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RESPONSES OF MOLE SALAMANDERS TO CLEARCUTTING: USING FIELD EXPERIMENTS IN FOREST MANAGEMENT

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Abstract. Impacts of forest management practices on amphibian populations have received growing attention in the last 10 yr. However, to date, measured responses include only comparisons of species diversity indices and population counts without true spatial and temporal controls. We used an experimental approach to test for differences in growth rate, fecundity, age at maturity, and whole-body storage lipids in individual mole salamanders, *Ambystoma talpoideum,* placed in differently managed habitats. Four 100-m² field enclosures were built in each of two habitats, a 4-mo-old clearcut and an adjacent 40-yr-old pine forest. On 19 July 1994, 80 recently metamorphosed and individually marked, weighed, and measured (snout–vent length) *A. talpoideum* were randomly assigned to field enclosures ($n = 640$ salamanders). Between 31 October 1994 and 31 March 1995, salamanders were collected from the enclosures using pitfall traps. Body mass and length, whole-body nonpolar storage lipids, clutch size, and egg nonpolar lipids were determined for sexually mature salamanders. After an average of 5–6 mo exposure to clearcut and 40-yr-old pine forest, there were no significant differences between habitats for number of recaptured salamanders, final body mass, final body length, percent whole-body storage lipid, clutch size, or percent storage lipid of eggs. Our results suggest, in contrast to expectations based on many comparative studies with other species, that habitat modification resulting from clearcutting may not have detrimental effects on newly metamorphosed *A. talpoideum*. We contrast our experimental approach, with its strengths and weaknesses, to previous comparative studies and identify the inherent complexities involved in establishing a causal link between habitat management (clearcutting) and effects on amphibians.

Key words: Ambystoma talpoideum; *amphibians; clearcuts; forest management; mole salamanders; pine forests.*

Introduction

A challenging task currently faced by managers of forest resources is the growing need to accommodate multiple demands of conserving biodiversity and protecting nutrient cycling and water quality, while maximizing forest productivity (Harris 1984, Petranka et al. 1993). In general, resource managers approach conservation of biodiversity by focusing their attention on the management of single species perceived to be at greatest risk (e.g., "endangered" or "threatened"). However, it is becoming increasingly clear that managing for a single species may have unintended consequences for species not explicitly considered in management plans (e.g., Liu et al. 1995).

Unfortunately, comprehensive forest management plans are currently limited by both an uncertainty about which taxa should be explicitly considered, as well as a lack of information about the actual effects of specific

forest management practices on identified taxa (Beiswenger 1988). For example, amphibians have been recognized as an important component of ecological communities (Burton and Likens 1975, Heyer et al. 1994, deMaynadier and Hunter 1996); nevertheless, data on amphibian responses to forest management are limited (Harlow and Van Lear 1987). Consequently, amphibians are often overlooked in management decisions concerning biodiversity (Petranka et al. 1993, Grant et al. 1994).

In the southeastern U.S., many amphibian species use temporary, isolated freshwater wetlands, and surrounding terrestrial habitat (Gibbons and Semlitsch 1991). Maintenance of these populations may depend on the exchange of animals among ponds and successful breeding at new locations (Gill 1978, Reading et al. 1991, Sinsch 1992); however, forest management practices may effectively isolate populations by leaving uninhabitable forest around wetlands. A few comparative studies have examined the effects of forest management practices on amphibians by comparing population sizes and species richness between logged and undisturbed (or older) habitat (e.g., Bennett and Gibbons 1980, Enge and Marion 1986, Pough et al. 1987, Ash 1988, Welsch and Lind 1988, Dodd 1991, Ray-

mond and Hardy 1991, Petranka et al. 1993, Grant et al. 1994, Petranka et al. 1994). Taken together, comparative data suggest that both amphibian population size and species richness are lower in disturbed habitat than in undisturbed habitat. However, conclusions about the effects of clearcutting on amphibians from comparative studies are ultimately limited by the absence of spatial and temporal controls (deMaynadier and Hunter 1996). Complementary evidence from experiments that directly demonstrate the effect of specific silvicultural practices on amphibian populations is entirely lacking.

In this paper we report the results of an experiment designed to test the effects of clearcutting on survival, growth, body condition, and reproduction of 1-yr-old mole salamanders, *Ambystoma talpoideum.* Our experiment measured effects of clearcutting between the time salamanders emerged from their natal pond to the onset of their first breeding season (~6 mo later). We focused on the effects clearcutting has on the life history traits of individual salamanders because variation in individual life history traits has direct consequences for population dynamics (Dunham et al. 1989).

Our experiment provides a specific test of the emerging hypothesis suggested by comparative data, that clearcutting negatively affects the survival and reproduction of forest-dwelling salamanders. Moreover, our study provides an example of how experimental manipulations can reveal complexities underlying even the most drastic kinds of habitat disturbance (i.e., clearcutting). We test the hypothesis that clearcutting will negatively impact growth rates, fecundity, age at maturity, and whole body and egg storage lipids of metamorph *A. talpoideum* during the terrestrial stage between emergence from a natal pond and the first breeding season 6 mo later.

METHODS

Study animal

Ambystoma talpoideum is a common pond-breeding salamander in the southeastern United States that exhibits a complex life cycle with an aquatic larval stage and a terrestrial adult stage. Metamorphosing juveniles emigrate on rainy nights between May and November (Semlitsch 1985*a*) into the terrestrial habitat surrounding natal ponds. Apart from recent work on the effects of density on survival and reproduction during the terrestrial phase of some ambystomatid salamanders (Pechmann 1995), little is known about the terrestrial stage of *A. talpoideum.* Terrestrial home ranges of adult *A. talpoideum* extend 100–300 m and juveniles 12–67 m from the edge of their breeding pond (Semlitsch 1981), but some individuals can range more widely (A. C. Chazal et al., *unpublished data*). Salamanders remain in the terrestrial habitat most of the year (usually 43–46 wk) and are fossorial, typically found in small-mammal burrows on average 4.5 cm below the surface

(Semlitsch 1981). In the terrestrial habitat, *A. talpoideum* exhibits high survival to first reproduction (as high as 40%; Pechmann 1995). High proportions of both males (84%) and females (75%) mature the first fall following metamorphosis (i.e., at 1 yr of age [Pechmann 1995]).

