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HEADSTARTING AS A MANAGEMENT TOOL: A CASE STUDY OF THE PLAINS GARTERSNAKE

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Abstract: The use of headstarting and related techniques as management tools for threatened and endangered species remains controversial, due in part to a lack of empirical data on their effectiveness. Here, we present data on pre-natal mortality, growth, and survival during headstarting as well as growth, survival, and reproduction following release for an unprotected population of plains gartersnakes. We combine these data with data on growth and survival of comparably sized wild-caught snakes to provide an overall evaluation of the potential effectiveness of headstarting. Depending on rearing conditions, proportions of live births varied from 0.79 ('worst-case') to 0.94 ('best-case'), survival during headstarting ranged from 0.74 ('worst-case') to 0.88 ('best-case'), and second-year survival following release ranged from 0.11 ('worst-case') to 0.40 ('best-case'). In comparison, survival of free-ranging snakes was 0.16 in their first year and 0.40 in their

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second year. Assuming the proportion of live births in nature is close to 1, expected survival to reproductive maturity among free-ranging snakes is 0.06, whereas that for headstarted snakes ranges from 0.07 ('worst-case') to 0.33 ('best-case'). The growth rate of headstarted snakes following release was similar to that of similar-sized free-ranging snakes, and headstarted snakes were successful at reproduction. Together, these results suggest that, if carefully implemented, headstarting may be an effective management tool for endangered plains gartersnake populations in Ohio and for other natricine snakes with similar demographic characteristics.

Key words: Gartersnake; Growth rate; Headstarting; Natricine Snakes; Survivorship

THE RARITY of threatened and endangered species can preclude the use of experimental manipulations to test alternative management strategies. Consequently, the effectiveness of management tools used to aid recovery of threatened and endangered species is sometimes poorly known. For taxa in which only some populations are of management concern or for which related (e.g., congeneric), ecologically similar unprotected taxa exist, experimental manipulations of these unprotected populations or taxa may provide guidance in the design of management strategies. Here, we report the results of an investigation of one potential management technique, headstarting, in an unprotected population of plains gartersnake, *Thamnophis radix*, and make recommendations regarding its potential effectiveness for protected populations of this and other North American natricines (gartersnakes, watersnakes, and allied taxa; Gibbons and Dorcas, 2004; Rossman et al., 1996). To be an effective management tool, headstarting must result in greater recruitment into the population of reproductive adults than would occur naturally. Whether this goal is met depends on both (1) growth and survival during headstarting, and (2) the fate of headstarted animals following release as compared to nonheadstarted animals. We present data on prenatal mortality (stillbirths), first-year growth and survival during headstarting, and growth, survival, and reproduction of headstarted animals following release. Using data on comparably sized wild-caught snakes, we compare growth rates (using Analysis of Covariance) and survival (using AIC criteria in MARK, White, 2004; White and Burnham, 1999) between snakes that were headstarted and those that were not. In this way, we provide an overall evaluation of the potential effectiveness of headstarting.

The plains gartersnake is a diurnal, medium-sized nonvenomous snake. It is commonly found in river valleys and near prairie ponds and feeds on earthworms, slugs and small amphibians (Conant and Collins, 1991; Harding, 1997; Phillips et al., 1999; Walley et al., 2003). Primarily a species of the Great Plains, it ranges from southern Alberta and northeastern New Mexico eastward into Minnesota, southern Wisconsin, and northern Indiana. Two disjunct populations also exist, one in west central Ohio (where this snake is listed as endangered, Ohio Department of Natural Resources, 2003) and another in western Illinois and adjacent eastern Missouri. Population declines in Ohio are attributed to conversion of wet-prairie to agriculture, and headstarting has been identified as a potential management tool for this species (Ohio Department of Natural Resources, 2003).

