

MATERNAL NEST-SITE CHOICE AND OFFSPRING FITNESS IN A TROPICAL SNAKE (*TROPIDONOPHIS MAIRII*, COLUBRIDAE)

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Abstract. Do reproducing female reptiles adaptively manipulate phenotypic traits of their offspring by selecting appropriate nest sites? Evidence to support this hypothesis is indirect, mostly involving the distinctive characteristics of used (vs. available) nest sites, and the fact that physical conditions during egg incubation can modify hatchling phenotypic traits that plausibly might influence fitness. Such data fall well short of demonstrating that nesting females actively select from among potential sites based on cues that predict fitness-determining phenotypic modifications of their offspring. We provide such data from experimental studies on a small oviparous snake (the keelback, *Tropidonophis mairii*) from the wet-dry tropics of Australia. When presented with a choice of alternative nesting sites, egg-laying females selected more moist substrates for egg deposition. Incubation on wetter substrates significantly increased body size at hatching, a trait under strong positive selection in this population (based on mark-recapture studies of free-ranging hatchlings). Remarkably, the hydric conditions experienced by an egg in the first few hours after it was laid substantially affected phenotypic traits (notably, muscular strength) of the hatchling that emerged from that egg 10 weeks later. Thus, our data provide empirical support for the hypothesis that nesting female reptiles manipulate the phenotypic traits of their offspring through nest-site selection, in ways that enhance offspring fitness.

Key words: Australia; egg incubation; keelback snake; nest-site selection; offspring fitness; phenotypic plasticity; reptile; *Tropidonophis mairii*.

INTRODUCTION

Within most animal populations, and especially in sexually reproducing species, a cohort of neonates displays substantial phenotypic variation. Charles Darwin's greatest insight was that such variation provides an opportunity for natural selection to modify the distribution of fitness-relevant traits, thereby increasing the frequency of characteristics that enhance an organism's probability of surviving and reproducing. The degree to which such selective forces result in evolutionary change within the population depends, however, upon the proximate mechanisms that generate that phenotypic variation. In the simplest case, the phenotypic variation is engendered entirely by genetic variation, so that fitness differentials will directly modify underlying gene frequencies. Unfortunately, the reality is more complex. One important complication is the fact that phenotypic variance within a cohort is the result of environmental influences as well as genetic factors. Indeed, a high proportion of the quantifiable variation in many traits is induced by environmental factors, not by genes (Bull 1987, Sultan 1987, Warrentin 1995, Scheiner and Callahan 1999).

This sensitivity of phenotypic traits to environmental conditions has strong implications for the operation of

natural selection. In the extreme case in which all phenotypic variation within a cohort of offspring is due to environmental, not genetic, factors (as in a clone of parthenogens), even intense selection on offspring traits will not generate any longer term (evolutionary) response because of the absence of genetic variation at the critical loci. This is not to say, however, that the system cannot evolve (Via et al. 1995). If specific environmental conditions result in the development of "fitter" phenotypic traits, we expect selection for any behaviors that expose the offspring to such environments at the appropriate time within their life history. Often, this will involve early development, generally the most critical phase because even small deviations in early embryos can later cascade through into major phenotypic modifications as development unfolds (Taning 1952, Albon et al. 1983, Henry and Ulijaszek 1996). Thus, one of the most important proximate influences on offspring phenotypes may be the conditions that eggs experience in natural nests. Minor shifts in traits such as nest temperatures and water potentials can have major impacts on phenotypic traits of hatchlings such as sex, size, shape, color, locomotor ability, and behavior (Burger et al. 1987, Deeming and Ferguson 1991, Rhen and Lang 1995). Hence, one major route by which natural selection can modify offspring traits in such a system is via genes that control the nest-site selection behavior of reproducing females (Bull et al. 1982, Bull 1983, Packard and Packard 1988, Packard 1991).