Study site

Researchers at the Savannah River Ecology Laboratory have been monitoring the amphibian community, including *A. talpoideum,* at Rainbow Bay, a Carolina bay community (Barnwell County, South Carolina), since September 1978 (see Pechmann et al. 1991 for a detailed description of monitoring protocol). In February 1994, the pine forest west of Rainbow Bay was clearcut to within ~300 m of the edge of the bay. Within 1 yr of the harvest, we introduced juvenile *A. talpoideum* into experimental enclosures (described below) located within an uncut pine forest buffer (FO; control) around the bay and the adjacent clearcut habitat (CC; treatment).

Enclosures were built on well-drained soils with a sand to loamy-sand composition, low in organic content, strongly acid, and with low available water capacity (Rogers 1990). In the FO pens, the canopy was primarily loblolly pine (*Pinus taeda*) with an understory made up of wax myrtle (*Myrica cerifera*), black cherry (*Prunus serotina*), *Quercus* sp., and *Carya* sp. The CC pens also had these species present as either seedlings or coppice growth in addition to herbaceous cover such as winged sumac (*Rhus copallina*), Japanese honeysuckle (*Lonicera japonica*), Carolina jessamine (*Gelsimium sempervirens*), and broomsedge (*Andropogon terrarius*).

Experimental design

In 1994, eight 10 × 10 m field enclosures were constructed. Four were located in the clearcut and four were in adjacent 40-yr old loblolly pine (*Pinus taeda*) forest. CC enclosures were ~300 m from the edge of Rainbow bay, which is at the limit of the range of home ranges of *A. talpoideum* reported by Semlitsch (1981); however, sample sizes in this home range study were small (*n* = 17 salamanders). *Ambystoma talpoideum* are found at distances >300 m from breeding ponds, as suggested by movement of individuals between Carolina bays >1 km apart (A. C. Chazal, *unpublished data*). In the absence of more exhaustive data on home range movements, we suggest it is reasonable to assume that the CC enclosures were placed within an area accessible to and utilized by *A. talpoideum.* We decided to construct four replicates in each habitat based on an a priori power analysis. Comparative studies suggest that the effects of clearcutting are profound, so we assumed that our treatment effect (habitat modification by clearcutting) and error variance would be of a magnitude similar to that produced by experimental larval density manipulations (Pechmann 1994). In other

words, we assumed that the magnitude of the effect of clearcutting on terrestrial salamanders would be similar to that of the effect of larval density on metamorphs. Our calculations suggested that four replicates would give us ≥80% power for tests of main effects (Cohen 1977).

Our experiment was a standard split plot; it tested the treatment effect in a single plot, half of which was clearcut and half left undisturbed. Replicate enclosures were not randomly assigned to ''forest'' or ''clearcut'' treatments independently of one another, making our design pseudoreplicated (Hurlbert 1984). There are two main ways we could have avoided pseudoreplication. First, we could have randomly assigned treatments (clearcut or undisturbed) to each 10×10 m enclosure, and then created a patchwork of 100-m² clearcut and undisturbed habitats around Rainbow Bay. However, since clearcut and undisturbed patches around natural Carolina bays do not occur on this small spatial scale, interpreting the biological significance of the treatment effect would be problematic, even if statistically rigorous. Alternatively, we could have built enclosures in clearcut and undisturbed habitats around four different Carolina bays. Such an approach would have avoided the nonindependence of treatment assignment in our design and would have allowed drawing inferences about the effect of clearcutting on a larger spatial scale, but has one important shortcoming; Rainbow Bay is the only Carolina bay on the Savannah River Site (SRS) with detailed long term data on salamander demography and population dynamics.

The importance of relevant background demographic information in judging the realism of experimental manipulations cannot be overstated. For example, long term demographic data from the very site around which we built our enclosures allowed us to set appropriate densities within our enclosures, as well as compare survival and reproduction responses of salamanders from enclosures within the undisturbed habitat of the split plot to those of free-ranging salamanders in previous years (see Discussion). In other words, our design gives us the ability to recognize anomalous results due to a ''pen'' effect, if they exist. We chose to trade off a statistically rigorous ability to draw inferences about clearcuts on the SRS in general, with the ability to draw inferences about the effects of clearcutting around a single Carolina bay having a rich background of data from an intensively studied natural population.

Enclosure construction

Walls of the field enclosures were constructed of aluminum flashing that was buried 80–90 cm deep and stood 80–90 cm above the surface (Pechmann 1995). All seams were closed with cable ties the entire height of the wall and holes around cable ties were sealed with gutter sealant to further insure against the possibility of escape. On the inside and outside of each enclosure, an ~1 m wide strip of soil along the enclo-

sure edge was disturbed during trench digging and installation. Each 10×10 m enclosure was one of four enclosures within a block containing four different species/age combinations of salamanders (Fig. 1). Results of other species/age combinations will be reported elsewhere.

Release and recapture procedures

Because size at metamorphosis can have a large effect on age at first reproduction and fecundity (Scott 1994), juveniles were collected from three sites to incorporate a wider range of initial sizes and perhaps lipid classes than may have been represented at just one collection site. Recently metamorphosed *A. talpoideum* were collected using drift fences with pitfall traps as they dispersed from three Carolina bays: Ellenton Bay (EB: area 11.3 ha, located 6.1 km from the study site), Ginger's Bay (GB: 1.5 ha, 7.2 km), and Flamingo Bay (FB: 5.6 ha, 4.5 km) (see Scott 1990, and Semlitsch 1985*a* for descriptions of the sites and fences). Animals were captured between 27 June 1994 and 5 July 1994 and kept in containers with clean, damp paper towels at a temperature of 6°C until released into the enclosures on 19 July 1994. Prior to release, animals from the three collection sites were assigned randomly to one of nine groups (eight groups to be released in pens, one group to provide estimates of body lipid reserves); the proportion of metamorphs from the three collection sites was equal in each group, with a total of 80 animals per group (Table 1). Eighty animals per pen gave a stocking density of 0.8 salamanders/m². Previous terrestrial enclosure experiments detected no effect on growth or survival of *A. talpoideum* due to terrestrial densities as high as 0.62 salamanders/m² (Pechmann 1995). However, even though our pen densities were higher, our enclosures theoretically permitted (assuming an even distribution of salamanders) home range sizes of 1.25 m²/salamander, which is between the median summer home range sizes observed by Semlitsch (1981) for juveniles (0.25 m²/salamander) and for adults (3.61 m²/salamander).