The plains gartersnake sometimes reaches exceedingly high densities (Reichenbach and Dalrymple, 1986; Rossman et al., 1996; Seibert, 1950), making it an attractive species for population studies. A population of plains gartersnake on the Northern Illinois University campus (the NIU population) has been the focus of ecological research since 1995 (Stanford and King, 2004). Furthermore, ecological similarities and close phylogenetic affiliation suggest that demographic information for the plains gartersnake might be used to guide management decisions for other North American natricine snakes which share a number of life-history characteristics typical of early-maturing temperate, colubrid snakes (Parker and Plummer, 1987). Although geographically widespread and sometimes locally abundant, a surprising number of North American natricines have been listed as Endangered, Threatened, Vulnerable, or Species of Special Concern by Federal, State, or Provincial agencies in at least a portion of their range (26 of 38 species, Levell, 1997). Thus, our experimental approach to evaluating headstarting as a possible management technique seems both timely and desirable.

Methods

A 2.65-hectare study site was located along the banks of the Kishwaukee River on the campus of Northern Illinois University (NIU), DeKalb, Illinois. The site is in an urban area and is bordered by a paved bicycle path, homes, and mowed lawns. Vegetation adjacent to the river was typically allowed to grow until late summer or early fall before being mowed. Beginning in 1995, field surveys were conducted in which snakes were hand captured, measured to obtain snout–vent length (SVL), uniquely marked by clipping ventral scales (Brown and Parker, 1976), and released. Field effort varied among months and years with most captures occurring in April–June and in 1998–2001.

In most years, gravid females were captured and maintained in captivity until parturition to obtain reproductive data and so that offspring could be marked. Females were housed individually in 40–l glass aquaria lined with cage paper and provided with ceramic tile shelters. Fresh water was available ad libitum and ca. 3–6 large earthworms were provided as food 2–5 times weekly. The room in which animals were housed was maintained at 24–26 C and at about 50% relative humidity with a 12 light:12 dark photocycle. A heat tape running under one end of aquaria provided a thermal gradient up to about 32 C for 12 hours a day. Following parturition, females and their offspring were measured to obtain SVL and mass, and offspring were classified by sex and as stillborn or live. Females were released at their site of capture soon after parturition.

Headstarted gartersnakes consisted of offspring born to wild-caught females in 1995 (n = 26 in 4 litters), 1996 (n = 46 in 3 litters), and 1999 (n = 190 in 13 litters). Offspring born in 1995 and 1996 were reared in captivity for 327–335 days and released in July, and offspring born in 1999 were reared for 253–260 days and released in April. Offspring were housed individually in plastic shoe-storage boxes in a room maintained at 24–26 C and at about 50% relative humidity with a 12 light:12 dark photocycle. Two to three small earthworms were offered as food twice weekly starting within several days of birth (earthworms too large for neonates to consume were cut into pieces). Snakes that did not feed voluntarily were induced to do so by offering food via forceps or by placing snakes in smaller containers with food. A few animals that still refused to eat were force-fed. Number and size of earthworms offered as food was increased as snakes grew. Headstarted animals were released at locations within the study site where plains gartersnakes were most commonly encountered. Offspring born in 1998 (n = 137 in 8 litters) and 2000 (n = 188 in 14 litters), and most offspring born in 2001 (n = 71 in 6 litters) were not headstarted but were released at their mother's site of capture 2–27 d after parturition (in August).

To determine if frequency of stillbirths could be reduced and survival could be increased during headstarting, 24 offspring born in 2001 were provided with heat tape (heat tape was not provided to neonates born in 1995, 1996, or 1999) and were fed earthworms three times (rather than twice) weekly. Once these snakes reached an age of 365 days, females were switched to a diet of juvenile mice (purchased frozen and thawed prior to use). Males and females underwent a simulated hibernation from Aug 2002–Jan 2003 after which a single female was placed with multiple males and videotaped to monitor courtship and mating.

