Herpetological Conservation and Biology 8(2):359−365.
Submitted: 1 November 2012; Accepted: 9 July 2013; Published: 15 September 2013.

Population Declines of Eastern Indigo Snakes (*Drymarchon couperi*) over Three Decades in the Gulf Hammock Wildlife Management Area, Florida, USA

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***Abstract.*—Habitat loss, degradation, and fragmentation are thought to be the primary causes of declines in the distribution and abundance of the Eastern Indigo Snake (*Drymarchon couperi*) throughout its range, although no long-term studies have verified these effects. We report dramatic declines in the relative abundance of this species in the Gulf Hammock of Levy County, Florida, USA. Radio-tracking of *D. couperi* in an 8,628-ha portion of the Gulf Hammock Wildlife Management Area from 1981 to 1983 documented catch-per-unit-effort and habitat conditions and use by snakes. Using similar sampling methods (road cruising and visual encounter surveys), an intensive survey on the same study area from 2005–2009 indicated that the number of individual indigo snakes observed per field day and per field hour had declined by 97.6% and 98.9%, respectively. Potential indigo snake habitat did not become more fragmented, decrease in total amount, or substantially change in cover types in our study area or regionally over these three decades. Circumstantial evidence suggests that cumulative, unsustainable mortality from vehicular traffic, intentional killing, and perhaps intensive forestry operations contributed significantly to the population crash. Predation of nests by Red Imported Fire Ants (*Solenopsis invicta*) also may be important, but environmental pollution, disease, and climate change seem to be insignificant or discountable factors at this site. Similar environmental conditions may be present over much of the remaining range of this threatened species.**

Key Words.—Drymarchon couperi; Eastern Indigo Snake; Florida; fragmentation; population decline; unsustainable mortality

Introduction

Declines in the distribution and abundance of many species of amphibians (Alford and Richards 1999; Blaustein and Kiesecker 2002; Collins and Storfer 2003; Beebee and Griffiths 2005) and reptiles (Gibbons et al. 2000; Gardner et al. 2007; Reading et al. 2010) are of global conservation concern. Habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable harvest, and global climate change are widely recognized threats to many populations (Gibbons et al. 2000). However, the proximate and ultimate causes of these declines remain enigmatic for many species, including a number of snakes in the southeastern USA, such as the Eastern Kingsnake, *Lampropeltis getula* (Krysko and Smith 2005; Winne et al. 2007; Stapleton et al. 2008) and the Southern Hog-nosed Snake, *Heterodon simus* (Tuberville et al. 2000).

The Eastern Indigo Snake (*Drymarchon couperi*) was federally listed as a threatened species in 1978, primarily because of population declines caused by habitat loss, over-collecting for the pet trade, and mortality from gassing Gopher Tortoise (*Gopherus polyphemus*) burrows (USFWS 1978). A recent re-evaluation of the federal status of the species (USFWS 2008) suggested that because of its large home range size, the loss, degradation, and fragmentation of habitat remain the primary threats to the species. Although the Eastern Indigo Snake remains widespread on large tracts in southeastern Georgia and peninsular Florida (USFWS 2008; Enge et et al. 2013), it is now rare on similar-sized tracts in the Panhandle of Florida (Gunzburger and Aresco 2007) and functionally extirpated in Alabama and Mississippi (USFWS 2008). Despite a recent surge in peer-reviewed papers on various aspects of the biology of this charismatic species (≥ 15 published since 2005), no long-term studies of population trends on the same site have been published. Herein, we report dramatic declines in the relative abundance of *D. couperi* in the Gulf Hammock Wildlife Management Area (GHWMA) of Florida over two study periods (1981–1983 and 2005–2009), spanning almost three decades. Having documented the decline, we then evaluate likely causes.

