testis are liberated into the ductus deferens; sperm are stored here throughout most, if not all, of the year (fig. 13). All adult males in the 1958 sample (March to November) carried sperm in this organ, with the exception of one individual (March 29) that had an abnormal kidney. Two specimens collected in Duval County in October 1960 had sperm in the ducts when killed 3 January 1961. Both ontogenetic (fig. 15) and seasonal changes are evident in the width of the ductus deferens, the duct measurements of adults averaging smaller in summer than in spring. Four adults collected in August have a smaller mean duct width (by 0.10 to 0.27 mm) than 6 specimens collected in March, 14 in April, and 4 in May; the differences cannot be accounted for on the basis of body size, for the April and May samples have smaller bodies than the August specimens. The ducti deferentia, therefore, decrease in size at the same time that the testes are increasing. Probably the ducts are at their greatest circumference in the fall and winter after all sperm have been released from the testes; use of spermatozoa in mating (probably in the spring), and perhaps sperm mortality and assimilation, cause a decrease in duct size until spermatogenesis is next completed.

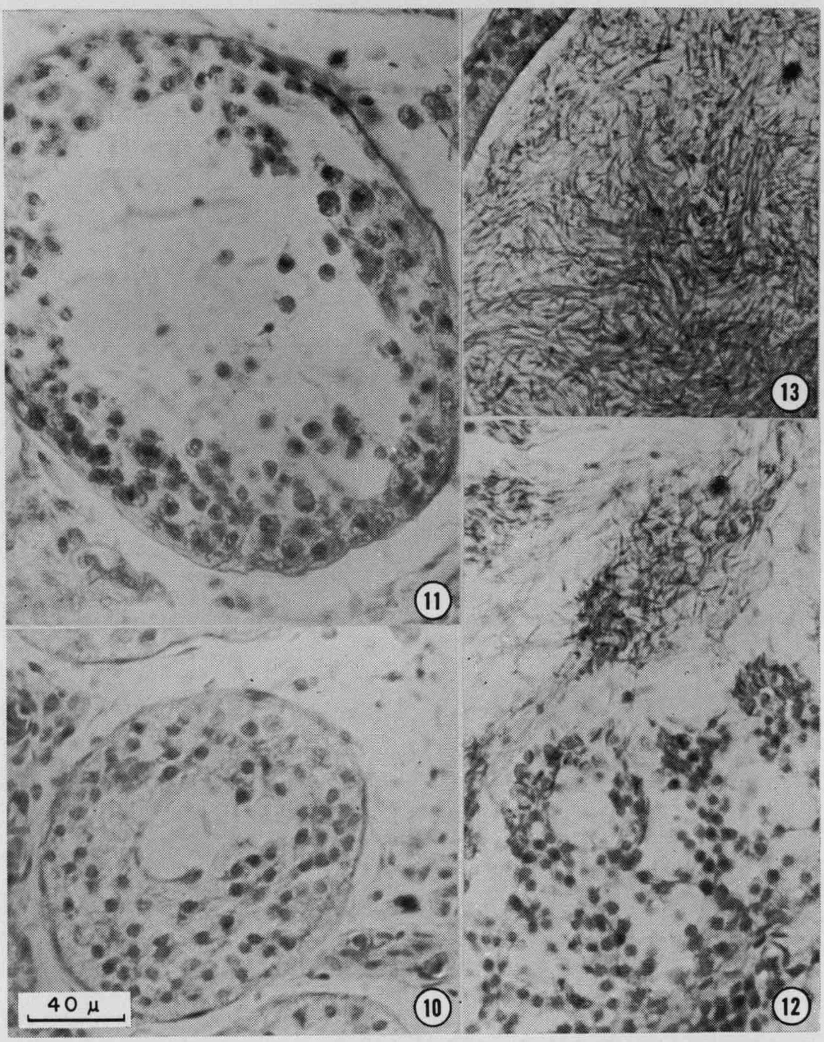

Fig. 10. Cross section of a seminiferous tubule in the testis of a *Diadophis punctatus* collected in March. Spermatogonia surround the small lumen.

Fig. 11. Seminiferous tubule cross section (May). Tubule diameter is much larger than in March; spermatogonia and spermatocytes are present.