To determine whether headstarting influenced survival, capture records were used to estimate survival rates of headstarted snakes and similar-sized wild-caught snakes using MARK 4.1 (White, 2004; White and Burnham, 1999). Initially, a twelve-parameter (saturated) model was fit, providing separate estimates of capture (p) and survival (Φ) probabilities for both male and female snakes in three groups: headstarted snakes born in 1995 and 1996 (group 1), headstarted snakes born in 1999 (group 2), and similar-sized wild-caught snakes (group 3). To examine variation in survival and capture parameters among the groups, nine additional models, allowing unequal survival and capture probabilities were compared to the saturated model. In these subsequent models, males and females were pooled to increase sample size and because sex-differences in survival are apparently lacking prior to adulthood in plains gartersnakes (Stanford, 2002; Stanford and King, 2004). All models were derived using the Cormack–Jolly–Seber model (the 'recaptures only' model with default link function and variance estimation in MARK, White and Burnham, 1999). The parameter combinations tested were not exhaustive, but rather were chosen to illuminate differences among groups while maintaining biological realism. In particular, we selected models that allowed us to determine whether survivorship and capture probability differed between snakes headstarted for different durations (groups 1 and 2) and between snakes that were headstarted and those that were not (group 3). Recent literature has suggested that the use of Akaike's Information Criterion (*AIC*) is the most appropriate method for this type of model selection (Burnham and Anderson, 2002). Models were compared using the small sample version of this criterion, (*AICc*), and the corresponding Akaike weights (w_i) provided within MARK. These values indicate how well a given model is supported relative to the best-fit model.

Growth of headstarted snakes following release was compared to that of wild-caught snakes of similar size using data from individuals captured multiple times. Daily growth rate was calculated as the difference in SVL between captures divided by number of days spent growing. An annual active season of 212 days was estimated from the earliest (March 17) and latest (October 15) capture dates between 1995 and 2000 (Stanford, 2002; Stanford and King, 2004). Because snakes grow only during the active season, growth intervals of snakes captured in two or more seasons were adjusted by subtracting the number of inactive days (daily growth rates estimated in this way did not differ from those based on multiple captures within seasons, R. B. King, unpublished data). Some individuals appeared to decrease in SVL by up to 5.6% between captures within a year presumably because of measurement error. To minimize this error, only first and last captures within a season were used, and growth increments less than 5.6% were omitted (as in Stanford, 2002; Stanford and King, 2004). Daily growth rate was compared between males and females and between headstarted and wild-caught snakes using Analysis of Covariance with sex and status (wild-caught vs. headstarted) as factors and mean SVL (averaged over the growth interval) as a covariate.

RESULTS

Offspring Production

Among 38 litters born to wild-caught females, 128 stillborn and 473 live offspring were obtained, giving a stillbirth rate of 21.3%. Two litters consisted entirely of stillborn offspring and 12 litters consisted entirely of live offspring. Stillborn offspring typically were fully developed and lacked obvious developmental defects but often showed signs of decay at midbody due to the action of digestive enzymes contained within the gall bladder. Parturition was induced using oxytocin in 18 additional litters. Among these, 112 stillborn and 343 live offspring were obtained, giving a stillbirth rate of 32.6%. Four of these litters consisted entirely of stillborn offspring and 8 litters consisted entirely of live offspring. The higher mortality among induced litters was a consequence of some litters being born prematurely as evidenced by incomplete absorption of yolk and incomplete closure of the umbilicus. In addition to litters produced by wild-caught females, four captive-reared females born in 2001 mated and produced offspring in spring 2003. These females produced 3 stillborn and 45 live offspring for a stillbirth rate of just 6.3%.

Survival and Growth During Headstarting

Overall survival during headstarting was 76% but varied somewhat with rearing conditions (Table 1). In particular, in 2001 when snakes were reared under conditions promoting rapid growth, survival was 87.5%. Most mortality occurred soon after parturition (36 of 47 deaths among offspring born in 1999 occurred within 2 mo of birth) and often involved animals that were reluctant to eat.

TABLE 1.—Survival of plains gartersnakes during headstarting.

Year of Birth	Initial #	# Surviving	% Survival	Time period
1995 & 1996	72	53	73.6%	327–335 days
1999	190	143	75.3%	253–260 days
2001	24	21	87.5%	367 days
Total	286	217	75.9%	

Growth rate was similar among headstarted animals born in 1995, 1996, and 1999 but was markedly higher among animals born in 2001 (Table 2). Based on an estimated size at sexual maturity in nature of 350 mm SVL in males and 380 mm SVL in females (Stanford, 2002; Stanford and King, 2004), seven (3.6%) headstarted snakes born in 1995, 1996, and 1999 had reached sexual maturity prior to release. All 21 of the surviving snakes born in 2000 had reached sexual maturity by age 367 days. These snakes were placed in simulated hibernation from August 2002–January 2003. One female and four males died soon after removal from hibernation. Of the remaining eight females and eight males, four females and three males mated and mated females all produced litters.

