

## Structural Aspects of Microhabitat Selection by the Skink *Lampropholis delicata*

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**ABSTRACT.**—*Lampropholis delicata* is a small skink common in eastern Australia. The species is heliothermic and uses the ground litter layer. This study examined whether *L. delicata* showed preferences for particular structural features of the ground litter layer by observing their response to a number of pairwise choices of ground litter type. *Lampropholis delicata* showed a clear preference for a ground litter layer with an open structure. Difference in catch rates between pairwise comparisons was positively correlated with an index of habitat accessibility. It is suggested that this habitat preference is associated with the ability of the lizard to trade-off different activities. Selection of a habitat with some form of open structure may reduce the conflict between the need for foraging and basking, and the need to find shelter from predators.

Habitat selection is an important component of animal ecology (Cody, 1985; Huey, 1991). Animals must “trade-off” costs and benefits associated with avoiding predators and competitors, and obtaining food and shelter. In spite of the significance of habitat selection, few experimental studies have determined the relative importance of key variables that might influence selection by terrestrial vertebrates (e.g., food, refuge from predators).

For ectothermic species such as lizards, thermal conditions also influence habitat choice because of their strong effect on short-term physiological performance (Pounds, 1988; Huey, 1991). Attributes associated with habitat choice by lizards include factors that influence degree of insolation or exposure such as canopy cover, and aspects of ground cover such as presence of grasses and forbs, structure of the litter layer, or amount of woody debris or rocks (e.g., Heatwole, 1977; Lunney et al, 1991; Block and Morrison, 1998; Hecnar and M'Closkey, 1998). All these variables are likely to influence an individual's ability to thermoregulate, feed, and avoid predators.

Although many studies of ground-dwelling lizards have inferred microhabitat selection from associations between relative abundance and habitat features (e.g., Diaz and Carrascal, 1991; Brown and Nelson, 1993; Hadden and Westbrooke, 1996), or from examination of habitat availability versus use (e.g., Burrow et al, 2001), there are also some experimental studies. For example, retreat site characteristics (size, thermal properties) have been manipulated to determine the relative importance of different factors in influencing site selection in rock dwelling snakes (Huey et al, 1989) and geckos (Downes and Shine, 1998; Webb and Shine, 1999). Downes and Shine (1998) demonstrated that predator avoidance had a higher priority than thermal advantage in the retreat site selected by a gecko, but they also noted that social interactions influenced choice. However, experimental studies of microhabitat selection by ground-dwelling lizards in nonrocky habitats are rare (e.g., lizards found in the leaf litter layer of the forest floor).

We present a preliminary experimental study of microhabitat selection in a small ground dwelling

lizard. Small lizards must thermoregulate, feed, and find refuge, and the structure of the leaf litter layer may influence these activities. Therefore, we experimentally varied the structure of the leaf litter layer to determine its role in the microhabitat selection of the lygosomid skink, *Lampropholis delicata*. This species is common in eastern Australia where it occupies a range of habitats including forest edge, wet and dry sclerophyll forest, coastal heath and woodland, and suburban gardens (Cogger, 2000). *Lampropholis delicata* is a small (to 40 mm SVL), diurnally active, heliothermic, and locally abundant generalist feeder that uses both active foraging and sit-and-wait methods to prey on a range of invertebrates (Rawlinson, 1971; Lunney et al, 1989).

### MATERIALS AND METHODS

Experiments were conducted from December 1998 to March 1999 in three enclosures that were erected in similar insolation conditions in open forest at Yandina in southeast Queensland, Australia (26°34'S 152°57'E). The forest was eucalypt dominated open woodland with a ground layer of kangaroo grass (*Themeda* sp.). Enclosures measured 3.5 m × 2.5 m and were constructed of clear PVC set 30 cm high, buried to a depth of 10 cm and held in place with wooden stakes. Enclosures were divided into two equal sections and three pitfall traps (22 cm diameter by 17 cm deep plastic buckets) were placed in each section. Traps were two-thirds filled with leaf litter. For each trial, the enclosure was raked clear and leaf litter treatments were assigned at random to each half and given one day to settle. Twenty new lizards, captured by hand or pitfall trap in the surrounding area, were then added to the enclosure and allowed one day to settle. Lizards used in trials were not sexed, but all individuals used in trials were adults. Each trial involved six one-hour trapping periods (0600–0700, 0800–0900, 1000–1100, 1200–1300, 1400–1500, and 1600–1700) per day for three consecutive days. Pitfall traps were closed at all other times. Lizards were released in the center of the enclosure after each trapping period. Experiments usually involved three replicates of a trial run either consecutively in one enclosure, or synchronously in three enclosures, although rainfall did limit replication in some experiments. A range of substrate types was compared (Table 1), and the depth and distribution of these litter types were varied in a number of the pairwise trials.