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Many studies of this topic have been based on reptiles. Laboratory-based experimental work has shown a high degree of phenotypic plasticity in hatchling reptiles as a result of the conditions experienced during embryogenesis (e.g., Joanen et al. 1987, Ji and Brana 1999, Warner and Andrews 2000, Webb et al. 2001). Quantitative comparisons of natural nests with available nest sites often reveal substantial differences, providing strong (albeit indirect) evidence that reproducing females actively select particular types of sites for nesting (Muth 1980, Packard and Packard 1988). Lastly, field studies suggest that a neonate's phenotype may influence its probability of survival (e.g., Fox 1975, Ferguson and Fox 1984, Arnold and Bennett 1988, Jayne and Bennett 1990). In combination, these three kinds of studies support the hypothesis that mothers may be able to manipulate the phenotypic traits of their offspring by exploiting norms of reaction of reptilian embryogenesis in relation to physical conditions during egg incubation (Beuchat 1986, 1988, Beuchat and Ellner 1987, Shine and Harlow 1996, Arnold and Peterson 2002). That is, some component of selection on offspring phenotypes in such systems is mediated not through differential fitness of alleles that determine specific offspring traits, but instead through selection on genes in females for nest-site selection criteria.

Unfortunately, the available evidence remains indirect. One problem is that maternal choice among alternative potential nesting sites has been inferred mostly from nonrandom attributes of natural nests rather than from experimental studies that manipulate nest availability. Correlational evidence cannot identify the actual cue(s) used by nesting females, because so many of these cues (e.g., temperature/moisture/soil depth/type and size of cover object) covary in nature. Ideally, we need to manipulate the array of available nest sites with respect to a specific attribute (such as temperature or moisture) relevant to the reaction norms of the offspring. Only then can we make a strong link between nest-site selection and its impact on offspring phenotypes to discern (1) whether or not the female actively selects among potential nest sites, and if so, (2) which cues does she use. We can then (3) examine the impact of variation in that cue on hatchling phenotypes, to construct a direct causal link between female behavior and offspring traits. Lastly, we need field data to (4) explore the ways in which this environmentally induced variation translates into fitness differentials. Our studies on the ecology of snakes in tropical Australia provide such data.

METHODS

Study species and area

The keelback, *Tropidonophis mairii*, is a small, non-venomous snake (adult size <80 cm snout-vent length [SVL hereafter]) belonging to the natricine lineage within the Colubridae (Malnate and Underwood 1988,

Cogger 2000). This species is abundant through many tropical and subtropical areas within the Australasian region, especially around bodies of water (O'Shea 1991, Cogger 2000), and feeds primarily upon frogs (Shine 1991). Keelbacks have been extensively studied on the Adelaide River floodplain 60 km east of Darwin in the Australian wet-dry tropics (Webb et al. 2001, Brown and Shine 2002, Brown et al. 2002). Ambient temperatures at this site are high year-round (mean monthly temperature 27.0°C), but precipitation is highly seasonal. More than 78% of the 1394 mm mean annual rainfall comes from monsoonal downpours within the relatively brief (four-month) "wet season" (December-March). Thus, much of the floodplain is inundated (and soils in surrounding higher areas are saturated) during the wet season, but soil moisture levels fall gradually over the course of the next several months (Shine and Brown 2002).

Keelbacks on the Adelaide River floodplain nest over an eight-month period (April-November), with some females producing multiple clutches within the same year (Brown and Shine 2002). Eggs are laid in relatively shallow (<20 cm) burrows in the floodplain soil (Shine and Brown 2002). Thus, clutches laid at different times of year experience different hydric conditions during incubation. Experimental studies have shown that the phenotypic traits of hatchling keelbacks are influenced significantly by the physical conditions that the eggs experience during incubation. In particular, hatchling phenotypes are affected by the magnitude of diel variation in nest temperatures (Webb et al. 2001) and by the water potential of the incubation medium (Shine and Brown 2002).

