

Ecology of an Aquatic Snake (*Thamnophis marcianus*) in a Desert Environment: Implications of Early Timing of Birth and Geographic Variation in Reproduction

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ABSTRACT.—We studied the ecology of the checkered garter snake, *Thamnophis marcianus*, in a desert grassland in southeastern Arizona. The adult sex ratio was 0.67 M:F and varied significantly among seasons. As with other species of *Thamnophis*, adult females were significantly larger than males in SVL and body mass, and females also had longer jaws. Activity occurred both during the day and nighttime, but was confined to aquatic areas or their immediate vicinity. Mating occurred in late March and females gave birth to a single brood of an average of 15 offspring in late May and early June. The timing of birth in this population was among the earliest on record for any live-bearing snake in North America and was much earlier than for other checkered garter snake populations. In comparison with populations of *T. marcianus* from northern and southern Texas, females from Arizona had larger maternal body sizes and their offspring were larger as well; conversely, we found no significant differences in brood size among localities once maternal body size was taken into account. The implications of early timing of birth and geographic variation in reproductive traits are discussed.

INTRODUCTION

Although the garter snakes (*Thamnophis*) are arguably among the best studied snakes in the world, much of our knowledge of the 30 species in the genus is based on studies of north-temperate zone species, especially *T. elegans*, *T. ordinoides*, *T. sauritus* and *T. sirtalis* (see summary in Rossman *et al.*, 1996). Information on species from tropical and southern parts of north temperate-zone areas (*i.e.*, southern United States and northern Mexico) is relatively limited; exceptions include data on dietary and habitat use patterns of *T. cyrtopsis*, *T. proximus* and *T. rufipunctatus* in Texas, New Mexico and Arizona (Fouquette, 1954; Fleharty, 1967; Jones, 1990), reproduction, feeding habits and behaviors of *T. eques* and *T. melanogaster* in Mexico (Drummond, 1983; Macias Garcia and Drummond, 1988; Halloy and Burghardt, 1990; Manjarrez, 1998) and body temperatures of *T. cyrtopsis*, *T. eques* and *T. rufipunctatus* in New Mexico and Arizona (Fleharty, 1967; Rosen, 1991). However, long-term field studies on populations in the southern United States and Mexico are rare, especially in comparison to the numerous long-term studies on populations in the northern United States and Canada (*e.g.*, Carpenter, 1952; Gregory, 1977; Kephart and Arnold, 1982; Peterson, 1987; Jayne and Bennett, 1990; Whittier and Crews, 1990; Fitch, 1998). Clearly, field data are biased towards northern forms, thus limiting our understanding of the evolution of ecological patterns in the genus (Rossman *et al.*, 1996).

The checkered garter snake (*Thamnophis marcianus*) has a broad range in the southern United States and northern Mexico, with isolated populations in Central America (Rossman *et al.*, 1996) which makes it an interesting comparison with garter snakes from more north-

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ern areas. In addition, although the majority of garter snakes are wetland species, most of the habitat within the range of *T. marcianus* is arid, ranging from grasslands to true deserts (Rossman *et al.*, 1996). Little is known regarding the ecology of garter snakes in such arid environments.

Although experimental laboratory data are extensive for this species (Ford and Seigel, 1989, 1994; Perry-Richardson *et al.*, 1990; Ford and Cobb, 1992; Seigel and Ford, 1992), few detailed field studies have been conducted on *T. marcianus*. Ecological data are confined to museum studies on reproduction (Karges, 1983; Ford and Karges, 1987) and field data on diet (Fouquette, 1954) and body temperatures (Rosen, 1991).

From 1988–1998 we conducted a field study of checkered garter snakes in a desert-grassland area in southeastern Arizona. Here we report information on sexual dimorphism, activity patterns, reproductive traits and feeding ecology of this population. We pose three questions; (1) How are the ecological traits of this species influenced by existence in an arid environment, (2) how do the traits of this species compare with garter snakes from more northern localities and (3) how much geographic variation in reproductive traits occurs among populations of *Thamnophis marcianus*?