Fig. 12. Part of seminiferous tubule cross section (August). The tubule has greatly enlarged in diameter; spermatocytes, spermatids, and spermatozoa are shown.

Fig. 13. Section of the ductus deferens (vas deferens) showing a mass of sperm (November). The structure at the upper left is the ductus wall. Scales for figs. 11-13, the same as in fig. 10. *Photomicrographs by Jay Bergstrand.*

Comparisons with other snakes. Basic aspects of cell proliferation in Florida *Diadophis* agree closely with those of *Thamnophis elegans* in California (Fox, 1952), but the gonadal condition of a *Diadophis punctatus* collected in November suggests that spermatogenic activity may be carried on over a longer period in this species. Spermatogenesis in *Thamnophis elegans* declines rapidly during September and October.

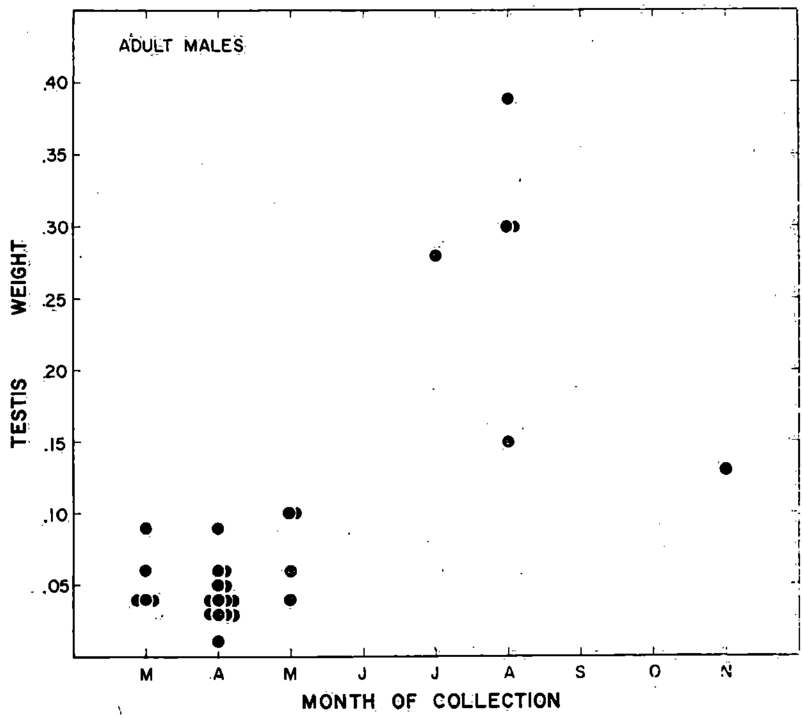

Fig. 14. Seasonal variation in weight of the left testis of adult *Diadophis punctatus* from Alachua County, Florida, 1958. Testis weight is expressed as (milligrams of testis per millimeter of body length) × 1000.

In *Thamnophis radix* of the Chicago region (Cieslak, 1945) spermatogenesis lags about 1½ months behind Florida *Diadophis* and California *Thamnophis* (Fox, 1952, 1954), probably because of more severe climatic conditions.

The peak of spermatogonial proliferation occurs from April to June in *Vipera berus* of Denmark (Volsøe, 1944), but the first spermatids do not appear until August. This differs considerably from the cycles of *Diadophis* and California *Thamnophis,* in which the peak of spermatogonial division apparently occurs at about the same time as in *Vipera,* but where spermatids make their entrance about 4 months earlier.

