Journal of Herpetology, Vol. 41, No. 3, pp. 492–500, 2007

Use of Posthatching Yolk and External Forage to Maximize Early Growth in *Apalone mutica* Hatchlings

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ABSTRACT.—**Posthatching yolk in oviparous vertebrates is thought to supply the hatchling with energy for a period of time after hatching in habitats that might require fasting. To examine strategies of posthatching energy use in *Apalone mutica*, hatchlings were fed or not fed over periods of nine weeks in 2003 and six weeks in 2004. Mass, plastron length, carapace width, and body condition changed during the course of the experiment; all trajectories of change, except carapace width in 2004, differed between fed and unfed hatchlings. Trajectories of fed hatchlings were significantly higher than unfed hatchlings. Fed and unfed hatchlings used internalized yolk at similar rates: 50% of the yolk was depleted by day eight after hatching and 90% by day 27. Metabolic rate (approximately 0.236 ml CO_2 h^{-1}) did not differ between fed and unfed hatchlings. Yolk reserves are insufficient to sustain hatchlings to the first overwintering season, but with access to external forage, hatchlings appear to use yolk reserves to meet maintenance demands to support maximal growth.**

In most vertebrate species, the energy parents provide to their offspring can be divided into two components: that used to make the embryonic body before birth (parental investment in embryogenesis, PIE) and that used to serve the offspring after birth (parental investment in care, PIC) (Congdon et al., 1983; Congdon and Gibbons, 1990; Nagle et al., 1998, 2003). In oviparous reptiles with no behavioral parental care, PIC takes the form of yolk remaining with the embryo after hatching, thus continuing yolk-based nutrition past birth (postnatal lecithotrophy, Lance and Morafka, 2001). Yolk reserves are thought to fuel the hatchling by providing energy for maintenance, activity, growth, and fat storage until the hatchling can attain a positive energy balance by foraging (Kraemer and Bennett, 1981; Congdon and Gibbons, 1990; Fischer et al., 1991; Nagle et al., 2003). These ideas are supported by studies of experimental yolk reduction in turtles (Yeomans, 1999), lizards (Radder et al., 2004), and birds (Murakami et al., 1992) and rates of yolk depletion in turtles (Kraemer and Bennett, 1981, Tucker et al., 1998), lizards (Troyer, 1983), snakes (Ji et al., 1997, 1999; Ji and Sun, 2000), and crocodilians (Whitehead, 1990; Fischer et al., 1991). The potential energetic contribution of postnatal lecithotrophy can be substantial (Ewert, 1991). For example, residual yolk in the turtle *Gopherus agassizii* permits hatchlings to emerge from their nest, disperse, grow, burrow, and hibernate over the first half year of their lives without ever successfully foraging (Lance and Morafka, 2001).

In the Smooth Softshell Turtle, *Apalone mutica*, only 25% of the yolk lipids deposited in the egg by the ovary are used to form the offspring, whereas 75% remain in the body as fat bodies and yolk reserves, rendering *A. mutica* with one of the largest PIC values reported for turtles (Nagle et al., 2003). This reserve could provide an important energy source for hatchlings of *A. mutica*, a species that nests close to water (within 20 m, Doody, 1995) on clean open sandbars of large rivers and whose hatchlings inhabit the relatively low-resource and unpredictable environment of the shallow water around sandbars (Plummer, 1976, 1977; Nagle et al., 2003). Demands on stored energy in this environment include digging out of the nest cavity, dispersal from the nest to the water, maintenance, growth, and activities such as foraging and escape from predators.

To examine strategies employed by hatchling *A. mutica* to use endogenous and exogenous energy sources and to estimate the time that yolk reserves are capable of meeting energetic requirements, we conducted laboratory experiments that address three questions: (1) Do fed hatchlings deplete yolk reserves at a slower rate than unfed hatchlings?, (2) Do fed hatchlings grow more rapidly than unfed hatchlings?, and (3) How long can stored yolk reserves fuel hatchlings?