Experimental methods

As is true for many species, natural nests of keelbacks are difficult to locate (Shine and Brown 2002). To examine the cues used by nesting females, we captured females that had migrated to the wall of Fogg Dam to lay their eggs (Brown and Shine 2002). After the females were measured and weighed, we offered them a choice of potential nest sites differing in hydric conditions. Females oviposited 2-18 days after collection (mean = 7.7 days). During this period, they were kept individually in clear plastic cages (40 × 30 × 20 cm) with a water bowl and four potential nest sites. These were circular black plastic bowls 10 cm in diameter and 4.5 cm high, covered by a plastic lid with a 3 cm diameter central opening. The bowls contained vermiculite moistened with water to produce substrates ranging from very dry (0.25 g water per 1 g vermiculite, = 25%) to very wet (6 g water per 1 g vermiculite, = 600%). Bowls were reweighed daily and water was added to bring them back to their original mass (i.e., to counteract evaporative water loss, generally <0.1 g/d). In 37 initial trials, we offered the snakes a choice of 25, 50, 100, and 300% treatments. Because most chose the wettest site (300%) for oviposition, we mod-

ified the protocol to use 100, 300, 400, and 600% treatments, in order to see whether the snakes simply selected the wettest available substrate. We ran 10 further trials with this combination.

Oviposition generally occurred at night, with all eggs within a single clutch being laid within a 60-min period. Cages were checked each morning and any eggs were removed, weighed, and measured, and the eggs from each clutch were separated for incubation under a range of hydric conditions. The postpartum females were also reweighed at this time, and then released at their site of capture. Eggs from each clutch were allocated to four incubation treatments (i.e., split-clutch design). Eggs were incubated separately in small plastic containers (6.5 cm diameter \times 4.5 cm high), partly buried in the vermiculite substrate. Each egg was incubated in twice its mass of vermiculite plus an amount of water determined by its treatment moisture regime. Water was added weekly to replace evaporative loss. The incubation containers were kept in a room with ambient temperatures $24.0^\circ \pm 8^\circ\text{C}$ (mean \pm 1 SD; range 16.0–32.0°C). Eggs were weighed every week and were checked daily for hatching; all hatchlings were immediately measured and weighed. Their muscular strength was tested at 1 day of age by attaching a spring balance to the tail and allowing the snake to pull against it seven times in rapid succession; we retained the mean and maximum strength scores for analysis (see Shine and Brown [2002] for details of this method). Hatchlings were then individually marked by scale-clipping, and were released at the site where their mother had been captured. None of these snakes has yet been recaptured. However, numerous hatchlings from similar incubation moisture experiments (but only incorporating 50% and 100% moisture regimes) during the 2000 and 2001 nesting seasons have been recaptured.

RESULTS

Maternal nest-site selection

Of 47 female keelbacks captured shortly prior to egg-laying, 38 oviposited within one of the four alternative nest sites provided in the cages. The remaining nine laid their eggs either on the cage floor or in the water bowl; these animals are excluded from our analyses of nest-site choice, but their eggs (if viable) were used for the study of incubation effects (incubated at extreme moisture levels of 6, 12, 400, and 600% water, to bracket the main experimental treatments of 25–300% water).

When female keelbacks were given a choice between incubation substrates offering 25, 50, 100, and 300% water by mass, most (21 of 29) selected the wettest treatment for oviposition. Another four oviposited in the driest treatment (25%), three in the 100%, and one in the 50%. Contingency-table analysis, against a null hypothesis of equal numbers of nests laid in each treatment, shows that the females significantly preferred the

wettest substrate ($\chi^2 = 35.41$, $df = 3$, $P < 0.0011$). In trials providing 100, 300, 400, and 600% water by mass in the alternative nest sites, females again tended to select the wetter treatments for oviposition (one in 100%, one in 300%, four in 400%, three in 600%) but the effect was not statistically significant ($\chi^2 = 3.0$, $df = 3$, $P = 0.39$).