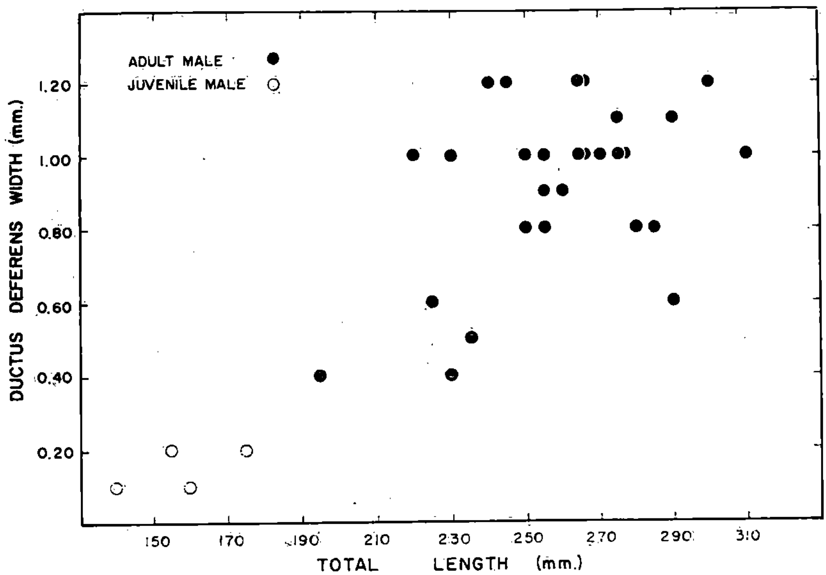

Fig. 15. Ontogenetic variation in the width of the right ductus deferens of *Diadophis punctatus,* Alachua County, Florida. The spread near the top of the graph is probably due, in part, to seasonal variation in the amount of stored sperm.

Seasonal Changes in the Female Genital Tract

The largest ovarian eggs in 15 adults collected 5 and 12 April, average 3.0 mm in greatest diameter (ranges of individual means, 2.0-4.5 mm). Large ova in two collected 10 May average 4.0 and 5.0 mm. Five July specimens show a considerable range in the size of their largest ovarian eggs: 17 July, 4.0 mm, 6.0 mm; 20 July, 15.8 mm; 27 July, 5.5 mm, 13.4 mm. Another individual collected 27 July had three large eggs (22.0, 22.5, 24.0 mm) in the oviducts. One taken 9 August was recently spent; it had enlarged, flabby oviducts, distinct corpora lutea (which seem to be of short duration in *Diadophis*), and no large ova.

Smaller sets of ova, the largest of which would have matured and been laid in the spring or summer of 1959, were often distinguishable by size from those currently maturing. Largest eggs in these second generation sets range from 1.0 to nearly 3.0 mm in April specimens, and from 2.0 to 3.0 in July. Mean size of the largest ovarian eggs for the 27 July specimen containing oviductal eggs is 2.5 mm, and for the recently spent individual in August, 2.8 mm.

These data, based on adult females collected at the Hatchet Creek locality in April and May and at Hale's Siding in July and August, show the largest ovarian eggs increase from a diameter of about 3.0 mm in April to a near maximum of 24 mm in July, when they move to the oviducts. Though yearly breeding is indicated, three late July specimens have ova 4.0-6.0 mm in diameter, smaller than to be expected at this time and larger than second generation ova in females that contain nearly mature eggs or have recently laid. The possibility of an earlier spring laying seems precluded, as these eggs seem too large to represent the next year's clutch, though possibly they might have matured in time to have been laid in late summer. Blanchard (1941) suggests that the act of mating may initiate the development of ovarian eggs in *Thamnophis sirtalis*. If this is true in *Diadophis*, these individuals might not have mated and therefore had eggs that did not undergo full development.

Surface (1906) claims that in Pennsylvania, "The latent gonads or undeveloped eggs are one-fourth inch [6.3 mm] in length and commence to develop in May, when they reach a length of one-half inch [12.7 mm], and by the middle of June they are practically developed, or over one inch [25.4 mm] long." Evidently the eggs in these specimens must have started developing at least a month before those in Florida during 1958. Also, McCauley's (1945) measurements of eggs (18.5-25.6 mm) of four Maryland specimens carried in late June indicate that eggs develop there about a month earlier than in Florida. As discussed below, these differences may be annual variations and not constant geographically.

Period of Egg Deposition

The egg-laying period is evidently rather long in the South. Wright and Bishop (1915) mention a specimen collected 11 June 1912 in southeastern Georgia that contained six eggs 18-21 mm in diameter; it probably would have laid in late June. Smith and List (1955) record a nest of three eggs found on 12 July 1951 in southern Mississippi that hatched on 29 July and might have been laid in June. Telford (verbal communication) found a nest of seven eggs on 19 July 1946 and had a captive ringneck that laid two eggs 12 August 1946 in Polk County, Florida. He sent me a clutch of three eggs a captive specimen from Payne's Prairie, Alachua County, deposited in late May 1961; these eggs were accidently destroyed in the laboratory, but one opened 5 July contained a well developed and pigmented embryo. A gravid female collected in Marion County, Florida, 7 August 1960, was kept refrigerated for nearly a week while being taken to Illinois; it laid one egg about 24 August and two others on 2 September, but all spoiled within a few days after laying. Under normal conditions these eggs probably would have been laid earlier in August, and they may have been spoiled by chilling during development and retained past the normal deposition time.

