
FEMALE REPRODUCTION IN WESTERN HOGNOSE SNAKES (*HETERODON NASICUS*) IN THE NEBRASKA SANDHILLS, USA

JOHN B. IVERSON

Department of Biology, Earlham College, Richmond, Indiana 47374, USA, email: johnni@earlham.edu

Abstract.—I studied reproduction in female Western Hognose Snakes (*Heterodon nasicus*) in the Sandhills of western Nebraska opportunistically from 1993 to 2017. Females matured at 37–38 cm SVL (estimated 80–90 g preoviposition body mass), and some apparently reproduced for the first time in their third year (about 33 mo of age). Oviposition occurred primarily in late June to early July, with a tendency for earlier nesting in years with warmer daytime temperatures in May. In the field, females may reproduce less than biennially (e.g., skipping reproduction following climatically harsh years), even though in captivity they can double-clutch within a year. Eggs averaged 29.6×17.0 mm, and 5.23 g, which is about 6% of spent body mass. Eggs decreased in length and increased in width with increasing female body size, such that smaller females laid extremely elongate eggs. Egg mass was not correlated with female body size, however, suggesting selection for optimal egg size (OES). Clutch size averaged 8.0, ranged from two to 16, and was positively correlated with female size, as was clutch mass. As females increased in size, they directed increased energy into clutch size, not to egg size, as predicted by the OES hypothesis. Very few reproductive data are available from other parts of the range of the species, but they suggest very little geographic variation in female body size or reproductive output despite a latitudinal distribution of over 1,900 km.

Key Words.—clutch size; ecology; egg size; life history; snake

INTRODUCTION

It is clear that limited sample sizes have hampered natural history studies of most snake species, often precluding an understanding of variation in life-history traits and their correlates (but see Fitch 1975; Madsen and Shine 2001). This applies particularly to diurnal but secretive Western Hognose Snakes (*Heterodon nasicus*), which range from Alberta, Manitoba, and Saskatchewan, Canada, to eastern New Mexico and west Texas, USA (Powell et al 2016), and for which body size, clutch size, and egg size measurements have all been reported from only two studies with samples larger than one. One of those provided data from five snakes from Kansas (Platt 1969), and the other just six (Iverson 1995, at the same site as this study).

Although apparently rarely encountered over much of its range, the Western Hognose reaches high densities in the Nebraska Sandhills (Imler 1945; Ballinger et al. 1979; Iverson, unpubl. data). While engaged primarily in studies of turtles on and near the Crescent Lake National Wildlife Refuge in western Nebraska from 1980 to 2018 (Iverson and Smith, 1993; Iverson et al. 1997; Converse et al. 2005; Hedrick et al. 2017), I opportunistically collected reproductive data on *Heterodon nasicus* during 17 y between 1993 and 2017. This study examines the reproductive ecology of this poorly studied snake in western Nebraska, with comparisons across the range of the species.

MATERIALS AND METHODS

I collected *H. nasicus* opportunistically (by hand, from roads, or along drift fences) on or near the Crescent Lake National Wildlife Refuge in Garden County, Nebraska, USA. Descriptions of the study area (Imler 1945; Gunderson 1973) as well as the general Nebraska Sandhills region (Weaver 1965; Bleed and Flowerday 1990) have been published previously. Sampling was uneven across years but focused primarily during mid-April to mid-July. I did not undertake mark-recapture of snakes, so it is possible a female could have been sampled in more than one year over the course of the 17-y study.

I determined the sex of snakes by cloacal probing (Schaefer 1934) and by the much longer tail in males. I measured and released most captured snakes, and some were preserved as voucher specimens, but I held many females captured from late May through June in captivity at $28^\circ \pm 2^\circ$ C) in plastic containers until they oviposited ($n = 40$) or not. I identified non-reproductive females by their low body mass relative to body length when captured in May or early June (Platt 1969; see below), and by holding them until mid to late July until I was certain that they were non-reproductive. I had no evidence that females at my site ever oviposited before mid-June, based on body masses, snakes held in captivity, or dissections of road-killed snakes for diet items. While captive, I regularly fed females

ambystomatid larvae and provided them with water *ad libitum* until their pre-oviposition ecdysis (generally one week before oviposition; Munro 1949a; Mattison 1992). I released most spent females near their capture site but their clutches were carried back to Indiana, USA, for incubation (see below). I also removed a few females to Indiana until they oviposited, and they (and their offspring) were subsequently returned and released. Hatching measurements reported here were all from snakes hatched in captivity. I preserved road-kills and voucher specimens and deposited them in the Herpetology Collection of the Florida Museum of Natural History (UF 62621, 65323-65348, 71412, 71415-71433, 73261-73264, 78130-78137, 78139-78153, 93698-93699, 99919-99920, 100650-100659, 150168-150169, 154871).

I measured snout-vent length (SVL, in cm) by gently laying each snake on a counter with the rostrum aligned with a mark on the counter top, and then releasing the head and sliding two pairs of fingers posteriorly along the body in a straight line, and marking the level of the cloaca on the counter with a pencil. I measured the distance between the two marks with a metric ruler and recorded it as SVL to the nearest 0.1 cm. I repeated the process at least once to verify repeatability. I measured tail length directly to the nearest 0.1 cm with an aligned metric ruler.

Body mass (BM) refers to pre-nesting (for females) or total body mass recorded on capture using a Pesola™ scale (Pesola Präzisionswaagen AC, Schindellegi, Switzerland). I measured spent body mass (SBM) immediately following oviposition. I also measured length (mm), maximum width (mm), and mass (g) of eggs within 4 h of oviposition, when I placed the eggs in plastic shoeboxes containing moistened vermiculite. I incubated clutches in a closed, insulated building at $25^{\circ} \pm 3^{\circ}$ C until mid July, when they were returned to Indiana, and placed in an environmental chamber at $29^{\circ} \pm 1^{\circ}$ C until hatching. I measured neonates in some clutches to the nearest 0.1 cm and 0.1 g within 72 h of hatching and then returned them to Nebraska for release.

One to five (mean and mode = 2) ovipositing females were available from each of 17 y between 1993 and 2017 (total = 40 clutches). Sample sizes (number of females) were three or more for only 5 y (1994, 1998, 1999, 2005, and 2007). Hence, I used data from these 5 y to test for annual variation in reproductive output (see below). Sample sizes in some analyses do not total 40 due to missing data from some clutches.

Statistical analyses.—I used partial correlation analysis to remove body size effects on reproductive variables. In addition, despite criticisms of the use of ratios of reproductive traits to body size (e.g., Packard and Boardman, 1988), and because of their direct practical use in the field (unlike residuals), I included ratios in this

analysis for comparison to the partial correlation results and to previously published data; the statistical conclusions for both approaches were identical in every case. I compared variation across samples (e.g., body size by sex, reproductive output by year, etc.) using *t*-tests (for two samples) or ANOVA, with post-hoc comparisons of sample means calculated using Fisher's (Protected) Least Significant Differences (PLSD) with $\alpha = 0.05$. I examined log-log Regressions of SVL versus measures of reproductive output (following King 2000 and Iverson et al. 2019) to test for isometry (i.e., an expected slope of 3 when relating a reproductive measure of mass [three dimensions] to body length [one dimension]). Means are followed by ± 1 standard deviation (SD). Alpha was set at 0.05. I performed all calculations on MacIntosh hardware with Statview™ software (Abacus Concepts, Berkeley, California, USA).

Taxonomy.—The taxonomy of the *Heterodon nasicus* complex is controversial. Described in 1860 on the basis of two head scale counts, *H. kennerlyi* was accepted as a southern subspecies of *H. nasicus* from 1939 (Stejneger and Barbour 1939) until the late 1990s. At that time Walley and Eckerman (1999) synonymized *kennerlyi* with *nasicus* based on their weak morphological differences; however, Smith et al. (2003) re-examined scale morphology across the group and found a discontinuity in a single scale character (number of loreals) between southern (*kennerlyi*) and northern (*nasicus*) populations. Based on this single character they argued for species recognition for these two forms, and the two taxa have generally been recognized as full species since then (but see Collins and Taggart 2009).