MATERIALS AND METHODS

Our research was conducted at Roper Lake State Park, located in Graham Co., southeastern Arizona, ca. 260 km southeast of Phoenix. Mean elevation is approximately 950 m. The park is surrounded by typical desert vegetation (*e.g.*, mesquite, ocotillo, prickly pear and creosote bush). Most of our work was done at the Dankworth Pond subunit of the park. Dankworth Pond consists of a man-made 4.9 ha wetland originally established in the 1930s to rear commercial fish. The water source for Dankworth Pond is a natural artesian spring which emerges from the ground at a water temperature of 35 C. Most of the pond maintains water at ambient temperatures, but about 25% of the pond has elevated water temperatures. Most of Dankworth Pond is open water; about 1/3 of the pond is dominated by cattails (*Typha* sp.). Water flows from Dankworth Pond via a small stream that drains into a riparian habitat. We also collected data along a narrow (1-m width) drainage stream at the main Roper Lake unit located 8 km north of Dankworth Pond. This stream (hereafter Roper Stream) flows intermittently from a nearby artesian spring and is also fed from overflow from a nearby reservoir. Common aquatic species in Dankworth Pond and the surrounding canals include Sonoran mud turtles (*Kinosternon sonoriense*), introduced bullfrogs (*Rana catesbeiana*) and several species of introduced fishes [*e.g.*, bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*) and channel catfish (*Ictalurus punctatus*)].

We conducted 10 sampling trips to Roper Lake State Park from 1988–1998 for a total of 49 field days. Most trips were made in May (21 d during 4 y) and August (18 d during 4 y), with lesser sampling effort in March and October (5 d per month). Garter snakes were collected primarily by hand or by wire-mesh minnow traps. Hand captures were made mostly along the edges of Dankworth Pond and Roper Stream, although we made specific efforts (by hand searches and road hunting) to find snakes in areas away from wetlands as well. After 1992 the uncontrolled growth of cattails made hand-hunting extremely difficult and we relied mainly on minnow traps (although minnow traps were also used extensively in 1988–1992). Standard commercial minnow traps were set along shallow water areas in the wetland habitats described above. Minnow traps were not baited by us, but captured bullfrog tadpoles and small fish on a daily basis. Traps were usually checked twice daily, once 1–3 h after sunrise and again at dusk.

All snakes were measured [snout–vent length (SVL), tail length (TL) and body mass

(BM)] using a cloth tape measure and a Pesola balance, respectively. Head width (HW) was measured at the hinges of the jaw and jaw length (JL) was measured from the tip of the rostral scale to the posterior end of the labial scale; both measurements were made using electronic calipers to the nearest 0.1 mm. We forced snakes to regurgitate any stomach contents and determined gender by the presence or absence of hemipenes (Fitch, 1987). Gravid females were palpated to determine the number of developing follicles, and some females were brought back to our laboratory where they gave birth (methods in Ford and Seigel, 1989). Offspring were processed in the same manner as were adults, but were weighed on an electronic balance to the nearest 0.01 g. Before release at the capture site all snakes were given either an individual mark or a cohort mark by clipping ventral or subcaudal scales (Brown and Parker, 1976; Fitch, 1987). Air temperatures were measured with either a Reotemp electronic thermometer or a quick-reading mercury thermometer (Miller and Weber, New York).

Relative clutch mass (RCM) was calculated as brood mass divided by female mass after parturition (Shine, 1980; Ford and Seigel, 1989). Following Brodie (1989), we also calculated effective relative clutch mass (ERCM) using the difference between pre- and postpartum female mass as the numerator and postpartum mass as the denominator. We used analysis of covariance (ANCOVA) to contrast size-dependent variables using SVL as the covariate. In all ANCOVA results differences reflect differences in y-intercepts, not slopes of regression lines. Differences in offspring size among localities used litter means rather than using individual offspring as independent data points. We used Tukey's HSD to make multiple comparisons among means. Statistical procedures were conducted on SYSTAT (SPSS Inc., 1996). Means are followed by ± 1 SD and the alpha level was 0.05.

In order to assess the degree of geographic variation in reproductive traits in *Thamnophis marcianus* we used data from wild-caught females taken from La Salle and McMullin counties in southern Texas (Ford and Karges, 1987) and Lubbock County in northern Texas. These samples consisted of females that were gravid when captured in the field, and which gave birth within several weeks in our laboratories in either Texas or Louisiana. *see* Ford and Karges (1987) and Ford and Seigel (1989) for details of captive maintenance. Clutch size and offspring size measurements for these females followed the methods outlined above.