If captivity prolongs egg retention in *Diadophis* as Blanchard (1942) suspects, the observations cited above can conservatively be taken to mean that egg-laying under natural conditions usually occurs in June and July, and possibly as early as late May and as late as August. The genital tracts of specimens collected in Alachua County in 1958 show no signs of June or early July depositions. A spent individual on 9 August and one with large eggs in its oviducts 27 July indicate late July or early August. Two with average ovarian egg lengths of 15.8 mm on 20 July and 13.4 mm on 27 July surely could not have laid before August.

The time of egg deposition for *D. punctatus* north of the 36th parallel is June and July (table 6); this excludes instances where abnormal eggs have been laid in May (McCauley, 1945) and August (Blanchard, 1930), and also where midwestern specimens have been transported to Michigan and laid eggs in July and August (Blanchard, 1942). In nature the peak of the breeding season probably occurs before mid-July in northern states; I am unaware of a single authenticated case where a northern *Diadophis* has laid normal eggs in August. Nearly 200 sets of eggs (extrapolated from Blanchard) are recorded as being laid before August in Michigan alone. In this light, the Florida evidence for egg-deposition in August takes on significance. Theoretically Florida *Diadophis* could perhaps have a later or longer breeding season than northern populations because of a longer activity season and the absence of a long hibernation period; it is probably to the advantage of northern reptiles to produce broods as early as possible, so that both adults and young can attain maximum physical fitness before winter. Nevertheless in the few other studies comparing northern and southern populations of a snake (Stille, 1954; Tinkle, 1957) the southern populations have bred somewhat earlier, seemingly because of milder temperatures, or more hours per day that body temperatures can be kept within optimum ranges. The August layings in northern Florida may have resulted from the un-

TABLE 6. TIME OF EGG DEPOSITION OF *Diadophis punctatus* BY STATES

State	Time of egg deposition	Basis	Authority
Florida	Late May to early August	Specimens collected and captive layings	This paper
Georgia	Probably late June	Specimen containing large (18-21 mm.) eggs, middle June, 1912	Wright and Bishop (1915)
Illinois	June 30 and July 23	Layings by two captives in 1945	Langebartel (1947)
Kentucky	Late June or early July	13 egg-bearing females June 8-24, and none thereafter, although 6 additional females taken in July and 8 in August	Barbour (1950)
Maryland	a) June 6	a) Captive laid one abnormal egg (on May 26) and later two normal ones in 1919	McCauley (1945)
	b) Late June and early July	b) Four specimens killed in June, 1936-1938, had eggs 18.5-25.6 mm	
Michigan	Late June throughout July	Many captive layings	Blanchard (1926, 1930, 1937a, 1942)
Mississippi	June or early July	Natural nest found July 12, 1951	Smith and List (1955)
Nebraska	Probably June	Specimen containing eggs (largest 18 x 5.5 mm.), May 21	Hudson (1942)
New York	June 28	Captive laying	Ditmars (1951)
Ohio	June 22	Captive laying in 1932	Conant (1951)
Oklahoma	June 20	Captive laying in 1928	Force (1930)
Pennsylvania	Middle of June to July or August	No substantiating data; probably based on dissections	Surface (1906)
Tennessee	Late June or July	Natural nest found July 28	Parker (1937)

seasonably cold weather in the winter of 1957-1958, one of the coldest recorded in the state.

The significance of reports (Ditmars, 1951; Peterson, 1956) that *Diadophis punctatus* may bear living young on occasion cannot now be determined.

TIME OF MATING

Copulation does not seem to have been reported for any species of *Diadophis*. In *D. punctatus* sperm are released into the ductus deferens in late summer and fall and stored there until late into the next summer. The most viable sperm would probably be present in the fall, but large congregations of snakes in early spring might afford more opportunity for mating. The fact that sperm are stored throughout the year might be an adaptation for an extended mating period, but I suspect that mating occurs during the spring as in most reptiles.

