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Lifetime Reproduction in a Northern Metapopulation of Timber Rattlesnakes (*Crotalus horridus*)

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Abstract: Lifetime reproduction is a fundamental demographic variable for all vertebrate species, but rarely has been examined in snakes. In the southeastern Adirondack Mountains of New York, I used a capture–recapture method over a 36-yr period to study the lifetime reproductive biology of *Crotalus horridus* in a metapopulation of communal overwintering dens. These longitudinal data allowed analysis of the following parameters for many females throughout their reproductive lives: age and size at first reproduction, reproductive cycle length, duration and frequency of reproduction, body mass changes, and fecundity. Within the metapopulation, first reproduction occurred at a mean age of 9.6 yr, mean length of reproductive cycles was 4.2 yr, mean reproductive life span was 9.6 yr, and average fecundity was 7.7 offspring per litter. Nonviable offspring were observed in 20% of field litters. Although several female snakes produced multiple broods (as many as seven litters over spans as long as 32 yr), most females reproduced only once—the mean number of lifetime reproductive events was 1.7 efforts per female. During their gravid year, most females lost 2–3% of their initial mass, but gains and losses as great as 15–20% indicate feeding during gestation. Microgeographic differences were evident within the metapopulation and might be correlated with (1) resource levels that could influence growth rates, or (2) human encounters that could influence survival rates. Conserving *C. horridus* in its northern range depends on recognizing the importance of a suite of reproductive constraints—late age of maturity, long reproductive cycles, and low number of lifetime efforts—that clearly influence the viability and persistence of local populations.

Key words: Age at maturity; Fecundity; Female body size; Life history; Reproductive cycles; Viperidae

Lifetime reproduction is a fundamental demographic variable that has been studied in a number of vertebrate species, particularly birds (e.g., Fitzpatrick and Woolfenden 1988; Ollason and Dunnet 1988; Spendelow et al. 2002) and mammals (e.g., Clutton-Brock et al. 1988; Wauters and Dhondt 1995; Barlow and Clapham 1997). In these and other studies, sometimes conducted over impressive time spans of three or more decades, researchers have focused on quantifying parturition or oviposition intervals, the observed reproductive history of females, litter or clutch sizes, and offspring survival. Long-term, individual-based studies of animal populations are increasingly invoked in explaining the evolution of age-related reproductive, behavioral, and demographic characteristics (Clutton-Brock and Sheldon 2010).

Lifetime reproductive success is generally recognized to consist of three components: (1) reproductive life span, (2) offspring survival between birth and reproductive age, and (3) average annual fecundity over the reproductive life span (D. Brown 1988; Clutton-Brock 1988). Researchers have often focused on the relative benefits of two patterns of reproduction: (1) income breeding, using resources gathered and expended during the current reproductive period—a strategy associated with iteroparity and common among endothermic taxa, or (2) capital breeding, using energy gathered at some previous time and stored for a future reproductive event—a strategy associated with either iteroparity or semelparity, and common among ectothermic vertebrates.

In snakes, several aspects of reproductive biology were reported in early decades of the 20th century (reviewed in Nilson 2011), as well as in more recent studies (Parker and Plummer 1987; Shine 2003; Gregory 2009; Aldridge and Sever 2011). In the context of the ecology and life history of reproduction, several authors have analyzed models of relative clutch mass and reproductive effort (Seigel and Fitch 1984; Shine and Schwarzkopf 1992); phenotypic plasticity in reproductive traits (Ford and Seigel 1989, 1994); clutch or litter size variation (Seigel and Ford 1992; Shine and Seigel 1996; Seigel and Ford 2001); comparative methods for measuring breeding frequency (Bonnet and Nalleau 1996); lifetime reproductive success and costs of reproduction (Bonnet et al. 2002; Bonnet 2011); and documenting effects of resource levels, thermal constraints, and food supply on physiological condition and reproductive effort (Nilson 1981; Andren 1982; Seigel and Fitch 1985; Naulleau and Bonnet 1996; Diller and Wallace 2002; Lourdais et al. 2002, 2004; Beaupre 2008; Gardner-Santana and Beaupre 2009; Jenkins et al. 2009; Schuett et al. 2011, 2013). The capital-breeding strategy is common among snakes (Bonnet et al. 1998). Documenting the variance of reproduction in long-lived species depends on carrying out long-term studies of "the reproductive performances of individuals over... the entire lifetime of the organism in question" (Madsen and Shine 1994:561).

Timber Rattlesnakes (*Crotalus horridus*) are moderately large, monotypic but geographically variable crotalines that are widely distributed in the eastern half of the United States and, formerly, extreme southeastern Canada (Clark et al. 2003; Allsteadt et al. 2006; Martin et al. 2008; Ernst and Ernst 2012; Rowell 2012). The spatial and seasonal biology of *C. horridus* in the northern sectors of North America are centered on hibernacula (dens) into which local populations communally retreat with high fidelity through the winter months. In its northern range, important reproductive characteristics in female Timber Rattlesnakes include late age at maturity and infrequent reproduction. In addition, female snakes in these areas likely have a low lifetime birthing frequency, but this aspect of their reproductive biology remains elusive because of the extended longevity of

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individuals in undisturbed populations, not to mention the paucity of the latter. In summarizing the reproductive life history of snakes, Seigel and Ford (1987:227) stated: "The frequency of reproduction is both the most important and the least understood aspect of snake reproductive biology." The current investigation focuses on this life-history trait.

The data that I present on the reproductive biology of Timber Rattlesnakes are part of my long-term field investigation of the natural history of this species. I examined female reproductive patterns in a northern metapopulation (a series of dens) of *C. horridus* in the Adirondack Mountains of northern New York. For the female snakes returning to each den, gestation requires a sufficiently large (radius ~2 km) and undisturbed area around the den to provide critical basking habitat for reproductive females. As documented by Brown (1991) and Martin (1993, 2002), most female *C. horridus* in three montane populations do not reach an age of first reproduction until they are at least 7–8 yr old, reproduce only at 2- to 7-yr intervals, and apparently undertake few reproductive attempts in a lifetime.

My analysis of female reproduction in *C. horridus* focuses chiefly on measurements of two components of reproductive success—reproductive life span and fecundity—while also expanding the data on reproductive frequency and cycle lengths (Brown 1991). My approach examines these variables over a time sufficient to encompass several snake generations, and measures the age of first reproduction and iteroparity in a longitudinal data set that spans more than three decades. Additional data on body mass changes of reproductive females in several reproductive states (e.g., vitellogenic, gravid, postpartum) provide inferential insights into the evolution of a variable reproductive strategy.

Materials and Methods

Environmental Setting

Brown (2008) described the geographic setting, habitat features, and den characteristics of the study site. Briefly, the elevation range is ~150–400 m at the dens that are situated in a habitat matrix of southeast- to southwest-facing wooded ridges, ledges, and grassy knolls within a region composed largely of unbroken northern hardwood forests. The summer ranges of rattlesnakes at this locality encompass a wide variation of elevations, as some snakes move to habitats at elevations lower than their dens, whereas others move to areas of higher elevation than their dens (≤680 m). Glacial surface features in grassy clearings are utilized by pregnant females, and these features and shelter boulders or crevices provide basking opportunities and protection, respectively, for females at these gestation sites. Prominent woody vegetation near gestating areas consists of red oak (*Quercus rubra*), shagbark hickory (*Carya ovata*), hophornbeam (*Ostrya virginiana*), and common juniper (*Juniperus communis*). Within a recent 25-yr period (1979–2002), the pattern of surface activity for *C. horridus* has occurred consistently between their periods of emergence (5–25 May) and ingress (7–27 September); 95% of the capture records occurred between 29 April and 5 October, a 5.2-mo active season (Brown 2008).