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TABLE 1. Substrates examined in pairwise choice trials. Depth of each litter type was recorded at sites where they were collected, and depth and structure emulated in trials.

Bare	Substrate raked clear of all leaf litter.
Native	Native leaf litter collected from surrounding open woodland (dominated by eucalypts and acacias). This litter type has an open structure because it is composed of material of a range of sizes.
Pine	Pine leaf litter ( <i>Pinus elliotii</i> ) collected from Beerwah State Forest 40 km south of the study site. Pine needles form a dense closed mat of litter material with largely uniform components. Pine litter was removed in $\approx 50 \times 50$ cm squares so that basic structure of the litter layer could be replicated in enclosures.
Casuarina	Leaf litter from beneath <i>Casuarina</i> sp. collected in the study area. Casuarina litter forms a closed mat similar to pine and was moved to experimental enclosures in a similar manner.
Artificial litter	Paper was used as an artificial litter layer. Shredded paper was used to simulate a compact litter layer and torn paper to simulate open litter layer.

Availability of food may influence habitat use, but we did not quantify aerial-arboreal or ground-dwelling invertebrates that make up the *L. delicata* diet. However, we made a preliminary assessment of the possible importance of food in three trials where we added a food supplement (40 diced mealworms distributed uniformly over the selected section) to one habitat. *Lampropholis delicata* were observed consuming the diced mealworms. Because of a limited supply of experimentally naive lizards and time, not all pairwise combinations of varied litter layer or food-supplemented litter were attempted.

Refuge in the litter layer, and its accessibility are key attributes of habitat use by many small skink species. To measure refuge availability and accessibility a 1.5-cm diameter glass marble (mass = 5.3 g) was dropped into the leaf litter from a height of 1.8 m. The enclosure was then examined from a standing position to see whether the marble was visible. This was repeated 30 times for each leaf litter type. In microhabitats where lizards could quickly move to refuge within the litter layer, marbles would not be expected to be visible, whereas in a microhabitat with few refuges or refuges that were difficult to access, marbles would be visible. Therefore, we assumed that refuge availability and accessibility was directly proportional to the percentage of marbles that were not visible.

Preference was examined using paired *t*-tests on mean catch rate per trial in each enclosure half. These tests lacked power (i.e., unlikely to reject false null hypotheses) because a maximum of three trials were conducted for each comparison. However, this conservative approach was used instead of comparisons for each one-hour trapping period caused by possible lack of independence of lizard habitat selection within trials.

#### RESULTS

The overall average catch per enclosure-half per hour was 3.7 lizards, with minimum and maximum average catches per enclosure-half over a trial being 0.7 and 5.8 lizards per hour, respectively. The maximum number of lizards caught in both enclosure-halves in any one-hour period was 17, and total captures exceeded 10 lizards in only 9% of the one-hour trapping periods (Table 2).

We checked for positional bias within enclosures by comparing catch rates when both halves of the enclosure had identical litter layers. No differences in

catch rate occurred between different halves of the enclosures (Table 2). *Lampropholis delicata* preferred leaf litter substrate to bare substrate (native vs. bare:  $t_1 = 7.57$ ,  $P = 0.084$ ; pine vs. bare:  $t_1 = 15.9$ ,  $P = 0.040$ ). Native leaf litter was preferred to pine ( $t_2 = 12.5$ ,  $P = 0.006$ ), and casuarina ( $t_1 = 21.1$ ,  $P = 0.030$ ) leaf litter, but catch rates did not differ significantly between pine litter and casuarina ( $t_1 = 3.42$ ,  $P = 0.181$ ; Table 2).

Changing the depth, structure or distribution of the litter layer also influenced comparative catch rates (Table 2). For example, reducing native litter to small patches that covered half the substrate in comparison to a standard pine litter layer produced similar catch rates (native patchy vs. pine:  $t_1 = 1.84$ ,  $P = 0.317$ ), and loosening the pine litter layer to create a more open structure decreased differences in catch rate in comparison with native litter layer, though catches were still higher in native leaf litter ( $t_2 = 4.85$ ,  $P = 0.040$ ). Increasing the depth of native litter produced higher catch rates than in thin and thick pine, and casuarina (Table 2), though this difference was significant only for thin pine (native thick vs. pine thin:  $t_2 = 7.57$ ,  $P = 0.017$ ; vs. pine thick:  $t_2 = 3.20$ ,  $P = 0.085$ ; vs. casuarina:  $t_1 = 5.12$ ,  $P = 0.123$ ). Increasing the depth of casuarina altered its importance relative to native and pine litter layers (casuarina thick vs. native:  $t_1 = 0.65$ ,  $P = 0.632$ ; vs. pine:  $t_1 = 1.00$ ,  $P = 0.500$ ; vs. pine thin:  $t_1 = 9.80$ ,  $P = 0.065$ ). In a comparison of artificial litter layers *L. delicata* preferred the more open structure of ripped paper to shredded paper ( $t_2 = 3.96$ ,  $P = 0.058$ ).