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Materials and Methods

Eggs of *A. mutica* were collected from 31 May to 20 June 2003 and 3 to 25 June 2004 from nests constructed on sandbars of the White River near Georgetown, White County, Arkansas. Mean clutch size ± SE in 2003 was 11.8 ± 0.70 (range 7–17) eggs and 14.4 ± 0.76 (8–22) eggs in 2004. Eggs were individually marked according to clutch with a felt-tipped pen, packed in moist sand, and transported to the laboratory where they were half-buried in 600 g of a 50 : 50 vermiculite/water mixture in a covered 7 × 20 × 27 cm (H × W × L) plastic tray. Water potential of the mixture was approximately −200 kPa (Plummer and Snell, 1988). Eggs were incubated at 30 ± 0.5 C in Hovabater (GFQ Corporation, Savannah, GA) incubators (Plummer et al., 1994). Each incubator contained two egg trays, each of which initially contained 20 eggs. In contrast to the flexible-shelled eggs of some reptiles, including many turtles, the rigid-shelled eggs of *Apalone* spp. are relatively insensitive to variation in substrate water potential (Packard et al., 1979, 1981; Gettinger et al., 1984). Nevertheless, to minimize variation in substrate water potential, we periodically weighed each egg tray and added water to the vermiculite to replace mass loss by evaporation.

When an egg pipped, we placed a small wire cage over the egg to contain the hatchling for identification. Hatchlings were randomly assigned to one of two experimental groups, fed and unfed. The two treatments contained approximately equal numbers of hatchlings from each of 16 (2003) or 24 (2004) clutches and five incubators. Food was withheld from the hatchlings in the unfed group, whereas hatchlings in the fed group were fed ad libitum three times a week, beginning on day eight after hatching, with a diet alternating between crickets and chopped minnows dusted with Reptivite® vitamins. The contents of the diet were consistent with the natural diet of *A. mutica* (Plummer and Farrar, 1981). Hatchlings were maintained on a 12 : 12 L : D photoperiod, a day length contained within the posthatching activity season for *A. mutica* in Arkansas (August to October), at room temperature (25°C) without the opportunity to regulate body temperature by basking. Normal field body temperatures are unknown for *A. mutica*. However, *Apalone spinifera*, the sister species of *A. mutica* (Meylan, 1987), is active within a broad range of body temperatures that average 25°C (Plummer et al., 2005). Hatchlings were housed in individual 5 × 12 × 12 cm (H × W × L) plastic containers with 1.3 cm of water. Water in containers was changed three times a week on the days following feeding.

We took several morphological measurements beginning on day seven after hatching, to allow time for flattening of the hatchling's body from the spherical shape while in the egg, and repeated approximately every two weeks (13–15 days; 2003) or weekly (2004) thereafter. We towel-blotted the hatchlings until dry and then weighed them. We also measured their carapace length, maximum carapace width, and plastron length, and calculated body condition (body mass/plastron length). The original experimental design required morphological measurements on each turtle over an approximate 60-day period during August to October 2003. This time frame was chosen because previous energetic calculations with turtle (*Trachemys scripta*) and alligator (*Alligator mississippiensis*) hatchlings suggested that posthatching yolk reserves could sustain the hatchlings for approximately 60–140 days (Fischer et al., 1991). However, a rapid decline in physical condition of unfed turtles caused us to terminate the experiments earlier. The 2004 experiments were conducted for approximately 40 days during August and September. After experiments were terminated, the 2003 hatchlings were overwintered in the laboratory and released near their nest sites in the White River in early May 2004; the 2004 experimental hatchlings were released in September 2004.

Hatchlings for yolk depletion measurements were taken from eight of the clutches collected in 2004: three to four hatchlings selected randomly from each treatment group were sacrificed by freezing at −80°C every four days, beginning at age four days, over a period of 44 days. In addition, yolks were obtained from eight hatchlings from four clutches immediately after pipping (age 0 days). Internalized yolk reserves were dissected out, oven dried at 45°C for 36 h, and weighed on an analytical balance. We measured rates of CO_2 production of one-month-old hatchling *A. mutica* randomly selected from each of three clutches within each treatment (seven fed, seven unfed) at 25°C using a Sable Systems TR-3 configured as an open-flow system (Beaupre and Zaidan, 2001). We measured CO_2 production for each hatchling every 30 seconds for 7.5 continuous minutes during each hour between 2100 and 0800 h, the normal inactive period for *A. mutica*. The SMR of each hatchling was calculated as the mean of its lowest four hourly CO_2 production rate measurements.

This experiment was designed as a repeated measures multivariate analysis of variance (MANOVA) experiment. Data were analyzed using the General Linear Model (GLM) statement in SAS (SAS Institute, Inc., Cary, NC). The primary independent variable was feeding re-

TABLE 1. Repeated-measures MANOVA to test for within subject effects on plastron length, body mass, carapace width, and body condition.