Similarly, Edgren (1952) described what at that time was a third subspecies of *H. nasicus*, *H. n. gloydi*, based on differences in the number and color of the dorsal blotches. His new subspecies included southeastern populations of *H. nasicus* and those across most of Texas. However, Platt (1969) quantified blotch patterns across the entire range of *H. nasicus (sensu lato)* and found that the patterns changed clinally, and questioned whether *gloydi* even deserved subspecies recognition. Walley and Eckermann (1999) subsequently formally synonymized *gloydi* under *nasicus*, and recognized only a monotypic *H. nasicus* at that time. This synonymy was accepted by Smith et al. (2003) in their description of *H. n. kennerlyi*; however, without any new analysis, Werler and Dixon (2000) recognized *gloydi* as a valid subspecies of *H. nasicus*. Subsequently, *gloydi* was elevated to full species status by Crother et al. (2003; see also Powell et al. 2016) based solely on their allopatric distributions and descriptions of the subspecies by Werler and Dixon (2000), although Collins and Taggart (2009) continued to recognize *gloydi* and *kennerlyi* as subspecies of *nasicus*.

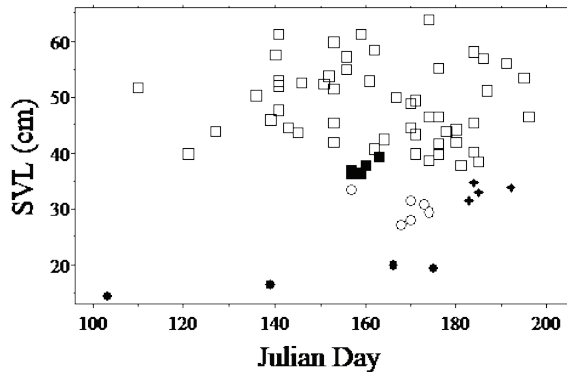


FIGURE 1. Body size (SVL = snout-vent length, in cm) versus date for female Western Hognose Snakes (*Heterodon nasicus*) captured in western Nebraska, USA. Symbols indicate estimated ages (see text): solid circles, 8–10 mo; open circles, about 22 mo; crosses, about 22.5 mo; solid squares, about 33.5 mo; and open squares, > 34 mo.

Hence, the last 20 y have seen the subspecies *kennerlyi* and *gloydi* disappear into synonymy and then be resurrected as full species. Clearly a molecular phylogeographic study of this complex is sorely needed. Therefore, given the uncertainty in the current taxonomy, I have included (and labeled) reproductive data for all three forms in this report. Given the meager data available from populations outside Kansas and Nebraska, however, and the lack of clarity in the phylogeographic relationships within the genus *Heterodon*, no attempt was made to apply comparative phylogenetic methods to my analyses. For comparative purposes I made an exhaustive search of the literature for reproductive data using the names *nasicus*, *kennerlyi*, and *gloydi*. For that compilation I estimated some missing reproductive parameters from appropriate regression equations based on the Nebraska population (see Results).

RESULTS

Size and sexual maturity.—The smallest reproductive female in Nebraska was 37.8 cm SVL (55.9 g spent body mass), whereas the three largest non-reproductive females (captured in June 2010) were 37.0, 36.4, and 33.6 cm SVL (45, 36, and 38 g body mass, respectively, when captured 6 June). These data suggest that females mature at 37–38 cm SVL (estimated pre-oviposition BM 80–90 g, see below). Because some sexually mature females skip reproduction in a given year (see below), however, there is some uncertainty in that estimate.

Based on body size clusters of subadult snakes captured in June (Fig. 1), juveniles in the first year of growth averaged mean $19.7 \pm (SD) 0.42$ cm SVL (range, 19.4–20.0 cm; $n = 2$), those in June of the presumed second year of growth averaged 30.2 ± 2.33 cm (range, 27.3–33.6 cm; $n = 16$), and those in July of the presumed

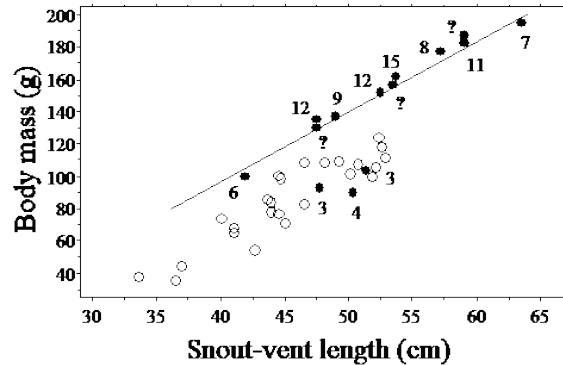


FIGURE 2. Relationship between snout-vent length (SVL in cm) and body mass (BM) of Western Hognose Snakes (*Heterodon nasicus*) during June in western Nebraska, USA, for gravid (solid circles) and non-gravid females (open circles). Numbers indicate clutch size for gravid females. Regression line for 11 gravid females (excluding three underweight gravid females) is plotted ($BM = 4.496(SVL) - 83.06$; $n = 11$; $F_{1,9} = 501.29$; $r^2 = 0.982$; $P < 0.001$).

second year averaged 33.3 ± 1.30 cm (range, 33.3–34.6 cm; $n = 4$). This rate of growth from June to June (about 10.5 cm SVL/year) suggests that females require at least two full activity seasons to reach maturity (37 cm SVL), with the potential for breeding in some females in their third season (about 33 mo post-hatching).

Females > 37 cm SVL averaged 49.1 ± 7.4 cm SVL (range, 37.8–77.5 cm; $n = 96$). Males > 30 cm SVL (estimated size at maturity by Platt 1969) averaged 39.1 ± 4.8 cm (range, 30.2–49.7 cm; $n = 68$). For 36 females that laid eggs, spent body mass (SBM) was highly related to SVL ($SBM = 4.244(SVL) - 121.059$; $F_{1,34} = 217.98$; $r^2 = 0.87$; $P < 0.001$). For 10 females with body mass data both before and after oviposition, spent BM averaged $66.6 \pm 10.3\%$ (range, 57.8–84.1%) of gravid BM. For females, SVL averaged 0.879 ± 0.010 of total length (range, 0.86–0.90; $n = 55$); for males it averaged 0.821 ± 0.022 of total length (range, 0.79–0.88; $n = 26$).

Female reproductive cycle.—My earliest capture of a female was on 12 April 1988 (earliest male, 20 April 1994). I never observed courtship in the field in April through mid-July during any year at the site from 1981 to 2019, nor even captured two hognose snakes (of more than 200 total sightings) in close proximity. Gravid females in June nearly always weighed more than non-reproductive females (Fig. 2). The three exceptions were females with very small clutches. Samples for only 2 y were large enough to estimate reproductive frequency. Of 13 females captured in June 1993 (all > 44.5 cm SVL), six (46%) were gravid. In contrast, of 11 females captured in June 2004, only two (18%) were gravid; however, three of the non-reproductive females were 40.1, 41.0, and 41.0 cm SVL. If those three females were immature, reproductive frequency that year would

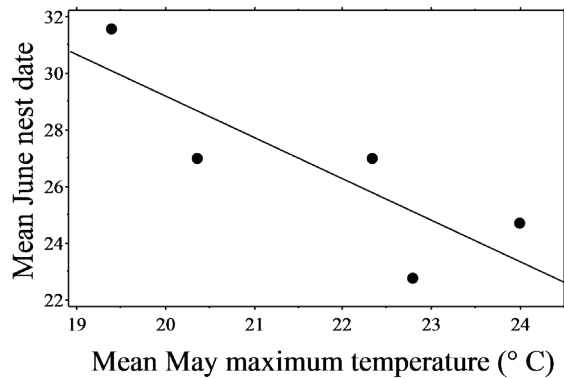


FIGURE 3. Relationship between mean daily maximum temperature ($^{\circ}$ C) in May and average June oviposition date for Western Hognose Snakes (*Heterodon nasicus*) from western Nebraska, USA, for the five best sampled years ($F_{1,3} = 6.315$; $r^2 = 0.678$; $P = 0.084$).

still have been only 25% (two of eight). Of five females > 45 cm SVL, only one (20%) was reproductive in 2004.

Of 40 females held in captivity for 3 to 50 d until oviposition, average deposition date was 29 June (± 7 d; range, 15 June - 20 July; Table 1) and the number of days in captivity was not correlated with oviposition date ($P = 0.550$; $n = 18$). The mean deposition date for eight females held fewer than two weeks was 26 June ± 7 d (15 June to 3 July), not significantly different from the 32 females held longer than two weeks (29 June ± 7 d; 15 June to 20 July; $t = 0.28$, $df = 38$; $P = 0.390$). I found no evidence for the production of a second clutch within the same year.