Groups were assigned randomly to the eight treatment enclosures and the animals were marked individually (by toe-clipping), measured (snout–vent length, ±0.5 mm), and weighed (±0.01 g) using an electronic balance. We immobilized salamanders in the ninth group by cooling and then sacrificed them by freezing (Smith et al. 1986); they remained frozen at −60°C until subsequent lipid analysis. Salamanders assigned to enclosures were released after dark (between 2130 and 2200) while the ground was wet from an evening rain (2.0 mm at ~1800) in the area. Salamanders remained in the enclosures without further manipulation. On 13 January 1995, loblolly pine seedlings were mechanically planted outside of the CC enclosures and by hand within each CC enclosure. There was minimal soil and litter layer disturbance within and outside the enclosures.
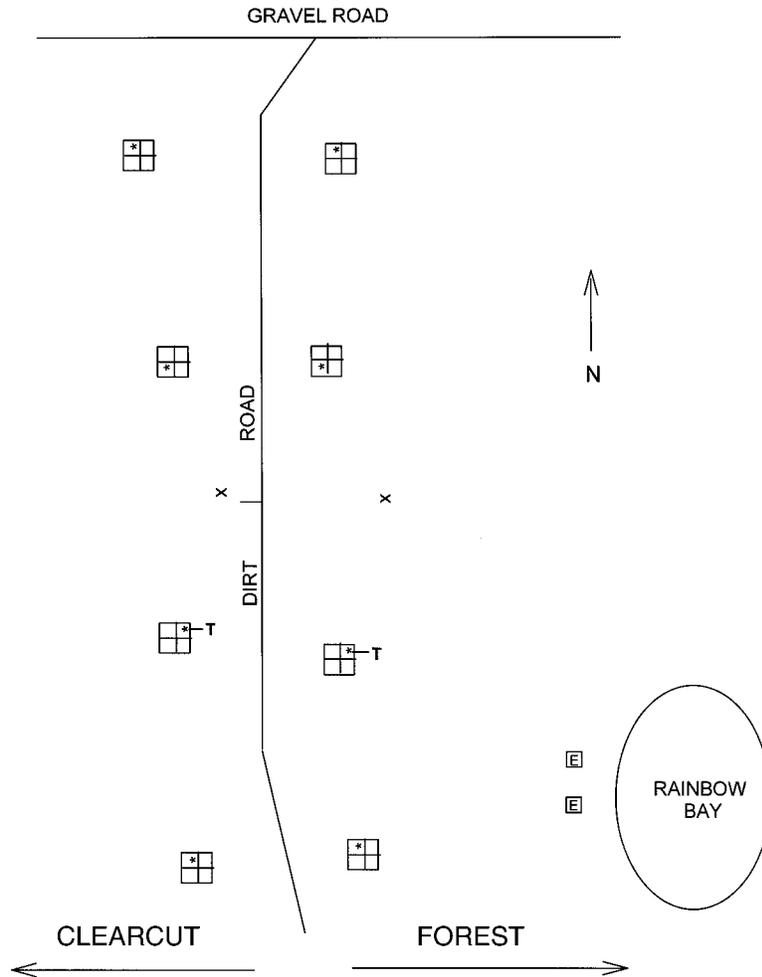
FIG. 1. The study site. Eight 20 × 20 m blocks, each divided into four 10 × 10 m sections (enclosures), were constructed near Rainbow Bay (RB). The dirt road is ~300 m west of RB and divides the clearcut and forest habitats. Two extra plots (E, each 100 m² and 75 m west of RB) were delineated for soil and litter comparisons. The enclosure sections used for this experiment are indicated with an asterisk (*). Temperature probes (T) were placed in two enclosures. Rain gauge locations are marked with an ×.

We placed pitfall traps (3-L buckets) in each corner of enclosures on 31 October 1994 to collect salamanders emerging from underground retreats to breed (Pechmann 1995). A sponge was placed in each trap to prevent desiccation or drowning. Beginning 1 November 1994, traps were checked after every rain event or every other day in dry conditions. Initially, all trapped salamanders were collected and taken to the laboratory for processing. We measured body mass with an electronic balance (±0.01 g), and snout–vent length (SVL, ±0.5 mm) for each individual. Salamanders with a swollen cloaca were considered to be sexually mature males. Only gravid salamanders (determined by candling) were considered to be sexually ma-

TABLE 1. Characteristics of the *Ambystoma talpoideum* salamanders initially stocked into pens in a South Carolina pine plantation in a study of the effects of clearcutting on resident amphibians.

Collection site	SVL (mm)	Body mass (g)	Stocking No./pen	Total	Initial percentage body lipid
Ellenton Bay	49.3 ± 2.7	4.45 ± 0.72	48	384	14.4 ± 2.5
Flamingo Bay	50.7 ± 2.7	4.67 ± 0.67	8	64	14.4 ± 3.3
Ginger's Bay	39.3 ± 1.8	2.23 ± 0.29	24	192	8.6 ± 2.9
All sites			80	640	12.5 ± 1.9†

Note: Data shown with variation are given as mean ± 1 SD.
† Grand mean ± 1 SE.

ture females (Pechmann 1995). All other salamanders were considered immature. Sexually mature salamanders were sacrificed and stored at $-60°C$ for subsequent lipid extraction and immatures were released back into the enclosures within 24 h of capture. As the season progressed, immature animals that had been caught previously (determined by reading their toe-mark) were left undisturbed in the enclosures to avoid any stress to the animal associated with transport to and storage at the laboratory. We captured only two unmarked *A. talpoideum* (i.e., animals resident before enclosures were constructed) and immediately released them outside the pen. By comparison, Pechmann (1995) recaptured 25 unmarked *A. talpoideum* in his experimental enclosures, which covered slightly more than five times the area of our enclosures. Pitfall traps were removed from the enclosures on 31 March 1995 after the end of the breeding season.

Prior to lipid extraction, salamanders were thawed and their stomachs removed; in females, egg masses were also removed and placed into 10% formalin for clutch size determination. Carcasses were extracted using petroleum ether to remove nonpolar storage lipids according to the methods of Fischer et al. (1991). Total and percentage lipid of samples were determined gravimetrically. Clutch size was determined by counting enlarged, vitellogenic, pigmented eggs (Semlitsch 1987). Clutches were counted within 72 h to minimize the effect of formalin on extractable lipids (D. Fletcher, *personal communication*), then rinsed with water, frozen, and analyzed for nonpolar lipids.