The Adirondack metapopulation forms a roughly linear series of nine dens spanning 12 km; two dens chosen for detailed study are located ~9.2 km from each other, with four dens positioned between them, and three located peripherally (Fig. 1). I consider this system to be a composite population or metapopulation, wherein local populations interact via individuals that move from one to another (Hanski and Gilpin 1991). Many basking sites are shared by snakes from neighboring hibernacula, thereby facilitating females from one den being located by males from another during the summer mating season. As such, relatively low levels of genetic differentiation have been noted among individuals representing populations local to each den (Clark et al. 2008; WSB, personal observation).

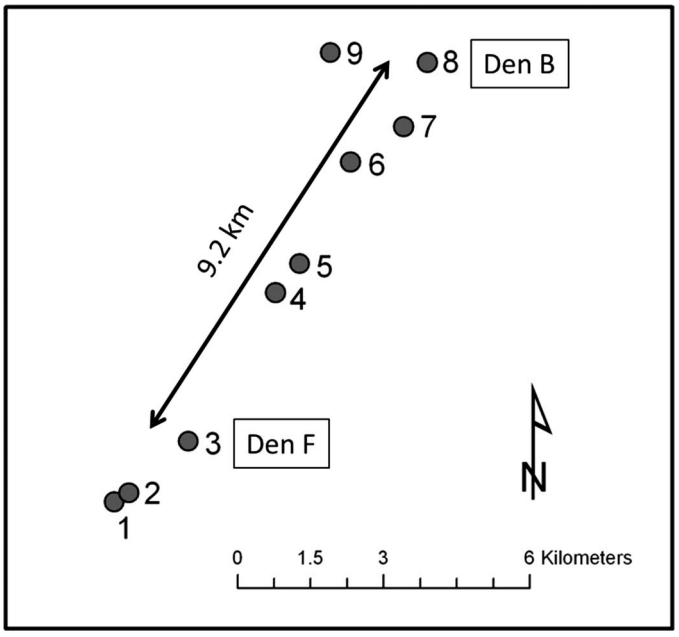


Fig. 1.—Map of den sites for a metapopulation of Timber Rattlesnakes (*Crotalus horridus*) in northeastern New York, USA. Data from two dens (F, B) were the basis for reporting comparative reproductive variables.

Sampling and Processing

The basic method to measure the long-term reproductive histories of female *C. horridus* involved capturing, marking, and recapturing individual snakes. I followed the most accurate of three methods evaluated by Bonnet and Nalleau (1996) to estimate breeding frequency: direct observation of gravid females captured in successive annual samples in the field. At the study site, reproductive females use summer gestating habitats predictably, allowing them to be sampled every year. Although all dens in the metapopulation have contributed data concerning female reproductive histories, the gestating habitats around many of the dens could not be adequately sampled regularly every year because the local topography effectively prevented knowing where all (or most) of the gestating sites were located. Among the dens in the study area, Dens B and F (Fig. 1) were tractable in terms of habitat and terrain. These two sites provided reliable knowledge of the traditional gestating areas associated with them.

I located individual *C. horridus* by visual encounter surveys, an opportunistic approach generally ranked high among methods for sampling snakes (Dorcas and Willson 2009). Surveys were guided by pre-existing knowledge or

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prediction of habitat areas to be searched, rather than conducting randomized block or transect surveys. Sampling was conducted around the target dens—usually at higher elevations—where a number of gestating sites, both previously known and new, were monitored on each survey. The sampling days were irregularly spaced and sites were checked repeatedly, mainly over 3 mo (June, July, August). Each day's sampling covered different sectors of the available gestating habitats within ~1.5 km of the dens. Complete coverage of the area surrounding each focal den usually required 2–4 d; surveys were repeated as weather permitted. Female snakes were typically captured and processed at the gestating sites.

Once the gestating sites around the two focal dens, and their use by females, had been incorporated into my survey routine over the first 2–3 field seasons, these dens were specifically targeted by consistent sampling procedures. Although gestating sites around the other dens were sampled less regularly, they too yielded numerous captures of females and provided life-history data that complemented the more extensive data from the two focal dens. This study took place continuously over periods of 35 and 36 yr at Dens F and B, respectively.

Processing rattlesnakes included the following procedures: (1) weighing each snake with a Pesola spring scale (± 1–5 g, depending on snake size, cf. Brown 2008); (2) determining individual identity; (3) recording the general body condition, injuries, or lesions; and (4) noting the segment count and morphology of the rattle. A subset of captured individuals was returned to the lab in order to measure total length (TL) in a squeeze box with the use of a calibrated map wheel. All snakes were released at site of capture. Permanent marking was accomplished by ventral scale clipping (Brown and Parker 1976) supplemented by temporary paint marking of the rattle (Brown et al. 1984). Once clipped, the scars persisted permanently over the natural life span of *C. horridus* at this locality.

Estimating Den Sizes

Several reproductive parameters reported here pertain exclusively to the two selected focal dens, separately or combined. I defined "capture days" (CD) as the number of days during which at least one female was captured in a given year (CD provides a metric for comparing yields between dens and years). Brown et al. (2007) estimated detectability (p; Williams et al. 2002) of *C. horridus* at this site to equal ~0.20. Therefore, to compare the two target dens with the use of the annual capture totals of both sexes, the annual counts were multiplied by five. This approach yielded adjusted counts that were averaged across years to produce a crude abundance estimate for each focal den.

Reproductive States and Body Mass

Reproductive states classified were immature (I), nongravid (N), vitellogenic (V), gravid (G), and postpartum (P). I snakes had small values for TL and body mass, as well as short rattles. G females were visibly distended posteriorly, with sagging abdomens when held vertically for a few seconds (I avoided palpation to prevent possible damage to the embryos). V females were diagnosed as being heavy posteriorly and having palpable enlarging oocytes; their later gravid status was confirmed by recaptures. N females lacked the characteristics of either G or V females. P females were thin and diagnosed by posterolateral integumentary folds, low body mass, and occasional residue of dried amniotic fluids on the skin. These females were recorded in autumn (typically in September) shortly after having given birth, or (less often) in spring or summer of the year following parturition.

Because fidelity to gestating sites was generally high, it was possible to recapture some G females within their reproductive year. On these occasions, mass measurements recorded at each capture event provided G-to-G comparisons of mass during pregnancy. Similarly, it was often possible to record the postpartum masses of females in the autumn or following spring, after they had delivered their litters. Changes in mass during the G-to-P transition were calculated in grouped samples, as well as in samples composed of individuals recaptured within that period of time. V females were generally recorded in August or September, a full year prior to their expected parturition (Brown 1995; McGowan and Madison 2008). Some of those subjects captured when gravid provided limited data on body masses in the V-to-G transition.

Aging Methods and Age Transitions

I estimated the ages of first-time G females by two methods: (1) rattle measurements, and (2) sequential recaptures of individuals initially caught as I snakes. For most females, a combination of both methods was available. The records of females with extended capture histories from I to G states—usually encompassing about 3–10 yr—allowed accurate estimates of the initial rattle-based age, which I then extrapolated to the gravid year. Most of these young individuals (n = 102, or 80%) had a capture history that included a combination of recaptures and rattle sizes; fewer individuals (n = 25, or 20%) were based on rattle size only (i.e., rattles of snakes lacking intermediate captures prior to the gravid year).

Rattle size was recorded as complete (i.e., included the natal button) or broken (missing the button and/or one or more subsequent segments). If broken, I also visually estimated the number of missing segments (based on the remaining segment widths). The missing-segment estimates were restricted to three levels of broken rattles: missing the button only (b); missing the first segment plus button (1 + b); or, missing the first two segments plus button (2 + b). No broken rattles greater than 2 + b segments missing were utilized in estimating ages. Stand-alone rattle size corroborated an individual's earlier rattle when accompanied by intervening shedding events, as evidenced by the loss of paint marks on the rattle (Brown et al. 1984; W.S. Brown 1988). For young females and males (age 1–10 yr), a mean rate of 1.4 sheds/yr was utilized to estimate age. Because the range of possible ages of an individual increases with rattle size, ages of first-time G females reported here (mainly 9–11 yr) should be interpreted as falling within an approximate deviation of ±1 yr of the actual age.