For the five largest annual samples (each with 3–5 clutches), average oviposition date ranged from 23 June to 2 July, and despite the small sample sizes, approached significant variation across years ($F_{5,31} = 2.64$; $P = 0.072$). In addition, average nest dates in those five small samples tended to be inversely correlated with mean May maximum temperatures ($r = 0.83$; $P = 0.084$; Fig. 3) and May degree days above 15.6° C ($r = 0.82$; $P = 0.088$), but not with June mean maximum temperatures ($P = 0.390$) or June degree days ($P = 0.290$). Average oviposition date during these five years was not correlated with rain in May, June, or May-June combined ($P > 0.510$ in all cases). In addition, although complicated by interannual variation in nest season timing, oviposition date was not correlated with either SVL ($P = 0.700$), clutch size ($P = 0.130$), egg mass ($P = 0.980$), or clutch mass ($P = 0.120$).

For 21 clutches monitored daily, incubation took 45–53 d (49.4 ± 2.3 d; Table 2). On average, hatching commenced on 16.5 August ± 10.2 d (19 July to 4 September; $n = 21$). Hatchling size averaged 14.6 ± 0.7 cm SVL (range, 12.5–15.7 cm; $n = 49$ from six clutches) and 4.35 ± 0.54 g BM (range, 3.16–5.96 g; $n = 79$, from 10 clutches; Table 3). SVL averaged $85.8 \pm 2.1\%$ (81.4–

89.2%; $n = 23$) of total length, but males had longer tails than females (SVL/total length, 82.6% vs 86.7%; $F_{1,6} = 68.1$; $P < 0.001$). Mean hatchling size (SVL or BM) per clutch, however, was not correlated with female body size (SVL or SBM) or mean clutch EM ($P > 0.05$ in all cases). Mean hatchling BM, however, approached a significant positive correlation with mean clutch EM ($r = 0.61$; $P = 0.060$; $n = 10$).

Egg size and shape.—Although Western Hognose Snake eggs are generally reported to be non-adherent with one another (e.g., Ernst and Ernst 2003), I recorded adherence in three of 40 clutches. In a clutch of four, two eggs were adherent; in another clutch of 10 eggs, three were adherent; and in a clutch of eight, two pairs of eggs were adherent. Eggs laid by 40 captive females averaged 29.6 ± 3.7 mm in length (range, 23.0–40.8 mm; $n = 249$), 17.0 ± 1.3 mm in width (range, 11.8–19.8 mm; $n = 248$), and 5.23 ± 0.74 g in mass (range, 3.25–7.19 mm; $n = 245$). Egg length (EL) was negatively related to egg width ($EW = -0.157(EL) + 21.657$; $F_{1,246} = 59.03$; $r^2 = 0.194$; $P < 0.001$; $n = 248$). EL and EW were each related to egg mass ($EM = 0.100(EL) + 2.247$; $F_{1,225} = 79.35$; $r^2 = 0.261$, $P < 0.001$; and $EM = 0.259(EW) + 0.806$; $F_{1,225} = 66.25$; $r^2 = 0.227$; $P < 0.001$, respectively; $n = 227$). EL and EW were related to EM by the equation $EM = 0.169(EL) + 0.461(EW) - 7.668$ ($F_{2,224} = 618.47$; $r^2 = 0.847$; $P < 0.001$; $n = 227$).

Egg elongation (EL/EW) averaged 1.76 ± 0.32 (range, 1.23–3.39; $n = 248$) and tended to be positively correlated with individual EM ($r = 0.13$; $P = 0.06$; $n = 227$). Mean egg elongation in a clutch for 32 clutches averaged 1.85 ± 0.32 (range, 1.40–2.72) and was negatively correlated with SVL ($r = -0.65$; $P < 0.001$; Fig. 4), SBM ($r = -0.65$; $P < 0.001$), CS ($r = -0.68$, $P < 0.001$) and CM ($r = -0.64$; $P < 0.001$), but not EM ($P = 0.520$). Mean clutch EL was negatively correlated with SVL ($r = -0.59$; $P < 0.001$; $n = 31$; Fig. 4) and spent BM ($r = -0.52$; $P < 0.001$; $n = 32$), whereas mean clutch EW was positively correlated with SVL ($r = 0.68$; $P < 0.001$; $n = 31$; Fig. 4) and SBM ($r = 0.76$; $P < 0.001$; $n = 32$). Mean clutch EM was not correlated with SVL ($P = 0.560$; Fig. 4) or SBM ($P = 0.180$; $n = 36$). Annual variation in mean clutch EM across the five largest sample years was negligible ($F_{4,15} = 0.870$; $P = 0.504$). The slope of the regression of log EM on log SVL was not significantly different than zero ($F_{1,33} = 0.213$; $P = 0.647$; $n = 35$).

Relative egg mass (REM: mean clutch EM/gravid BM) averaged 0.038 ± 0.012 (range, 0.026–0.061; $n = 9$). Egg mass relative to spent body mass (SREM = EM/SBM), however, averaged 0.062 ± 0.020 (range, 0.025–0.099; $n = 36$) and was negatively correlated with female SVL ($r = -0.85$; $P < 0.001$; $n = 35$; Fig. 4) and SBM ($r = -0.86$; $P < 0.001$; $n = 36$). SREM did not

TABLE 1. Literature records of oviposition dates for Western Hognose Snakes (*Heterodon nasicus*), Dusky Hog-nosed Snakes (*H. gloydi*), and Mexican Hog-nosed Snakes (*H. kennerlyi*) held in captivity. Populations listed by decreasing latitude. Asterisk indicates long-term captive.

Location	Date captured	Date gravid	Date laid	Source
<i>H. nasicus</i>				
Alberta			Mid-June to late July	Russell and Bauer 1993
Alberta		15 June	early July	Pendlebury 1976
Alberta	13 July		19–23 July (n = 1)	Moore 1953
Manitoba		22, 23, 24, 26, 27 June and 8 July		Leavesley 1987
Manitoba			12–17 June (n = 1)	Truill in Platt 1969; Preston 1982
Minnesota			first week of June (n = 1), first week July (others)	Hoaglund and Smith 2012
Minnesota		13 July*		Breckenridge 1944
Montana		20 July		Mosimann and Rabb 1952
Montana		11 June, 13, 20 July		Stebbins 1954
Iowa	20 July		4 August	Ruthven 1910
Nebraska	3–47 d captive		15 June - 20 July (n = 40) (mean 29 June ± 8 d)	Iverson 1995, this paper
Nebraska	< 14 d captive		15 June - 3 July (n = 8) (mean 27 ± 7 June)	This paper
Nebraska	14 May		9 July	Iverson 1975
Kansas	4–36 d captive		2–23 July (n = 8)	Platt 1969
Kansas	28 June		2 July	Taggart 1992
Kansas	3 June		5–6 July	Munro 1949a, 1949b
Kansas		27, 29 May, 2, 3, 4, 10, 18 June		Marr 1944
New Mexico			early June (n = 1)	Degenhardt et al. 1996
Unknown			15 August*	Bakker 1997
<i>H. gloydi</i>				
Texas			17 July	Sabath 1960
Texas			24 August	Sabath and Worthington 1959
Texas		17 June*		Anderson 1965
Unknown			March–June*	Mattison 1992
<i>H. kennerlyi</i>				
Texas			3 June*	Werler 1951

vary across the five best sampled years ($F_{4,15} = 0.756$; $P = 0.570$), nor did the residuals of EM regressed against SVL ($F_{4,14} = 0.867$; $P = 0.507$).