Addition of food had some influence on preference. Catch rates in supplemented pine were higher than in unsupplemented pine ( $t_2 = 7.86$ ,  $P = 0.016$ ). However, supplemented native leaf litter was not favored over unsupplemented native litter ( $t_1 = 1.00$ ,  $P = 0.50$ ), and unsupplemented native litter was still favored over supplemented pine litter ( $t_2 = 4.18$ ,  $P = 0.053$ ), although the magnitude of this difference was not as great as when both litter types were not food supplemented (Table 2).

Leaf litter with more open structure (native) showed high accessibility (Fig. 1; 66%), whereas pine litter, which forms a dense mat, showed low accessibility (9%). If differences in accessibility of the litter layer influence selection by *L. delicata* then the difference in capture rates should reflect the difference in accessibility to refuge of the litter layers being compared: difference in catch rate between enclosure halves was

TABLE 2. Mean number of lizards caught per hour (SE) in each half of the enclosures for all pairwise comparisons. *N* is the total number of one-hour trapping sessions. Note that comparisons marked with # were trials where there was only one pitfall trap per enclosure half, and where only one trial was conducted.

Comparison	Litter types compared (depths in cm)	<i>N</i>	Number caught/hour $\bar{x}$ (SE)
Same types #	Native (2.3)	18	1.22 (0.23)
	vs. Native (2.3)		1.16 (0.20)
	Pine (5.5)	18	1.05 (0.22)
	vs. Pine (5.5)		1.16 (0.24)
Cover bare	Casuarina (2.2)	18	1.38 (0.28)
	vs. Casuarina (2.2)		1.44 (0.18)
	Native (2.3)	36	5.08 (0.30)
	vs. Bare		0.66 (0.16)
Basic types	Pine (5.5)	36	3.88 (0.21)
	vs. Bare		0.80 (0.17)
	Native (2.3)	48	4.75 (0.18)
	vs. Pine (5.5)		2.68 (0.24)
Varying structure	Native (2.3)	32	5.12 (0.25)
	vs. Casuarina (2.2)		2.13 (0.24)
	Pine (5.5)	36	5.13 (0.25)
	vs. Casuarina (2.2)		3.33 (0.24)
Varying depth	Native (patchy)	34	4.35 (0.25)
	vs. Pine (5.5)		4.00 (0.26)
	Native (2.3)	45	4.22 (0.21)
	vs. Pine (loosened)		3.44 (0.18)
Artificial litter	Native (thick) (5.3)	54	5.27 (0.21)
	vs. Pine (thin) (2.4)		1.77 (0.18)
	Native (thick) (5.3)	54	4.46 (0.17)
	vs. Pine (thick) (9.8)		2.66 (0.17)
	Native (thick) (5.3)	36	4.97 (0.26)
	vs. Casuarina (2.2)		2.55 (0.18)
	Native (2.3)	36	4.63 (0.24)
	vs. Casuarina (thick) (4.8)		3.80 (0.25)
	Pine (5.5)	32	4.06 (0.28)
	vs. Casuarina (thick) 4.8		3.84 (0.30)
	Pine thin (2.4)	36	3.02 (0.25)
	vs. Casuarina (thick) (4.8)		4.38 (0.22)
Food added	Ripped paper	54	4.25 (0.20)
	vs. Shredded paper		3.24 (0.17)
Food added	Pine (supplemented)	54	4.05 (0.19)
	vs. Pine (unsupplemented)		3.38 (0.19)
	Native (supplemented)	36	4.41 (0.28)
	vs. Native (unsupplemented)		4.13 (0.27)
Food added	Native (unsupplemented)	54	4.20 (0.16)
	vs. Pine (supplemented)		3.35 (0.18)

positively and significantly correlated with difference in accessibility between enclosure halves ( $r_s = 0.73$ ,  $P < 0.003$ ,  $N = 14$ ; supplementary feeding trials excluded).