Based on the long-term average earliest date of annual birthing (Brown et al. 2007), I set the date of the annual age transition to 1 September. If a snake's capture occurred in spring prior to shedding, its age (X_i) would have been attained in the prior year, so its age in the current year was X_i + 1; if its capture occurred in summer after shedding, X_i

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TABLE 1.—Sampling data (mean ± SD) for gravid female Timber Rattlesnakes (*Crotalus horridus*) recorded at two focal dens in a long-term field study (1979–2014) in northeastern New York. G = gravid, CD = capture days (see text).

Den	Years	G females	CD	CD per year	G females per year
F	35	264	274	Mean = 7.83 ± 3.78	Mean = 7.51 ± 5.52
				Median = 7.0	Median = 6.0
				Range = 2–14	Range = 1–26
B	36	194	221	Mean = 6.14 ± 3.19	Mean = 5.39 ± 2.72
				Median = 5.5	Median = 5.0
				Range = 2–18	Range = 0–11

applied to the current year. All of the snakes' estimated ages were adjusted uniformly to reflect this timing difference in capture dates so that each snake's age pertained to its current year of life.

Fecundity and Reproductive Efficiency

The use of palpation for counts of oocytes, ovulated ova, or embryos can be unreliable; also, I wanted to minimize the risk of injury during handling to a female or her fetuses. Instead of abdominal palpation, I obtained fecundity estimates in a 5-yr interval (1982–1986) early in the study when 31 G females were captured during late gestation and returned to the lab where parturition occurred within 1–24 d (mean = 10.3 d following capture). These data were supplemented in 1988 and 1992, when four litters were counted in the field.

I calculated reproductive efficiency (Lourdais et al. 2002) as the proportion of nonviable offspring in a litter for female snakes that produced any one of three brood categories: (1) normal neonates (NEO); (2) stillborn neonates of both normal and stunted body size (SB); and (3) arrested fertilized ova or infertile oocytes (yolky masses, or so-called "yolk plugs;" OO). Litters were grouped into two categories: Type A litters = NEO; and Type B litters = NEO + SB + OO. In the field, yolky masses and stillborn or stunted fetuses were found, usually in association with recently born litters observed with their postpartum mothers. The frequency of yolk plugs seen with their normal littermates was compared with the frequency of the nonviable output from those females returned to the lab.

Reproductive Life Span and Cycle Lengths

A reproductive interval includes successive reproductive events, and thus, is 1 yr longer than a reproductive cycle length (e.g., a 4-yr interval would encompass a 3-yr cycle). Because biennial cycles made up only 1% of all observed cycles, I was confident that all longer (3–7 yr) cycles were real (i.e., not composed of two shorter cycles). This interpretation is supported by the fact that I rarely captured iteroparous females in the intervening years between the gravid years. It was unusual to find any female other than a gravid one at a gestating site (rarely, an I or a N female, or even an occasional male, might be found). Many summer recaptures of females in their nonreproductive years occurred in forested summer habitats distant from the gestation sites. As such, I was confident that longer cycles were not attributable to lack of a recapture while gravid.

In estimating the number of lifetime reproductive efforts, I established an arbitrary cutoff year of 2009 in order to eliminate those females that reproduced only once (probably their first attempt), thus reducing bias of this estimate. This procedure removed a small number of G female captures (seven records from Den B, nine from Den F) during the last 5 yr of the study (2010–2014) that would have been treated as one-time-only events.

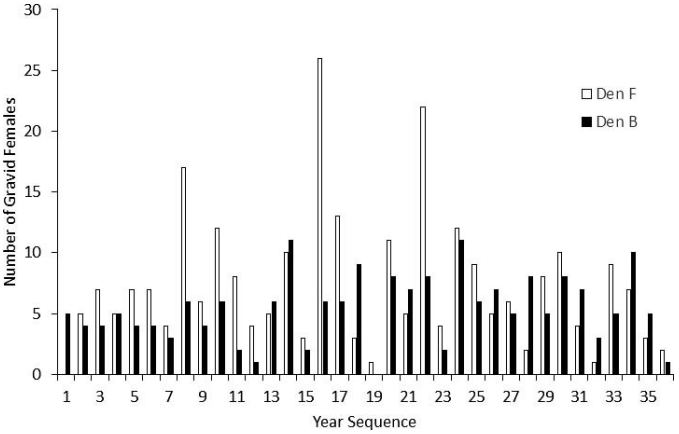


FIG. 2.—Time series of gravid female Timber Rattlesnakes (*Crotalus horridus*) captured annually over a 36-yr sampling period (1979–2014) at two focal dens in northeastern New York, USA.

Statistical Procedures

Parametric and nonparametric tests and other procedures followed Woolf (1968), and were performed with the use of Statistix (v9, Analytical Software, Tallahassee, FL); significance levels were set at $\alpha = 0.05$. Unless stated otherwise, mean values are reported ±1 SD.

RESULTS

Sampling Effort and Den Population Estimates

At the focal dens, female CD averaged 7.8 d per year at Den F and 6.1 d per year at Den B (Table 1). There was no correlation between the number of G females caught and the total CD per year ($r^2 = 0.02$, $F = 1.36$, $P = 0.25$), and no difference in the frequency distributions of CD and G females (Kruskal–Wallis statistic = 7.83, $P = 0.80$). The total number of snakes captured (all age classes of both sexes) was 1042 at Den F (range = 10–78 individuals per year) and 785 at Den B (range = 6–55 individuals per year). Thus, the estimated number of snakes at Den F was 148.9 ± 85.1 (range = 50–390 per year, $n = 35$ yr), and at Den B it was 106.1 ± 48.5 (range = 30–275 per year; $n = 37$ yr).

Number of Females Reproducing

The number of G females recorded each year peaked in three different years at each den (Fig. 2). Values ranged from 1–26 G females per year (mean = 7.5, median = 6.0, CV = 73.4) at Den F, and from 0–11 G females per year (mean = 5.4, median = 5.0, CV = 50.4) at Den B (Table 1). The three peak years at Den F occurred in Year 8 (1986), 16 (1994), and 22 (2000), and at Den B in Year 14 (1992), 24 (2002), and 34 (2012); thus, peak years differed asynchronously between the two dens. Low levels of reproduction (1–3 females) were recorded in 7 of the study years (20%) at Den F, and in 8 of the study years (22%) at Den B. A near-reproductive failure occurred in 1997 (zero G females

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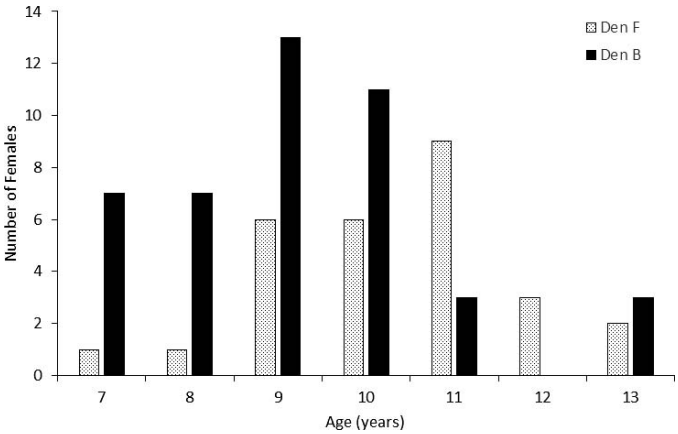


FIG. 3.—Age at first reproduction for female Timber Rattlesnakes (*Crotalus horridus*) at two focal dens in northeastern New York, USA. Den F ($n = 28$), Den B ($n = 44$).

