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Life history constraints contribute to the vulnerability of a declining North American rattlesnake

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ABSTRACT

Delayed maturation and age-biased dispersal work in concert under past selection to maximize individual fitness and contribute to population viability; however, these life history attributes can become dysfunctional in a dynamic, anthropogenic landscape when important population demographics cannot redistribute in response to novel landscape change. We used long-term monitoring data to estimate age at maturity, potential longevity, survival, and fidelity for the declining eastern diamondback rattlesnake (EDB), *Crotalus adamanteus*. We used radio telemetry data and known-fate models to examine adult survival, and we combined mark-recapture and radio telemetry data to examine survival and fidelity using a combined recapture/recovery model. Monthly adult survival was higher during the active season (April–November; 99.5%) as compared to the inactive season (December–March; 96.3%), despite a higher probability of detecting human-caused mortalities during the active season. Rattlesnakes matured in 7.1 years and potential longevity exceeded 20 years. Fidelity estimates indicated mature EDBs had a low probability of dispersing from the study area, while younger, sexually immature individuals were more likely to emigrate. The combination of a slow life history and an ontogenetic shift in emigration suggests EDB life history limits the species' ability to respond to landscape change, shedding further light on EDB imperilment. Management efforts will benefit from activities that maintain high adult survival. Furthermore, EDB fidelity should be considered in conservation plans, particularly in light of the species' longevity, as these characteristics suggest that mature EDBs may not readily redistribute at the landscape scale in response to habitat degradation.

1. Introduction

Within certain constraints, life history traits (e.g., age at maturation, dispersal rates) naturally vary across populations, reflecting environmental variation and local selection that shift the balance of tradeoffs to maximize fitness and contribute to population viability (Stearns, 1992). Tradeoffs link competing life history traits to maximize fitness, but can constrain the ability of a population to respond to abrupt changes in selection (Roff, 2002). For instance, species with low dispersal abilities are highly susceptible to local extirpation due to rapid anthropogenic landscape change (Parvinen, 2004). Thus, life history attributes, such as generation time, age at maturation, and dispersal ability, can interact with the spatial and temporal dimensions of a disturbance, resulting in a lag time between anthropogenic activities and extirpations (e.g., the extinction debt, see Jackson and Sax (2010) for review). Identifying such interactions is extremely important for conservation because wildlife biologists can then focus management efforts on specific demographics to maintain viable populations. For example, long-lived species are more likely to suffer population declines due to decreased adult survival, regardless of changes in juvenile survival (Crone, 2001; Legendre, 2004; Raimondo and Donaldson, 2003); in this scenario, biologists can influence population viability by managing adult survival (Crone, 2001; Enneson and Litzgus, 2008).

Within the context of life history theory (Roff, 2002; Stearns, 1992), delayed maturation, high adult survival, and age-biased dispersal work in concert, linked under past selection, to maximize individual fitness and contribute to population viability. However, the novel dynamics of anthropogenic landscapes can abruptly change selection, and these linked attributes can become dysfunctional if population viability is strongly affected by a demographic that is unlikely to respond to habitat degradation by redistributing at the landscape-scale (Ewers and Didham, 2006).

In this study, we quantified age at maturation, survival, and redistribution probability for a declining rattlesnake (eastern

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diamondback rattlesnake, *Crotalus adamanteus*; EDB), with the goal of examining these attributes within the framework of species imperilment. Insight into these life history parameters is currently lacking for EDBs. The species' status is being reviewed by the IUCN viper specialist group (IUCN, 2011), and the species is currently being reviewed for federal protection under the Endangered Species Act (United States Fish and Wildlife Service, 2012). We used long-term monitoring data to examine several life history parameters that are potential contributors to the species' overall decline. We estimated age at maturity and modeled survival because these attributes are often linked (Roff, 2002; Stearns, 1992), characterizing a 'slow life history,' and are commonly cited as contributors to species vulnerability (Anderson et al., 2011; Purvis et al., 2000; Webb et al., 2002). Our assessment of EDB survival included intra-annual time intervals (e.g., seasonal effects) and causes of mortality, allowing us to examine potential conflicts between EDB conservation and human land use. We used a combined recapture/recovery model to examine redistribution probabilities and test for an apparent ontogenetic shift in dispersal behavior at the landscape-scale. Even through EDBs can have rather large home-ranges, e.g., up to 320 ha for the study population (Waldron et al., 2006), we suspected a high degree of landscape-scale site fidelity based on individual recaptures that occurred in close spatial proximity over multiple years. Further, despite the species' high degree of habitat specificity (Waldron et al., 2006, 2008), some individuals appeared to continue occupying a location even after portions of the area experienced habitat degradation (e.g., fire exclusion and pine plantation forestry). This pattern of spatial fidelity was more apparent in larger individuals, and thus we suspected an ontogenetic shift in dispersal behaviors, with mature (larger) individuals having a very low probability of redistributing at the landscape scale.