#### DISCUSSION

Numerous studies have indicated that the geometric configuration of a habitat can serve as a key stimulus in the selection of suitable habitats by reptiles (e.g., Heatwole, 1977; Díaz and Carrascal, 1991; Hadden and Westbrooke, 1996; Martín and Lopez, 1998). However, the majority of studies infer this relationship rather than test it experimentally. Our manipulative studies indicate that *L. delicata* prefers leaf litter to bare substrate, but also shows a preference for different types of leaf litter layer. Altering the depth, structure, and distribution of the litter layer influenced their choice.

Although the hypothesis tests for each pairwise choice experiment generally lacked power, the combined data for catch rate and accessibility to refuge suggest that *L. delicata* prefer litter with a relatively open structure. This preference can be interpreted in terms of the general habitat requirements of small lizards. Habitats must be thermally suitable and also provide sufficient food and refuge (Adolph, 1990). Open litter could provide all these requirements for a small, ground-dwelling lizard such as *L. delicata*. Thermoregulation would be more efficient as lizards could move to different positions in the litter layer to either raise temperature to optimum levels, or avoid overheating. Attaining optimal temperature should improve efficiency of prey capture and predator avoidance (Tracy and Christian, 1986; Huey and Bennett,

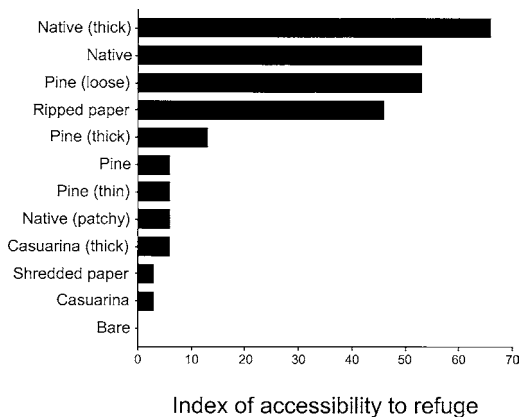


FIG. 1. Index of accessibility to refuge (measured by the percentage of marbles not visible) for the different leaf litter types.

1987; Huey, 1991). Use of a more open litter layer would also allow rapid access to refuge for predator avoidance in comparison to a litter layer with closed structure where lizards would have few access points and movement through the litter layer would be impeded (Diaz and Carrascal, 1991). An open litter layer would also allow more efficient foraging movements.

The role of food in habitat choice is not clear because invertebrate abundance was not monitored in the different litter types, and there were only limited trials in which food manipulation was attempted. Trials involving manipulation of food levels suggested that food was not as important as structure, although an overabundance of food in enclosures before adding supplement could also explain lizard responses. However, in the absence of food within the litter (artificial litter layer), *L. delicata* preferred an open litter structure. As for other lizard species (e.g., Law and Bradley, 1990; Diaz, 1994), attributes linked to maintaining optimal thermal environment may be the key factors influencing habitats selected by *L. delicata*.

If availability of suitable basking sites influences *L. delicata* abundance (e.g., as per other species; Law and Bradley, 1990), then habitat modifications that alter the structure of the litter layer should influence abundance of *L. delicata*. For example, exotic pine plantations with similar canopy cover and food conditions to native open woodland might still have low densities of skinks because the litter layer is unsuitable.

In this study, we assumed that catch rates in each litter layer reflected habitat use. Catch rates in pit-fall traps will depend on the number of lizards and the amount that they move. Movement could be influenced by litter layer, food availability and intraspecific interactions. Densities used in this study were at the high end of natural densities and may have influenced the amount of interaction between individuals. However, it seems unlikely that social interactions or foraging activity would be lower in bare substrate and litter layers with closed structure and, therefore, that these factors could lead to significantly different catch rates between leaf litter types if lizards were distributed at random.