Clutch size.—Clutch size (CS) based on oviposited eggs averaged 7.93 ± 3.59 (range, 2–16; n = 40; Table 4), and was positively correlated with both female SVL ($r = 0.50$; $P = 0.001$; n = 38; Fig. 5) and SBM ($r = 0.42$; $P = 0.010$; n = 36). The slope of the regression of log CS on

log SVL was 1.56 ($F_{1,36} = 11.493$; $r^2 = 0.242$; $P = 0.002$; 95% confidence interval [CI] = 0.63–2.50). CS was not correlated with mean clutch EM ($P = 0.700$; n = 36). In addition, partial correlation analysis of CS versus EM to remove the effect of SVL also showed no correlation ($P = 0.403$), suggesting no trade-off between clutch size and egg size. CS for oviposited clutches did not vary across the five best sampled years ($F_{4,15} = 0.393$; $P = 0.816$). Relative clutch size (SRCS = CS/spent BM) for

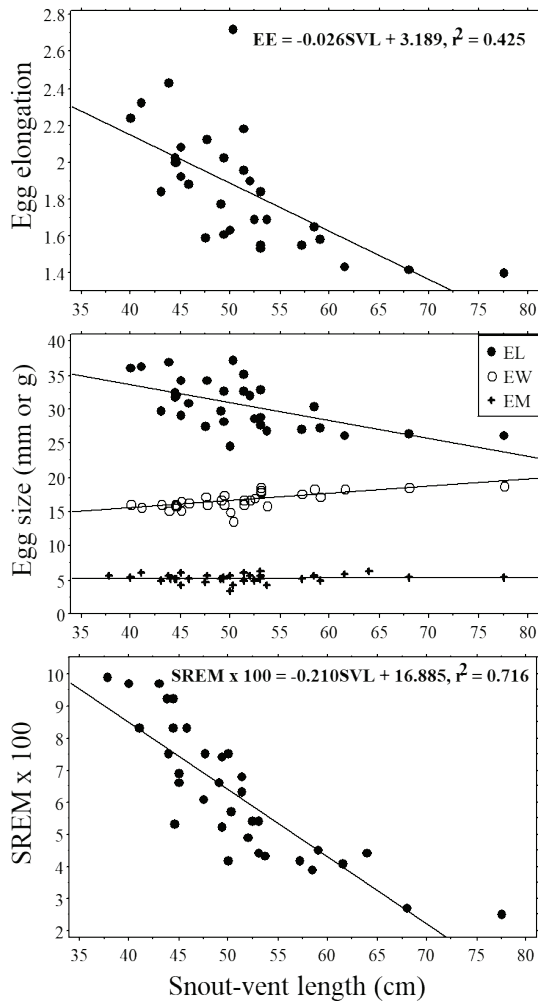


FIGURE 4. Relationship between female snout-vent length (SVL in cm) and egg traits in Western Hognose Snakes (*Heterodon nasicus*) in western Nebraska, USA. (Top) mean egg elongation (length/width); least squares regression is significant ($F_{1,29} = 21.45$; $r^2 = 0.425$; $P < 0.001$). (Center) mean egg length (mm; $F_{1,29} = 15.20$; $r^2 = 0.344$; $P < 0.001$), width (mm; $F_{1,29} = 25.05$; $r^2 = 0.463$; $P < 0.001$), and mass (g; $F_{1,33} = 0.340$; $r^2 = 0.010$; $P = 0.563$) per clutch. (Bottom) relative egg mass (SREM = mean clutch egg mass/spent female body mass); Least squares regression equation is significant ($F_{1,29} = 83.16$; $r^2 = 0.716$; $P < 0.001$).

oviposited clutches averaged 8.8 ± 0.4 eggs/100 g BM (range, 2.1–15.5; $n = 37$), and did not vary across the five best sampled years ($F_{4,15} = 0.244$; $P = 0.909$), nor did the residuals of CS regressed against SVL ($F_{4,14} = 0.180$; $P = 0.945$). SRCs was not correlated with female SVL ($P = 0.235$; $n = 36$).

Clutch mass.—Clutch mass (CM) for 35 females that oviposited in captivity averaged 41.9 ± 20.8 g (range, 10.2–88.4 g; Table 5), and was positively correlated with SVL ($r = 0.52$; $P < 0.002$; Fig. 5), and SBM ($r = 0.47$; $P = 0.005$). The slope of the regression of log CM on log SVL was 1.69 ($F_{1,32} = 10.536$; $r^2 = 0.248$; $P = 0.003$; 95% CI = 0.63–2.74). CM did not vary significantly

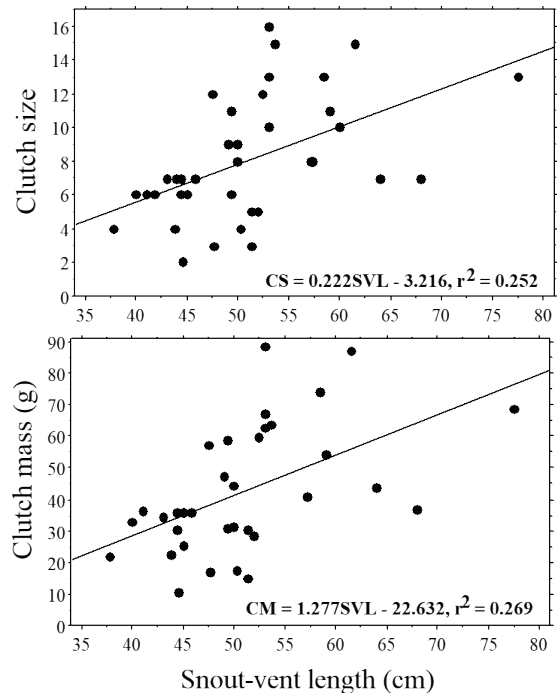


FIGURE 5. Relationship between female snout-vent length (in cm) and reproductive output in Western Hognose Snakes (*Heterodon nasicus*) from western Nebraska, USA. (Top) clutch size; least squares regression line is significant ($F_{1,36} = 12.12$; $r^2 = 0.250$; $P = 0.001$), and virtually identical to that calculated for data from 12 females from Manitoba (Leavesley 1989; see text). (Bottom) clutch mass; least squares regression is significant ($F_{1,32} = 11.75$; $r^2 = 0.270$; $P = 0.002$).

across the five best sample years ($F_{4,15} = 0.528$; $P = 0.717$). Relative clutch mass for gravid females (RCM = clutch mass/gravid female mass) averaged 0.29 ± 0.11 (range, 0.144–0.425; $n = 9$). Relative clutch mass for spent females (SRCM = CM/spent female BM) averaged 0.45 ± 0.18 (range, 0.105–0.858; $n = 35$), and was not correlated with female SVL ($P = 0.318$; Fig. 6) or SBM ($P = 0.113$). SRCM for oviposited clutches also did not vary across the five best sample years ($F_{4,15} =$

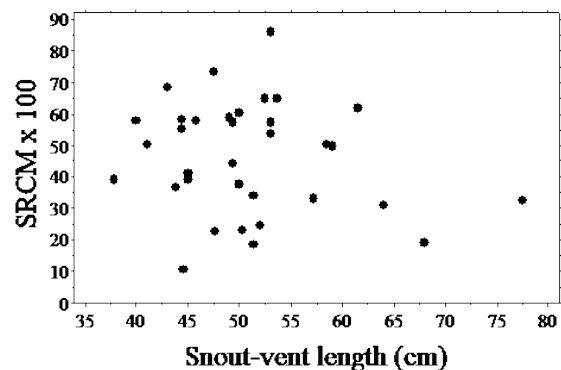


FIGURE 6. Relationship between female snout-vent length (in cm) and relative spent clutch mass (SRCM = clutch mass/spent female body mass) in Western Hognose Snakes (*Heterodon nasicus*) in western Nebraska, USA. Least squares regression is not significant ($F_{1,32} = 1.029$; $P = 0.318$).

TABLE 2. Length of laboratory incubation (in d) for Western Hognose Snakes (*Heterodon nasicus*) and Dusky Hog-nosed Snakes (*H. gloydi*) from across the geographic range (listed by decreasing latitude). Means are followed by range in parentheses. The abbreviation NR indicates that the incubation conditions were not reported in the original reference.

Location	Length	No. of clutches	Conditions	Source
<i>H. nasicus</i>				
Manitoba	51	1	NR	Preston 1982
Manitoba	47–52	1	NR	Platt 1969
Nebraska	49 (45–53)	21	25–30° C	This study
Nebraska	52	1	28° C	Iverson 1975
Kansas	56 (52–64)	4	27° C (22–31° C)	Platt 1969
Kansas	81 (70–89)	1	23° C	Platt 1969
Kansas	55	1	< 32° C	Munro 1949a, 1949b
captive	44	1	NR	Bakker 1997
<i>H. gloydi</i>				
Texas	55	1	NR	Sabath 1960
captive	57 (53–60)	9	28° C	Mattison 1992

0.100; $P = 0.981$), nor did the residuals of CM regressed against gravid SVL ($F_{4,14} = 0.283$; $P = 0.884$). The ratio of spent to gravid body mass for 10 females (41.9–59.1 cm SVL) averaged 0.666 ± 0.103 (range, 0.577–0.841), and was negatively correlated with SBM ($r = -0.65$; $P = 0.005$), but not correlated with female SVL ($P = 0.874$).