Survival and Growth Following Release

Offspring released as newborns were recaptured up to two years later. Those released following headstarting were recaptured up to three years later. Overall, 27 of 362 (7.4%) offspring released as newborns and 2 of 15 (13.3%) wild-caught newborns were recaptured one or more years after release or initial capture. Similarly, 14 of 53 (26.4%) 1995–96 headstarted snakes (group 1), 7 of 142 (4.9%) 1999 headstarted snakes (group 2), and 16 of 80 (20.0%) similar-size wild-caught snakes (group 3) were recaptured one or more years after release or initial capture. *AICc* values generated using MARK indicated that a three-parameter model (designated $\Phi_{1=3\neq2}\ p_{1=2=3}$) was best supported (*AICc* weight = 0.39, Table 3). In this model, survival was equal in groups 1 and 3 (Φ = 0.40, 95% CI = 0.30, 0.51) but not group 2 (Φ = 0.11, 95% CI = 0.05, 0.22) and capture probabilities were equal in all groups (P = 0.43, 95% CI = 0.27, 0.61) Under the criterion of Burnham and Anderson (2002), two other models received similar support. The model $\Phi_{1=3\neq2}\ p_{1=3\neq2}$ ($\Delta AICc$ = 0.95, Table 3) had equal survival and capture probabilities in groups 1 and 3 (Φ = 0.41), but not group 2 (Φ = 0.05). The model $\Phi_{1\neq2\neq3}\ p_{1=2=3}$ ($\Delta AICc$ = 1.84, Table 3) had unequal survival in all 3 groups (Φ = 0.38 for group 1, 0.11 for group 2, 0.42 for group 3) but equal capture probabilities in all groups. Other models received poorer support ($\Delta AICc \geq 2.68$, Table 3).

Growth increments were obtained for 34 headstarted snakes (23 males, 11 females) following release and for 25 comparably sized wild-caught snakes (15 males, 10 females). Analysis of Covariance revealed no difference in slopes (sex-by-group-by-SVL interaction: $F_{3,51} = 0.305$, $P = 0.822$), no sex-by-group interaction ($F_{1,54} = 0.760$, $P = 0.387$), and no group effect ($F_{1,54} = 2.512$, $P = 0.119$). There was a significant covariate (SVL) effect ($F_{1,54} = 17.148$, $P < 0.001$) and a significant sex effect ($F_{1,54} = 9.626$, $P = 0.003$). Growth rate decreased with increasing SVL and females grew faster than males (Fig. 1). Based on SVL, seven snakes released as newborns and aged 20–22 mo and 21 headstarted snakes aged 20–34 mo had reached sexual maturity by their final recapture. Furthermore, two

TABLE 2.—Growth of headstarted plains gartersnakes during captivity. Shown are means ± SE (range).

Year of Birth (sample size)	Birth		200–229 days[1]		327–367 days[1]	
	SVL (mm)	Mass (g)	SVL (mm)	Mass (g)	SVL (mm)	Mass (g)
1995 & 1996	131.7 ± 1.15	1.39 ± 0.03	299.0 ± 4.37	13.9 ± 0.57	321.4 ± 4.38	18.9 ± 0.85
(n = 53 in 7 litters)	(117–152)	(1.0–1.9)	(230–380)	(5.5–24.2)	(245–390)	(7.6–33.3)
1999 (n = 143 in 13 litters)	141.2 ± 0.76	1.50 ± 0.02	266.7 ± 2.66	11.2 ± 0.31		
	(115–158)	(0.9–2.0)	(173–334)	(3.2–20.1)		
2001 (n = 21 in 6 litters)	136.4 ± 1.18	1.63 ± 0.04	394.7 ± 6.44	34.0 ± 1.71	492.9 ± 9.05	66.4 ± 5.18
	(127–143)	(1.4–2.0)	(334–445)	(19.1–47.5)	(418–574)	(35.3–114.5)

[1] Snakes born in 1995 & 1996 were measured at 204–229 and 327–335 days of age, snakes born in 1999 were measured at 200 days of age, and snakes born in 2001 were measured at 220 and 367 days of age.