Methods and Materials

***Study area.*—**Historically, the Gulf Hammock in Levy County supported the largest (> 40,000 ha), contiguous hydric hardwood hammock in Florida (Simons et al. 1989). Positioned immediately interior to the coastal salt marshes, these seasonally flooded, freshwater wetland hammocks were characterized by a diverse overstory of hardwood evergreen trees and Cabbage Palms (*Sabal palmetto*) growing on thin soils overlying limestone bedrock (Vince et al. 1989). Interspersed within these low-lying (< 5 m in elevation) hammocks were numerous, shallow seasonal ponds and sloughs (Vince et al. 1989). Beginning in the late 1960s, a network of elevated, limestone logging roads was constructed in the Gulf Hammock (Simons et al. 1989). This entire road network was completed prior to our initial surveys. By 1984, about 80% of the Gulf Hammock had been clearcut, mechanically site prepared, and converted to commercial pine (*Pinus taeda* and *P. elliottii*) plantations (Simons et al. 1989). Since that time, planted pines have been cut on about a 25-y rotation, and in areas too wet for planting, the hardwoods are harvested on about a 40-y rotation.

Our study took place in an 8,628-ha portion of the 12,000-ha GHWMA, centered about 8 km north of Yankeetown, Florida (Fig. 1). Since 1948 the GHWMA has been continuously leased for public hunting from commercial timber companies by the Florida Fish and Wildlife Conservation Commission (FFWCC). It is bordered to the west by Waccasassa Bay State Preserve Park (WBSPP) and to the east by U.S. 19, a 4-lane divided highway. About 300 private inholdings exist within the GHWMA, most of which have retained the native hammock except for small, permanent hunting camps. Land uses surrounding the GHWMA are similar, consisting of commercial silviculture, hunting, and conservation. With the exception of a small (5.6 km) segment of Co. Rd. 326, no primary (paved) roads exist within a 433 km² section of the Gulf Hammock surrounding the GHWMA, although limestone logging roads are numerous (Fig. 1).

Sampling techniques.—Moler (1985) and his colleagues radio-tracked Eastern Indigo Snakes in the GHWMA from December 1981 through April 1983. Most indigo snakes initially were captured crossing roads in GHWMA by Florida Department of Natural Resources (FDNR) personnel traveling to and from WBSPP. Several individuals were located while radio-tracking other instrumented snakes. From January 2005 through March 2009, Godley and his colleagues conducted extensive ecological surveys in this same area of GHWMA as part of environmental permitting activities for a proposed regional limestone mine. All observations of *D. couperi* and other listed species were recorded during this field work and while driving these same roads. During the 8 y of combined field work, Moler and Godley recorded a total of 10 indigo snakes in this 8,628-ha study area of the GHWMA.