Source	df	Plastron length		Mass		Carapace width		Body condition	
2003; $N = 100$		F	P	F	P	F	P	F	P
Time	4, 83	1.64	0.172	0.70	0.591	0.26	0.903	1.32	0.270
Time×Egg mass	4, 83	1.75	0.147	1.11	0.358	0.19	0.944	1.91	0.1167
Time×Clutch	44, 344	2.34	<0.001	1.45	0.037	1.19	0.200	2.24	<0.001
Time×Treat	4, 83	3.57	0.010	23.74	<0.001	10.32	<0.001	24.79	<0.001
2004; $N = 60$									
Time	5, 37	0.99	0.435	2.02	0.098	2.74	0.033	3.01	0.022
Time×Egg mass	5, 37	0.87	0.512	1.67	0.167	2.79	0.031	2.71	0.035
Time×Clutch	55, 205	0.97	0.540	1.02	0.449	1.15	0.249	1.19	0.197
Time×Treat	5, 37	3.01	0.022	7.42	<0.001	0.83	0.540	8.11	<0.001
Time×Block	10, 76	1.68	0.102	2.80	0.005	0.91	0.530	1.69	0.098

gime (Treat). Egg mass, clutch, and block (physical position of hatchling; 2004 only) were included to remove variability in growth data caused by these factors and maximize our ability to detect variation resulting from our experimental treatments. Dependent variables were body mass, plastron length, carapace width, and body condition. Because carapace length was difficult to measure as health deteriorated in unfed turtles, it was eliminated from the analyses. For graphically presenting morphological measurements over time, we expressed each mean as a percentage of its initial value. To meet the assumption of normality, body mass data were transformed by squaring, and carapace width data were transformed with natural logarithms in 2003. Dried internalized yolk mass was regressed on days after hatching for each treatment group; regression equations were compared by Analysis of Covariance (ANCOVA). Metabolic rates were compared between treatment groups with a t-test, and means were reported ± SE. Regression analyses and t-tests were conducted with SYSTAT Version 11 (SYSTAT Software Inc., Richmond, CA).

RESULTS

Clutch and egg mass were included in our statistical analysis to remove variability in the data caused by genetic and maternal differences. Clutch accounted for significant variability in body mass, body condition, and plastron length in 2003 (Table 1). Egg mass accounted for a significant amount of variability in body condition and carapace width in 2004, whereas block accounted for a significant amount of variability in mass in 2004 (Table 1).

We predicted that fed hatchlings would increase in mass, whereas unfed hatchlings would decrease in mass as they used their yolk reserves. Consistent with our predictions, fed and unfed hatchling mass diverged through time in 2003 ($P < 0.001$; Table 1) with fed hatchlings slowly gaining mass, whereas unfed hatchlings slowly lost mass (Fig. 1). By week five, and continuing through the rest of the experiment, univariate tests indicated that the fed hatchlings had greater mass than unfed hatchlings (Table 2, Fig. 1). In 2004, both fed and unfed hatchlings lost mass, but fed hatchlings lost mass at a slower rate than unfed hatchlings (Fig. 1). By week two, and continuing through the rest of the experiment, fed hatchlings consistently had greater mass than unfed hatchlings (Table 2).

We predicted that turtles in both treatments would increase plastron length and carapace width until the yolk could no longer sustain growth, at which point only the fed hatchlings would continue to increase in size. Consistent with our prediction, plastron length initially increased in both feeding treatments (Fig. 1). Furthermore, plastron length diverged between treatments: as the plastron length of unfed hatchlings began to decrease, the plastron length of fed hatchlings continued to increase in both years (Fig. 1; 2003: $P = 0.010$; 2004: $P = 0.022$; Table 1). Plastron length was significantly greater in fed hatchlings by week nine of 2003 and beginning in week four in 2004 (Table 2). Also consistent with our prediction, carapace width diverged between feeding treatments in 2003 ($P < 0.001$; Table 1). Carapace width increased initially in both treatments, but only the fed hatchlings continued to increase in carapace width after week five (Fig. 1). However, univariate tests indicated a significant difference between the fed and unfed carapace widths only during week three (Table 2). Although there were significant differences in carapace width between feeding treatments during all weeks in 2004 (Table 2), the hatchlings in both treatments responded similarly through time ($P = 0.540$; Table 1); thus, we could