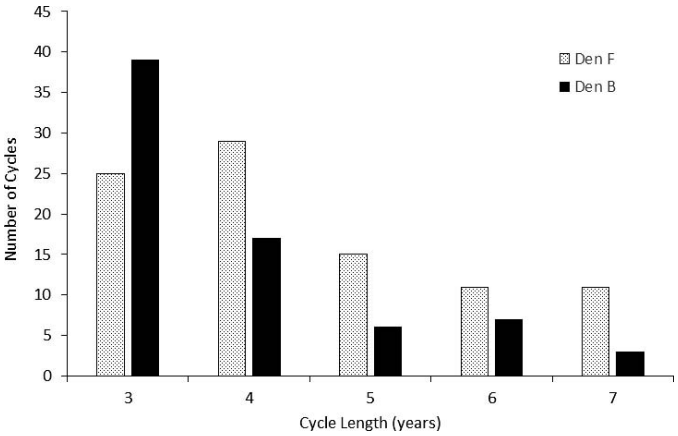


FIG. 5.—Reproductive cycles of female Timber Rattlesnakes (*Crotalus horridus*) at two focal dens: Den F ($n = 72$ cycles), Den B ($n = 91$ cycles).

captured at Den B, one at Den F). Relative to the total number of all snakes captured, G females represented 25.2% of the total at Den F and 27.2% of the total at Den B.

Age of First Reproduction

Averaged across both focal dens, first reproduction for female snakes occurred at a mean age of 9.6 ± 1.6 yr (range = 7–13 yr, $n = 72$; Fig. 3). This value is consistent with that of females representing six other dens (9.6 ± 1.3 yr, range = 7–12 yr, $n = 55$; Fig. 4). When comparing between focal dens, however, Den B females (9.2 ± 1.6 yr, $n = 44$, median and mode = 9 yr) underwent their first parturition at an earlier mean age than Den F females (10.4 ± 1.4 yr, $n = 28$, median = 10.5, mode = 11 yr; Wilcoxon rank sum test, $P = 0.001$).

Reproductive Cycles

Reproductive cycles for both focal dens consisted of 3-yr (39%), 4-yr (28%), 5-yr (13%), 6-yr (11%), and 7-yr (8%) cycles; the mean cycle length across both focal dens was 4.2 yr ($n = 163$ cycles; Fig. 5). Females from Den B had a shorter mean cycle length (3.9 yr) than those from Den F (4.5 yr; two-tailed Kolmogorov–Smirnof statistic = 0.27, $P = 0.006$). This pattern is likely explained by Den F having a greater number of females exceeding a 3-yr cycle ($n = 66$, 72%) than Den B ($n = 33$, 46%; Fisher's exact test, $P < 0.05$).

The mean cycle length among female snakes at six other dens within the metapopulation was 4.4 yr ($n = 84$). Taken together with data from the focal dens ($n = 247$ cycles among 162 individuals), the mean cycle length was 4.2 yr (Fig. 6). Whereas no female snakes from the two focal dens exhibited a 2-yr reproductive cycle, three females representing two other dens within the study area (No. 5 and 6; Fig. 1) reproduced biennially between 1996 and 2001.

Span of Active Reproduction and Iteroparity

The reproductive life span of those female snakes from Dens F and B that produced multiple broods ranged from 4 to 32 yr (mean interval = 9.6 yr, $n = 108$; Fig. 7). The distributions of the reproductive life spans of females representing the two focal dens were similar (Kruskal-Wallis statistic = 0.01, $P = 0.94$). Of particular interest is the maximum observed history of 32 yr in one individual (inconsistent recaptures did not allow counting all of her efforts over a span of three decades).

Across both focal dens, female snakes experienced a mean of 1.70 reproductive efforts per lifetime. Overall, most

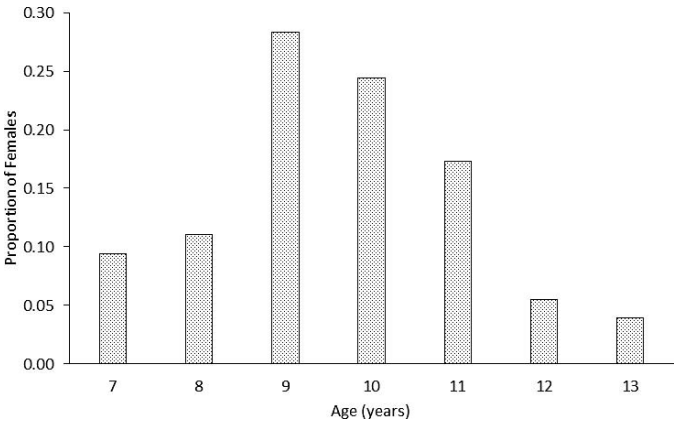


FIG. 4.—Age at first reproduction for female Timber Rattlesnakes (*Crotalus horridus*) in proportion to the total number of known-aged females ($n = 127$) for all dens sampled in northeastern New York, USA.

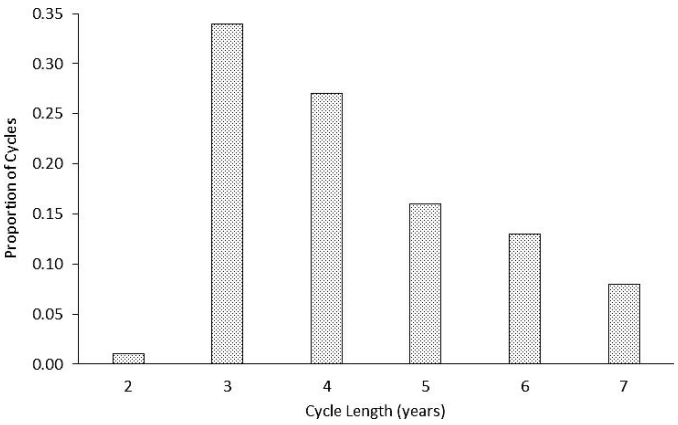


FIG. 6.—Reproductive cycles ($n = 247$) of female Timber Rattlesnakes (*Crotalus horridus*) in dens sampled in northeastern New York, USA, from 1979–2014.

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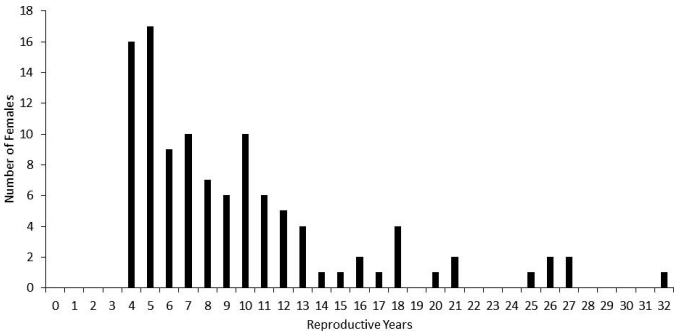


FIG. 7.—Reproductive life span of iteroparous Timber Rattlesnakes (*Crotalus horridus*) from two focal dens in northeastern New York, USA. Den F ($n = 64$); Den B ($n = 44$).

females (148, or 60%) reproduced once, followed by 61 (25%) reproducing twice, and 26 (10%) reproducing three times (Fig. 8). Only three individuals (1%) reproduced six or seven times; the seven-event individual had six successive cycles without interruption during a 20-yr period—one 4-yr cycle, followed by five 3-yr cycles (she was still alive at the end of the 2015 season).