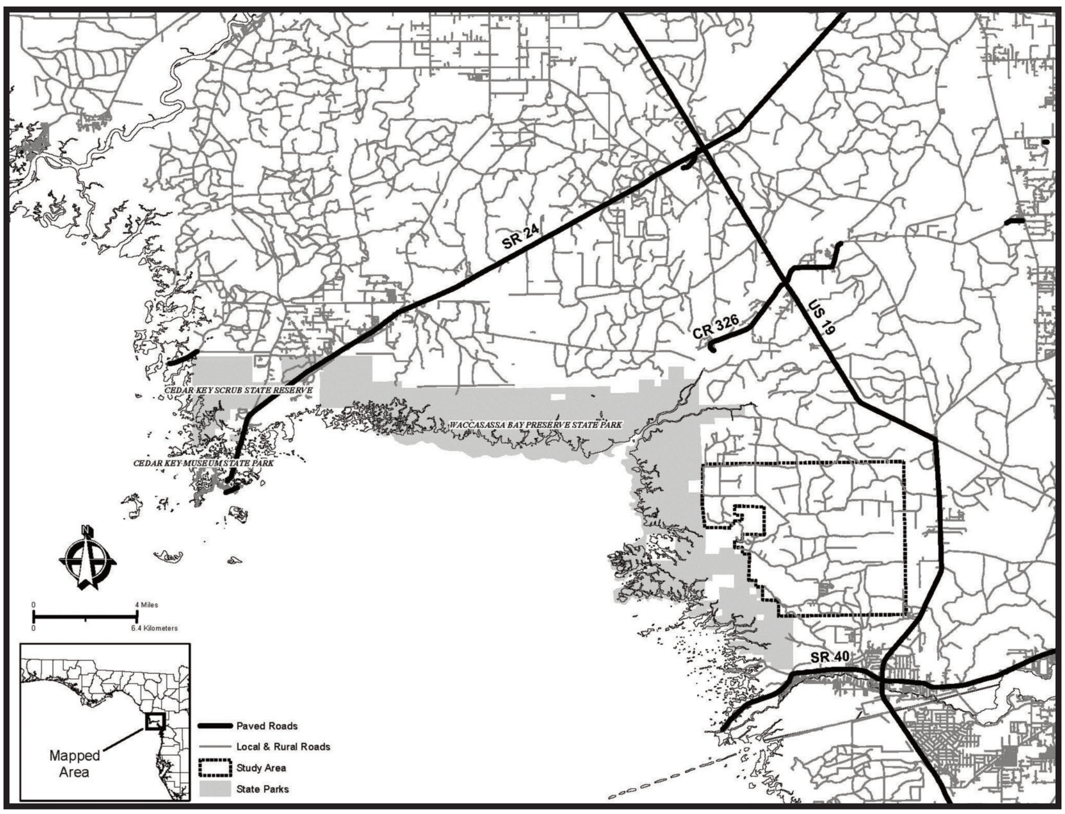

Figure 1. Map of roads and conservation lands in vicinity of the Gulf Hammock study area, Florida, USA.

Data analysis.—We do not have exact records of sampling effort in all cases, but we can provide reasonable estimates. During the Moler (1985) study, we estimate that FDNR personnel spent approximately 32 h (32 person-d) in November 1981 traveling roads in the GHWMA (capturing any indigo snakes encountered), and that Moler and his colleagues spent an average of 5 h/d in the field on each of 72 d of radio-tracking. During the Godley study, the number of field d and h was determined from time sheet entries. Relative abundance (catch-per-unit-effort) of Eastern Indigo Snakes for each study period was estimated by comparing the total number of individuals observed per sampling effort (field h and field d).

To evaluate historical changes in the landscape, we obtained and ortho-rectified 1944, 1952, and 1970 black and white digital imagery of our study area. Using ArcGIS, we also mapped the vegetative communities in the study area during our two study periods from ortho-rectified, false-color infra-red digital imagery dated 1984 and 2007. Moler (1985) found that recent (≤ 10-y-old) pine clearcuts were particularly important habitats to indigo snakes in the GHWMA. He mapped these clearcuts and all mature hammocks in the vicinity of radio-tracked snakes. Godley and his colleagues had timber stand data and used the Florida Land Use and Forms Classification System to Level IV (FDOT 1999) to map community types, including pine stands ≤ 10-y-old. By superimposing Moler's (1985) habitat maps on the 1984 imagery and comparing the vegetative signatures of this imagery to the 2007 mapped imagery, we were able to comparably map and quantify recent clearcuts, older pine stands, and mature hammocks in the study area in 1984 as well. To determine if land use changes in our study area were somehow unique, we visually inspected the 1984 and 2007 imagery for the region (Fig. 1).

Results

During the Moler (1985) study, a total of seven individual indigo snakes were captured or observed in approximately 104 field d and 392 field h of sampling effort for an observation rate of one snake/14.7 d or 56.0 h in the field. Three of the snakes were adult males first found crossing roads and four (two females, one male and one juvenile) were found while radio-tracking. Months of initial observation were November (1), December (1), January (3) and April (2). During the Godley study, only three indigo snakes were observed in 1,875 field d and 15,000 h of sampling effort for an observation rate of one indigo snake/625 d or 5,000 h in the field. All three were adults found crossing roads: two males in December and one of undetermined sex (escaped) in October.

In 1984, there were 11 recent clearcuts (≤ 10-y-old) totaling 3,565 ha (41.3% of study area) with a mean size of 324.2 ha (range = 2.1–2,204.1 ha). By 2007, the number of ≤ 10-y-old clearcuts had increased to 24 but the mean size had decreased to 96.1 ha (2.3–380.1 ha), so only 26.7% (2,306.4 ha) of the study area had been recently harvested. No significant difference in the mean size of clearcuts was detected between the study periods (Mann-Whitney U = 111, P = 0.466), perhaps because of small sample sizes and unequal variances. No change in old-growth hydric hammock or seasonal ponds and sloughs was apparent from the imagery.