To examine whether phenotypic traits of a female snake or her eggs influenced her choice of incubation sites, we conducted one-factor ANOVAs with nest hydric category as the factor and female traits or clutch mean values as the dependent variables. We combined data from both sets of trials for this analysis. Females using the different hydric categories of nests did not differ in mean body sizes (SVL, $F_{5,32} = 0.26$, $P = 0.93$; mass postpartum, $F_{5,32} = 0.49$, $P = 0.78$), clutch sizes ($F_{5,32} = 0.40$, $P = 0.84$), or egg sizes (length, $F_{5,32} = 0.73$, $P = 0.61$; width, $F_{5,32} = 1.13$, $P = 0.37$; mass, $F_{5,32} = 1.87$, $P = 0.13$; see Fig. 1).

Effects of incubation regimes on hatchling phenotypes

Hatching success was high for eggs in all treatments, regardless of hydric conditions in the nest of origin (78% of 157 eggs laid in 300% water by mass, 83% of 72 eggs laid at drier conditions, and 100% of 28 eggs laid in wetter conditions; $\chi^2 = 3.06$, $df = 2$, $P = 0.22$) or during incubation (84% of 68 eggs incubated at 300%, 82% of 208 eggs kept in drier conditions, 80% of 10 eggs kept in wetter conditions; $\chi^2 = 0.1$, $df = 3$, $P = 0.95$). In this study, eggs incubated only briefly in the initial nest site (from oviposition until they were removed the following morning, typically a few hours) and then spent the rest of incubation (\sim 10 weeks) at the regime to which they were allocated. Intuition suggests that the initial brief phase will be of trivial importance, but to test this assumption, we included the initial as well as incubation nest conditions in our analysis of hatchling phenotypes. These data were analyzed with three-factor nested ANOVA, with the factors being clutch ID number nested within the hydric treatment for the initial nest; the initial nest hydric conditions; and the incubation hydric conditions. Both of these latter factors were tested against the nested term (among-clutch variation) rather than the residual error term. The analysis also included the interaction between hydric conditions in the initial and final nests. To simplify the analysis, hydric conditions were scored as a trichotomous variable ($<300\%$, 300% , and $>300\%$ water). Initial analyses showed that many of the variables that we measured (tail length, head length, mass, mean and maximum strengths) were highly correlated with SVL ($P < 0.001$ in all cases), so we calculated residual scores from the general linear regressions of all these traits against SVL. This procedure generated size-independent measures, so that apparently “significant” effects on traits were not simple consequences of their correlation with body size.