Body Size

Regardless of the number of times they had reproduced, G females averaged 886 ± 179 g ($n = 365$ records for 180 individuals); snakes from Den B (956 ± 201 g, $n = 160$ records for 77 individuals) were heavier than those from Den F (831 ± 137 g, $n = 205$ records for 103 individuals; $t = 7.05$, $P < 0.001$; Table 2). G females from Den B reproducing for the first time also were heavier (mass = 827 g) than those from Den F (737 g; $t = 2.84$, $P < 0.01$). The distribution of body masses at the first reproductive event shows a modal range of 700–900 g at Den B and 650–850 g at Den F (Fig. 9). Females from Den B (mean = 103 cm) had larger TL values than those from Den F (mean = 99 cm; $t = 2.94$, $P < 0.01$; Table 2). Snake mass increased with TL ($r^2 = 0.98$, Fig. 10), and those females from Den B achieved greater relative body masses than those from Den F (TL held as a covariate; $F = 19.08$, $P < 0.001$).

Regardless of the month of their capture, P females from Den B (mean mass = 593 ± 147 g, $n = 43$) were heavier than those from Den F (527 ± 95 g, $n = 76$; $t = 2.94$, $P = 0.004$). This difference in postpartum mass was consistent whether the subjects were measured in September or in the following May (Table 2). Furthermore, the mass lost by P females following parturition—already evident as depleted body condition in September—typically included further losses over the succeeding winter and spring.

TABLE 2.—Morphometric values (mean ± SE) of female Timber Rattlesnakes (*Crotalus horridus*) in northeastern New York in two reproductive states (G = gravid, P = postpartum) at two focal dens sampled from 1979–2014. "First-time" refers to individuals determined to be primiparous based on estimated age and capture records; "all" includes females of all ages. Postpartum mass values recorded in autumn (September) or spring (May) following parturition.

Measurement/state	Den B	Den F
Total length, G all	102.9 ± 1.18 cm ($n = 39$) Range = 90–118 cm	99.1 ± 0.69 cm ($n = 48$) Range = 87–109 cm
Body mass, G all	956.3 ± 15.9 g ($n = 160$) Range = 527–1364 g	831.4 ± 9.6 g ($n = 205$) Range = 527–1189 g
Body mass, G first-time	827.4 ± 20.8 g ($n = 40$) Range = 620–1207 g	737.6 ± 18.1 g ($n = 21$) Range = 605–903 g
Body mass, P all (Sept)	664.2 ± 51.1 g ($n = 13$) Range = 386–918 g	546 ± 16.3 g ($n = 34$) Range = 378–851 g
Body mass, P all (May)	547.8 ± 22.0 g ($n = 21$) Range = 442–792 g	482.9 ± 17.5 g ($n = 25$) Range = 402–757 g

Changes in Body Mass Associated with Reproduction

For those female snakes reproducing more than once, body mass tended to increase with the number of efforts. This relationship reinforced the differences in female body size: reproductively active females from Den B ($n = 159$) reached a plateau in body mass of ~1150 g, whereas Den F females ($n = 205$) plateaued at ~900 g (Fig. 11).

Gravid to postpartum.—The decrease in body mass attributable to parturition did not differ between the two dens or between years (i.e., whether postpartum mass was recorded in the same year or the following year; for both, $t = -0.65$, $P = 0.52$). The relative mass loss of female snakes from Den F (0.405) tended to be higher than that of females from Den B (0.306; Table 3).

Gravid to gravid in the same season.—Gravid females were first captured at median dates of 2 June (3 May–23

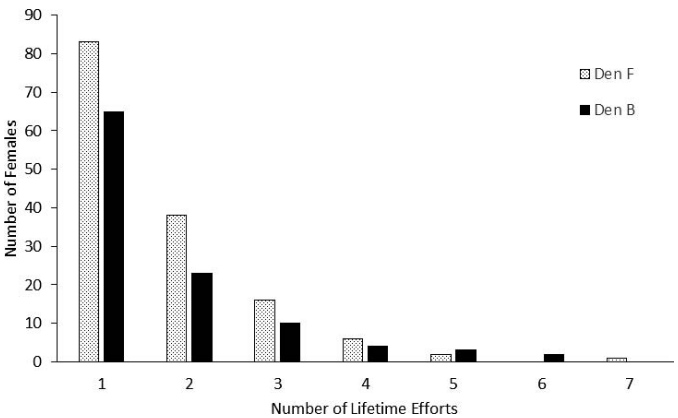


FIG. 8.—Lifetime reproductive efforts of female Timber Rattlesnakes (*Crotalus horridus*) at two focal dens based on 432 gravid records in 253 individuals sampled in northeastern New York, USA.

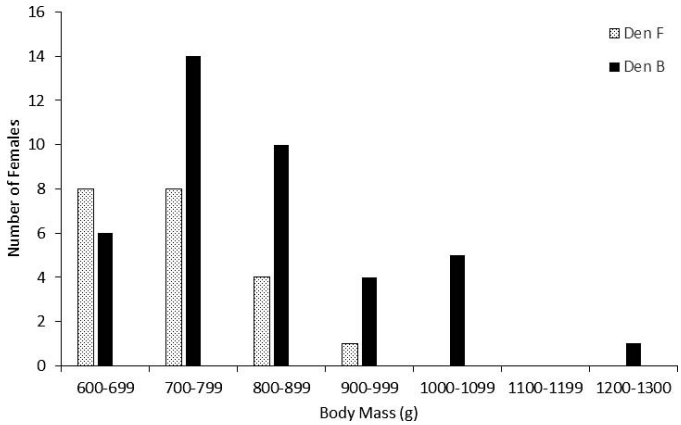


FIG. 9.—Distribution of body mass at first reproduction for female Timber Rattlesnakes (*Crotalus horridus*) sampled from two focal dens in northeastern New York, USA.

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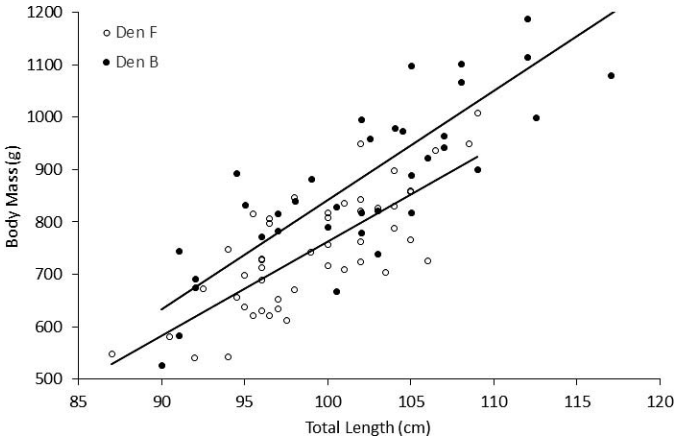


FIG. 10.—Body mass (g) as a function of total length (cm) in gravid female Timber Rattlesnakes (*Crotalus horridus*) sampled from two focal dens in northeastern New York, USA. Lines are based on least-squares regressions: filled circles and upper line depicts Den B females ($n = 39$, $r^2 = 0.74$; $Y = 20.9 \cdot X - 1244$); open circles and lower line depicts Den F females ($n = 48$, $r^2 = 0.60$; $Y = 18.0 \cdot X - 1035$).

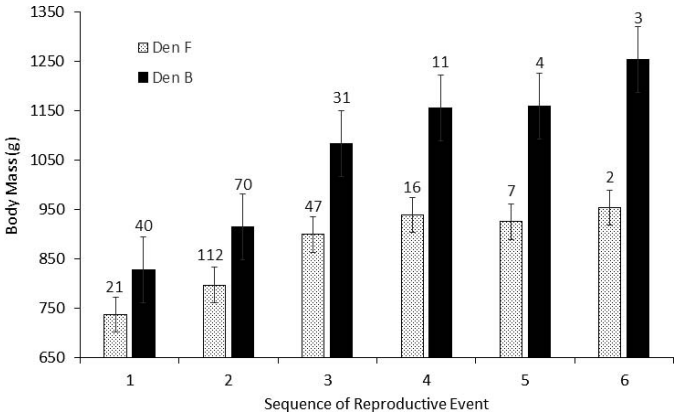


FIG. 11.—Body mass (mean ± 1 SE) of gravid female Timber Rattlesnakes (*Crotalus horridus*) from two focal dens as a function of the sequence of their reproductive events. Sample sizes are indicated above each error bar.