Discussion

In less than three decades on the same 8,628-ha patch of GHWMA, the relative abundance of *Drymarchon couperi*, as measured by the number of snakes observed per field d or field h of sampling effort, declined by 97.6% and 98.9%, respectively. Both studies used seasoned field biologists familiar with the species and similar sampling methods (primarily road cruising and visual encounter surveys). Radio-tracking did increase the sample size, as one instrumented adult male was found accompanying an adult female in the breeding season. A reduction in the acreage of recent clearcuts in the latter study period may have affected the relative detectability of snakes while on foot in the field. However, the same number of indigo snakes (three) was seen while traversing the identical road network in both study periods, despite an estimated 30.7-fold increase in field h of sampling effort in 2005–2009. While we acknowledge that natural fluctuations in populations of amphibians and reptiles occur and are difficult to detect and distinguish from anthropogenic causes (Pechmann et al. 1991; Gibbons et al. 2000; Blaustein and Kiesecker 2002; Gardner et al. 2007; Reading et al. 2010), we infer that the apparent dramatic declines of Eastern Indigo Snakes on GHWMA are real, not temporary, and human-caused. In relatively intact, natural landscapes, annual survivorship of adult Eastern Indigo Snakes is high (Breininger et al. 2004; Breininger et al. 2012; Hyslop et al. 2012) and exceeds that of most other large, late-maturing, temperate colubrids (Parker and Plummer 1987). Below, we discuss in order each of the six major threats implicated in the global decline of reptiles (Gibbons et al. 2000) that are applicable to *D. couperi* on this site: habitat loss and degradation, unsustainable use (mortality in this case), introduced invasive species, environmental pollution, disease, and global climate change.

By the time Moler (1985) initiated his study, all secondary limestone roads in the GHWMA (and in the region) had been constructed, 80% of the hydric hardwood hammock in the Gulf Hammock had been clearcut (Simons et al. 1989), and 41.3% of the planted pine in the study area had undergone its first rotational cut. Although four of his five radio-tracked indigos had mature hammock within their home range, this hammock was used infrequently and mostly to exploit the edges of ponds during spring and summer for foraging. Moler (1985) also found that clearcuts were important overwintering sites, where indigo snakes sheltered in rodent burrows, hollow root channels, and other refugia (Gopher Tortoise burrows were absent). He suggested that early successional pine plantations almost certainly supported greater *D. couperi* populations than did mature hammock; like Speak et al. (1978) and Hyslop (2007) in Georgia, Moler (1985) found windrows to be commonly used by indigo snakes as well.

Compared to 1984, by 2007 the total acreage of recent clearcuts had decreased 35.3%, their mean size decreased by 70.4%, and about half of the original clearcuts had also been harvested a second time. The reduction in size of clearcuts was mandated by changes in forestry best management practices over the years (Siry and Cubbage 2002). Aerial application of herbicides to control hardwoods also largely eliminated windrowing as a management practice, decreasing the availability of these temporary sheltering sites. However, the amount of old-growth hammock and important indigo snake foraging sites, such as seasonal ponds in the study area, did not change detectably over time. We surmise that regionally and in our study area (Fig. 1), potential indigo snake habitat did not become more fragmented, decrease in total amount, or substantially change in cover types over the time of our study. We infer that changes in habitat quality and quantity cannot account for the observed population declines. The few indigo snakes captured in the 2000s appeared healthy, and the prey base (other snakes, amphibians, and rodents) seemed robust.

We have no evidence that Eastern Indigo Snakes were collected as pets in our study area, but several lines of evidence suggest that cumulative, unsustainable mortality from vehicular traffic, intentional killing, and perhaps intensive forestry operations contributed significantly to the population crash. During the 2005–2009 study period, we observed hundreds of dead-on-road (DOR) snakes, but none were indigos, perhaps because of their relative rarity by that time. Of the 16 species of snakes that we recorded during this period, about half also were found DOR and at least six species (*Agkistrodon piscivorus, Coluber constrictor, Crotalus adamanteus, Sisturus miliarius*, *Nerodia fasciata,* and *Pantherophis alleghaniensis*) had been shot. Deliberate killing of snakes on roads is common world-wide (Andrews et al. 2008).