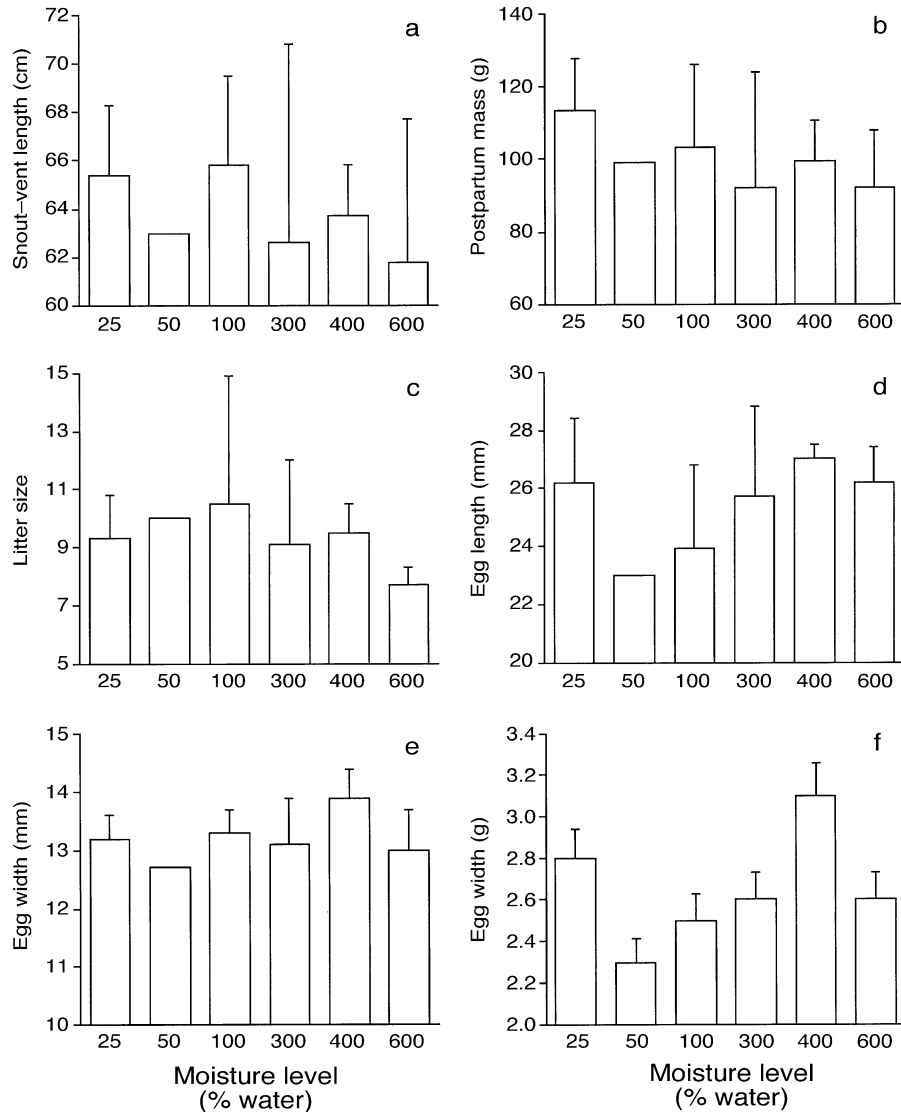


FIG. 1. Phenotypic traits (mean + 1 SD) of female keelback snakes (*Tropidonophis mairii*) and their clutches, as a function of the hydric conditions in nest sites in which the captive females laid their eggs. Sample sizes of females in each category were as follows: 25% water, $n = 4$; 50%, $n = 1$; 100%, $n = 4$; 300%, $n = 22$; 400%, $n = 4$; 600%, $n = 3$. See *Maternal nest-site selection* for statistical tests of these data.

Table 1 shows the main results from these analyses. Maternal effects were strong for all traits, with significant differences among clutches for all of the hatchling characteristics that we measured. After allowing for this source of variation, some traits also were significantly affected by the incubation regimes experienced during the egg stage (Fig. 2). Surprisingly, the initial nest in which an egg was laid (and remained for only a few hours) had as much influence in this respect as did the incubation regime to which eggs were transferred and kept throughout the remainder (>99%) of development (Table 1). Thus, although hatchling body size was affected mostly by incubation regime, a neonate's muscular strength relative to size was strongly influenced by the hydric conditions that it experienced

in the first few hours after the egg was laid, more than two months previously (Table 1). Our analyses did not reveal any significant interactions between oviposition conditions and incubation conditions in these respects (Table 1). Sex ratios of hatchlings were not significantly affected by any of our incubation treatments (range 50–63% male, $\chi^2 = 0.42$, $df = 2$, $P = 0.77$).

Determinants of survival rates of free-ranging snakes

We released 750 individually marked hatchlings that had been incubated on either 50% or 100% moisture substrates (including 239 hatchlings from the incubation experiments reported in the current paper) between July 2000 and September 2002. Hatchlings from wet-substrate incubation were larger than those from dry-

TABLE 1. Three-factor nested ANOVA F values showing the effects of clutch ID number, and hydric conditions in the initial nest and during the subsequent incubation period, on phenotypic traits of hatchling keelbacks (*Tropidonophis mairii*).