July) at Den B ($n = 35$), and 29 May (28 April–4 July) at Den F ($n = 34$). Second captures in the gravid year occurred at median dates of 25 August (18 June–21 September) at Den B, and 28 August (23 June–19 September) at Den F. Mean intervals between the two measures of gravid mass were 67.0 ± 29.1 d ($n = 35$) at Den B and 78.0 ± 25.3 d ($n = 34$) at Den F. Female snakes tended to lose mass during these intervals, and the losses were similar between females representing each of the focal dens (2 × 2 contingency test, $P > 0.05$; Fig. 12). Noteworthy changes in body mass occurred among 8 G females (recorded in different years in the 21-yr interval 1992–2012), with increases as great as 114 and 150 g (+10% and +15%) over spans of 103 and 43 d, and decreases ranging from –105 to –65 g (–11% to –20%) over spans of 80–112 d.

The rates of mass change were similar among female snakes from each of the focal dens, whether considering absolute (Den B, –0.50 g/d ± 0.20 SE; Den F, –0.19 g/d ± 0.14 SE; $t = -0.26$, $P = 0.21$) or relative rates (Den B, –3.34% ± 1.07 SE; Den F, –1.83% ± 1.16 SE; $t = -0.96$, $P = 0.34$). Although these trends were similar between the dens ($r^2 = 0.014$, $F = 0.48$, $P = 0.62$), there was a weak interaction as a function of den site (Fig. 12).

Vitellogenic to gravid.—Changes in mass occurring in female snakes transitioning from V to G showed a mean loss of 25 g (range = –130 to +155 g, $n = 9$). Six individuals decreased in mass, two increased, and one remained unchanged over periods of 242 to 426 d between measurements of V (1034.0 ± 165.2 g) to G (1009.0 ± 159.0 g).

Fecundity and Reproductive Efficiency

Across all categories of reproductive output (Type B litters = NEO + SB + OO; $n = 330$) female snakes produced a mean of 9.4 offspring. For Type A litters (NEO only) females produced a mean of 7.7 offspring, within which the neonatal sex ratio was relatively equal (paired $t = -0.89$, $P = 0.38$; Table 4). Litter sizes were similar among females as grouped by den of origin (Kruskal–Wallace statistic = 0.28, $P = 0.86$). The mean sizes of litters were similar among females from the two focal dens, regardless of whether they were Type A (Den B, 8.4 ± 4.7, $n = 8$; Den F, 7.5 ± 2.8, $n = 11$; Kruskal–Wallace statistic = 0.20, $P = 0.66$), or Type B (Den B, 10.7 ± 3.8, $n = 9$; Den F, 9.3 ± 2.0, $n = 11$; Kruskal–Wallace statistic = 2.56, $P = 0.12$).

Nonviable offspring (stillborn or oocytes, or both) made up some portion of 16 lab-born litters (52% of the lab sample; Table 4). A few stunted stillborns weighed ca. 7–10 g, whereas normal neonates averaged 21–23 g at birth in the lab. Production of yolky oocytes might not impact future efforts as evidenced by one female (the only individual whose captures happened to allow a comparison of back-to-back lab births) that produced 11 yolky masses in 1982 followed by a litter of 14 normal neonates in 1986. Her relative clutch mass was 0.25 on the first occasion, and 0.31 on the second.

In the field, 93 litters with their recently postpartum mothers were observed. A mean of 2.3 yolky oocytes (range = 1–6, $n = 44$) were seen in 19 (20%) of the field litters. An additional four litters consisted of one underdeveloped or malformed stillborn in combination with normal neonates (two litters), or one passed oocyte plus a stillborn in combination with normal neonates (two litters). One cluster

TABLE 3.—Changes in body mass (g; mean ± 1 SD, range) of female Timber Rattlesnakes (*Crotalus horridus*) in transition from gravid (G) to postpartum (P) for the same individual within 1 yr (see text for timing of measurements). Interval (days, d) is the span between the G and P records. Proportional mass loss was calculated with respect to G mass.

Den (n)	Year	Interval (d)	Loss in mass (g)	Proportional mass loss
B ($n = 5$)	Same	37.6 ± 23.1, 5–67	391.4 ± 121.3, 226–548	0.359 ± 0.029, 0.334–0.405
F ($n = 18$)	Same	62.7 ± 33.7, 13–132	280.1 ± 64.5, 178–370	0.327 ± 0.073, 0.208–0.441
B ($n = 8$)	Next	325.9 ± 34.7, 263–373	256.4 ± 25.7, 222–297	0.306 ± 0.052, 0.245–0.382
F ($n = 6$)	Next	325.8 ± 40.3, 253–359	328.8 ± 36.7, 302–398	0.405 ± 0.016, 0.390–0.431

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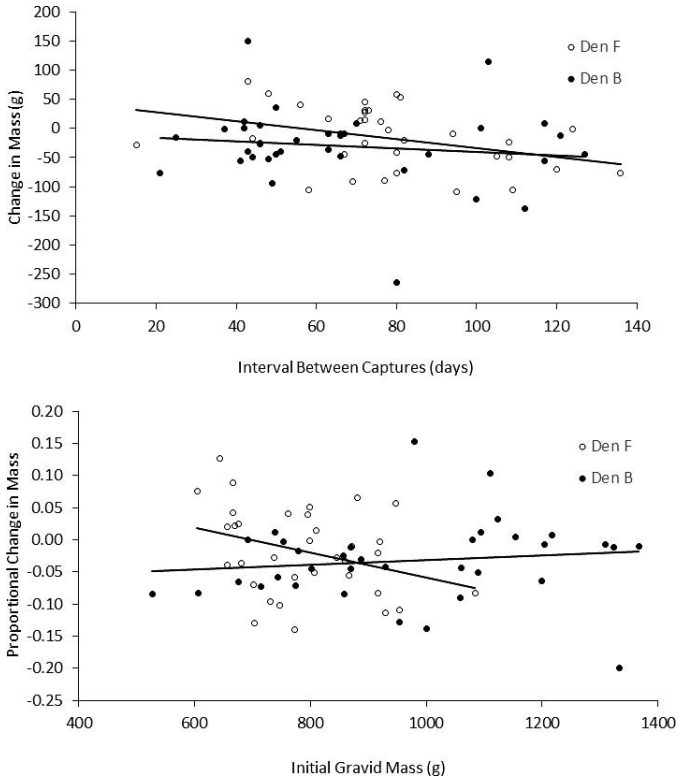


FIG. 12.—Change in body mass of gravid female Timber Rattlesnakes (*Crotalus horridus*) ($n = 69$) from two focal dens as a function of interval between capture of the same individual (d; upper panel) and mass at initial capture (g; lower panel). In both graphs, filled circles indicate individuals from Den B, whereas open circles indicate individuals from Den F.

of five yolky masses weighed 44 g, and another of four masses weighed 47 g at one birth site, each cluster apparently produced by each of two females sharing the site. Yolk plugs were usually seen under birth rocks, but in two cases, the yolky masses were found in the open.