RESULTS

Adult sex ratios, body size and sexual dimorphism.—Exclusive of neonates processed after birth, we captured 165 checkered garter snakes a total of 174 times. Using 45 cm SVL as the size at maturity (*see* below), we captured 54 adult males, 81 adult females, 17 juvenile males and 13 juvenile females. The overall adult sex ratio (0.67:1 M:F) was significantly different from 1:1 (χ^2 with Yates' correction = 5.00, df = 1, P = 0.025). However, adult sex ratios were not independent of season of capture; females outnumbered males in May (0.43 M:F, n = 43) and August (0.58 M:F, n = 65), but the opposite was true in March (1.5 M:F, n = 10) and October (1.83 M:F, n = 17) (contingency table analysis, $\chi^2 = 7.96$, df = 3, P = 0.047).

There were significant differences in SVL between the sexes, with an uncompressed sexual dimorphism index (SDI: Lovich and Gibbons, 1992) of 1.13 for SVL and 1.63 for body mass (Table 1). After correction for SVL using ANCOVA, males had significantly longer tails than did females (Table 1). Females also had relatively longer JL than did males, but there was no sexual dimorphism in HW (Table 1).

Activity patterns and habitat use.—We found checkered garter snakes active during all months in which we sampled (March, May, August, October). Based on both visual obser-

TABLE 1.—Sexual dimorphism in SVL, tail length (TL), body mass (BM), head width (HW) and jaw length (JL) for adult checkered garter snakes from southeastern Arizona. Length in mm, mass in g. Means \pm 1 SD. Differences between sexes were tested using ANCOVA (except for SVL, which was tested with ANOVA). * = $P < 0.05$; *** = $P < 0.001$; ns = not significant. Body mass, head width and jaw length were log-transformed to achieve normality

Sex	SVL	TL	BM	HW	JL
Female	609.83 \pm 88.18	151.3 \pm 20.09	122.0 \pm 55.35	14.4 \pm 2.77	22.88 \pm 3.66
n	82	55	81	62	62
Male	538.1 \pm 58.34	150.9 \pm 21.75	74.8 \pm 31.91	12.3 \pm 1.83	19.6 \pm 2.05
n	51	42	51	42	42
F	26.1***	22.6***	5.8*	1.2 ns	6.3*

vations and checking minnow traps at dusk and dawn, checkered garter snakes were active during both daytime and nighttime surveys. Of 90 captures made from 1988–1991, 71 were made during the day and 19 at night. Although we were not able to quantify seasonal differences in diurnal vs. nocturnal activity, some nocturnal activity was seen in all months. For example, an adult female was found foraging in the water at Dankworth Pond on 24 March 1991 about 1 h after dark with a water temperature of 15.2 C and air temperature of 15.4 C.

Of 101 captures of garter snakes made between 1988–1992 (when both capture methods were used), 26.7% were in aquatic minnow traps and 73.3% were by hand on land. However, despite numerous hours spent hand-hunting and road-hunting for garter snakes at sites both adjacent to, and well away from, wetlands, only four *T. marcianus* were ever found > 10 m from Dankworth Pond or one of the drainage canals. Most hand captures were also made in the immediate vicinity of the water, usually in thick bundles of dead cattails surrounding Dankworth Pond, where garter snakes would bask on top of the matted vegetation. Checkered garter snakes were also found basking in creosote bush habitats within 10 m of the drainage canals, especially during the summer monsoons in August when the relative humidity was high. One *T. marcianus* was found along a paved road, ca. 300 m from Dankworth Pond, but in the immediate vicinity of a then-flowing stream.

Reproduction.—Mating was seen only on 27 March 1991 when we found a mating ball of four males and one female. Gravid females were seen almost exclusively in May; of 30 females > 45 cm SVL examined in May, 22 were gravid and two were apparently post-parturient (80%). Conversely, only one gravid female was found in March, August or October, and that was a dying female with atretic follicles found in August 1988. Based on the presence of females with obvious signs of having recently been gravid (*e.g.*, extreme emaciation, flaccid oviducts), parturition occurred in mid to late May in the field. More specific data are available for 13 gravid females captured 20–25 May 1989 and immediately brought back to our laboratory. All gave birth to fully-formed offspring between 27 May and 30 June, with 50% giving birth by 19 June. This provides a minimum interval between mating and parturition of about 60 d. Given this interval and the absence of any gravid females during any of four sampling trips in early to mid-August, this population appears to produce a single brood per year.