TABLE 3.—Comparison of the fit obtained using alternative models of survivorship (Φ) and capture probability (*p*) generated with MARK. Subscripts denote equality and inequality of parameter estimates among groups (1 = headstarted snakes born in 1995 and 1996, 2 =headstarted snakes born in 1999, 3 = similar sized wild-caught snakes). Males (m) and females (f) were pooled in all except the 12 parameter model.

Model	Number of Parameters	*AICc*	*ΔAICc*	*AICc* Weight
$\Phi_{1=3\neq2}\ p_{1=2=3}$	3	297.49	0.00	0.390
$\Phi_{1=3\neq2}\ p_{1=3\neq2}$	4	298.43	0.95	0.243
$\Phi_{1\neq2\neq3}\ p_{1=2=3}$	4	299.32	1.84	0.156
$\Phi_{1=3\neq2}\ p_{1\neq2\neq3}$	5	300.17	2.68	0.102
$\Phi_{1\neq2\neq3}\ p_{1=3\neq2}$	5	301.09	3.60	0.064
$\Phi_{1\neq2\neq3}\ p_{1\neq2\neq3}$	6	302.24	4.75	0.036
$\Phi_{1\neq2\neq3,\ \mathrm{m}\neq\mathrm{f}}$ $p_{1\neq2\neq3,\ \mathrm{m}\neq\mathrm{f}}$	12	305.08	7.59	0.009
$\Phi_{2=3\neq1}\ p_{2=3\neq1}$	4	314.41	16.93	<0.001
$\Phi_{1=2\neq3}\ p_{1=2\neq3}$	4	316.45	18.96	<0.001
$\Phi_{1=2=3}\ p_{1=2=3}$	2	316.80	19.32	<0.001

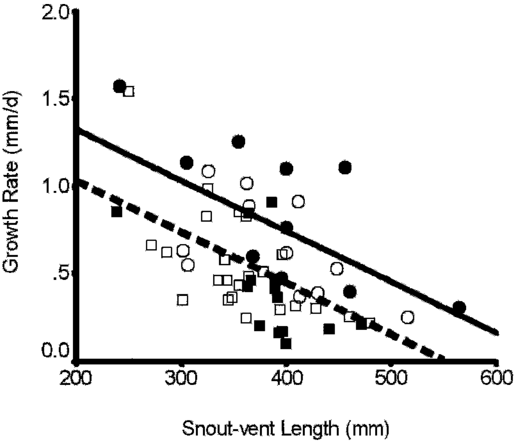

FIG. 1.—Growth in nature of headstarted and comparably sized wild-caught plains gartersnakes. Circles and solid line denote females, squares and dashed line denote males, open symbols denote headstarted snakes; solid symbols denote wild-caught snakes.

females released as newborns and aged 21–22 mo and three headstarted females aged 23–34 mo were gravid when recaptured and produced litters when brought into captivity.

DISCUSSION

The use of headstarting and related management tools (reintroduction, translocation, reinforcement/supplementation; International Union for Conservation of Nature and Natural Resources, 1995) remains controversial for many reasons ably reviewed elsewhere (Burke, 1991; Campbell, 1980; Conant, 1988; Dodd and Seigel, 1991; Fischer and Lindenmayer, 2000; Griffith et al., 1989; Mlot, 1989; Reinert, 1991; Sarrazin and Barbault, 1996). Despite potential shortcomings and sometimes limited success, these tools are likely to remain appealing to managers, perhaps due in part to a desire to 'do something' and to the public goodwill they may engender. Theory-driven evaluations of the potential utility of headstarting have focused on demographic parameters (juvenile and adult survival, age at first reproduction, fecundity) and suggest that headstarting is more likely to be effective in species falling near the 'fast' end of the 'slow-fast' life history continuum (Stearns, 1983). More specifically, species that mature rapidly, have relatively high juvenile survival, and have relatively low adult survival are more likely to benefit from headstarting than species that mature slowly, have lower juvenile survival, and have higher adult survival (e.g., Congdon et al., 1993; Heppell, 1996; 1998; Heppell et al., 2000). Among snakes, the plains gartersnake in particular and natricines in general seem to fall toward the fast end of this continuum (Bronikowski and Arnold, 1999; Brown and Weatherhead, 1999; Parker and Plummer, 1987; Stanford, 2002, Stanford and King, 2004). Clearly, however, appropriate demographic characteristics alone are not enough to ensure the success of headstarting. As discussed below, live birth rates, survival and growth during the captive phase, and growth, survival, and reproduction following release also influence success.