Storm (1955) found four *D. amabilis* at the base of a decaying fir stump in October. This stump probably was a place of hibernation, as three other species of snakes were in or near it. The position of the ringnecks, coiled about each other with much of the brightly colored underparts exposed, is suggestive of a mass courtship. A garter snake "ball," perhaps analogous to the above, contained two copulating individuals (Gardner, 1957).

FECUNDITY

The average number of large ova in 20 adults in which different size groups of ova could be distinguished was 5.2; number of ova per individual ranged from 2 to 10, with 4 being the most frequent number (in 7 of 20 cases). In 202 Michigan clutches Blanchard (1937a) found an average of 3.5 in a range of 1 to 7, with 3, 4, and 5 the most usual numbers. Whether southern *D. punctatus* actually lays more eggs than the larger-bodied northern ones is not certain, because differences between potential and realized reproduction are not known. One specimen collected in July was found carrying a desiccated egg; it had three seemingly normal ovarian eggs of 14.5-16.0 mm plus the bad one of 12.0 mm length.

Blanchard (1937a) demonstrated that the numbers of eggs laid by Michigan ringnecks increase with increasing body size of the individual and then apparently decrease with old age. Fig. 16 shows a trend for more ova per larger snake in specimens, but the data are not sufficient to determine conclusively the effects of old age in the Alachua County sample. One of the largest (and oldest?) Florida females examined also contained the greatest number of ova; this individual, from Marion County, measured 340 mm total length (preserved) and contained at least 15 first generation ovarian eggs. This estimate is conservative, as there was no appreciable size break between the first and second generation ova.

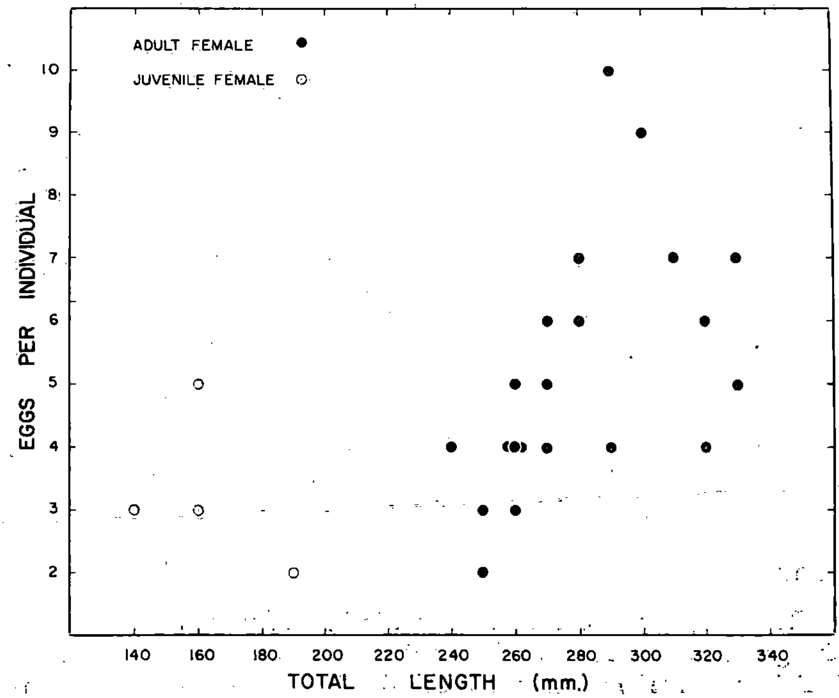

Fig. 16. Number of ovarian or oviductal eggs per female *Diadophis punctatus*, Alachua County, Florida, plotted to nearest 10 mm of snake's total length.

The Egg and Nest

No natural nests were found during this study. Telford (1952) mentions finding several clutches of 3 to 7 eggs in Polk County, Florida, which he told me were all under several inches of litter at the base of an old haystack in a slash pine flatwoods. The University of Florida has an empty shell and two hatchlings (UF 3056) from Hale's Siding. A note with these states that two eggs were found in a rotten log on 23 September 1950; one egg was opened and the other hatched several hours later. The empty shell that was saved measures 23 mm in length.

Telford (1952) states that the hatching time of two clutches in Polk County was about 43 days, but this was for eggs found in natural nests of unknown deposition dates (Telford, verbal communication).