DISCUSSION

Female Survival and Lifetime Reproduction

Bull and Shine (1979) outlined the selective trade-offs in viviparous ectotherms between less-than-annual reproduction and increased survival rate. They pointed out that "low-frequency reproduction must be an adaptation superior to yearly reproduction" (p. 298), and argued that important factors favoring this prediction should include fecundity and survival. In habitats less favorable for energy acquisition (e.g., short activity season, fluctuations in prey abundance), low-frequency reproduction might be favored (Bull and Shine 1979). Researchers have examined the relative benefits of reproduction among capital-breeding ectotherms that use resources gathered at some previous time and stored for a future reproductive event without compromising thermoregulation, body maintenance, or foraging (e.g., Bonnet et al. 1998). Longevity and fecundity depend on the continued growth of females and increased reproductive success with age (Madsen and Shine 1994). This strategy requires a long time (years) in long-lived sedentary predators with prolonged reproductive cycles as typified by most rattlesnake species.

TABLE 4.—Fecundity data for female Timber Rattlesnakes (*Crotalus horridus*) based on litters born in captivity ($n = 31$) or field ($n = 4$) settings. Birth categories are identified as follows: early embryos or stillbirths (SB), yolky masses or infertile oocytes (OO), and neonates (NEO). See text for explanation of two litter types (Lit. A, Lit. B).

Birth category	Total *n*	Number of females	Mean ± SD	Median (range)
Stillborns (SB)	21	12	1.75 ± 1.05	1 (1–4)
Oocytes (OO)	47	13	3.61 ± 3.30	3 (1–11)
Normal (NEO) (Lit. A)	262[a]	34	7.71 ± 3.15	8 (2–14)
NEO + SB + OO (Lit. B)	330	35	9.43 ± 2.56	10 (4–14)

[a] Neonatal sex ratio ($n = 251$): 118 males, 133 females (0.47:0.53).

My findings show that in those female *C. horridus* achieving at least a second effort, the reproductive life span averaged almost 10 yr. Female snakes produced a mean of 1.7 litters per reproductive lifetime; most individuals (60%), however, reproduced only once. As such, this population appears to deviate from a pattern of prolonged iteroparity as has been documented in other long-lived capital breeding viperids (reviewed in Madsen and Shine 1992; Bonnet at al. 2002). The reproductive life history of *Vipera aspis* (Naulleau and Bonnet 1996; Bonnet 2011) emphasizes a marked tendency toward a single lifetime effort, reflecting a high mobilization cost of vitellogenesis as opposed to the costs of gestation and parturition. In *C. horridus*, however, the body mass of V females during the year preceding parturition was similar to that of G females. In contrast, in the 8-mo interval between parturition and the following spring, losses in body mass of an additional 12–17% occurred. Skin folds in a few P females persisted into the second year following parturition and some were in an emaciated condition, indicating that slow postpartum recovery produced a weakened body condition with a concomitant greater susceptibility to eventual starvation or predation.

Some individuals reproduced over spans exceeding 20 yr, but lifetime reproductive events were fewer than predicted based on the longevity of the species. I suggest that reproduction in each generation falls disproportionately on a few long-lived and successful females. Work on *V. aspis* has suggested a positive relationship between current reproduction and future reproductive success, whereby individual females with the highest rate of mass recovery show an increased likelihood of reproducing again (Bonnet and Nalleau 1996; Bonnet et al. 2002). At a mean cycle length of 4.2 yr and a mean breeding lifetime of 9.6 yr, female *C. horridus* at my study site could expect to achieve a mean of 2.3 reproductive efforts per lifetime. Because of the high proportion of females reproducing only once, however, the observed level of iteroparity (1.7 events per lifetime) falls short of this expectation. If my study is representative of northern populations of *C. horridus*, the reproductive life history might be better described as facultative semelparity.

The question of survival of females is critical to understanding the role of iteroparity and costs of reproduction in low-frequency capital-breeding ectotherms. One survival-curve model demonstrates a lower expected survival in viviparous than in oviparous species because of the longer reproductive season experienced by gestating females (Seigel and Fitch 1984). For females on 3- and 4-yr cycles, estimated survival costs favor a strategy of semelparity (Bonnet et al.

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1999), and survival costs, rather than fecundity costs, are considered more important in determining the level of reproductive effort (Shine and Schwartzkopf 1992). In Western Rattlesnakes (*Crotalus oreganus*), the finite population growth parameter (λ) was most sensitive to juvenile and adult survivorship; reproductive constraints (late age at maturity, long cycle length, low litter size) produced relatively small reductions in λ (Gregory 2009). In the *C. horridus* metapopulation studied here, the annual survival rate among first-year juveniles is estimated at ~65%, whereas in adults of both sexes, the rate is 90% or greater (Brown et al. 2007). In Indiana populations of *C. horridus*, female survival declined from 95% to ~75% after a year of low prey abundance (Olson et al. 2015). If applied to individuals based on reproductive state, I suspect that modeling results will show decreased survival in postpartum females, arguably making them the most vulnerable cohort.

Limitations of the Empirical Approach

Any multiyear field study necessarily incorporates a matrix of individuals and years with arbitrary cutoff dates that define the boundaries of the longitudinal data set, but that lacks any predictions about where the ages and reproductive states of the included individuals might fall. A similar problem in analyzing long-term records of Northern Fulmars (*Fulmarus glacialis*) was solved by excluding the beginning and ending periods of the breeding histories (Ollason and Dunnet 1988). I used an arbitrary terminal cutoff preceding by 5 yr the actual end date of the study, thus providing a temporal sample of sufficient duration to yield unbiased estimates of the key variables (cycle length, lifetime reproductive span). By extending the study to 30+ yr—about three times longer than the mean reproductive span or the crude generation time—biased estimates are thought to have been minimized.

Effects of Field Sampling on Reproductive Females

My experience with this population showed that frequent visits to the gestation areas were counterproductive and not necessary; it was more efficient to sample G females on fewer field trips. This lower sampling effort decreased the level of disturbance to the females and thereby increased the number of them encountered. My surveys were usually predicated by weather conditions that were favorable for detecting females resting in a coiled position on the surface or under the overhanging edge of a shelter boulder. Over the first 25 yr, field time ranged from around 20 to over 300 hr per year (Brown 2008) but capture–recapture models detected no effect of search effort (annual field time) on the most parsimonious survival model (Brown et al. 2007). In the second half of the study, despite nearly a 50% reduction of CD, the total number of females and rates of capture actually increased. Evidently, discernment of field conditions rather than total time spent in the field made a nontrivial difference in the sampling results.

In this population of *C. horridus*, most of the gestating sites were considered "traditional" (sensu Graves and Duvall 1993) in that they were used annually, but not necessarily by the same individuals. After being processed, recaptures within the same season showed that G females frequently moved from the site of capture to another gestating location, an indication of disturbance-induced abandonment of the original gestating site. The snakes' response to disturbance might have evolved as a protective behavior. Females were usually calm when encountered but became agitated and defensive when captured, and were often temporarily disoriented at release. In an attempt to reduce stress, I often guided them to protective crevices; still, they usually abandoned the site later. Among the females with a sequence of repeated gravid years, however, the same gestating sites were often reused after several years, and the same sites were also used by first-time G females and by a few I females. Spatial occupancy and turnover of different females, sometimes between closely related individuals (e.g., mothers and daughters) returning to the natal nesting site, is a phenomenon that has been recognized in snakes (Brown and Shine 2007)—and certainly deserves further study. In this population of *C. horridus*, genetically related G females of different generations have been shown to aggregate preferentially with one another (Clark et al. 2012).

Body Mass, Fecundity, and Reproductive Efficiency

The typical pattern seen among viviparous squamates is that feeding during gestation is reduced or absent (gestational anorexia; Gregory et al. 1999). A few female individuals had large changes in mass, gaining as much as 150 g or losing between 100 and 265 g. Such departures from what I observed among most G females (2–3% loss in mass) indicate that these individuals must have ingested a meal, providing indirect evidence of opportunistic feeding during gestation. In spite of these observations of large changes in mass, the nonfeeding model might still be true for the majority of pregnant females in this study.