Trait	Clutch ID number	Influence of hydric conditions		
		Initial nest	Incubation nest	Interaction of initial \times incubation conditions
Egg mass				
At laying	71.82***	1.59	0.02	0.83
At 2 weeks	41.65***	1.46	0.37	0.16
At 3 weeks	25.49***	2.70	0.89	0.19
At 4 weeks	18.66***	3.63*	1.90	0.28
At 5 weeks	13.86***	3.28	3.50*	0.46
At 6 weeks	8.00***	3.63*	7.50**	0.43
At 7 weeks	6.82***	3.27	11.83**	0.59
At 8 weeks	2.61***	0.56	3.29	0.27
At 9 weeks	6.77***	0.24	14.54***	0.03
At 10 weeks	6.13***	0.50	15.18**	0.89
Snout-vent length (mm)	4.80***	3.21	18.37***	0.82
Relative tail length	9.27***	0.85	0.27	1.14
Relative head length	7.95***	0.07	0.25	0.83
Relative body mass	5.94***	0.67	0.44	1.60
Relative mean strength	2.94***	4.43*	0.76	0.93
Relative maximum strength	2.30**	4.06*	0.99	0.50

Notes: Clutch effects are nested within the initial nest hydric treatment, and the other main effects are tested against this interaction term rather than the residual term. For all variables except snout-vent length, the trait tested is the residual score from the linear regression of the trait against snout-vent length. For clutch ID, $df = 26, 197$; for tests of hydric conditions (last three columns), all $df = 2, 197$.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

substrate incubation (mean values 14.5 vs. 13.3 cm SVL, $F_{1,74} = 187.7$, $P < 0.0001$). In total, 42 of these animals were recaptured 109–1005 days after their release as hatchlings. The percentage of animals that was recaptured was higher from wet-substrate incubation (29 of 393, = 7.4%) than from dry-substrate incubation (13 of 357, = 3.6%; $\chi^2 = 5.94$, $df = 1$, $P = 0.026$). Logistic regression showed that snakes were more likely to be recaptured if they were large at hatching (log-likelihood ratio test, $\chi^2 = 9.68$, $df = 1$, $P = 0.002$; see Fig. 3).

DISCUSSION

Our study shows that female keelbacks actively select moist nest sites; that such nests produce larger hatchlings; and that larger body size at hatching enhances offspring survival. Hence, our data show a direct link between a female's nest-site choice and her reproductive success, mediated via phenotypically plastic responses during embryogenesis. The hypothesis that reproducing females enhance their own fitness by manipulating the phenotypic traits of their offspring (via nest-site selection) is consistent with indirect evidence from a variety of previous studies. However, our study is unusual in providing direct evidence for each of the major links in the hypothesis, rather than relying upon assumptions about critical aspects such as maternal criteria for nest choice, and the phenotypic determinants of hatchling fitness.

The idea that females select nest sites based upon cues that predict hatchling viability is an obvious one, with a long history (e.g., Fitch 1954, Fitch 1964, Muth 1980). Detailed analyses of several taxa have shown that the physical conditions inside natural nests constitute a highly nonrandom sample of the incubation environments available in potential nest sites (e.g., Packard and Packard 1988, Shine and Harlow 1996). Fewer studies, however, have looked at active nest-site selection behavior using appropriate experimental designs to identify the specific cues used by nesting females. Such cues include nest temperatures (Bull et al. 1988) and hydric conditions (Plummer and Snell 1988, Warner and Andrews 2002).

Analogous phenomena occur in viviparous reptiles also, with pregnant females maintaining distinctive thermal regimes (often, with low diel variance), and thus controlling the physical conditions under which their offspring develop (Beuchat 1986, Charland and Gregory 1990, Gregory et al. 1999). This behavior may substantially affect the phenotypic traits of offspring (Beuchat 1988, Shine and Harlow 1993, Swain and Jones 2000, Wapstra 2000, Arnold and Peterson 2002). Active maternal control over the incubation environment thus is widespread among reptiles. Although thermal factors have been the primary focus of previous studies, this probably reflects the concentration of research on temperate-zone (cool-climate) reptile taxa. In many tropical areas, high temperatures are available