Soil analysis

On 24 January 1995, following a rain (CC = 14 mm; FO = 12 mm), six soil samples (three 2 cm diameter cores taken to 10-cm depth, divided into transversely 5-cm halves) were collected from each enclosure and from two 100-m² locations between the enclosures and Rainbow Bay (Fig. 1). On 24 March 1995, after 1 wk without rain, six similar soil samples and three leaf litter samples (taken from three 0.5-m² areas) were collected from each enclosure and the 100-m² locations (outside of experimental pens). Each sample was taken from a randomly determined spot within the 100-m² area. Water content was determined for the soil and litter samples by drying to a constant mass and the soil samples were ashed at 500°C to determine percent organic content.

Statistical analyses and precipitation data

We measured rainfall at two gauges, one in an FO pen and one in a CC pen (Fig. 1). Monthly rainfall was summed for each gauge. Between 20 December 1994 and 31 March 1995, soil temperature was monitored with two Hobo-dataloggers randomly located in one enclosure from each habitat (Fig. 1). The sensor probes of both dataloggers were buried 5 cm deep (below litter), the approximate depth at which *A. talpoideum* are

found (Semlitsch 1981); (Fig 1). Soil temperature readings were taken every 3 h. Mean maximum and minimum soil temperatures were calculated monthly for each habitat.

We used analysis of variance (ANOVA) to test for differences between clearcut (CC) and forest (FO) treatments for salamander recapture counts, body length and mass, percent nonpolar lipid for both the carcass and eggs, clutch size, and total number of days spent in the enclosures (time to emergence). Proportions were arcsine square-root transformed and count data, lengths, and body masses were $\log_e$ transformed (Sokal and Rohlf 1981).

For data with multiple observations per enclosure (e.g., SVL) we calculated enclosure means; where there is only one observation per enclosure (i.e., percent recaptured) the single enclosure value was used. Enclosure means were used as the unit of replication, because individuals within an enclosure are not statistically independent (Hurlbert 1984, Wilbur 1987). Using the enclosure means is equivalent to using the treatment $\times$ enclosure interaction term as the error term in an ANOVA model with each individual as the unit of observation (Wilbur 1987, Scott 1990).

To account for the variance of final body size due to initial size, we regressed final SVL and mass on initial SVL and tested the enclosure means of the residuals (equivalent to using an analysis of covariance, with initial SVL as a covariate [Hayes and Shonkwiler 1996]). Similarly, residuals of percent lipid, total lipid, and clutch size regressed on final SVL were analyzed to account for differences in these variables due to size variation. Main effects of treatment, collection site, sex, and their interactions were included in the statistical models (sex was not included in models for egg lipid and clutch size). All statistical tests were conducted using the General Linear Models (GLM) procedures of the Statistical Analysis System (SAS 1987).

Soil parameters (percent soil water content, percent soil organic content, percent litter water content, litter mass, and soil temperature) were analyzed using ANOVA models with GLM in SAS (1987). Percentages were arcsine square-root transformed and mass data were $\log_e$ transformed (Sokal and Rohlf 1981). Soil samples were tested using day and core depth as main effects, with enclosure means used to test for differences between habitats. With the exception of soil temperature means, we compared clearcut, forest, and extra plots for significant differences. Extra plots provided estimates of soil parameters for the forest habitat farther from the edge of the clearcut habitat. No statistical procedures were performed on precipitation data.

RESULTS

Statistical power for treatment effects on the main dependent variables ranged from 8 to 100% (Table 2). Power to detect differences in SVL, mass, and clutch size was particularly low; however, differences in mean

TABLE 2. Observed statistical power tests of the null hypothesis of treatment effect on selected dependent variables.

Variable	Observed difference between means	Power (%)	Mean difference at 80% power
SVL	0.56 mm	25	1.23 mm
Mass	0.1 g	34	0.21 g
Number recaptured	10	100	...
Body lipid	0.8%	100	...
Clutch size	7.7 eggs	8	52 eggs
Egg lipid	1.5%	100	...
Time to emergence	11.6 days	88	...

Note: ''Mean difference at 80% power'' refers to the difference between treatment means required for 80% power to detect significant differences.

responses between treatments were exceptionally small. Power of tests of the null hypothesis for no treatment effect on SVL and mass quickly increased to ≥80% for only modest increases in the difference between treatment means (Table 2).

Demographic parameters

Number of recaptures was not significantly different between treatments for either the main effect or for any interaction term which included treatment (Table 3).

Of 476 total recaptures, 243 (51.1%) were from the CC and 233 (48.9%) were from the FO. The sex, site, and the sex × site interaction terms were significant for number of recaptures (Table 3). Males were recaptured at apparently higher rates than females or juveniles ($n = 220$ males [46.5%]; $n = 158$ females [33.2%]; $n = 98$ juveniles [20.6%]). Apparently more salamanders were recaptured from EB ($n = 310$ individuals [65%]) than from FB ($n = 49$ individuals [10.0%]), or GB ($n = 117$ individuals [24.6%]). This may be a function of the initial stocking percentages (Table 1). An apparently higher percentage of the recaptured animals from Ginger's Bay ($n = 117$ salamanders) was recaptured as immatures ($n = 70$ individuals [71.4%]) than as females ($n = 11$ individuals [6.7%]) or males ($n = 36$ individuals [16.4%]). More salamanders from EB and FB were captured as adults.

Final mass and SVL of the salamanders were not significantly different between treatments (Table 3). In both habitats, mean mass (± 1 SE) decreased (in CC, from 3.98 ± 0.18 g to 3.54 ± 0.08 g; in FO, from 3.97 ± 0.21 g to 3.64 ± 0.08 g; Fig. 2) and mean SVL increased (in CC, from 46.9 ± 0.50 mm to 48.8 ± 0.53 mm; in FO, from 47.3 ± 0.25 mm to 49.3 ± 0.24 mm; Fig. 2). There was a significant effect of sex on final body size (Table 3). Immatures appeared shorter (46.7

TABLE 3. Analysis of variance showing the effects of clearcutting on growth, reproduction, fat storage, and survival of mole salamanders (*Ambystoma talpoideum*).