DISCUSSION

Size and sexual maturity.—The largest Western Hognose Snake captured in Nebraska (a female) measured 77.5 cm SVL. The record length for the species is 91.8 cm total length for a female from Kansas (Collins et al. 2010; Powell et al. 2016), with

an estimated SVL of 80.7 cm. The largest specimen of *H. nasicus* from Texas measured 90.2 cm total length (Werler and Dixon 2000; estimated SVL 79.3 cm). The smallest reproductive female in Nebraska was 37.8 cm SVL, and the smallest from Kansas measured 36.6 cm SVL (Platt 1969). Platt (1969) estimated sexual maturity at 35.0 cm SVL in females and 30.0 cm SVL in males. The available data on adult body size across the species range (Table 5) suggest minimal geographic variation.

At least some females in Nebraska apparently begin producing eggs during their third full activity season (about 33 mo post-hatching), the same timing as females in Kansas based on juvenile size classes and meager recapture data (Platt 1969). These growth rates

TABLE 3. Hatching sizes of Western Hognose Snakes (*Heterodon nasicus*) and Dusky Hog-nosed Snakes (*H. gloydi*) across the geographic range (listed by decreasing latitude). Means are followed by sample size and appear above ranges (in parentheses). Abbreviations include SVL (snout-vent length in cm), and BM (body mass in g). Asterisks indicate data estimated from SVL-total length ratios (0.858) reported in text, and NR = not reported.

Location	SVL	Total length	BM	Source
<i>H. nasicus</i>				
Nebraska	14.6; 49 (12.5–15.7)	17.0*	4.35; 79 (3.16–5.96)	Iverson 1995; this study
Nebraska	14.6*; 5	17.0; 5	—	Iverson 1975
Kansas	15.3; 20 (12.8–16.7)	17.8*	—	Platt 1969
Kansas	—	—	6.1; 11	Munro 1949c
New Mexico	15.0; NR	15.8; 2 (15.0–16.5)	—	Degenhardt et al. 1996
NR	—	17.5; 21 (14.0–20.0)	4.2 (3) (3.9–4.6)	Ernst and Ernst 2003
<i>H. gloydi</i>				
Texas	—	16.5 (1)	—	Sabath 1960

Iverson.—Western Hognose Snake reproduction.

TABLE 4. Variation in clutch size in Western Hognose Snakes (*Heterodon nasicus*), Dusky Hog-nosed Snakes (*H. gloydi*), and Mexican Hog-nosed Snakes (*H. kennerlyi*) across their ranges. Clutch size values are followed by sample size for that clutch size in parentheses. Asterisks (*) indicate clutch sizes based on counts of ovarian follicles. The abbreviation MWO = mean without ova.

State	Clutch sizes	Mean (n)	Range	MWO	Range	Sources
<i>H. nasicus</i>						
Alberta	9, 12	10.5 (2)	9–12	10.5 (2)	9–12	Moore 1953; Pendlebury 1976
Manitoba	5*, 6 (4)*, 7 (2)*, 8 (3)*, 9*, 11*, 12(3)*	8.0 (16)	5–12	12.0 (1)	NA	Stebbins 1954; Platt 1969; Leavesley 1987
Montana	7	7 (1)	NA	7 (1)	NA	Mosimann and Rabb 1952
Minnesota	9	9 (1)	NA	9 (1)	NA	Breckenridge 1944
Iowa	5	5 (1)	NA	5 (1)	NA	Ruthven 1910
Nebraska	2, 3 (2), 4 (4), 5 (2), 6 (8), 7 (6), 8 (3), 9 (3), 10 (2), 11 (2), 12 (2), 13 (3), 15 (2), 16	7.95 (41)	2–16	7.95 (41)	2–16	Iverson 1975; Iverson 1995; this paper
Nebraska	mean, 12.6; range 10–16; N = 11	12.6 (11)	10–16	12.6 (11)	10–16	Ballinger et al. 2010
Kansas	7*, 7*, 11*, 13 (2)*, 14*, 17*, 23*; 11; 4 (3), 5 (6), 6, 7 (3), 14, 15, 16	9.2 (25)	4–23	7.35 (17)	4–16	Marr 1944; Munro 1949a; Platt 1969
Unknown	6	6 (1)	NA	6 (1)	NA	Bakker 1997
<i>H. gloydi</i>						
Texas	2; 16	9 (2)	2–16	9 (2)	2–16	Sabath and Worthington 1959; Anderson 1965
Unknown	6, 7, 9,(3), 10, 11 (2), 13, 14, 15, 16	10.8 (12)	6–16	10.8 (12)	6–16	Mattison 1992 (captive)
<i>H. kennerlyi</i>						
Texas	7	7 (1)	NA	7 (1)	NA	Werler 1951
Means for <i>nasicus</i> only		8.80 (99)	2–23	8.55 (76)	2–16	

also match those for females in Manitoba (Leavesley 1987) based on size class data and limited recapture data, although size at maturity was not determined for that population. In captivity, however, females can reach 45 cm SVL and begin reproducing in 14.5 mo (Bakker 1997). Assuming a six-month season of winter inactivity (Platt 1969), 14.5 mo in captivity would be approximately equivalent to 38.5 mo in nature. Another captive female first laid eggs after just 21 mo (Mattison 1992). Clearly captive conditions (e.g., optimal food and temperatures; no brumation) can alter life-history traits in reptiles such as *H. nasicus*, and hence, comparative studies should be cautious about including only captive data for included taxa. Hatchlings from Kansas averaged 15.3 cm SVL (from six clutches; Table 3; Platt 1969), which was not significantly different from average SVL from Nebraska (14.6 ± 0.7 cm) based on their overlap in variation. The smallest hatchling captured in the fall in Manitoba, however, was 16.8 cm

SVL (Leavesley 1987), but the larger size in Manitoba is likely the result of post-hatching growth rather than larger hatchling size in Manitoba.

Female reproductive cycle.—Although the literature generally reports *H. nasicus* as a biennial breeder (e.g., Ernst and Ernst 2003, and references therein), only 46% of females were gravid during one climatically typical year in Nebraska (1993), whereas only 18% were reproductive in a particularly harsh year (2004). The low clutch frequency in 2004 may have been related to the fact that 2003 (the previous year) was the seventh driest year from 1970–2018 (NOAA climate data at the study site) and the fifth warmest (including the hottest October across all years), followed by the seventh driest May and June in 2004 and a slightly warmer than normal spring in 2004 (Iverson, unpubl. data).

In Kansas, Platt (1969; Table 20) reported that of 29 females > 35 cm SVL, only 10 (34.5%) were

TABLE 5. Mean reproductive outputs of Western Hognose Snakes (*Heterodon nasicus*), Dusky Hog-nosed Snakes (*H. gloydi*), and Mexican Hog-nosed Snakes (*H. kennerlyi*) across their range. Populations are listed by decreasing latitude (to the nearest half degree, in parentheses below location). Values are means of samples reported in the listed source. Abbreviations are SVL (adult female snout-vent length in cm), CS (clutch size), EL (egg length in mm), EW (egg width in mm), EM (egg mass in g), SRCM (clutch mass relative to spent body mass x 100), and REM (egg mass relative to spent body mass x 100). See text for further explanations of outputs. Means are followed by sample size (in number of clutches) in parentheses, and appear above ranges in parentheses. Asterisks indicate data estimated from egg size-egg mass or SVL-spent body mass regressions in text and NR = not reported.