We do not have estimates of traffic volumes in our study area, but we presume that it has increased over time (the resident human population in Levy County increased 105.3% from 1980 to 2010; U.S. Census Bureau), and we observed that traffic varied seasonally. In addition to traffic from timber operations and the 300 inholdings with hunt camps within the study area, the FFWCC annually issues 450 recreational hunting permits for the GHWMA. The hunting season coincides with the breeding season of *D. couperi* (October-March; Hyslop et al. 2012), and thereby increases the likelihood of mortality (run over and shot) as males are encountered on roads in their search for mates. The limestone road network also is open to the public year-round.

Moler (1985) reported that the five radio-tracked *D. couperi* in the GHWMA moved locations on 124 of 215 total radio-locations (57.7%). By overlaying the road network on indigo snake locations and assuming straight-line movements between consecutive points, we calculate that 70 roads were crossed by indigo snakes during these 124 movements (mean = 56.5% of movements; range = 42.9–84.0% per individual). Further, of the six individual indigo snakes observed crossing roads during our study, at least five were adult males during the breeding season likely searching for mates. *Drymarchon couperi* has the largest home range size reported for any snake species in North America (Hyslop 2007), and males move more frequently and greater distances than females (Layne and Steiner 1996; Hyslop 2007). In east-central Florida, telemetry studies of Eastern Indigo Snakes (Breininger et al. 2004) found that adult males had an average home range of 120 ha, snakes living along primary (paved) roads soon died, and the species was extirpated from habitat fragments < 120 ha (based on a larger dataset, Breininger et al. [2011] later expanded mean home range size to 202 ha for males and 76 ha for females). Overlaying 120-ha cell grids on our study area showed that 76 of 77 cells contained at least one limestone road, and this density of roads is common in much of the Gulf Hammock and the adjacent region (Fig. 1). Layne and Steiner (1996), Hyslop et al. (2009, 2012), and Breininger et al. (2011, 2012), all reported road kill to be a common source of mortality for this diurnal species on paved, limestone, and dirt roads.

Independent of logging truck mortality, intensive forestry operations in our study area almost certainly contributed directly to the decline of this long-lived (Snider and Bowler

1992) reptile. Indigo snakes spend about 77% of daylight h below cover or underground (Hyslop 2007), and in the Gulf Hammock hollow root channels and rodent burrows were the most important den sites (Moler 1985). At this site, the soil depth beneath the limestone bedrock rarely exceeds 30 cm. Tree harvest, site preparation, and planting are done mechanically, in succession. Some unknown proportion of the population of indigo snakes and their clutches is likely injured or killed during these episodic events.

During intensive surveys from 2005–2007, invasive introduced plant species (i.e., *Dioscorea bulbifera, Lonicera japonica, and Imperata cylindrica*) that might depress the diverse prey base of *D. couperi* (Stevenson et al. 2010) were uncommon and localized in the GHWMA (J. Steve Godley, unpubl. data). Red Imported Fire Ants (*Solenopsis invicta*) were abundant in clearcuts at our study site from 2005–2009 and may have been present during Moler's (1985) study (see Fig.1 of Langkilde 2009). To our knowledge, predation of indigo snakes by this ant species has not been reported, although it is known that fire ants prey on the eggs and hatchlings of a variety of reptiles and they have been implicated with the decline of several species of snakes and other reptiles in the southeastern USA (reviews in Tuberville et al. 2000; Wojcik et al. 2002; Allen et al. 2004). As other species of egg-laying reptiles were common in the latter part of our study, it seems unlikely that *S. invicta* would prey differentially on indigo snake eggs or hatchlings. Although environmental pollution, disease, and global climate change have all been implicated as causes of declines in other species of reptiles and amphibians, we have no evidence that such factors contributed to the decline of Eastern Indigo Snakes in the Gulf Hammock region of Florida.