Dependent variable	Independent variable	df	ss	F	P
Number of recaptures	TRT	1	0.0926	0.36	0.5528
	SX	2	3.9083	7.55	0.0015
	ST	2	16.2480	31.38	0.0001
	SX × ST	4	25.8951	25.01	0.0001
	Error	45	11.6498		
SVL	TRT	1	0.001	0.05	0.8208
	SX	2	0.0130	5.07	0.0103
	ST	2	0.0012	0.47	0.6300
	Error	45	0.0575		
Mass	TRT	1	0.0005	0.05	0.8269
	SX	2	0.0790	3.57	0.0365
	ST	2	0.0050	0.22	0.8001
	SX × ST	4	0.0963	2.17	0.0875
	Error	45	0.4988		
Body lipid	TRT	1	0.0003	0.09	0.7684
	SX	2	0.0004	0.06	0.9410
	ST	2	0.0013	0.23	0.7985
	Error	45	0.923		
Egg lipid	TRT	1	0.0014	0.91	0.3550
	ST	2	0.0103	3.35	0.0626
	Error	15	0.0229		
Clutch size	TRT	1	0.0284	0.48	0.4991
	ST	2	0.0749	0.63	0.5456
	Error	15	0.8907		
Emergence	TRT	1	0.1452	12.61	0.0010
	SX	2	0.8876	38.54	0.0001
	ST	2	0.0746	3.24	0.0493
	TRT × SX	2	0.1309	5.68	0.0066
	TRT × ST	2	0.0601	2.61	0.0856
	Error	45	0.4721		

Notes: Independent variables were treatment (TRT), sex (SX), and collection site (ST). Body lipid is percentage whole-body, nonpolar lipid. Interaction effects not shown had F statistics with P values >0.1.
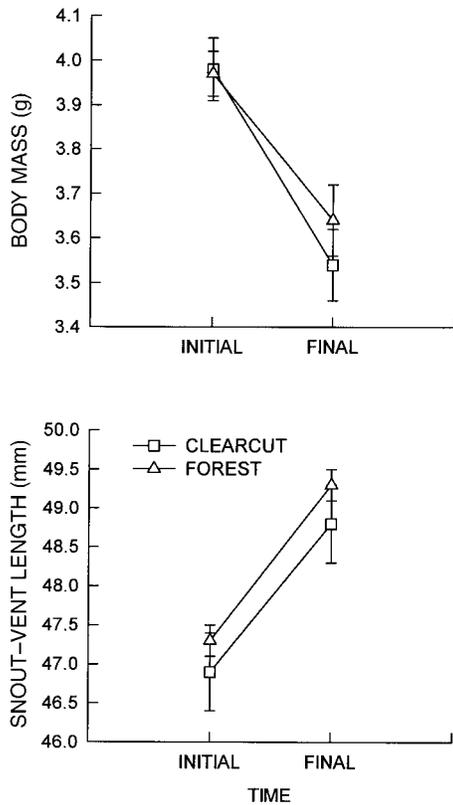
FIG. 2. The change in body size (mass and SVL) between stocking (initial) and recapture (final) for *Ambystoma talpoideum* recaptured from the clearcut and forest treatments. There were four pens per treatment; data show mean ± 1 SE for each treatment.

± 1.1 mm) and lighter (3.11 ± 0.19 g) than both males (49.6 ± 1.0 mm; 3.68 ± 0.2 g) and females (48.8 ± 0.8 mm; 3.56 ± 0.14 g). Females appeared to lose more mass than males and males appeared to gain more length than females (change in mean mass: females: −0.64 g, males: −0.26 g, immatures: −0.26; change in mean SVL: females: 1.11 mm, males: 2.68 mm, immatures: 1.65 mm). The main effect of site and all its interactions were not significant (Table 3).

Percentage whole body nonpolar lipids was not statistically different at any tested level (Table 3). Mean lipid fraction was 7.0 ± 1.1% of dry mass for CC animals and 6.2 ± 0.9% for FO salamanders. Mean lipid fraction of the initial stock population was estimated to be 12.4 ± 0.03% of dry mass (Table 1). Neither percent lipid of the eggs nor clutch size was significantly different between treatments, site, or the interaction (Table 3). Mean percent egg lipid was 14.7 ± 1.3% in the forest compared to 13.2 ± 1.1% in the clearcut (Fig. 3). Females in the forest treatment had 247.2 ± 6.42 yolked ova vs. 239.5 ± 7.20 in the clearcut (Fig. 3).

The treatment × sex interaction term was significant for the time to emergence and there were significant main effects for treatment, site and sex (Table 3). An-

imals in the FO treatment were first recaptured after 137.0 ± 2.86 d on average whereas CC animals were first recaptured after 148.6 ± 2.2 d. Males spent 128.4 ± 1.6 d and females spent 144.1 ± 3.9 d while immatures were not captured again for 174.8 ± 8.14 d. If we assume that the time to emergence has implications for the arrival time to the breeding site, then it is reasonable to consider only sexually mature animals. After dropping the immatures from the data set, only the significant main effect of site remained ($F_{2,45}$ = 6.05, P = 0.0070).

Environmental parameters

Mean percent water content and mean percent organic content of the soil generally were not significantly different between the habitats (there was a marginal difference for the second sample day's top core-halves; Table 4). In general, CC soils had higher percent water and organic content than the FO or extra plots. Mean percent water content of the leaf litter was not different between treatments nor was litter mass (Table 4). Mean maximum and minimum temperatures did not differ between habitats (maximum: $F_{2,27}$ = 0.07, P = 0.363; minimum: $F_{2,27}$ = 0.02, P = 0.888; Fig. 4). Forest soils tended to have a smaller range between maximum and minimum temperature means than did
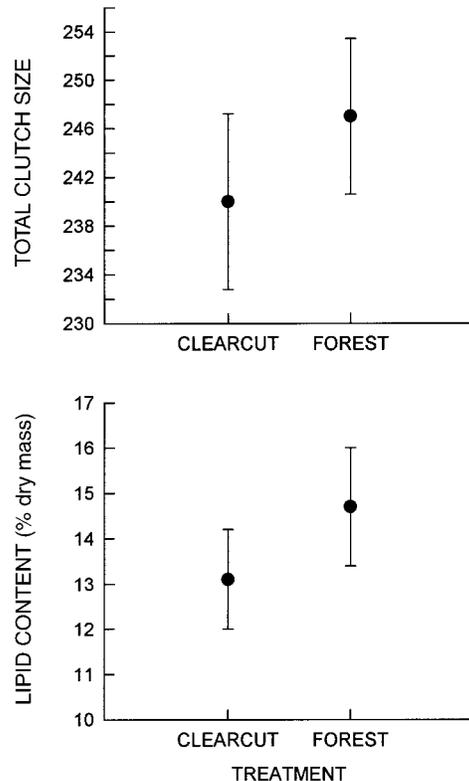

FIG. 3. Two measures of reproductive investment for female *Ambystoma talpoideum* recaptured from the clearcut (n = 4 pens) and forest (n = 4 pens) treatments. Lipid measure was of nonpolar compounds. Data show means ± 1 SE.