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#### LITERATURE CITED

- ADOLPH, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* 71:315–327.
- BLOCK, W. M., AND M. L. MORRISON. 1998. Habitat relationships of amphibians and reptiles in California oak woodlands. *Journal of Herpetology* 32:51–60.
- BROWN, G. W., AND J. L. NELSON. 1993. Influence of successional stage of *Eucalyptus regnans* (Mountain Ash) on habitat use by reptiles in the central highlands, Victoria. *Australian Journal of Ecology* 18:405–417.
- BURROW, A. L., R. T. KAZMAIER, E. C. HELLGREN, AND D. C. RUTHVEN. 2001. Microhabitat selection by Texas Horned Lizards in southern Texas. *Journal of Wildlife Management* 65:645–652.
- CODY, M. 1985. An introduction to habitat selection in birds. In M. Cody (ed). *Habitat Selection in Birds*, pp.3–56. Academic Press, San Diego, CA.
- COGGER, H. G. 2000. *Reptiles and Amphibians of Australia*. 6th ed. Reed New Holland, Sydney, New South Wales, Australia.
- DÍAZ, J. A. 1994. Field thermoregulatory behaviour in the Western Canarian lizard *Gallotia galloti*. *Journal of Herpetology* 28:325–333.
- DÍAZ, J. A., AND L. M. CARRASCAL. 1991. Regional distribution of a Mediterranean lizard: influence of habitat cues and prey abundance. *Journal of Biogeography* 18:291–297.
- DOWNES, S., AND R. SHINE. 1998. Heat, safety, or solitude? Using habitat selection experiments to identify a lizards priorities. *Animal Behaviour* 55: 1387–1396.
- HADDEN, S. A., AND M. E. WESTBROOKE. 1996. Habitat relationships of herpetofauna of remnant buloke woodlands of the Wimmera plains, Victoria. *Wildlife Research* 23:363–372.
- HEATWOLE, H. 1977. Habitat selection in reptiles. In G. Gans and D. W. Tinkle (eds.), *Biology of the Reptilia*. Vol 7. Ecology and Behavior, pp. 137–155. Academic Press, New York.
- HECNAR, S. J., AND R. T. MCCLOSKEY. 1998. Effects of human disturbance on Five-Lined Skink, *Eumeces fasciatus*, abundance and distribution. *Biological Conservation* 85:213–222.
- HUEY, R. B. 1991. Physiological consequences of habitat selection. *American Naturalist* 137:S91–S118.
- HUEY, R. B., AND A. F. BENNETT. 1987. Phylogenetic studies of co-adaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41:1098–1115.
- HUEY, R. B., C. PETERSON, S. ARNOLD, AND W. PORTER. 1989. Hot rocks and not-so-hot rocks: retreat site selection by garter snakes and its thermal consequences. *Ecology* 70:931–944.
- LAW, B. S., AND R. A. BRADLEY. 1990. Habitat use and basking site selection in the water skink, *Eulamprus quoyii*. *Journal of Herpetology* 24:235–240.
- LUNNEY, D., E. ASHBY, J. GRIGG, AND M. O'CONNELL. 1989. Diets of scincid lizards *Lampropholis guichenoti*

- (Dumeril and Bibron) and *L. delicata* (de Vis) in Mumbulla State Forest on the south coast of New South Wales. Australian Wildlife Research 16:307–312.
- LUNNEY, D., P. EBY, AND M. O'CONNELL. 1991. Effects of logging, fire and drought on three species of lizards Mumbulla State Forest on the south coast of New South Wales. Australian Journal of Ecology 16:33–46.
- MARTIN, J., AND P. LOPEZ. 1998. Shifts in microhabitat use by the lizard *Psammodromus algirus*: response to seasonal change in vegetation structure. Copeia 1998:780–786.
- POUNDS, J. A. 1988. Ecomorphology, locomotion and microhabitat structure: patterns in a tropical mainland *Anolis* community. Ecological Monographs 58:299–320.
- RAWLINSON, P. A. 1971. Reptiles of Victoria. In V. H. Arnold (ed.), Victorian Yearbook 85, pp. 11–36. Government Printer, Melbourne, Victoria, Australia.
- TRACY, C. R., AND K. CHRISTIAN. 1986. Ecological relations among space, time and thermal niche axes. Ecology 67:609–616.
- WEBB, J., AND R. SHINE. 1999. Paving the way for habitat restoration: can artificial rocks restore degraded habitats for endangered reptiles? Biological Conservation 92:93–99.

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### Analysis of Spotted Salamander (*Ambystoma maculatum*) Growth Rates Based on Long-Bone Growth Rings

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**ABSTRACT.**—Amphibians experience indeterminate growth, but although factors affecting larval growth are relatively well studied, less is known about correlates of postmetamorphic growth. We measured areas between lines of arrested growth (inter-LAG) to determine yearly growth rates to test whether the post-metamorphic growth of 32 Spotted Salamanders (*Ambystoma maculatum*) was related to age, sex, or year of emergence. Growth decreased with age and was not associated with sex or year of emergence. Using interLAG area as a metric of growth provides growth information in the years before first capture and can be done using the toe-clips commonly taken for marking individuals.

Growth rate and body size are important intraspecific characteristics for adult amphibians. First, rapid growth immediately following metamorphosis reduces the time to sexual maturity for anurans, allowing them to reproduce earlier (Turner, 1960). Second, reproductive output is often correlated with body size. For example, larger Spotted Salamanders (*Ambystoma maculatum*) and Wood Frogs (*Rana sylvatica*) produce significantly larger clutches than do smaller conspecifics (Woodward, 1982; Howard, 1988), and larger male Bullfrogs (*Rana catesbeiana*) mate more frequently each year than do smaller males (Howard, 1988). In some *Ambystoma*, larger individuals breed earlier in the season than do smaller individuals (Lowcock et al., 1992), perhaps offering a time advantage to their offspring in a rapidly fluctuating environment. Finally, larger male body size may be important in species where individuals defend territories (Howard, 1988; Regosin et al., in press).