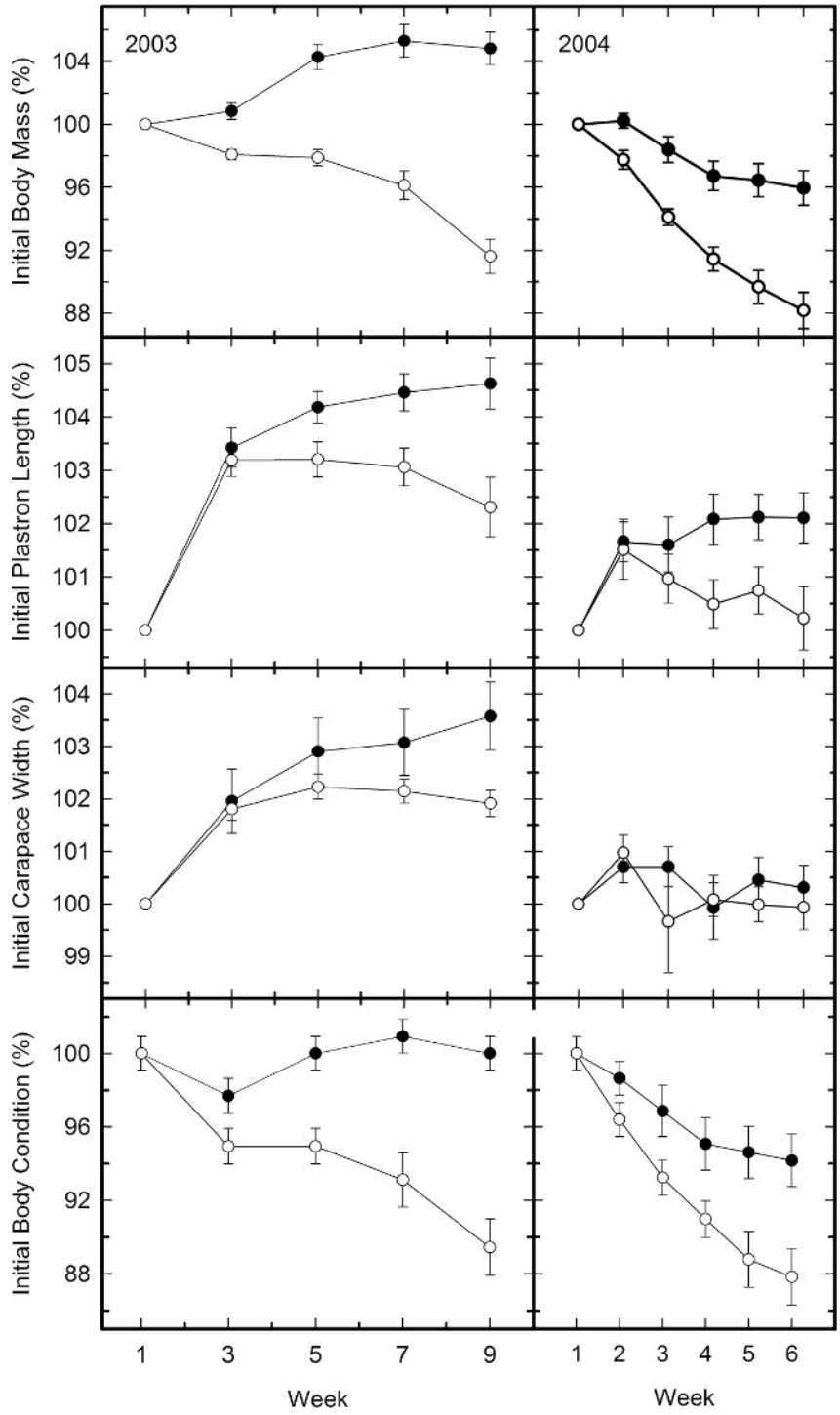

FIG. 1. The relationship between percent of initial body mass, plastron length, carapace width, and body condition to age in fed (closed symbols) and unfed (open symbols) *Apalone mutica* hatchlings in 2003 (left column) and 2004 (right column). Plotted are mean ± SE.

TABLE 2. Analyses of variance results for effects of feeding treatment on morphological traits within each week. All df = 1.