Over the lifetime events for each iteroparous female snake, the body mass estimates increased as the number of reproductive events increased with age. These data show a general growth trend that reached an asymptote in the reproductive females. The two focal dens showed a body-size difference in this estimate, with Den B snakes achieving a plateau about 250 g heavier than Den F snakes by the time of the fourth reproductive event. I suggest that snakes from both dens might have attained a maximum body size, but further analysis is needed.

Vipera berus produces a number of undeveloped eggs with normal developing embryos (Nilson 1981); in *V. aspis*, 8.7% of litters were composed entirely of ova and stillborns (Lourdais et al. 2002, 2004). In comparison, 52% of the lab-born litters and 20% of the observed field litters of *C. horridus* were composed of a small number of stunted nonviable stillborns, yolk plugs, or both, in addition to normal neonates. Only 1 of 31 (3.2%) of the litters contained 100% yolk plugs. In *Crotalus cerastes*, stillborns and yolk plugs made up 15% of the total offspring of one female over her lifetime (Blomsten et al. 2016); in *C. horridus*, these nonviable products composed 21% of the total offspring among all females.

Regional Variation in Reproductive Biology

Selection by environmental factors on the life history of Timber Rattlesnakes might have produced geographically divergent populations across its range (Martin et al. 2008). In northern portions of the *C. horridus* distribution, demes tend to cluster within physiographic regions of the landscape (Bushar et al. 2014). In two areas (New York, Missouri),

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TABLE 5.—Comparative life history and female reproduction data for Timber Rattlesnakes (*Crotalus horridus*) at two northern study sites, Appalachians (Allegheny Front of West Virginia, Martin 2002) and Adirondacks (northeastern New York, present study); at the latter site, (B) and (F) refer to two focal dens (see text). Where appropriate, means are reported with ranges and sample sizes.

Variable	Appalachians	Adirondacks
Latitude	39°N	43°N
Den elevation	1075 m	225 m
Duration of study	12 yr	36 yr
Active season	5 mo	5.2 mo
Population estimate[a]	60–120	100–150
Gravid females captured	6.7/yr	6.4/yr
Years of lowest reproduction[b]	1992, 1993	1990 (B), 1997 (B, F)
Years of highest reproduction[b]	1998	1992 (B), 1994 (F)
Reproductive cycle length[c]	4.8 yr, 3–7 yr; $n = 12$	4.2 yr, 2–7 yr; $n = 247$
Female body size[d]	780 g, 563–1005 g; $n = 11$	886 g, 527–1364 g; $n = 365$
Age of first reproduction[e]	10.7 yr, 9–14 yr; $n = 38$	9.6 yr, 7–13 yr; $n = 127$
Fecundity (litter size)[f]	8.8, 6–14; $n = 25$	7.7, 2–14; $n = 34$

[a] All adults; revised estimates of total population range from ca. 250–375 (W.H. Martin, personal communication).

[b] Years of lowest and highest reproduction between 1989–2001 (cf. Martin 2002).

[c] Cycle length in Appalachians revised from that originally reported (W.H. Martin, personal communication); Adirondacks cycle length pertains to all dens in the metapopulation.

[d] Gravid females, all ages.

[e] Age for Appalachians calculated from author's data.

[f] Mean litter size of neonates only (no stillborns or oocytes) for comparison between studies.

movements among dens by long-ranging males to intermediate basking areas facilitate interden mating and minimize genetic differentiation among subpopulations (Clark et al. 2008; Anderson 2010). In addition to metapopulations, there are scattered isolated dens composed of small populations. The long-term viability of these geographic isolates might be analogous to small populations of other long-lived vertebrates that are sustained by a few adult females ("tenacious adults" sensu Shoemaker et al. 2013).

In the high-elevation Appalachians, the number of G females varied between years and recaptures were low except in years when the females reproduced (Martin 2002). In comparison to my study site, the cycle lengths of those females were slightly longer, body sizes were smaller, and first reproduction occurred at a later age (Table 5). The lower mean temperatures and a wetter climate at the higher elevation site were likely important in affecting reproduction and contributed to these constraints: (1) 2 yr of total reproductive failure caused by embryos not completing development; (2) ~33% of pregnant females failing to produce litters; and (3) ~25% of the females entering hibernation while still pregnant, presumably aborting their litters during the winter (Martin 2002). In contrast, I did not observe such severe impacts on reproduction in the southeastern Adirondacks.

Local Variation in Reproductive Biology

I did not anticipate the interden differences within the metapopulation because of the fairly close proximity of the focal dens and their similar phenology. However, considerable variation in life-history traits is not unexpected among demes within a metapopulation (Hanski and Simberloff 1997). Female snakes representing the two focal dens of *C. horridus* showed microgeographic divergence in several life-history traits: size at maturity, age at first reproduction, and mean cycle length. A relatively small number of individuals moved permanently between dens. Among closely situated local populations of some snakes, low rates of gene exchange and/or periodic extirpations followed by founder effects may explain the presence of distinctive phenotypic variation (Shine et al. 2012).

Several variables might contribute to the reproductive differences observed among the female *C. horridus* representing the two focal dens. Biotic factors such as prey abundance are implicated as being important for successful reproduction (e.g., Seigel and Fitch 1985; Diller and Wallace 2002; Lourdais et al. 2002; Beaupre 2008; Jenkins and Peterson 2008; Jenkins et al. 2009; Schuett et al. 2011; Olson et al. 2015). Prey species that likely contribute to snake energy budgets at my study site include Eastern Chipmunks (*Tamias striatus*) and White-footed Mice (*Peromyscus leucopus*). Human impacts such as roads and incidental disturbance might also differentially affect the dens in the Adirondack metapopulation. One example is a paved highway along the northwest border of the study area. The highway traverses about 10 km in a narrow forested valley roughly paralleling the metapopulation, unequally bisecting it. The highway affects the dens by causing genetic separation of one of the two dens north of the road (Den B) from other dens south of the road (including Den F). Snakes from Den B differ genetically from those representing dens that are south of the road (that also cluster genetically; Clark et al. 2010). Both focal dens as well as most others in the metapopulation are located within typical summer movement distances from the highway on which roadkills have long been recorded (cf. Aldridge and Brown 1995). In the case of Den B, however, snakes tend to move away from the road, migrating into relatively undisturbed forest habitats (Brown et al. 1982). In the case of Den F, individuals can encounter a greater density of human-occupied sites (e.g., private camps, hiking trails, public campsites) than those from Den B and therefore might experience a human interaction with greater frequency, and possibly a negative outcome.

Many populations of *C. horridus*, particularly in northern portions of its range, continue to be threatened by habitat alteration, poaching, and persecution (cf. Martin et al. 2008). Conserving Timber Rattlesnakes in North America is increasingly viewed in the context of their coexistence with other wildlife resources. Given that the determination of a species' conservation status typically requires multiyear data collection in natural settings (Brown 1993; Dodd 1993; Furman 2007; Martin et al. 2008; Shine and Bonnet 2009), it is imperative that populations receive protection at both human-impacted localities and research sites. The completeness of understanding the reproductive biology of this species was possible in part because my investigations focused on an area where habitat disturbance and collecting were curtailed through vigilance. The reproductive characteristics of *C. horridus* reported here—(1) high annual variability of small numbers of G females, (2) late age of maturity, (3) restricted lifetime reproductive rate, (4) lengthy reproductive cycles, and (5) limited fecundity—all point to the fact that this species must be protected to achieve a

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lasting recovery. These are major demographic constraints characterizing northern populations of *C. horridus* in which female reproduction is a limiting factor affecting the continued viability of the species.

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