Amphibians exhibit indeterminate growth continuing to grow beyond reproductive maturity (Perrin and

Sibley, 1993). Therefore, factors that affect growth and body size may act during the larval stage and continue well after metamorphosis. In contrast to amphibian postmetamorphic growth, larval growth has been well studied, and important correlates have been identified. Higher temperatures and greater food availability, for example, can increase larval growth (Duellman and Trueb, 1986), but increased density of conspecifics, regardless of prey density, decreases larval growth rates (Petranka, 1989; Scott, 1990; Van Buskirk and Smith, 1991). Also, some species of anurans produce a chemical that can inhibit growth of both conspecific larvae and larvae of other amphibian species (Richards, 1958; Rose, 1960; West, 1960).

Larval growth rates can affect size at metamorphosis and, thus, can impact adult body size (Semlitsch et al., 1988; Scott, 1994); however, patterns and correlates of adult amphibian growth are relatively poorly known. Several early studies, however, have identified factors affecting postmetamorphic anuran growth (e.g., Raney and Ingram, 1941; Fitch, 1956; Martof, 1956; Turner, 1957), and there are a few studies specific to salamanders (Flageole and Leclair, 1992; Wake and Castenet, 1995; Caetano and Leclair, 1996; Castenet et al., 1996; Russell et al., 1996). An animal's age is one factor often

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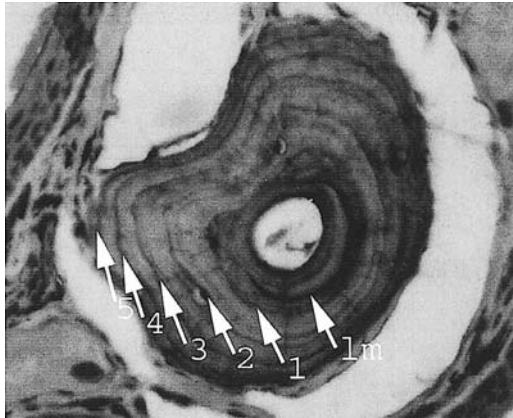


FIG. 1. Example of Spotted Salamander phalangeal bone cross-section of a five-year-old individual. The arrow labeled "lm" demonstrates the line of metamorphosis in this individual. Arrows labeled 1 to 5 show the postmetamorphic annuli, or annual lines of arrested growth (LAGs). Lighter gray areas between the LAGs are the interLAG areas measured to estimate relative growth rates.

related to both anuran and salamander postmetamorphic growth rates, with animals exhibiting more rapid growth during the early years of postmetamorphic life, followed by reduced growth in later years (Raney and Ingram, 1941; Ryan, 1953; Turner, 1957; Caetano and Leclair, 1996; Castenet et al., 1996; Russell et al., 1996). Growth rates differ between the sexes in some species, with females typically growing faster than males, particularly in the first season postmetamorphosis (Ryan, 1953; Fitch, 1956; Flageole and Leclair, 1992). Finally, month and/or environmental temperature have been correlated with postmetamorphic anuran growth rates. For example, Green Frogs (*Rana clamitans*) and Spotted Frogs (*Rana pretiosa*) grew most rapidly during mid-summer (July; Martof, 1956; Turner, 1957), and growth of the North American Desert Spadefoot Toad (*Scaphiopus couchii*) is affected by rainfall (Tinsley and Tocque, 1995). Russell et al. (1996) also suspected that environmental heterogeneity, such as differences in food availability, affected growth rates in the Northern Long-toed Salamander (*Ambystoma macrodactylum krausei*). In this study, we examined postmetamorphic growth rates of *Ambystoma maculatum* from two populations to evaluate the relative importance of age, sex, and year for growth in this species.

#### MATERIALS AND METHODS

*Ambystoma maculatum* are common in eastern North America, and individuals demonstrate a cyclic pattern of activity, being active during the spring, summer and fall, and quiescent during the winter (Downs, 1989; Windmiller, 1996). This variation in activity is associated with seasonal growth, in particular seasonal patterns of long-bone deposition, which combined with their indeterminate growth (Duellman and Trueb, 1986) allows one to age and measure growth in individuals up to and beyond reproductive maturity (Flageole and Leclair, 1992). The slower winter growth results in the bone formation of annual lines of arrested

growth (LAGs), which can be counted to determine the age of a particular animal in years (Flageole and Leclair, 1992). We used the area of bone deposition between LAGs as a measure of growth (e.g., Flageole and Leclair, 1992; Kellner and Green, 1995; Tinsley and Tocque, 1995).