Location	SVL	CS	EL	EW	EM	CM	SRCM	SREM	Source
<i>H. nasicus</i>									
Alberta (51)	60.7 (1) –	12 (1) –	–	–	–	–	–	–	Moore 1953; Pendlebury 1976
Manitoba (50)	59.1 (12) (51–75)	7.9 (12) (5–12)	–	–	–	–	–	–	Leavesley 1987
Alberta (49)	47.3 (1) –	9 (1) –	–	–	–	–	–	–	Pendlebury 1976
Illinois (42)	49.3 (21) (41–63)	–	–	–	–	–	–	–	Kolbe et al. 1999, pers. comm.
Nebraska (41.5)	49.8 (65) (38–78)	7.9 (40) (2–16)	30.6 (32) (24.7–37.2)	16.7 (32) (13.7–18.8)	5.25 (36) (3.47–6.27)	41.9 (35) (10.2–88.4)	45.5 (35) (10.5–85.8)	6.2 (35) (2.5–9.9)	Iverson this paper
Nebraska (40.5)	63.0 (1) –	9 (9) –	37.0 (9) –	18.0 (9) –	6.88* (1) –	61.9* (1) –	42.3 (1)* –	4.70 (1)* –	Iverson 1975
Kansas (38.5)	58.4 (1) –	11 (1) –	33.5 (11) (31.5–35.5)	19.5 (11) (18.5–20.0)	6.46 (1) (6.05–6.80)	71.1 (1) –	69.5 (1) –	6.3 (1) –	Munro 1949a, 1949b
Kansas (38)	51.7 (9) (37–65)	7.5 (13) (4–16)	32.3 (5) (26.0–38.0)	17.0 (5) (14.0–23.0)	5.53 (5) (4.1–8.7)	29.9 (5) (18.0–45.5)	65.8 (4) (42–83)	–	Platt 1969
<i>H. gloydi</i>									
Texas (30)	54.0 (1) –	2 (1) –	32.0 (1) (31–33)	20.0 (1) –	6.96* (1) –	13.9* (1) –	12.9* (1) –	6.44* (1) –	Sabath and Worthington 1959
Texas (29)	48.4 (1) –	5 (1) –	32.6 (1) (30–34)	19.6 (1) (19–20)	6.88* (1) –	34.4* (1) –	40.8* (1) –	8.15* (1) –	Sabath 1960
Texas (NR)	60.3 (1) –	16 (1) –	31 (1) –	17 (1) –	5.41* (1) –	86.5* (1) –	64.1* (1) –	4.01* (1) –	Anderson 1965
<i>H. kennerlyi</i>									
Texas (26.5)	58.0 (1) –	7 (1) –	22.5 (1) (20–24)	14.5 (1) (14–15)	2.86* (1) (2.50–3.13)*	20.0* (1) –	16.0* (1) –	2.29* (1) –	Werler 1951

reproductive, but of 16 females > 40 cm SVL eight (50%) were reproductive. In Manitoba, Leavesley (1987) reported that eight of 10 large females (> 50 cm SVL) were gravid when captured in late May to early July, but only eight of 16 total adult females (50%) were known to be reproductive. These data suggest that reproduction in this species may frequently be less than biennial, that reproductive frequency increases with female body size, and that extremely hot and dry

conditions during the year prior to nesting season may reduce reproductive frequency that summer.

An increase in reproductive frequency with body size is a common pattern in snakes (see review in Iverson et al. 2012). In addition, climatic conditions, and hence, resource availability during the year prior to oviposition, are known to impact reproductive frequency in many snakes (e.g., Andr n and Nilson 1983; Whittier and Crews 1990; Lourdais et al., 2002; Iverson et al. 2012;

Baron et al. 2013, among others). Although *H. nasicus* are less than a biennial breeder in the field, Mattison (1992) demonstrated that well-fed females maintained under warm captive conditions are capable of producing two clutches per year at intervals of 53–60 d ($n = 9$; mean 57.1 d, excluding two outliers of 26 and 39 d). This corroborates the importance of resource availability and thermal history to reproductive frequency in this species. Because ovipositing females lost about 33% of their body mass on average, and second clutches in captivity required nearly 2 mo between clutches (Mattison 1992), the production of a second clutch in the field in Nebraska is very unlikely.

Across populations gravid female *H. nasicus* have been collected from 27 May to 20 July (Table 1); however, oviposition dates ranged from early June to early August, with most dates falling between mid-June and mid-July (as in my study). Some of the variation no doubt reflects the length of time and the conditions under which the female was held prior to oviposition. Surprisingly, there was no evident latitudinal pattern of timing despite the effect of warmer May temperatures on earlier nest timing in Nebraska.

Laboratory incubation times across populations generally ranged from 44–64 d (Table 2), although a clutch kept in a cold (about 23° C) basement by Platt (1969) required an average of 81 d (70–89 d). There is no evidence of geographic variation in incubation times in *H. nasicus*, although there is a weak indication that they might be longer for *H. gloydi* from Texas (Table 2). The available data, however, are too few to evaluate that pattern statistically.

Egg size and shape.—The eggs of *H. nasicus* generally weigh 5–6 g (Table 5) and no clear pattern of geographic variation is evident, although samples are meager outside of Kansas and Nebraska. Egg mass does not vary with female body size, although egg width increases and egg length decreases with body size. Hence, small females produce elongate eggs, whereas the eggs of large females are considerably more blunt. Egg elongation and its correlates have been examined in only one other species of snake (Bullsnake, *Pituophis catenifer*; Iverson et al. 2012), where elongation increased with egg size but not body size. Future work should address the lack of these data.

Eggs of *H. nasicus* in a clutch are generally reported to be non-adherent with one another (e.g., Ernst and Ernst 2003); however, I observed adherence between two to three eggs in three of 40 clutches from Nebraska, and Platt (1969) mentioned that they may adhere (presumably in Kansas) but usually do not. In addition, Sabath (1960) observed two adherent eggs of five in a clutch from *H. gloydi* from Texas. Unfortunately, no clutch has ever been observed in the field, so it is

unclear how common adherence is in nature. Adherence is apparently uncommon among snakes, and hence, a comparative study of its occurrence across snakes might reveal the adaptive significance of the trait for those that exhibit it.

Relative egg mass (REM: mean clutch EM/gravid BM) averaged 0.038 for nine female *H. nasicus* from western Nebraska, but data for this metric are unavailable for other populations of this species (Table 5). The Nebraska value is similar to those of other oviparous colubrids calculated from the data compiled by Dunham et al. (1988: mean = 0.047; $n = 17$ taxa). REM for 39 *Pituophis catenifer* from my Nebraska site averaged 0.039 (Iverson et al. 2012).

Egg mass relative to spent body mass (SREM: mean clutch EM/spent BM) averaged 0.062 in Nebraska, nearly identical to the only other published value for the species (0.063; $n = 1$) from Kansas (Munro 1949a, 1949b; Table 5). In addition, the mean SREM estimated for three female *H. gloydi* from Texas (Table 5) was also 0.062. The lack of a relationship between female size and egg mass, the apparent absence of annual or geographic variation in raw or relative egg mass suggest that egg size may be under strong selection for optimal size (Smith and Fretwell 1974; Brockelman 1975; see below).

Clutch size.—Clutch size (CS) based on deposited eggs varied from a mean of 7.9 in this study (Table 4), to 8.6 across 15 other studies (Table 4). Wright and Wright (1957), however, reported a maximum clutch size of 24 eggs (without details), and Platt (1969) recorded 23 ova in a Kansas female. Based on the data in Figure 7, I question the possibility of actual deposited clutches this large.

Clutch size was highly correlated with SVL in my sample, as it is both within and across snake populations in general (Fitch, 1970, 1985; Dunham et al., 1988; among many others). The SVL-CS regression equation from my data was nearly identical to that calculated from 12 gravid females reported from Manitoba by Leavesley (1987; $CS = 0.277(SVL) - 8.471$; $F_{1,10} = 32.45$; $r^2 = 0.764$; $P < 0.001$). In addition, these regressions were consistent with the mean clutch sizes reported from small, medium, and large snakes by Platt (1969). Together, these data suggest little geographic variation in clutch size, except that related to body size. Neither raw clutch size nor relative clutch size varied across years in my study, a pattern typical in snakes (Seigel and Fitch 1985; Seigel and Ford 1987, 1991; Iverson et al. 2012).

Clutch size in *H. nasicus* scaled logarithmically with SVL at half the predicted slope (1.56 versus 3.0). This relationship has been examined in only one other snake, the Red-backed Ratsnake, *Oocatochus* (formerly

Elaphe rufodorsatus (King 2000), which scaled close to the expected slope (2.9; 95% CI = 2.2–3.5). Given that data are available for only two snake species, the significance of the extreme hypoallometry in *H. nasicus* is unclear.

No egg size-clutch size tradeoff existed in Nebraska *H. nasicus*. Instead, larger females increased their reproductive output almost exclusively by increased CS rather than egg mass, precisely as predicted by optimal egg size (OES) theory, but under stable conditions (Smith and Fretwell 1974; Brockelman 1975). Reproductive frequency in *H. nasicus*, however, appears to be constrained by resource availability, and under that scenario OES theory predicts a trade-off between number and size of offspring. No such trade-off was evident in my population. Nevertheless, my data suggest that egg size in *H. nasicus* is being strongly optimized by selection. On the capital- versus income-breeding spectrum (Stephens et al. 2009), like most snakes (e.g., Lourdaï et al. 2002), *H. nasicus* is likely a capital breeder, using stored nutrients from previous years for later reproduction, rather than relying on resources acquired during the year of reproduction.