Headstarting as a Management Tool in Plains Gartersnakes

Stillbirths were discouragingly common (21.3%) among offspring born to wild-caught plains gartersnakes. Additionally, the general lack of obvious developmental defects makes it difficult to determine the cause of these stillbirths. The observation that most stillborn offspring were fully developed suggests that environmental conditions or cues important in inducing parturition may be lacking in captivity. However, it is unclear what these conditions or cues might be. Interestingly, four captive-reared females produced litters with markedly lower numbers of stillbirths (6.3%)

than observed among wild-caught females, suggesting that perhaps wild-caught females experience greater stress associated with captivity. Possibly, higher success in offspring production might be achieved through captive breeding than by holding wild-caught females captive until parturition. However, inbreeding effects either due to the small size of source populations (e.g., Madsen et al., 1996; Ujvari et al., 2002) or reduced genetic variation within captive colonies (Templeton, 2002) may constrain such efforts.

Mortality during headstarting also was fairly common (ca. 25%) but was markedly reduced (to 12.5%) when snakes were reared under conditions maximizing growth (i.e., in snakes born in 2001, Table 1). As noted earlier, mortality often occurred soon after birth and involved animals that were reluctant to begin feeding. Maintaining relative humidity ≥ 50% to prevent desiccation and ensuring that snakes start feeding shortly after birth (e.g., by hand-feeding those snakes that do not feed voluntarily) appear necessary to minimize mortality in species such as plains gartersnakes that produce small (< 2 g) offspring. Rapid growth can be elicited by providing food at frequent intervals (e.g., every 2 days) and using heat tape to generate a thermal gradient. Under such conditions, captive plains gartersnakes reach sexual maturity in as little as one year. In animals with indeterminate growth, rapid growth can shorten generation time of headstarted individuals (free-ranging plains gartersnakes typically mature in their second year, Stanford, 2002; Stanford and King, 2004), thus promoting population increase.

Results obtained here indicate that some offspring born in captivity were recruited into the adult population and succeeded in reproducing either when released as newborns or following headstarting. Snakes released as newborns did not appear to differ from comparably sized wild-caught snakes in likelihood of recapture. However, the sample of wild-caught newborn snakes was small (n = 15). Survivorship of headstarted snakes born in 1995 and 1996 (group 1) did not differ from that of similar-size wild-caught snakes (group 3, $\Phi = 0.40$) but was higher than that of headstarted snakes born in 1999 (group 2, $\Phi = 0.11$). Thus, conclusions regarding the utility of headstarting depend on which group of headstarted snakes is considered. Reasons for this difference are unclear, but snakes in group 1 were larger and older at release (Table 2) and were released later in summer than were those in group 2 (July vs. April). Survivorship in headstarted redbelly turtles, *Pseudemys rubriventris*, is positively correlated with size at release (Haskell et al., 1996), a pattern also seen in free-ranging reptiles (Janzen et al., 2000), including other gartersnakes (Jayne and Bennett, 1990). Additionally, population viability analysis of the Ohio population of *T. radix* indicates that release of juveniles and adults should have a more positive effect on population growth rate than release of neonates (K.M. Stanford, unpublished data). These results suggest that maximizing the size of snakes at release would be desirable in a headstarting program for plains gartersnakes.