We measured growth of *A. maculatum* from two populations in Sudbury, Massachusetts (N42°22', W71°25'), taken in 1998, 1999, and 2000. The two populations used breeding ponds that are approximately 56 m apart and separated by a narrow paved road. Ponds were similar in hydroperiod, vegetation, and surrounding terrestrial habitat. Phalanges were clipped at the base to assign identification marks to each salamander for a related study, and clipped phalanges were kept in a solution of 10% formalin. Bone samples were rinsed thoroughly in distilled water, allowed to dry, and sent to Matson's Laboratory, LLC (Milltown, Montana) for sectioning. Eight cross-sections of phalangeal bone per individual were made at 0.2-mm intervals. Sections were 10  $\mu$  thick and stained with hematoxylin. After receiving the sectioned phalangeal bones for each individual, we identified and photographed the clearest of the eight sections.

We assumed that one line of arrested growth represented one period of slow winter growth and, therefore, was equivalent to one annual ring (e.g., Flageole and Leclair, 1992). Where the innermost LAG was irregular in shape, relative to the other LAGs, and had differently stained bone inside than outside, it was considered to be the line of metamorphosis, with all outer LAGs representing postmetamorphic annuli (Flageole and Leclair, 1992; Russell et al., 1996). Only postmetamorphic LAGs were counted to determine age (Fig. 1). Potential LAGs were not counted if they were very lightly stained relative to the clearest LAGs or if the ring could not be followed around the circumference of the bone section (Russell et al., 1996). Phalanges were excised from the animals within 1–2 months following the end of winter hibernation, so we assumed that the final LAG was either very close to or at the edge of the periosteal, or postmetamorphic, bone. Two observers independently estimated age for each salamander. If we initially disagreed on the age by one year, we conferred and included the individual only if a consensus could be reached. If our age estimates disagreed by more than one year, we did not include that individual in our study.

We determined age and interLAG area for the first five years of postmetamorphic growth for 32 *A. maculatum* (18 males, 14 females) that were between five and seven years old at the time of capture, because we were most confident in the age assignments for animals in this age group. Each animal was toe-clipped for aging only once. We did not always use the same phalange across individuals for aging, introducing the possibility of between-individual error. However, we do not suspect significant problems, because we measured relative growth, and age estimates have been found to be independent of the phalange measured (Russell et al., 1996). InterLAG areas were measured using Scion Image (Scion Corp., Frederick, MD, 2000), by electronically tracing neighboring LAGs and calculating the area between them. Areas for a given year are presented as the percent of the total postmetamorphic growth, because differences in toe sizes and possible

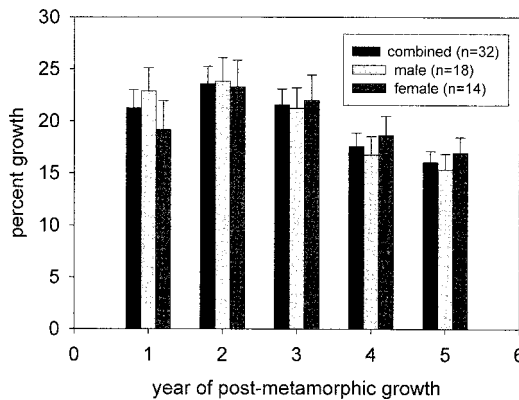


FIG. 2. Mean percent growth ( $\pm$  standard error) of *Ambystoma maculatum* across their first five years of life ( $N = 32$ ). Percent growth values represent the postmetamorphic growth in one year relative to the total growth across the first five years of life. The first year of postmetamorphic growth may have been any date from 1992 through 1995.

small differences in magnification across photos might introduce error in absolute area measures. We looked for relationships between relative growth and capture site, sex, year of emergence and age. Year of emergence and age are not necessarily related, because our samples came from animals captured any time over a period of three years, so that individuals sharing an age did not necessarily emerge in the same year. For all hypotheses, we tested for significant differences in percent growth across years using repeated measures ANOVA (SAS, vers. 8, Statistical Analysis Institute, Inc., Cary, NC, 1999).