TABLE 4. Water and organic content by treatment for the top 5 cm and bottom 5 cm of soil cores taken 24 January 1995 after a rain, and 24 March 1995 after a week without rain. Percentage of water and dry mass of litter samples are shown for 24 March. Data are means, with 1 SE in parentheses.

| Treatment	Soil water content (%)		Soil organic content		Litter	
	Top	Bottom	Top	Bottom	Water (%)	Mass (g)
Substate data						
Clearcut ($n = 4$ cores)						
24 January	17.3 (2.6)	11.4 (2.3)	7.9 (1.9)	3.0 (0.7)		
24 March	20.4 (4.3)	9.9 (2.7)	16.7 (6.8)	3.7 (1.3)	32.4 (9.2)	234.3 (42.5)
Forest ($n = 4$ cores)						
24 January	15.0 (1.1)	7.9 (6.0)	6.3 (1.0)	1.7 (0.3)		
24 March	8.5 (0.8)	4.3 (0.2)	5.2 (0.8)	1.4 (1.0)	27.7 (4.0)	222.8 (28.6)
Extra plots ($n = 2$ cores)						
24 January	20.1 (1.2)	9.9 (0.6)	7.0 (0.9)	2.7 (0.4)		
24 March	12.0 (1.1)	6.0 (0.9)	10.6 (0.6)	2.4 (0.1)	29.9 (3.9)	180.9 (13.3)
ANOVA results						
24 Jan						
$F_{2,27}$	1.32	1.45	0.28	2.14		
P	0.326	0.298	0.767	0.188		
24 Mar						
$F_{2,27}$	4.47	2.40	2.00	2.24	0.36	1.17
P	0.056	0.161	0.205	0.177	0.707	0.363
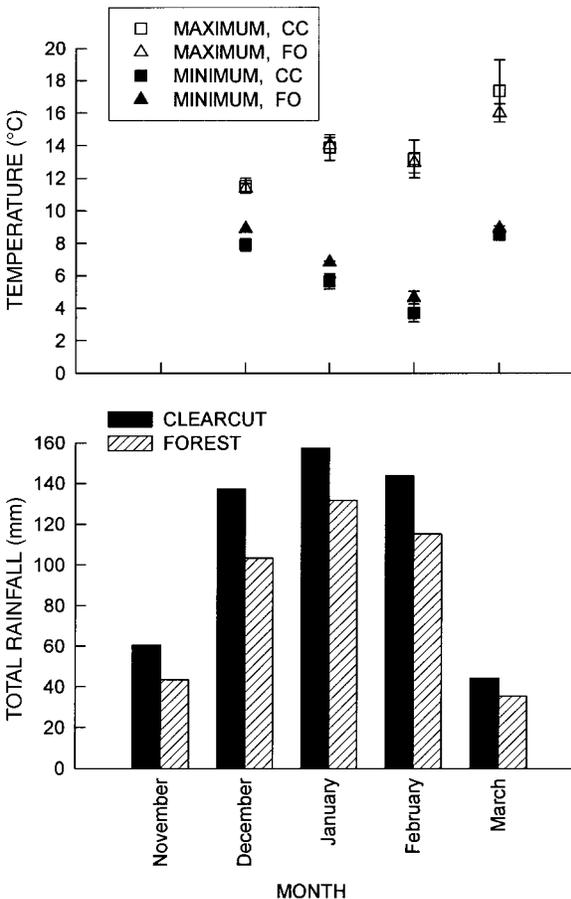
FIG. 4. Maximum and minimum temperatures from 1 December 1994 to 31 March 1995 are shown. Total rainfall is shown for the time between 1 November 1994 and 31 March 1995. Data show means ± 1 SE.

the clearcut soils (Fig. 4). The monthly sum of rainfall received was consistently higher in the clearcut than in the FO (Fig. 4).

DISCUSSION

Numerous comparative studies have reported declines in amphibian population size and species richness within clearcut habitats. Our study, in contrast, shows no significant main effects of clearcutting on individual traits including survival, body size, whole body and egg nonpolar lipid percentages, and time to emergence for 1-yr-old *A. talpoideum.* Although salamanders in our experiment were only exposed to treatments for a period of ~5–6 mo, on average, we expected habitat differences between clearcut and undisturbed pens to have their strongest effect immediately following the process of clearcutting. We also expected effects on all or many of the dependent variables to be very strong, given comparative data on the effects of clearcutting. Lack of differences between clearcut and control pens cannot, however, be reasonably attributed to anomalous effects of the enclosures; our data are well within ranges reported for local, unmanipulated populations on the SRS. For example, mean clutch sizes reported here (Fig. 3) are comparable to those reported by Semlitsch (1985b) who counted 248 ± 21 ova/female in 1-yr-olds. Similarly, we found an increase in SVL of ~2 mm for both treatment groups (Fig. 2). Semlitsch et al. (1988) saw SVL increases of 2–5 mm from size at metamorphosis to size at first reproduction. Overall, our data suggest that salamanders in both treatments may have experienced conditions similar to those they would have encountered outside our experimental pens.

Although statistical power was too low to detect differences between clearcut and control pens given the variance between treatments we observed, relatively

small increases in the mean effect for all of the dependent variables measured, except clutch size, would have produced tests with power >80% (Table 2). For example, we would have detected a statistically significant effect of clearcutting on SVL if the mean difference between clearcut and control pens was roughly twice what we actually observed (0.56 vs. 1.23 mm, respectively), all else being equal. Given the drastic population consequences associated with clearcutting reported in comparative studies, we expected effects on growth rate to be larger than we observed. However, even a difference of 1.23 mm between treatment and control that would have led to statistical significance would appear to be biologically insignificant in some contexts. For example, Semlitsch et al. (1988) showed that over a range of body sizes (SVL) including the range observed in our experiment, there were no size-specific differences in the probability of survival to first reproduction. Similar reasoning applies to observed differences in body mass. In general, statistical power to detect differences in all other dependent variables (number recaptured, percent body lipid, percent egg lipid, and time to emergence) was high. In contrast to each of the dependent variables above, we had low power to test our hypothesis that clutch size is not affected by clearcutting. Consequently, definitive conclusions cannot be drawn about effects on clutch size, and we suggest that future studies should consider increasing number of replicates, at least for tests on the effects on clutch size.