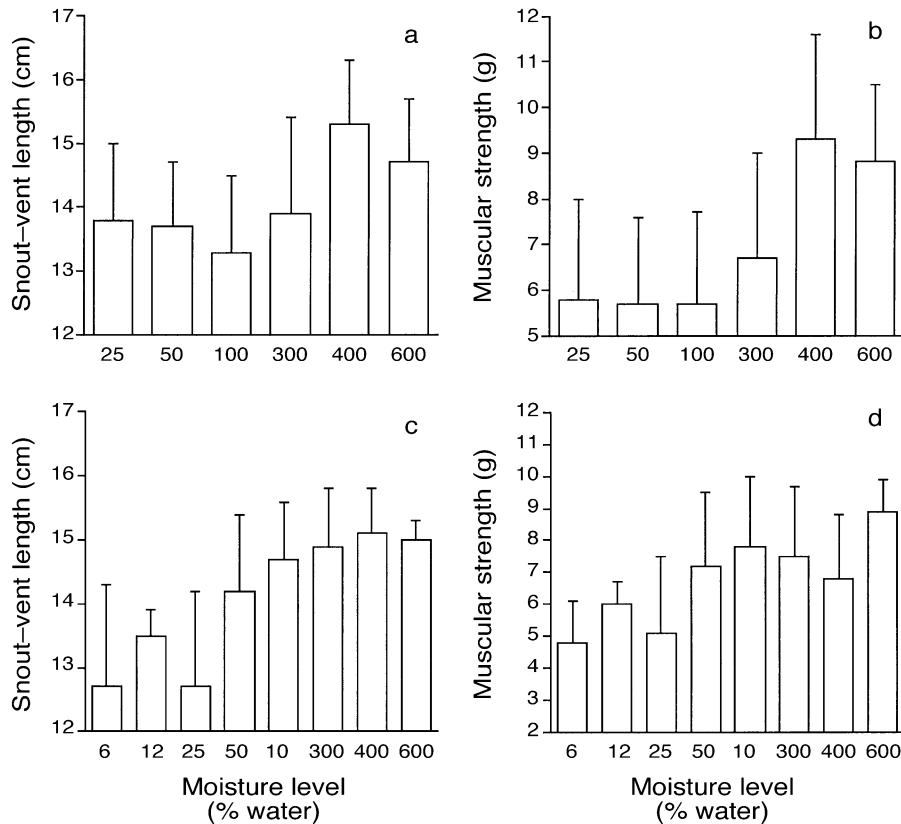


FIG. 2. Phenotypic traits (mean + 1 SD) of hatchling keelbacks (*Tropidonophis mairii*) as a function of (a, b) the hydric conditions in nest sites in which the captive females laid their eggs and (c, d) the hydric regimes under which eggs were kept during the 10-week incubation period. Sample sizes (number of eggs) were as follows: for initial treatment, 25% water, $n = 37$; 50%, $n = 10$; 100%, $n = 25$; 300%, $n = 163$; 400%, $n = 28$; 600%, $n = 15$; for subsequent incubation treatment, 6%, $n = 5$; 12%, $n = 5$; 25%, $n = 72$; 50%, $n = 66$; 100%, $n = 60$; 300%, $n = 68$; 400%, $n = 5$; 600%, $n = 5$. See Table 1 for statistical tests of these data.

year-round and the most important seasonal variation for incubating eggs will be hydric, rather than thermal, in nature.

We obtained strong support for the hypothesis that female keelbacks base nest-site choice at least partly on moisture content of the substrate, but saw no hint that females match their choice of oviposition site to the reaction norms of their own offspring. One could imagine a situation whereby some females within the population specialize in dry-substrate incubation (i.e., produce eggs that benefit from incubation on drier substrates, and actively select such substrates), whereas other females specialize on moist substrates. If present, such an effect should be revealed by significant interactions between nest-site choice and incubation responses, but no such interactions were apparent in our analyses (Table 1). A study of montane lizards reached the same conclusion, based on field data (Shine et al. 1997).