2003; $N = 100$		Week 1	Week 3	Week 5	Week 7	Week 9	—
Plastron length	F	0.16	0.05	1.20	2.84	5.05	—
	P	0.692	0.827	0.277	0.096	0.027	—
Body mass	F	3.27	1.43	12.40	19.06	38.49	—
	P	0.074	0.234	<0.001	<0.001	<0.001	—
Carapace width	F	2.53	4.28	1.17	0.54	0.21	—
	P	0.116	0.042	0.283	0.463	0.649	—
Body condition	F	3.84	3.47	16.69	26.59	54.08	—
	P	0.053	0.066	<0.001	<0.001	<0.001	—
2004; $N = 60$		Week 1	Week 2	Week 3	Week 4	Week 5	Week 6
Plastron length	F	0.36	0.37	1.53	8.16	6.46	8.63
	P	0.554	0.544	0.223	0.007	0.015	0.005
Body mass	F	0.28	5.33	11.60	18.59	23.13	26.30
	P	0.600	0.026	0.002	<0.001	<0.001	<0.001
Carapace width	F	4.92	4.47	5.14	5.32	12.38	11.16
	P	0.032	0.041	0.029	0.026	0.001	0.002
Body condition	F	0.03	6.81	13.08	14.23	24.46	27.46
	P	0.863	0.013	<0.001	<0.001	<0.001	<0.001

not conclude that there was a difference in carapace width caused by the feeding treatment.

Body condition diverged between feeding treatments in both years (2003: $P < 0.001$; 2004: $P < 0.001$; Table 1). After an initial decrease in body condition, the fed hatchlings in 2003 increased in body condition, whereas the unfed hatchlings decreased in body condition (Fig. 1). Beginning in week five, and continuing throughout the experiment, fed hatchlings consistently had better body condition than unfed hatchlings (Table 2, Fig. 1). Body condition decreased in both feeding treatments during 2004, but unfed hatchlings decreased in body condition at a faster rate than fed hatchlings (Fig. 1). Univariate tests indicated that the fed hatchlings maintained a significantly better body condition beginning in week two and continuing throughout the rest of the experiment (Table 2).

Hatchlings used yolk reserves at a comparable rate regardless of feeding condition. A regression analysis showed a significant negative relationship between internalized yolk dry mass and time after hatching in both feeding treatments and indicated that hatchlings used yolk reserves at a constant rate (Fig. 2; fed: $\log_{10}$ dry mass $= -0.557–0.036$ age, $N = 42$, $R^2 = 0.785$, $F_{1,40} = 146.4$, $P < 0.001$; unfed: $\log_{10}$ dry mass $= -0.576–0.038$ age, $N = 42$, $R^2 = 0.813$, $F_{1,40} = 173.4$, $P < 0.001$). There was no significant difference in rate of yolk depletion between fed and unfed hatchlings (ANCOVA: $F_{1,81} = 0.639$, $P = 0.426$). Hatchling dry mass was not correlated with yolk dry mass ($R^2 = 0.064$, $P = 0.549$, $N = 90$). Because the effect of time on internalized yolk mass did not differ between treatments, we pooled the data and calculated a common regression equation ($\log_{10}$ yolk dry mass $= -0.547–0.038$ age, $N = 84$, $R^2 = 0.819$, $F_{1,88} = 397.7$, $P < 0.001$). This equation predicts that 50% of the internalized yolk in a hatchling is depleted by day eight, 75% by day 16, and 90% by day 27. The standard metabolic rate of fed hatchlings (0.236 ± 0.017 ml CO_2 h^{-1}, $N = 7$) did not differ from unfed hatchlings (0.235 ± 0.023 ml CO_2 h^{-1}, $N = 7$; $t_{12} = 0.035$, $P = 0.972$). Pooled SMR was 0.236 ± 0.014 ml CO_2 h^{-1} ($N = 14$).