Conservation implications.—Although the relative contribution of various causative agents remains unknown, it seems likely that we are witnessing the potential extirpation of *D. couperi* from the Gulf Hammock region of Florida. A suite of life-history traits that characterize indigo snakes (large body and home range sizes, male-biased sexual size dimorphism and movements, diurnal hunting for mates and prey, long generation time) appear to be incompatible with the landscape matrix (roads and industrial silviculture) and human activities (intentional and inadvertent killing of snakes) that became established in the Gulf Hammock shortly before our study began. A > 90% reduction in the relative abundance of *D. couperi* in only a few generations suggests that the "extinction debt" (Tillman et al. 1994) of this landscape has yet to be paid.

Nearly identical land uses (commercial forestry, hunting, and conservation), densities of paved and unpaved roads (U.S. Census Bureau, 2008. TIGER/Line Shapefiles. Available from http://www.census.gov/geo/www/tiger/tgrshp2008/tgrshp2008.html [Accessed 13 September 2012]), and human populations (U.S. Census Bureau) now also characterize most of the Big Bend and Panhandle regions of Florida, and these changes occurred over about the same timeframe as reported here for the Gulf Hammock (Kautz 1998). Perhaps not coincidentally, Eastern Indigo Snakes have disappeared or are very rare over most of this landscape (Gunsburger and Aresco 2007; USFWS 2008; Enge et al. 2013).

However, recent status reviews indicate that the Eastern Indigo Snake still remains widely distributed across portions of southeastern Georgia and peninsular Florida (USFWS 2008; Enge et al. 2013). Carefully designed long-term research could quantify key differences in the demographics, life-history traits, and/or landscape matrices that allow these populations to persist and to elucidate why other populations disappear. Such research would also inform conservation and recovery priorities for the species (USFWS 2008), including: (1) the location, size, and acceptable fragmentation level of Eastern Indigo Snake reserves across its remaining range; (2) where reintroductions should or should not be attempted; and (3) the levels and types of habitat connectivity and management needed to maintain populations. In the GHWMA, where roadkill and wanton killing threaten the persistence of the population, signage to alert the public of the listing status of the species, education, and increased law enforcement are clearly needed.

Acknowledgments.—We thank the USFWS for funding the Moler study and Tarmac America, LLC for funding the Godley study. Numerous individuals searched for *D. couperi*; only Tony Morrell, Tom Rooks, John Hintermister, Andrew M. Fuddy, and Annette L. Doyle were successful. A. Curtis Walker prepared Fig. 1 and the ArcGIS analyses. Kristan M. Robbins assisted with statistics and Neisa N. Smith formatted the manuscript. Kevin Enge shared the FFWCC database of Eastern Indigo Snake observations for Florida. We thank Roy W. McDiarmid, Henry R. Mushinsky, Dirk J. Stevenson, and Joseph T. Walsh for reviewing drafts of the manuscript.

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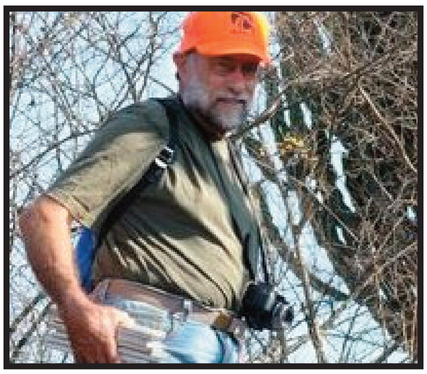
J. Steve Godley earned a Bachelor and Master of Arts in the College of Natural Sciences, University of South Florida. For the past 40 years he has been an environmental consultant in Florida with a focus on the management and conservation of endangered and threatened species, particularly herps. Steve continues to publish as time permits. For the phosphate mining industry he has led the development and implementation of large-scale reclamation and translocation projects that accommodate Gopher Tortoises and a variety of burrow commensals, including the Eastern Indigo Snake he is holding. (Time-release photograph by author with Steven P. Christman [left] and Ron E. Concoby [middle]).



Paul E. Moler attended Emory University (B.A.) and the University of Florida (M.S.). He went to work in 1977 as the first research herpetologist with the Florida Game and Fresh Water Fish Commission, a position he held until his retirement in 2006. Since retirement, he has continued herpetological and astacological research in Florida and herpetological surveys in Vietnam and southern Africa. (Photographed by Randy Babb).