The smallest gravid or newlyspent female was 515 mm SVL and the smallest male found in the mating ball was 478 mm (Table 2). The mean brood size of 14 gravid females that gave birth in the laboratory was 15.3 ± 7.97 offspring/female (14.1 with one statistical outlier removed), compared with a mean estimated brood size of 11.5 ± 3.99 ($n = 6$) via

TABLE 2.—Summary of major reproductive traits of checkered garter snakes from southeastern Arizona, contrasted with selected data from populations in southern and northern Texas. Data from southern Texas are from Ford and Karges (1987). Means \pm one sd, Sample sizes (# of litters) given below means. See text for statistical analysis and calculations of RCM and ERCM. F-values refer to either ANOVA or ANCOVA comparing reproductive traits among localities. Lengths are in mm, mass in g. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

Location	Maternal SVL	Brood size	Offspring SVL	Offspring mass	Clutch mass	RCM	ERCM
Arizona	639.8 \pm 77.45 n = 20	14.1 \pm 7.12 n = 20	176.6 \pm 12.91 n = 14	2.4 \pm 0.49 n = 14	43.7 \pm 24.72 n = 14	0.305 \pm 0.104 n = 14	0.367 \pm 0.136 n = 13
North Texas	582.7 \pm 80.88 n = 23	13.2 \pm 8.63 n = 23	159.3 \pm 9.29 n = 23	1.9 \pm 0.38 n = 23	—	—	—
South Texas	526.0 \pm 96.41 n = 14	9.5 \pm 4.88 n = 14	149.8 \pm 12.08 n = 14	2.3 \pm 0.68 n = 14	—	—	—
ANOVA or ANCOVA	$F_{2,54} = 8.01^{***}$	$F_{2,53} = 0.85^{ns}$	$F_{2,45} = 20.9^{***}$	$F_{2,48} = 6.1^{**}$	—	—	—

palpation, but these values were not significantly different regardless of whether the outlier was removed (ANCOVA, $F = 1.70$, $df = 1, 17$, $P = 0.210$). Using the combined data set, there was a significant relationship between \log_{10} maternal SVL and \log_{10} brood size ($F = 36.9$, $df = 1, 18$, $P < 0.001$), which explained 67.2% of the variation in brood size [regression equation: $-7.82 + 3.18(\log_{10} \text{ SVL in mm})$].

Of 194 offspring examined, 94 were males and 100 were females, which did not differ from a 1:1 ratio ($\chi^2 = 0.19$, $df = 1$, $P = 0.66$). The sex ratio per brood varied from 30.0 to 61.1% males. We found no significant relationship between log maternal SVL and log offspring SVL ($r^2 = 0.18$, $F_{1,11} = 2.5$, $P = 0.144$), but did find a significant negative relationship between log maternal SVL and log offspring mass once two outliers were removed ($r^2 = 0.43$, $F_{1,10} = 7.6$, $P = 0.020$).

Geographic variation in reproduction.—Females from Arizona were significantly larger than females from southern Texas, but not in comparison to females from northern Texas (Table 2; Tukey's HSD, $P = 0.093$). Arizona females had the largest raw brood size (Table 2), but when we adjusted for maternal size using an ANCOVA no significant differences were seen in mean brood size among the localities; in fact, the least-square mean values from Arizona were actually nonsignificantly lower than in the other populations. Both offspring SVL and offspring mass varied significantly among the three localities (Table 2); after adjusting for maternal SVL, offspring from Arizona had significantly longer SVLs than offspring from the two Texas localities, and had greater body masses than offspring from north Texas (Tukey's HSD, $P = 0.013$) but not south Texas (Tukey's HSD, $P = 0.994$).

Feeding.—Data from snakes captured in minnow traps are likely unreliable in this population because it became apparent that checkered garter snakes would feed while in minnow traps (*i.e.*, minnow traps that earlier in the day contained bullfrog tadpoles and no snakes later held no tadpoles but a garter snake whose stomach contained tadpoles). Using data from only hand-captured snakes, 12 snakes contained a total of 28 prey items, all small bullfrogs, bullfrog tadpoles or earthworms. Juveniles consumed primarily earthworms (three of five snakes), whereas adults fed primarily on tadpoles (five of eight snakes) and small frogs (three of eight snakes).