DISCUSSION

One function of residual yolk may be to increase hatchling fitness in unpredictable, low resource environments (Lance and Morafka, 2001). The productivity of lotic ecosystems, the preferred habitat of *A. mutica*, generally is considerably lower and more unpredictable than the productivity of lentic systems (Whittaker and Likens, 1973). Furthermore, fasting may be induced in these microhabitats and forced further by conflicts between fitness-enhancing activities. Mrosovsky and Sherry (1980) argue that the many examples of naturally occurring fasting that have been observed may arise from conflicts between feeding and more pressing activities such as thermoregulation, incubation, territory defense, and predator avoidance. For *A. mutica* hatchlings, the high risk of predation (Iverson, 1991; Morafka et al., 2000), especially by birds (Janzen et al., 2000; MVP, pers. obs.), may be a deterrent to foraging (Nagy, 2000) and force the hatchling to rely on its residual yolk. Reserves may also provide

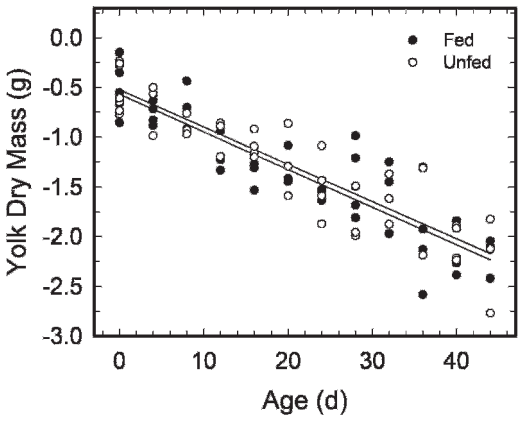

FIG. 2. The relationship between log dry mass of internalized yolk and age in fed and unfed *Apalone mutica* hatchlings. Upper regression line = fed (N = 42); lower regression line = unfed (N = 42). The common regression equation for pooled data is $\log_{10}$ dry yolk mass (g) = −0.547–0.038 age (days).

a sufficient supply of energy to allow the hatchlings to learn to maximize foraging at minimal cost. For example, many young animals reduce activity when at risk of predation (Skelly, 1992; Killen and Brown, 2006), and the reserves of hatchling *A. mutica* could provide an energy buffer to allow reduced foraging under predation pressure.

The primary energy budget components of hatchlings are maintenance, growth, associated costs of growth, and activity (Wieser, 1994). During times when fasting is not necessitated, juvenile animals with energy reserves could adopt different energy use strategies. For example, hatchlings with posthatching yolk reserves and access to external energy resources could conserve yolk reserves for later use (Radder et al., 2004), grow more quickly to escape size-limited predation (Troyer, 1983; Iverson, 1991; Janzen et al., 2000; Morafka et al., 2000), and increase adult body size and corresponding clutch size (Congdon and van Loben Sels, 1993; van Buskirk and Crowder, 1994) or increase activities such as foraging (Peach and Thomas, 1986; Vidal et al., 2002).

Yolk conservation does not appear to be a strategy of *A. mutica* hatchlings because hatchlings in both feeding treatments depleted yolk at the same rate. In chicks, posthatching yolk is depleted as it enters circulation as lipid and is assumed to be used for energy (Noy and Sklan, 2001). Thus, depletion may translate directly into use in *A. mutica* as well. Yolk reserves of newly hatched *A. mutica* contain approximately 1.75 kcal (M. V. Plummer, S. J. Beaupre, T. N. Lee, and N. E. Mills, unpubl. data), sufficient to sustain a hatchling at standard metabolic rate (SMR) for approximately 54 days at 25°C (using our pooled SMR estimate and assuming constant yolk composition). Because the metabolic rate of an active hatchling would likely be 2–3× SMR and because triacylglycerol, the primary storage lipid in *A. mutica* yolk (Nagle et al., 2003), may be preferentially used in development (Nagle et al., 1998), a more accurate estimate of sustainability would be about 40 days. This estimate may still be too liberal because the body condition of our unfed hatchlings significantly diverged from fed hatchlings as early as 14–35 days after hatching. This divergence suggests that it may be necessary for hatchlings to forage successfully before hibernation to obtain certain non-caloric nutrients not available in the reserve yolk. At the Georgetown locality on the White River, *A. mutica* hatchlings emerge from nests from late July to mid-August and begin hibernation in mid-October (MVP, pers. obs.), a period of approximately 60–80 days. According to our estimates of sustainability and yolk depletion results, the yolk reserve of an *A. mutica* hatchling is insufficient to sustain the hatchling until its first hibernation.