To assess the likelihood of success of headstarting in the plains gartersnake, we consider ‘no intervention,’ ‘headstarting worst-case,’ and ‘headstarting best-case’ scenarios (Table 4). For the no intervention scenario, proportion of live births was assumed to be 1.00 (information from nature is lacking, but a lower proportion of live births would improve the relative performance of headstarting and so our analysis is conservative with respect to the possible advantages of headstarting), overwinter survival comes from Stanford and King (2004), and second year survival is that estimated above for groups 1 and 3. For the worst-case scenario, proportion of live births is that observed for noninduced wild-caught females, headstarting survival is that observed in groups 1 and 2, and second year survival is that estimated above for group 2. For the best-case scenario, proportion of live births is that observed for four captive-reared females, headstarting survival is that observed in captive-reared snakes born in 2001, and second year survival is that estimated above for groups 1 and 3. Expected survival to reproduction was computed for each scenario as the product of live births, overwinter or headstarting survival, and second year survival. Given these parameter estimates, 6% of newborn plains gartersnakes are

Table 4.—Parameter estimates used in determining possible benefits of headstarting in the plains gartersnake. Expected survival to reproduction was computed as the product of live births, over winter/headstarting survival, and second year survival (see text for details).

		Headstarting	
Life Stage	No intervention	'Worst-case'	'Best-case'
Live Births	1.00	0.79	0.94
Over Winter/Headstarting Survival	0.16 (0.07–0.33)	0.74	0.88
Second Year Survival	0.40 (0.30–0.51)	0.11 (0.05–0.22)	0.40 (0.30–0.51)
Expected Survival to Reproduction	0.06	0.07	0.33

expected to survive to reproductive maturity with no intervention compared to 7% and 33% under worst-case and best-case headstarting scenarios, respectively (Table 4). These results suggest that a carefully implemented headstarting program could be a useful tool in the management of the plains gartersnake. The success of such a program will depend, in part, on the degree to which the life history of our study population matches that of managed populations. Admittedly, the potential success of headstarting that we report, based on analysis of a presumably stable population, may differ from what might be achieved in a declining or severely reduced population. Success also will depend on the degree to which causes of population decline have been identified and reduced. In the case of the plains gartersnake in Ohio, habitat protection and modified management practices (e.g., timing and extent of mowing) have been invoked to address inferred causes of population decline (C. Caldwell, personal communication). Economic factors (cost of headstarting vs. other management activities) could also contribute to the desirability of headstarting.

Headstarting as a Management Tool in Other Natricines

The results of this study suggest that headstarting might be a useful tool in the management of other natricine snakes, many of which are of management concern. Although few species have been studied in detail, available data indicate that demographic characteristics are similar among natricines (Bronikowski and Arnold, 1999; Brown and Weatherhead, 1999; Parker and Plummer, 1987; Stanford, 2002; Stanford and King, 2004); therefore, the results obtained here may be more widely applicable. However, other differences among species may reduce the effectiveness of headstarting as outlined below.

(1) Methods of captive husbandry may differ among species and require refinement as was necessary to maximize captive growth in this study. Furthermore, food requirements of diet specialists (e.g., crayfish snakes, Godley et al., 1984) or species with ontogenetic shifts in diet (e.g., from insect larvae and shrimp to crayfish; Franz, 1977; Godley, 1980) may be difficult to accommodate in captivity. (2) Environmental cues associated with normal parturition may be lacking in captivity and in their absence, wild-caught females may retain litters beyond completion of development, resulting in stillbirths (as possibly occurred in this study). (3) Headstarted animals may not participate in normal reproductive activities. Although headstarted plains gartersnake succeeded in reproducing both in captivity and in nature, normal reproduction by other natricines might be disrupted by conditions during headstarting. (4) Headstarted animals may disperse out of intended management areas or be at a disadvantage in finding hibernation sites, resulting in unacceptably high mortality (as in relocated hognose snakes, *Heterodon platirhinos*, Plummer and Mills, 2000). In snakes, 'soft release' (e.g., Wanless et al., 2002) could be achieved by using drift fences to restrict movements of headstarted animals until they are familiar with their environment and artificial hibernacula could be provided (Zappalorti and Reinert, 1994). It is possible that, in this study, dispersal or difficulty in finding hibernation sites contributed to lower survival of headstarted snakes born in 1999. (5) Headstarted animals may serve as inadvertent vectors of pathogens. Among snakes,