Prehatching Development

Telford also made available a small series of late embryonic stages from a clutch of seven eggs he found in Polk County, Florida, 19 July 1946. Starting on the date of collection, Telford opened one every 7th day until the last egg hatched on 30 August. Brief descriptions of the embryos follow; because date of deposition is unknown, age is expressed in terms of days before the hatching date of the one individual allowed to reach this point.

42 DAYS: Body without visible scales or pigment cells when examined under 40 magnifications. Head not yet formed; two pairs of visceral arches conspicuous, the first (mandibular) not fused but the second pair joined. Heart external. Sex unknown.

34 DAYS: Scales and head plates distinct, but head not perfectly formed, higher than it is wide; eyes well formed. Heart internal. Pigment cells sparse but uniformly distributed over dorsum except in region of neck ring; no markings indicated on venter. Male; hemipenes in everted position.

28 DAYS: As above, but head somewhat more normal in appearance, dorsal pigmentation darker, and black ventral spots now faintly indicated. Male; hemipenes in everted position.

21 DAYS: Head well formed except for a ridge between the parietal plates and a longitudinal depression down the center of the frontal plate. Pigmentation darker than above, the melanophores now most concentrated around the free edges of the dorsal scales; ventral markings distinct. Female.

14 DAYS: Much as above, but head nearly smooth and body more darkly pigmented. Male; hemipenes now in withdrawn position.

7 DAYS: As above, but apical pits on dorsal body scales now discernible as unpigmented spots. Male; hemipenes withdrawn.

HATCHLING (August 30): Male; normal in all respects.

Some Aspects of Growth

The following observations are based on 128 Florida specimens from the following counties: Alachua 93, Volusia 15, Dade 4, Gadsden 2, Jackson 2, Leon 2, Liberty 2, Marion 2, Putnam 2, Glades 1, Lake 1, Martin 1, unknown 1.

Weight-length relationship. Increases in body weight and total length occur simultaneously and seemingly at a rather uniform rate, except that juveniles appear to increase in length more rapidly than do adults (fig. 17). Carpenter's (1953) weight-length graphs for two species of *Thamnophis* in Michigan show similar differential increases.

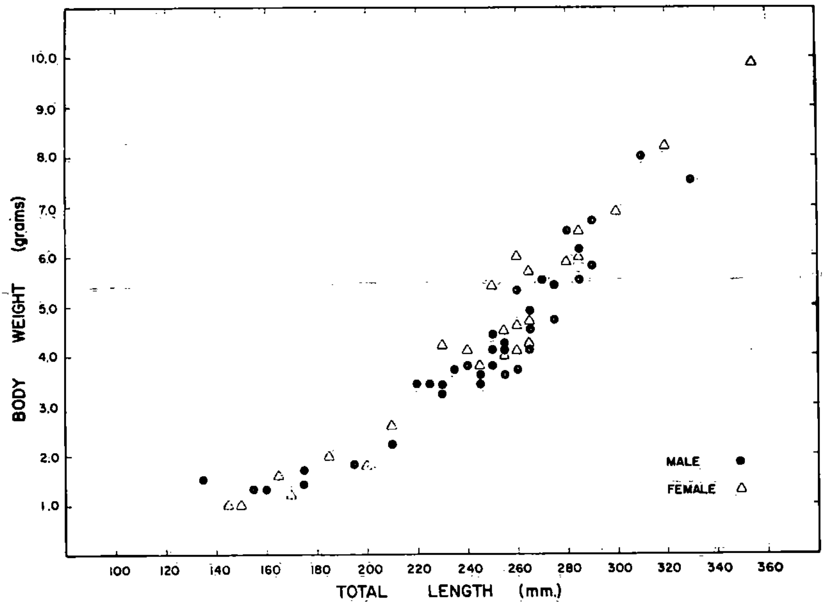

Fig. 17. Weight-length relationship of *Diadophis punctatus*, Alachua County, Florida. Females with eggs measuring more than 4 mm. in greatest diameter are not included.

Attainment of sexual maturity in males. Because sperm are present in the ductus deferens of adult ringnecks throughout most, if not all of the year, sexual maturity is easily determined in males. The time such secondary sex characters as anal ridges and enlarged kidney tubules appear can also be ascertained. Blanchard (1931) first described and illustrated the anal ridges of ringneck snakes; the kidney tubules are shown in figs. 8-9.