DISCUSSION

Comparisons with other species of garter snakes.—With one notable exception checkered garter snakes from southeastern Arizona show few major differences from congeners from more northern or less arid habitats. In terms of female-biased sexual dimorphism size at sexual maturity (515 mm), seasonal activity patterns (March–October), timing of mating (early spring), reproductive frequency (one brood per year), positive brood size-maternal size relationships and nonbiased offspring sex ratios, *T. marcianus* at Roper Lake are quite similar to other species of *Thamnophis* (see review in Rossman *et al.* [1996]). The only apparent effect of existing in an arid environment is that terrestrial activity appeared to be confined to areas immediately adjacent to the water, although there was some tendency for snakes to be found in more terrestrial areas during the summer rainy season. However, additional data using radiotelemetry are needed to confirm our findings that activity is restricted to areas immediately adjacent to the wetlands.

Perhaps the most interesting component of the ecology of the Roper Lake population is the extremely early period of parturition, from mid May–late June. Only one other species of garter snake (*Thamnophis eques* from Mexico) is known to give birth this early. In fact, the timing of parturition of *T. marcianus* at Roper Lake is the earliest timing of birth of any natricine snake in the United States (Table 3). Early parturition of checkered garter snakes at Roper Lake is not simply a function of latitude because populations of garter

TABLE 3.—Summary on early dates of parturition (defined as < 1 July) in North American viviparous snakes. Records based on abnormal broods (e.g., deformed, mainly stillborn) were not included

Species	Date(s) of parturition	Location	Reference
<i>Nerodia floridana</i>	19, 21 June	Florida	Fitch, 1970
<i>N. fasciata</i>	10, 21, 28 June	Florida	Fitch, 1970
<i>N. compressicauda</i>	13 June	Not specified	Fitch, 1970
<i>N. taxispilota</i>	15 June	Florida	Fitch, 1970
<i>Regina alleni</i>	24 June	Florida	Fitch, 1970
<i>Storeria dekayi</i>	11 June	Louisiana	Kofron, 1979
<i>S. occipitamaculata</i>	18 June	Not specified	Fitch, 1970
<i>Thamnophis cyrtopsis</i>	15 June	Arizona	Fitch, 1970
<i>T. cyrtopsis</i>	29 June	Arizona	Jones, 1990
<i>T. eques</i>	30 April–7 October	Mexico	Manjarrez, 1988
<i>T. marcianus</i>	27 May	Arizona	this study
<i>T. postremus</i>	20 June	Mexico	Rossman <i>et al.</i> , 1996
<i>T. proximus</i>	23, 25 June	Texas, Missouri	N. Ford (pers. obs.); Powell, 1982
<i>T. scalaris</i>	18–30 May	Mexico	Rossman <i>et al.</i> , 1996
<i>T. sirtalis</i>	24 June	Louisiana	Fitch, 1970
<i>T. validus</i>	6 June	Mexico	Rossman <i>et al.</i> , 1996

snakes from lower southern latitudes (e.g., *T. sauritus* from Florida) give birth much later than do *T. marcianus* from Arizona (Table 3). In addition, *T. marcianus* from Arizona are much more consistent in their timing of parturition than are the other species with early reproduction; *T. eques* from Mexico gave birth from 30 April–7 October (Manjarrez, 1998), whereas all females of *T. marcianus* at Roper Lake gave birth by late June and virtually no gravid females were seen during either August or October. The difference in consistency between *T. eques* and *T. marcianus* does not represent a phylogenetic effect since *T. marcianus* from south Texas also have wide variation in timing of parturition, with most births occurring from July to August but as early as May or as late as October (Ford and Karges, 1987; N. Ford, pers. obs.).