ophidian paramyxovirus infections have been a significant cause of mortality in a number of private and zoo collections (Jacobson, 1993, 1994). Although no outward signs of ill-health were noted among headstarted animals in this study, screening for potential pathogens was not conducted. Such screening would be well-advised should headstarting be used as a management tool. (6) Headstarting may result in selection for traits that are adaptive in captivity but not in nature (Heath et al., 2003).

Arguments for and against headstarting and related management tools will no doubt continue as human activities put more species in peril. Critics will remind us of failed programs, unrecognized dangers, and life-history constraints (e.g., Congdon et al., 1993; Dodd and Seigel, 1991; Woody, 1990, 1991), while proponents will point to spectacular successes, improved recognition and resolution of methodological problems, and integration of headstarting into multifaceted recovery programs (e.g., Cayot et al., 1994; Dobson and Lyles, 2000; Ralls and Ballou, 2004). Such debate is healthy in that it can prevent blind application of inappropriate management techniques and increase the level of sophistication with which appropriate techniques are applied. It also should stimulate further analyses like the one presented here to aid in determining when headstarting may be destined to failure and in ensuring success when headstarting appears warranted.

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FECUNDITY, REPRODUCTIVE ECOLOGY, AND INFLUENCE OF PRECIPITATION ON CLUTCH SIZE IN THE WESTERN SLIMY SALAMANDER (*PLETHODON ALBAGULA*)

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ABSTRACT: We investigated the reproductive ecology of the western slimy salamander (*Plethodon albagula*) in an abandoned mine shaft in the Ouachita National Forest of south-central Arkansas. The mine habitat provided an opportunity to observe nesting behavior, quantify reproductive output, and evaluate the influence of precipitation on fecundity for a population of *P. albagula* that utilize this particular mine shaft to brood and defend egg clutches. We collected reproductive data on 372 clutches between 1982 and 2004. There was no relationship between the number of eggs per egg clutch versus egg size; snout–vent length, body mass, and tail length were not correlated with clutch size. Thirteen females were found to exhibit nest site fidelity, and 10 females exhibited nest securing. Neither nest site fidelity nor nest securing was found to influence reproductive output by females. The amount of precipitation one year prior to oviposition was correlated with the average number of eggs per clutch. It appears, therefore, that precipitation influences fecundity in this population.

Key words: Arkansas; Fecundity; Nest securing; Nest site fidelity; Precipitation; *Plethodon albagula*; Plethodontidae; Reproduction

PLETHODONTID salamanders are excellent organisms for determining ecosystem integrity; for example, Welsh and Droege (2001) proposed that plethodontid salamanders are ideal indicator species for assessing the integrity of forest ecosystems in North America. This argument was based on the sensitivity of plethodontids to environmental variation and on the low temporal variation in counts of plethodontids from repeat surveys within a given site. Yet, because of their secretive nature, there is a lack of information concerning major aspects of plethodontid ecology. Data concerning reproduction by species of large *Plethodon* in a natural setting are especially sparse. Most information pertaining to the reproductive habits and productivity of some species has been gathered from necropsied specimens, laboratory observations, and anecdotal accounts. Furthermore, smaller eastern species of *Plethodon* (chiefly *P. cinereus*) are the focus of most laboratory studies. Other than seminal studies on the life history of large eastern *Plethodon* (Highton, 1956, 1962, 1995; Highton et al., 1989), little information is known concerning the reproductive ecology of most species within the *Plethodon glutinosus* complex (Highton and Larson, 1979).

Reproductive traits in salamanders are known to be contingent upon a number of factors. Reproductive output has been correlated with mass (Tucker, 1999), body size (Tilley, 1968), snout–vent length (Bruce, 1969; Fraser, 1980; Hairston, 1983; Lotter, 1978; Nagel, 1977; Semlitsch, 1980; Semlitsch and West, 1983), lipids (Scott and Fore, 1995),

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