One general conclusion that could be drawn from our study is that clearcutting has little or no measurable effect on 1-yr-old *A. talpoideum* on the SRS. However, comparative evidence on the effects of clearcutting on salamanders suggests the opposite. There are at least two kinds of explanations (not mutually exclusive) for such contrasting results. First, the lack of spatial and temporal controls in comparative studies limits inferences about causal relationships between clearcutting and measured variables. Indeed, our experiment was partly motivated by such a limitation. Even though our experiment was confined to a single clearcut and one 6-mo period, we nevertheless had ample replication within the clearcut to detect any strong effects of clearcutting within that site, if they had existed during that period.

Second, and in our view much more interesting from a management perspective, our experiment did not include some factors included in comparative studies of the effects of clearcutting. These include: exposure of resident animals to the mechanical disturbances of clearcutting and site preparation, differences in microhabitats as a result of clearcutting, and habitat choice of free-ranging animals. Below, we discuss the potential significance of omitting these factors in our experiment. Our discussion is not meant to discount our results; rather, we are interested in precisely defining the inferences that may be drawn from our experiment.

Secondarily, our discussion is meant to suggest the type of experiments that are needed in the future in order to reveal the potential effects of clearcutting on amphibians.

Ambystoma talpoideum in our experiment were not exposed to the mechanical disturbances of clearcutting and site preparation. It may be that reduced species abundance and diversity in clearcuts relative to undisturbed sites arises from direct mortality during tree removal and subsequent site preparation (e.g., disking, burning, and herbicide application). However, currently there are no data to allow a test of this hypothesis. Population surveys in comparative studies take place anywhere from 1 to 10 yr after the harvesting and typically the exact method of harvesting and site preparation, or replanting, is not reported. Enge and Marion (1986) censused clearcut areas with minimum and maximum site preparation techniques and a 40-yr-old pine forest. They reported no significant differences in amphibian species richness between the habitats but they did find reduced abundances in both site preparation treatments. From a microhabitat perspective, the method of clearcutting and site preparation affects soil and microhabitat properties differently (Switzer et al. 1978), including the magnitude of increased soil compaction, which reduces water infiltration and soil aeration (Hatchell et al. 1970, Gent et al. 1983). But the relationship of these habitat changes has not been satisfactorily linked to amphibian performance and needs to be addressed with experiments.

Our initial measurements of habitat parameters show that treatments in our study may not have been effectively different. Despite many reports of habitat differences measured in soil parameters (e.g., soil moisture and litter cover [Pough et al. 1987, Ash 1988, Dodd 1991, Grant et al. 1994]), our results, collected over one season, show no differences between the habitats in our study (Tables 3 and 4). It may be that the weather and coarse woody debris left on the surface of the clearcut contributed to the similarity in both hydric and thermal characteristics between habitats. For example, if the effect of clearcutting is to increase soil compaction (inhibiting drainage) and decrease moisture loss from evapotranspiration (Hatchell et al. 1970), then the higher amount of rainfall received by the clearcut in conjunction with increased soil compaction (Fig. 4) may have acted to ameliorate differences between CC and FO pens. Similarly, coarse woody debris which was left on the surface (in CC pens but not in FO pens) may have decreased the rate at which soil dried in CC pens. Such possibilities are intriguing and warrant further experimental investigation because of the obvious management implications (see also Petranka et al. 1994).

Lack of significant differences in microhabitat parameters that should be relevant to amphibians was unexpected and may be related to our sampling schedule. We sampled (temperature, soil, and litter data) dur-

ing the fall, winter, and spring months, while salamanders were resident in pens. Second, the forest enclosures are no farther than 30 m from the clearcut habitat. It might be more appropriate to term this forest habitat ''edge,'' however, neither the clearcut nor the forest plots differed from the extra plots (located ~225 m from the forest/clearcut edge) with respect to the measured environmental parameters. Parameters in our study were measured 5 cm deep, which is close to where *A. talpoideum* is known to be in forested areas (Semlitsch 1981). Soil depth may be an effective buffer for the salamander against any surface-soil changes.

Finally, our experiment differs from previous comparative studies in that animals were not able to choose a treatment through habitat selection. In comparative studies, reduced amphibian abundance and species richness could arise from effects of clearcutting on habitat choice though, to our knowledge, no study has quantified salamander habitat selection. Habitat selection could be especially important in sites or years where clearcuts and undisturbed habitats differ significantly in temperature and/or moisture properties. Raymond and Hardy (1991) reported that a clearcut 156 m from a breeding pond altered the arrival pattern of incoming adult *A. talpoideum.*

In conclusion, our experimental results suggest that the clearcut examined in this study had no effect on the survival, growth, lipid levels, clutch size, egg lipid levels, or to emergence of 1-yr-old *A. talpoideum* over one terrestrial activity season. Nevertheless, we do not believe that our results are necessarily at odds with previously published comparative results. Comparison of our experimental protocol with the design of previous comparative studies suggests that differences between experimental and comparative approaches must be examined and evaluated carefully. Our results imply an underlying biological complexity to the response of metamorph mole salamanders to habitat modification by clearcutting that is almost certainly relevant to management decisions. For example, it may be that different aspects of clearcutting (e.g., mechanical disturbance, site preparation, etc.) have clear consequences for amphibian populations, through their independent effects on fundamental demographic parameters such as growth, body condition, survival, and reproduction. If that is true, experiments designed to reveal the mechanistic relationships between habitat manipulation and amphibian populations may allow development of more focused and efficient management approaches especially required in multi-use landscapes.

LITERATURE CITED

Ash, A. N. 1988. Disappearance of salamanders from clearcut plots. Journal of the Elisha Mitchell Scientific Society **104**:116–22.