Phenotypic plasticity in response to physical conditions during egg incubation is widespread among reptiles, from a diversity of phylogenetic lineages and habitat types (see Deeming and Ferguson 1991; review by

Shine 1999). Studies on squamate reptiles have typically focused on thermal, rather than hydric, influences, with the latter found to exert little or no effect on embryonic pathways in some taxa (e.g., Ji and Brana 1999, Flatt et al. 2001). However, many turtles show strong responses to minor variation in water potential of the incubation medium (Packard 1991, Packard et al. 1993), and the same is clearly true for some squamate taxa also, including *Tropidonophis* (Shine and Brown 2002). Drier substrates result in hatchlings that are small because they are unable to resorb all of the yolk sac and thus leave this behind in the egg (Shine and Brown 2002). The most surprising result from our current analyses is that the water content of the incubation medium in which an egg is laid somehow exerts a significant influence on the muscular strength of the neonatal snake that emerges from that egg months later, even if the initial exposure is very brief (a few hours, out of a 10-week incubation period). The proximate basis for this effect may involve changes to the eggshell or embryonic membranes as they take up or lose water immediately after oviposition, and warrants further study.

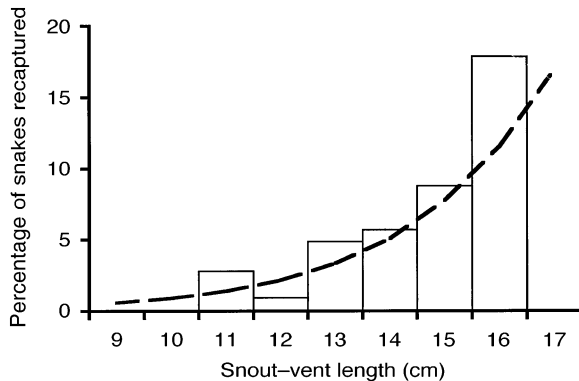


FIG. 3. Survival (recapture) rates of free-ranging keelbacks (*Tropidonophis mairii*) as a function of their body size at hatching. The histograms show the percentage of recaptured snakes of each 1-cm snout-vent length (SVL) class, except that SVL categories are combined where $N < 10$. Thus, the 11-cm class ($N = 71$) contains 14 offspring < 11 cm, and the 16-cm class ($N = 28$) contains three offspring > 16 cm. Sample sizes for the other size classes are as follows: 107 for 12 cm; 144 for 13 cm; 263 for 14 cm, and 137 for 15 cm. The dotted line shows the probability equation from the logistic regression of survival against body size at hatching.

The finding that larger body size at hatching enhances the probability of survival for young keelbacks accords well with intuition, and with results from several mark-recapture studies on other species of reptiles (e.g., Fox 1975, Ferguson and Fox 1984). Nonetheless, many other studies have failed to find any evidence that “bigger is better,” including a detailed analysis of survival rates in water pythons (*Liasis fuscus*) at the same study areas that we use for our keelback studies (Madsen and Shine 1998). The role of hatchling size in predicting survival may also vary among years even within a single population (Fox 1975, Sinervo and Huey 1990). This variability makes it difficult to infer the direction and magnitude of selective forces on offspring traits without very long-term data. In the case of *Tropidonophis* at Fogg Dam, larger hatchlings have survived significantly better than smaller conspecifics in each of the three years for which we have recapture data (G. P. Brown and R. Shine, unpublished data).

In summary, our results are encouraging for those who infer an adaptive significance to maternal nest site choice. Female keelbacks actively select among alternative nest sites based on a trait (substrate water potential) that influences the body size of hatchlings, which in turn affects the survival of these offspring. The direction of these effects conforms to the adaptationist prediction: that is, the females’ preference for moister sites enhances, rather than reduces, offspring fitness. By using a cue that directly predicts developmental responses of their embryos, female keelbacks can thereby maximize the fitness benefits from egg production.

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