Clutch mass.—As expected from previous research on snakes (Seigel et al. 1986), CM increased with body size, although at about half the rate expected by theory (King 2000; Iverson et al. 2019), i.e., hypoallometrically. Unfortunately, log-log standardized CS-body size data are not yet available for other snakes (King 2000). Relative clutch mass (RCM = CM/ gravid BM) averaged 0.29 at our Nebraska site, a value typical for other oviparous colubrids (mean 0.35 for 52 samples in Seigel and Fitch 1984; 0.32 for 19 samples in Dunham et al. 1988). Clutch mass relative to spent female body mass (SRCM) for Nebraska *H. nasicus* averaged 0.45, compared to a mean of 0.66 for four Kansas females (Platt 1969), and a mean of 0.39 for three *H. gloydi* from Texas (Table 5). Samples are still too few to assess latitudinal variation in relative clutch mass in *H. nasicus*, but the preliminary data suggest no pattern. I found no evidence of annual variation in SRCM in *H. nasicus*, a pattern also found in a number of other snakes (Seigel and Ford 1991; Madsen and Shine 2001; review in Iverson et al. 2012).

To summarize, reproduction in female *H. nasicus* seems to be highly resource limited, as evidenced by the fact that half or more of females skip reproduction in a given year, whereas in captivity they can produce two clutches in a year. However, long-term telemetry studies of individual snakes are sorely needed to test this assumption, which is based on sporadic captures of multiple individuals. Clutch and egg sizes relative to female body size are typical of snakes; however, clutch size increased with female body size but egg mass did

not. Small females produced decidedly elongate eggs, whereas the eggs of larger females were only slightly elongate. These data argue that egg mass is under selection for optimal size. Surprisingly, reproductive data from other populations of *H. nasicus* suggest little geographic variation in age or size at maturity, adult body size, nest timing, or raw or relative egg or clutch size, despite the fact the species ranges over 1,900 km of latitude.

Acknowledgments.—Refuge managers Fred Zeilemaker, Kevin Brennan, Mark Heisinger, Royce Huber, Bill Behrends, Larry Malone, Steve Knode, Neil Powers, Rod Wittenberg, Brian DeVries, and Marlin French permitted our work on the Crescent Lake Refuge. Permits to undertake research in Nebraska were provided annually from 1980 to 2017 by the Nebraska Game and Parks Commission, through the courtesy of Mike Fritz. Support for the project was provided by Earlham College, the Joseph Moore Museum of Natural History, the Howard Hughes Medical Institute, the Ford Foundation, the Sears Roebuck Foundation, and the National Science Foundation. Iverson's family patiently tolerated his frequent absences for field work in western Nebraska for nearly four decades. Frank Slavens shared critical obscure literature. Geoffrey Smith provided valuable comments on an early draft. Most of this work was done before the advent of the Earlham College Institutional Animal Care and Use Committee, but was approved by that committee beginning in 2014 (20140516-2JI). In any case, I abided by the ethical guidelines later published by the Guidelines for the Use of Live Amphibians and Reptiles in Field Research by the American Society of Ichthyologists and Herpetologists, The Herpetologists' League, and the Society for the Study of Amphibians and Reptiles (<http://erenweb.org/wp-content/uploads/2011/07/GUIDELINES-FOR-USE-OF-LIVE-AMPHIBIANS-AND-REPTILES-IN-FIELD-RESEARCH.pdf>).

LITERATURE CITED

- Anderson, P. 1965. The Reptiles of Missouri. University of Missouri Press, Columbia, Missouri, USA.
- Andr n, C., and G. Nilson. 1983. Reproductive tactics in an island population of Adders, *Vipera berus* (L.), with a fluctuating food resource. *Amphibia-Reptilia* 4:63–79.
- Bakker, J. 1997. Striking nest behaviour of *Heterodon nasicus nasicus*. *Litteratura Serpentina* 17:10–11.
- Ballinger, R.E., J.D. Lynch, and P.H. Cole. 1979. Distribution and natural history of amphibians and reptiles in western Nebraska with ecological notes on the herptiles of Arapaho Prairie. *Prairie Naturalist* 11:65–74.

Iverson.—Western Hognose Snake reproduction.

- Ballinger, R.E., J.D. Lynch, and G.R. Smith. 2010. Amphibians and Reptiles of Nebraska. Rusty Lizard Press, Oro Valley, Arizona, USA.
- Baron, J.P., J.-F. Le Galliard, R. Ferrière, and T. Tully. 2013. Intermittent breeding and the dynamics of resource allocation to reproduction, growth and survival. *Functional Ecology* 27:173–183.
- Bleed, A., and C. Flowerday (Eds.). 1990. An Atlas of the Sandhills. Conservation Survey Division, Institute of Agriculture and Natural Resources, Resource Atlas 5a:1–265.
- Breckenridge, W.J. 1944. Amphibians and Reptiles of Minnesota. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Brockelman, W.Y. 1975. Competition, the fitness of offspring, and optimal clutch size. *American Naturalist* 109:677–699.
- Collins, J.T., and T.W. Taggart. 2009. Standard Common and Current Scientific Names for North American Amphibians, Turtles, Reptiles, and Crocodylians. Sixth Edition. The Center for North American Herpetology, Lawrence, Kansas, USA.
- Collins, J.T., S.L. Collins, and T.W. Taggart. 2010. Amphibians, Reptiles, and Turtles in Kansas. Eagle Mountain Publishing, Eagle Mountain, Utah, USA.
- Converse, S.J., J.B. Iverson, and J.A. Savidge. 2005. Demographics of an Ornate Box Turtle (*Terrapene ornata ornata*) population experiencing minimal human-induced disturbances. *Ecological Applications* 15:2171–2179.
- Crother, B.I., J. Boundy, J.A. Campbell, K. De Quieroz, D. Frost, D.M. Green, R. Highton, J.B. Iverson, R.W. McDiarmid, P.A. Meylan, et al. 2003. Scientific and standard English names of amphibians and reptiles of North America north of Mexico: update. *Herpetological Review* 34:196–203.
- Degenhardt, W.G., C.W. Painter, and A.H. Price. 1996. Amphibians and Reptiles of New Mexico. University of New Mexico Press, Albuquerque, New Mexico, USA.
- Dunham, A.E., D.B. Miles, and D.N. Reznick. 1988. Life history patterns in squamate reptiles. Pp. 441–511 *In* Biology of the Reptilia, Volume 16. Gans, C., and R.B. Huey (Eds.). Alan R. Liss, New York, New York, USA.
- Edgren, R.A. 1952. A synopsis of the snakes of the genus *Heterodon*, with the diagnosis of a new race of *Heterodon nasicus* Baird and Girard. *Chicago Academy of Sciences Natural History Miscellanea* 112:1–4.
- Ernst, C.H., and E.M. Ernst. 2003. Snakes of the United States and Canada. Smithsonian Press, Washington, D.C., USA.
- Fitch, H.S. 1970. Reproductive cycles in lizards and snakes. University of Kansas Museum of Natural History, Miscellaneous Publications 52:1–247.
- Fitch, H.S. 1975. A demographic study of the Ringneck Snake (*Diadophis punctatus*) in Kansas. University of Kansas Museum of Natural History, Miscellaneous Publications 62:1–53.
- Fitch, H.S. 1985. Variation in clutch and litter size in New World reptiles. University of Kansas Museum of Natural History, Miscellaneous Publications 76:1–76.
- Gunderson, H. L. 1973. Recent mammals of Crescent Lake National Wildlife Refuge, Garden County, Nebraska. *Nebraska Bird Review* 41:71–76.
- Hedrick, A., Corichi, L., H. Klondaris, J.B. Iverson, and M. Dreslik. 2017. The effects of climate on annual variation in reproductive output in Snapping Turtles (*Chelydra serpentina*). *Canadian Journal of Zoology* 96:221–228.
- Hoaglund, E.P., and C.E. Smith. 2012. Lessons learned: notes on the natural history of the Plains Hognose Snake (*Heterodon nasicus*) in Minnesota. *Reptiles and Amphibians* 19:163–169.
- Imler, R.H. 1945. Bullsnares and their control on a Nebraska wildlife refuge. *Journal of Wildlife Management* 9:265–273.
- Iverson, J.B. 1975. Notes on Nebraska reptiles. *Transactions of the Kansas Academy of Sciences* 78:51–62.
- Iverson, J.B. 1995. *Heterodon nasicus*. Reproduction. *Herpetological Review* 26:206.
- Iverson, J. B., and G.R. Smith. 1993. Reproductive ecology of the Painted Turtle (*Chrysemys picta*) in the Nebraska Sandhills and across its range. *Copeia* 1993:1–21.
- Iverson, J.B., H. Higgins, A. Sirulnik, and C.M. Griffiths. 1997. Local and geographic variation in the reproductive biology of the snapping turtle (*Chelydra serpentina*). *Herpetologica* 53:96–117.
- Iverson, J.B., P.V. Lindeman, and J. Lovich. 2019. Understanding reproductive allometry in turtles: a slippery “slope.” *Ecology and Evolution* 9:11891–11903.
- Iverson, J.B., C.A. Young, T.S.B. Akre, and C.M. Griffiths. 2012. Reproduction by female Bullsnares (*Pituophis catenifer sayi*) in the Nebraska Sandhills. *Southwestern Naturalist* 57:58–73.
- King, R.B. 2000. Analyzing the relationship between clutch size and female size in reptiles. *Journal of Herpetology* 24:148–150.
- Kolbe, J.L., L.J. Harmon, and D.A. Warner. 1999. New state record lengths and associated natural history notes of some Illinois snakes. *Transactions of the Illinois Academy of Sciences* 92:133–135.
- Leavesley, L.K. 1987. Natural history and thermal relations of the Western Hognose Snake (*Heterodon nasicus nasicus*) in southwestern Manitoba. M.Sc. Thesis, University of Manitoba, Winnipeg, Canada. 161 p.