Beiswenger, R. E. 1988. Integrating anuran amphibian species into environmental assessment programs. U.S. Department of Agriculture Forest Service General Technical Report **RM-166**:159–165.

Bennett, S. H., and J. W. Gibbons. 1980. Terrestrial activity, abundance and diversity of amphibians in differently managed forest types. American Midland Naturalist **103**:412–416.

Burton, T. M., and G. E. Likens. 1975. Salamander populations and biomass in the Hubbard Brook experimental forest. Copeia 1975:541–546.

Cohen, J. 1977. Statistical power analysis for the behavioral sciences. Academic Press, New York, New York, USA.

DeMaynadier, P., and M. Hunter. 1996. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews **3**:230–261.

Dodd, C. K. 1991. The status of the red hills salamander, *Phaeognathus hubrichti,* Alabama, USA 1976–1988. Biological Conservation **55**:57–75.

Dunham, A. E., B. W. Grant, and K. L. Overall. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. Physiological Zoology **62**(2):335–355.

Enge, K. M., and W. R. Marion. 1986. Effects of clearcutting and site preparation on herpetofauna of a North Florida flatwoods. Forest Ecology and Management **14**:177–192.

Fischer, R. U., F. J. Mazzoti, J. D. Congdon, and R. E. Gatten. 1991. Post-hatching yolk reserves: parental investment in American alligators from Louisiana. Journal of Herpetology **25**:253–256.

Gent, J. A., Jr., R. Ballard, and A. E. Hassan. 1983. The impact of harvesting and site preparation on the physical properties of Lower Coastal Plain forest soils. Soil Science Society of America Journal **47**:595–598.

Gibbons, J. W., and R. D. Semlitsch. 1991. Guide to the reptiles and amphibians of the Savannah River Site. University of Georgia Press, Athens, Georgia, USA.

Gill, D. E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monographs **48**:145–166.

Grant, B. W., K. L. Brown, G. W. Ferguson, and J. W. Gibbons. 1994. Changes in amphibian biodiversity associated with 25 years of pine forest regeneration: implications for biodiversity management. Pages 355–367 *in* S. K. Majumdar, F. J. Brenner, J. E. Lovich, J. F. Schalles, and E. W. Miller, editors. Biological diversity: problems and challenges. Pennsylvania Academy of Science, Easton, Pennsylvania, USA.

Harlow, R. F., and D. H. Van Lear. 1987. Silvicultural effects on wildlife habitat in the South (an annotated bibliography) 1980–1985. Clemson University, Clemson, South Carolina, USA.

Harris, L. D. 1984. The fragmented forest. University of Chicago Press, Chicago, Illinois, USA.

Hatchell, G. E., C. W. Ralston, and R. R. Foil. 1970. Soil disturbance in logging. Journal of Forestry **68**:772–775.

Hayes, J. P., and J. S. Shonkwiler. 1996. Analyzing mass-independent data. Physiological Zoology **69**:974–980.

Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster. 1994. Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institute Press, Washington, D.C., USA.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**: 187–211.

Liu, J., J. B. Dunning, and H. R. Pulliam. 1995. Potential effects of a forest management plan on Bachman's Sparrows (*Aimophila aestivalis*): linking a spatially explicit model with GIS. Conservation Biology **9**:62–75.

Pechmann, J. H. K. 1994. Population regulation in complex life cycles: aquatic and terrestrial density-dependence in the mole salamander. Dissertation. Duke University, North Carolina, USA.

———. 1995. Use of large field enclosures to study the terrestrial ecology of pond-breeding amphibians. Herpetologica **51**:434–450.

Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science **253**:892–895.

Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management **67**:135–147.

Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on Southern Appalachian salamanders. Conservation Biology **7**:363–370.

Pough, F. H., E. M. Smith, D. H. Rhodes, and A. Collazo. 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecology and Management **20**:1–9.

Raymond, L. R., and L. M. Hardy. 1991. Effects of a clearcut on a population of the mole salamander, *Ambystoma talpoideum,* in an adjacent unaltered forest. Journal of Herpetology **25**:509–512.

Reading, C. J., J. Loman, and T. Madson. 1991. Breeding pond fidelity in the common toad, *Bufo bufo.* Journal of Zoology (London) **225**:201–211.

Rogers, V. A. 1990. Soil survey of Savannah River Plant area, parts of Aiken, Barnwell and Allendale Counties, South Carolina. Soil Conservation Service, U.S. Department of Agriculture, Aiken, South Carolina, USA.

SAS. 1987. SAS user's guide: statistics. SAS Institute, Cary, North Carolina, USA.

Scott, D. E. 1990. Effects of larval density in *Ambystoma opacum*: an experiment in large-scale field enclosures. Ecology **17**:296–306.

———. 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum.* Ecology **75**:1383–1396.

Semlitsch, R. D. 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). Canadian Journal of Zoology **59**:315–322.

———. 1985a. Analysis of climatic factors influencing migrations of the salamander *Ambystoma talpoideum.* Copeia 1985:447–489.

———. 1985b. Reproductive strategy of a facultatively paedomorphic salamander, *Ambystoma talpoideum.* Oecologia **65**:305–313.

———. 1987. Density-dependent growth and fecundity in the paedomorphic salamander *Ambystoma talpoideum.* Ecology **68**:1003–1005.

Semlitsch, R. D., D. E. Scott, and J. H. K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum.* Ecology **69**:184–192.

Sinsch, U. 1992. Structure and dynamics of a natterjack toad metapopulation (*Bufo calamita*) Oecologia **90**:489–499.

Smith, A. W., et al. 1986. Report of the AVMA Panel on Euthanasia. Journal of AVMA **188**(13):252–268.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York, New York, USA.

Switzer, G. L., D. M. Moehring, and T. A. Terry. 1978. Clearcutting vs. alternative timber harvesting—stand regeneration systems: effects on soils and environment of the South. Pages 477–507 *in* C. T. Youngberg, editor. Forest soils and land use. Proceedings of the Fifth American Forestry Soil Conference, Fort Collins, Colorado, USA.

Welsch, H. H., and A. J. Lind. 1988. Old growth forests and the distribution of the terrestrial herpetofauna. Pages 439–455 *in* R. C. Szaro, K. E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and mammals in North America. Technical Report RM-166, U.S. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Wilbur, H. M. 1987. Regulation of structure in complex systems: experimental temporary pond communities. Ecology **68**:1437–1452.