We hypothesized that EDB survival would be high and exhibit time-dependent variation reflective of seasonal differences in snake behavior and activity, e.g., Bonnet et al., 1999. We suspected survival would be lower during the inactive season (e.g., hibernation), particularly for individuals with low body condition. In other *Crotalus* species, adult survival is often higher than juvenile survival (e.g., Northern Pacific rattlesnakes, *C. viridis oreganus*, Diller and Wallace, 2002; timber rattlesnakes, *C. horridus*, Brown, 2008); thus, we expected EDB survival would increase with body size. Further, we hypothesized that differences between male and female reproductive behavior would affect survival. For example, we expected that male survival would be lower during the breeding season due to increased movement activity associated with mate searching (e.g., Bonnet et al., 1999). Lastly, we hypothesized that human-caused mortality would occur at a higher frequency during the active season as compared the inactive season. Specifically, we expected a greater frequency of human-caused mortality during the breeding season relative to the foraging and hibernation seasons.

2. Methods

2.1. Study area

This study was conducted in the South Carolina southeastern Coastal Plain, USA, on property managed by the South Carolina Department of Natural Resources. The study area is located within ca. 18 km of the western limit of the species' distribution in South Carolina. The 2 374-ha property contains a mosaic of habitats, including longleaf pine (*Pinus palustris*) flatwoods and savannas, loblolly pine (*Pinus taeda*) forests, oak-hickory mixed-pine hardwoods, hardwood bottoms, and cypress-tupelo swamp forests associated with the Savannah River floodplain. The area is managed with growing- and dormant-season prescribed fires, which maintain high vascular plant diversity (Porcher and Rayner, 2001) and support habitats for longleaf-pine endemic wildlife, including colonies of federally endangered red-cockaded woodpeckers (*Picoides borealis*). Game management at the study area includes maintenance of agricultural food plots in upland habitats, focuses on bobwhite quail (*Colinus virginianus*) and white-tailed deer (*Odocoileus virginianus*).

2.2. Study species

The EDB is endemic to the imperiled longleaf pine ecosystem (Martin and Means, 2000; Timmerman and Martin, 2003). Dependent on savanna structure at multiple spatial scales, the EDB is considered a remnant of the historical southeastern woodland–savanna landscape (Martin and Means, 2000; Waldron et al., 2006, 2008). It occurs in the southeastern Atlantic and Gulf Coastal Plains from southeastern North Carolina through eastern Louisiana, including Florida (Martin and Means, 2000; Timmerman and Martin, 2003), and it is listed as a species of conservation concern in Alabama, Mississippi, and South Carolina. North Carolina populations are endangered, and EDBs are critically imperiled in Louisiana. In addition to habitat loss, over-collection, rattlesnake round-ups (Means, 2009), indiscriminant killing by humans, and a lack of public policy regarding protection have accelerated the species' decline (Martin and Means, 2000).

2.3. Data collection

We monitored EDBs between 1994 and 2011 using mark recapture surveys and radio telemetry. We captured rattlesnakes using visual surveys, coverboard sampling, incidentally on roads, and while conducting radio telemetry surveys. We used hooks and clear snake tubes to safely restrain individuals while we collected morphological data. We determined sex by counting subcaudal scales and using cloacal probes. We measured snout-vent-length (SVL) to the nearest cm and subcutaneously injected a passive integrative transponder 13 ventral scale rows above (cephalad) the cloaca. After 2005, we cauterized ventral scales according to Winne et al. (2006), in addition to injecting transponders.

We implanted 29 adults (21 females, 8 males) with radio transmitters (SI-2, 11–13 g, Holohil Systems, Carp. ON) between 1997 and 2005 using modified surgical procedures outlined by Reinert and Cundall (1982). We monitored individuals $\leqslant$3 years using a radio receiver (Telonics, TR-2, Mesa, AZ), and thus some individuals required multiple transmitter implantation and removal surgeries. We located individuals three to five times weekly during the active season (April–November), and weekly to biweekly during the inactive season, which included hibernation and emergence. Our goal was to visually detect EDBs upon each radio location while maintaining 2–5 m between observer and rattlesnake.

2.4. Age at maturation

We used growth intervals from females to estimate age at maturity. We excluded males from the analysis due to insufficient recapture data, using female-based estimates for population-level inferences. Excluding neonates captured at birthing locations, all EDBs captured in this study were of unknown age. Estimating age-related parameters using mark-recapture interval data is widely accepted as a valuable conservation tool, even when the age of marked individuals is unknown (Eaton and Link, 2011). We used a modified von Bertalanffy growth model to estimate age at first reproduction (Frazer and Ehrhart, 1985; Isely and Grabowski, 2007) because the approach is robust with small data sets (Eaton and Link, 2011). To examine the assumption that