- Lourdais, O., X. Bonnet, R. Shine, D. Denardo, G. Naulleau, and M. Guillon. 2002. Capital-breeding and reproductive effort in a variable environment: a longitudinal study of a viviparous snake. *Journal of Animal Ecology* 71:470–479.
- Madsen, T., and R. Shine. 2000. Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. *Journal of Animal Ecology* 69:952–958.
- Madsen, T., and R. Shine. 2001. Conflicting conclusions from long-term versus short-term studies of growth and reproduction of a tropical snake. *Herpetologica* 57:147–156.
- Marr, J.C. 1944. Notes on amphibians and reptiles from the central United States. *American Midland Naturalist* 32:478–490.
- Mattison, C. 1992. Reproduction in the Dusty Hognose Snake, *Heterodon nasicus gloydi*. *Litteratura Serpentina* 12:98–101.
- Moore, J.E. 1953. The Hog-nose Snake in Alberta. *Herpetologica* 9:173.
- Mosimann, J.E., and G.B. Rabb. 1952. The herpetology of Tiber Reservoir area, Montana. *Copeia* 1952:23–27.
- Munro, D.F. 1949a. Food of *Heterodon nasicus nasicus*. *Herpetologica* 5:133.
- Munro, D.F. 1949b. Gain and size and weight of *Heterodon* eggs during incubation. *Herpetologica* 5:133–134.
- Munro, D.F. 1949c. Hatching of a clutch of *Heterodon* eggs. *Herpetologica* 5:134–136.
- Packard, G.C., and T.J. Boardman. 1988. The misuse of ratios, indices, and percentages in ecophysiological research. *Physiological Zoology* 61:1–9.
- Pendlebury, G.B. 1976. The Western Hognose Snake. *Heterodon nasicus nasicus*, in Alberta. *Canadian Field Naturalist* 90:416–422.
- Platt, D.R. 1969. Natural history of the Hognose Snakes *Heterodon platyrhinos* and *Heterodon nasicus*. University of Kansas Publications, Museum of Natural History 18:253–420.
- Powell, R., R. Conant, and J.T. Collins. 2016. Peterson Field Guide to the Reptiles and Amphibians of Eastern and Central North America. Houghton Mifflin Harcourt, Boston, Massachusetts, USA.
- Preston, W.B. 1982. The Amphibians and Reptiles of Manitoba. Manitoba Museum of Man and Nature, Winnipeg, Canada.
- Russell, A.P., and A.M. Bauer. 1993. The Amphibians and Reptiles of Alberta. University of Calgary Press, Calgary, Alberta, Canada.
- Ruthven, A.G. 1910. Contributions to Iowa herpetology. *Proceedings of the Iowa Academy of Sciences* 17:198–212.
- Sabath, M. 1960. Eggs and young of several Texas reptiles. *Herpetologica* 16:72.
- Sabath, M., and R. Worthington. 1959. Eggs and young of certain Texas reptiles. *Herpetologica* 15:31–32.
- Schaefer, W.H. 1934. Diagnosis of sex in snakes. *Copeia* 1934:181.
- Seigel, R.A., and H.S. Fitch. 1984. Ecological patterns of relative clutch mass in snakes. *Oecologia* 61:293–301.
- Seigel, R.A., and H.S. Fitch. 1985. Annual variation in reproduction in snakes in a fluctuating environment. *Journal of Animal Ecology* 54:497–505.
- Seigel, R.A., and N.B. Ford. 1987. Reproductive ecology. Pp. 210–252 *In* Snakes: Ecology and Evolutionary Biology. Seigel, R.A., J.T. Collins, and S.S. Novak (Eds.). McGraw-Hill, New York, New York, USA.
- Seigel, R.A., and N.B. Ford. 1991. Phenotypic plasticity in the reproductive characteristics of an oviparous snake, *Elaphe guttata*: implications for life-history studies. *Herpetologica* 47:301–307.
- Seigel, R.A., H.S. Fitch, and N.B. Ford. 1986. Variation in relative clutch mass in snakes among and within species. *Herpetologica* 42:179–185.
- Smith, C.C., and S.D. Fretwell. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108:499–506.
- Smith, H.M., D. Chiszar, C.M. Eckerman, and H.D. Walley. 2003. The taxonomic status of the Mexican Hognose Snake *Heterodon kennerlyi* Kennicott. *Journal of Kansas Herpetology* 5:17–20.
- Stebbins, R.C. 1954. Amphibians and Reptiles of Western North America. McGraw Hill, New York, New York, USA.
- Stejneger, L.H., and T. Barbour. 1939. A Check List of North American Amphibians and Reptiles. 4th Edition. Harvard University, Cambridge, Massachusetts, USA.
- Stephens, P.A., I.L. Boyd, J.M. McNamara, and A.I. Houston. 2009. Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology* 90:2057–2067.
- Taggart, T.W. 1992. Observations on Kansas amphibians and reptiles. *Kansas Herpetological Society Newsletter* 88:13–15.
- Walley, H.D., and C.M. Eckerman. 1999. Reptilia: Squamata: Colubridae *Heterodon nasicus*. *Catalogue of American Amphibians and Reptiles* 698:1–10.
- Weaver, J.E. 1965. Native Vegetation of Nebraska. University of Nebraska Press, Lincoln, Nebraska, USA.
- Werler, J.E. 1951. Miscellaneous notes on the eggs and young of Texan and Mexican reptiles. *Zoologica* 36:37–48.
- Werler, J.E., and J.R. Dixon. 2000. Texas Snakes: Identification, Distribution, and Natural History. University of Texas Press, Austin, Texas, USA.

Iverson.—Western Hognose Snake reproduction.

Whittier, J.M., and D. Crews. 1990. Body mass and reproduction in female Red-sided Garter Snakes (*Thamnophis sirtalis parietalis*). *Herpetologica* 46:219–226.

Wright, A.H., and A.A. Wright. 1957. *Handbook of Snakes of the United States and Canada*. Comstock Publishing Associates, Cornell University Press, Ithaca, New York, USA.



JOHN B. IVERSON holds a Ph.D. in Biology from the University of Florida, Gainesville, USA, and is Biology Research Professor at Earlham College in Richmond, Indiana, USA. Because of his interests in the natural history, ecology, and evolution of iguanas and turtles, he is currently on the steering committees (and founding member) of the International Union for Conservation of Nature (Species Survival Commission) Iguana Specialist Group, and Tortoise and Freshwater Turtle Specialist Group. He has been involved with the Turtle Survival Alliance since its inception in 2001 (currently a Board member), and serves on the Board of the Turtle Conservation Fund. He has been active in several herp societies, serving as Editor and President of the Herpetologists League. He has maintained long-term field research sites since 1980 for Rock Iguanas (*Cyclura cyclura*) in the Exumas in the Bahamas, and since 1981 for turtles at the Crescent Lake National Wildlife Refuge in western Nebraska, USA. His hobby is restoring a 76 ac woodlot/cornfield (now in a Conservation Easement) to a mature hardwood forest. (Photographed by Matt Lachiusa).