Hatchlings in the fed treatment had greater masses and body sizes, with the exception of carapace width in 2004, than unfed hatchlings. *Trachemys scripta* hatchlings with experimentally reduced reserves also grew more slowly than hatchlings with full reserves but did not feed differently (Yeomans, 1999). These results suggest that these species of turtles may use posthatching yolk for maintenance and any energy intake above maintenance requirements to maximize growth. However, although the masses and body sizes of fed *A. mutica* hatchlings were greater, they were not always increasing. Mass can only increase in animals obtaining external forage, but access to external resources does not guarantee an increase in mass. During both years, but more notably in 2004, some hatchlings in the fed treatment never fed and some fed only occasionally. The inclusion of these individuals in the analysis lowered the means of the fed treatment in all morphological measurements. Also, the initial increases of body size may not have indicated early growth but changes in body shape. Accurate linear body measurements on newly hatched softshells are difficult to obtain until the transformation from a spherical shape in the egg to the final flattened body shape is completed. We waited one week after hatching before taking initial body measurements; however, the sharp increases in plastron length and carapace width in week three of 2003 and week two of 2004 (Fig. 1) suggests the flattening process continued past one week. The initial

decrease in body condition in both years was likely in part caused by the continued increase in plastron length resulting from flattening disproportional to the change in mass.

Feeding condition may differentially affect the rate of yolk depletion in various taxonomic groups. For example, fed hatchlings of *A. mutica* used yolk at the same rate as unfed hatchlings but grew faster, indicating a strategy to meet maintenance demands with yolk and fuel growth costs with external forage. In contrast, depletion of reserve yolk is faster in fed fish (Mani-Ponset et al., 1996), chicks (Noy and Sklan, 1999), and a lizard (Pandav et al., 2006). Noy and Sklan (1999) suggest that the chick's strategy is to use the yolk to support preferential growth and final maturation of the small intestine, and Pandav et al. (2006) propose that the lizard may use the yolk to meet increased metabolic demands from specific dynamic action. Vidal et al. (2002) argued that reserve yolk was depleted more rapidly in unfed than fed newly hatched squid because the unfed squid must increase activity to learn to forage to avoid starvation.

The faster growth in fed *A. mutica* hatchlings theoretically should have been accompanied by a metabolic increase above SMR (cost of growth; Wieser, 1994; Nagy, 2000); however, we were unable to detect differences in metabolic rates between fed and unfed hatchlings. The similarity may be a result of the procedures used during SMR measurement, or it may have resulted from a behavioral or physiological compensation in the neonate's energy budget (Nagy, 2000). Indeed, the expected cost of rapid neonate growth has not been confirmed in most reptile species that have been studied (Nagy, 2000; Brown et al., 2005; but see Beaupre and Zaidan, 2001). Metabolic rates decreased and remained low for at least 60 days after hatching in *Chrysemys picta* (Peterson and Kruegl, 2005), and lower standard metabolic rates resulted in higher growth rates in hatchling *Chelydra serpentina* (Steyermark, 2002). In their exposed habitat, *A. mutica* hatchlings may also minimize energy expenditure by reducing metabolic rate through cryptic inactivity in response to predation risk (Janzen et al., 2000) and possibly through suboptimal body temperatures attained by relaxed basking. However, the limited amount of stored energy in reserve yolk necessitates successful foraging to avoid starvation before the first overwintering, and the effectiveness and timing of hatchling foraging are unknown.

In summary, when external forage is available and conflicts between feeding and other activities do not induce fasting, residual yolk of hatchling *A. mutica* indirectly supports growth by meeting maintenance costs to allow exogenous energy use for maximal growth. However, yolk reserves of *A. mutica* can sustain a hatchling in absence of external forage for approximately 40 days and cannot sustain the hatchling until the first overwintering. Future investigation is needed to elucidate the apparent paradox of fed hatchlings' increased growth rate at a metabolic cost similar to unfed hatchlings.

Acknowledgments.—Turtle eggs were collected under Scientific Collecting Permit 675 issued by the Arkansas Game and Fish Commission. This research was approved by the Harding University Animal Care Committee and is in accordance with the booklet ''Guidelines for Use of Live Amphibians and Reptiles in Field Research'' (1987; American Society of Ichthyologists and Herpetologists, The Herpetologists' League, and the Society for the Study of Amphibians and Reptiles). A Faculty Development Grant and a grant from the Margaret M. Plummer Memorial Research Fund at Harding University funded portions of this research. We thank S. Beaupre for use of his metabolic lab and J. Van Dyke for insightful comments on the manuscript.

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Accepted: 19 April 2007.