Fig. 18 shows that anal ridges, visually enlarged kidney tubules, and sperm usually appear at about the same time, but that any of these characters may appear independently of the others. Anal ridges are generally present only in adults or subadults, but occasionally show as a precocious character in the smallest juveniles (fig. 18; Blanchard, 1931, fig. 7). Nevertheless most adults have anal ridges and most juveniles lack them, which justifies Blanchard's (1931, 1942) use of these structures as an indication of the size at which sexual maturity is attained, at least in *Diadophis*. Two adults had anal ridges and sperm, but lacked visually enlarged kidney tubules. One adult had anal ridges but lacked sperm and enlarged kidney tubules; this individual had a diseased kidney which may have caused its sexual inactivity, although a sexual function of the kidney in *Diadophis* has not been proved. A few adults lacked visible anal ridges; all females except 4 in a sample of 60 lacked anal ridges. One female had weakly enlarged kidney tubules. The presence of typical male structures in these occasional females is probably a result of estrogen-androgen imbalance in the females. No attempt was made to measure possible seasonal size fluctuations of the secondary sex characters, but they are visible throughout the year.

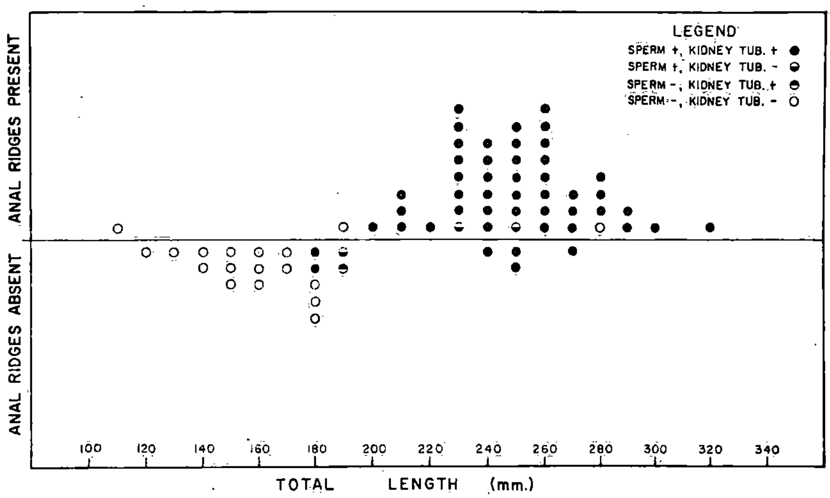

Fig. 18. Size of Florida *Diadophis punctatus* at time of appearance of visually enlarged kidney tubules, anal ridges, and sperm in the ductus deferens. The 280 mm specimen lacking sperm had a diseased kidney. Total length measurements were taken from preserved specimens.

Males attain sexual maturity at about 170-190 mm total length (preserved), or roughly 180-200 mm before preservation. A specimen collected 3 May and measuring 174 mm (169 mm after preservation) lacked all signs of sexual maturity except that the testis contained spermatocytes and was in phase with testes of aduts collected at that time. Although the yearly rate of growth is not known, this individual had probably hatched the previous summer or fall.

The evidence suggests that spermatogenesis probably begins in the first spring, and the snake reaches sexual maturity in late summer or fall when about one year of age. Whether mating takes place at this time or in the following (second) spring is not known.

Attainment of sexual maturity in females. Two juveniles, probably young of the year, collected 3 October and 6 December had total lengths of 157 mm and 140 mm respectively, and their largest ovarian eggs were about 1.0 mm in diameter. The largest ova in two other juveniles collected in April (163 mm) and May (185 mm) were 1.5 and 2.0 mm in diameter; these individuals probably had hatched the previous summer or fall (1957). A specimen measuring 212 mm, collected 20 December 1959 and probably in its second winter, was probably nearing sexual maturity, as its ova (2.0 mm) were as large as in some adults collected the previous April and its oviducts were about 1.0 mm wide, whereas the smaller females had oviducts less than 0.5 mm in width.

These data indicate that females hatched in late summer or fall have ova about 1.0 mm in diameter that fall and the following winter, and ova of about 1.5 or 2.0 mm in their first spring. Little subsequent increase takes place until the second spring when the ova undergo rapid development to be laid in late spring or summer.

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