Timing of reproduction in Temperate Zone snakes has been thought to represent a balance between the needs of offspring to be born early enough in the summer or fall to feed and grow before the onset of winter and the needs of females to emerge from hibernation after potentially lethal temperatures are unlikely to occur (Shine, 1977; Seigel and Ford, 1987). Although much of the wide variation in the timing of parturition shown in Table 3 is likely a result of yearly differences in weather patterns, differences in the timing of birth among populations and species may have a significant but untested impact on life history patterns in snakes (Greene *et al.*, 1999). For example, female garter snakes are known to reach sexual maturity in 24–36 calendar months, *i.e.*, without regard to months of actual activity (Rossman *et al.*, 1996, p. 76–77). For populations in northern areas where parturition occurs in late summer or fall, only 1–2 mo usually elapse between birth and hibernation, and sexual maturity is not achieved until at least the third spring after birth, after about 15 “activity months” of growth (e.g., Fitch, 1965). By contrast, parturition in May, coupled with activity from March to at least October, suggests that *Thamnophis marcianus* in Arizona may grow for up to 5 mo their first year of life (June–October), at least 8 mo their second year (March–October), and, thus, potentially reach maturity in their second spring after birth, at least one calendar year earlier than would be possible with parturition later in the year.

Because early reproduction may have large consequences for lifetime fitness (*e.g.*, Cole, 1954), this is a trait that should be strongly favored by natural selection, unless constrained by unfavorable conditions (*e.g.*, cold weather). This raises the question how such wide variation in the timing of parturition occurs within populations that apparently lack such a constraint, such as *Thamnophis eques* from Mexico (Manjarrez, 1998) and *T. marcianus* from southern Texas (Ford and Karges, 1987). Such wide variation may represent multiple clutches [although this remains unproven in snakes (Seigel and Ford, 1987)] or simply lack of synchronization in reproductive cycles among females. Additional data on the fitness consequences of early and/or variable timing of reproduction are needed badly (*see* Greene *et al.*, 1999).

Geographic variation in reproduction.—Wide-ranging species of squamates frequently show geographic variation in life-history traits, and considerable attention has been focused on trying to explain such variation (*e.g.*, Fitch, 1985; Gregory and Larsen, 1993, 1996). However, data from experiments on phenotypic plasticity in checkered garter snakes indicate clearly that geographic variation in some traits (especially clutch size) are likely the result of proximate environmental factors such as rainfall and food availability (*e.g.*, Ford and Seigel, 1989; *but see* Gregory and Larsen, 1993). These data also suggest that offspring size is canalized relative to food availability, making this trait more amenable to geographic comparisons (Ford and Seigel, 1989).

Comparisons of reproductive traits among three localities for *Thamnophis marcianus* showed that when maternal size effects are removed, apparent geographic differences in brood size are no longer apparent. Although this result could be a function of different diets for the wild-caught females, recent experiments in our laboratory with these populations suggest that when diet is controlled, geographic differences in brood size are primarily a function of maternal size. Conversely, females from Arizona produce much larger offspring (especially in SVL) than females from the other localities, and these differences are independent of diet in these populations (Ford and Seigel, 1989). Thus, these differences may reflect evolutionary shifts (*see* King, 1993; Gregory and Larsen, 1993, 1996; Shine, 1996 and Velhagen and Savitsky, 1998 for an examination of geographic variation and evolutionary trends in offspring size among snakes). Why larger offspring size would be favored in Arizona (or smaller offspring size favored in other sites) cannot be determined with our current data set, but we echo our earlier call (Ford and Seigel, 1989) for additional focus on geographic variation in traits (such as offspring size) that are apparently less subject to phenotypic plasticity than are highly plastic traits such as clutch size.

Acknowledgements.—For reviews of the manuscript we thank Henry S. Fitch, Brian D. Greene, Nadia Seigel and an anonymous reviewer. We are grateful to the staff of Roper Lake State Park for logistical support and to the Arizona Game and Fish Department for permits. We also thank the many students from Southeastern Louisiana University who helped collect these data, especially J. Sean Doody, Cliff Fontenot, Nadia Seigel and Ben Seigel. This research was supported by a grant from the Louisiana Education Quality Support Fund, the Department of Biological Sciences at Southeastern Louisiana University (SLU) and by Faculty Development Grants from SLU. Additional support was provided by the University of Texas–Tyler to NBF. This research was also supported by DOE contract number DE-FC09-96SR18546 with the University of Georgia Research Foundation and by the Faculty Research Participation Program of the Oak Ridge Institute for Science and Education (ORISE).

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SUBMITTED 22 MARCH 1999

ACCEPTED 10 SEPTEMBER 1999