#### RESULTS

We found that population, sex, and year of emergence were not correlated with percent yearly growth rates ( $F_{1,29} = 3.48$ ,  $P = 0.07$ ;  $F_{1,30} = 1.76$ ,  $P = 0.19$ ;  $F_{5,24} = 1.44$ ,  $P = 0.25$ , respectively). Consequently, for subsequent analyses, these variables were removed from the model. The only factor significantly associated with interLAG area was age ( $F_{4,124} = 3.25$ ,  $P = 0.009$ , Fig. 2). Growth rates were similar during the first three years postmetamorphosis, with a minor peak at age two, and declined over the remaining years (Fig. 2).

#### DISCUSSION

The ability to measure growth across multiple years and ages of a single individual from a single bone sample offers a relatively rare opportunity to study animal growth and its possible correlates, without having to measure individuals repeatedly across years. This is particularly true for amphibians, where toe-clipping is a standard marking technique (Martof, 1953), and the toe clip provides a suitable bone sample for measuring growth. The results we obtained using this technique indicate that postmetamorphic Spotted Salamander growth may be primarily influenced by an animal's age, rather than by sex or environmental factors. This result is consistent with several studies in which relatively rapid growth occurs in early years

after metamorphosis and is followed by slowed growth as the animal ages (Raney and Ingram, 1941; Ryan, 1953; Turner, 1957; Kellner and Green, 1995; Caetano and Leclair, 1996; Castenet et al., 1996; Russell et al., 1996). In contrast, our findings differ from some amphibian studies, including one on *A. maculatum*, where clear effects of sex were reported (Ryan, 1953; Pearson, 1955; Fitch, 1956; Flageole and Leclair, 1992). However, we measured relative growth, rather than absolute growth; thus, if one sex consistently grows faster, we would not necessarily observe sex differences. The lack of sex effect in our study ( $N = 32$ ) also may have been caused by lower statistical power relative to Flageole and Leclair's (1992) study of *A. maculatum* ( $N = 116$ ).

We also found no effects of environment, contrary to other studies (George, 1940; Thompson, 1942; Martof, 1956; Russell et al., 1996). Years of emergence from the pond were 1992 to 1995, and because we found no significant effect of year on growth rates, we concluded that environmental differences across these years were relatively insignificant to postmetamorphic growth. It is possible that environmental conditions in the years examined here were not sufficiently extreme to elicit a statistically significant change in growth rates or that sample sizes were insufficient to detect small, significant effects. An alternative explanation is that reports of temperature effects on adult amphibian growth might be confounded with other environmental factors. For example, George (1940) found that *R. catesbeiana* in Louisiana have a greater annual growth rate than *R. catesbeiana* in New York, but this could be the result of greater length of the growing season rather than with temperature per se.

Although age appears to be the primary determinate of yearly growth rates in *A. maculatum*, there is indirect evidence that the reduced growth rate might be an evolved response to reproduction. The trade-off between reproductive effort and growth is well known (Gadgil and Bossert, 1970; Wilbur, 1977). Since large body size appears to be an advantage to amphibians (Woodward, 1982; Howard, 1988; Lowcock et al., 1992; Regosin et al., in press), it might be expected that growth rates would not slow with age in an indeterminate grower. We observed, however, that yearly growth declined at or just before the average age of reproductive maturity for males and females. Although Flageole and Leclair (1992) found that *A. maculatum* mature at a wide age range, with maximums of six years for males and seven years for females, Wilbur (1977) suggests that *A. maculatum* are often reproductively mature by age two or three for males and age four for females. Indeed, in a related study of the same populations used in this study, we found that the modal ages of breeding *A. maculatum* are three years for males and four years for females (unpubl. data), suggesting an earlier reproductive maturity in our population than for that of Flageole and Leclair's (1992). Russell et al. (1996) also observed a similar pattern of slowed growth near the time of sexual maturity in another *Ambystoma*.

In future studies, it would be interesting to examine effects of size at metamorphosis on postmetamorphic growth to determine whether larval conditions play a role in adult growth patterns. Research by Semlitsch et al. (1988) and Scott (1994) on two other *Ambystoma* species showed that individuals that were larger at

metamorphosis were also larger adults during their first reproductive year. In another research direction, amphibians may be used as biomonitors of environmental conditions (Blaustein, 1994; Homan et al., 2003). Amphibian interLAG areas might be developed into an additional biomonitoring tool for identifying individuals from populations in which factors exist that negatively affect growth. Because the inter-LAG areas are maintained for years, the technique might be useful for evaluating the history of a pollutant or other stressor in the recent past that is no longer present, if such factors affect growth.

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## LITERATURE CITED

- BLAUSTEIN, A. R. 1994. Chicken Little or Nero's fiddle? A perspective on declining amphibian populations. *Herpetologica* 50:85–97.
- CAETANO, M. H., AND R. LECLAIR JR. 1996. Growth and population structure of red-spotted newts (*Notophthalmus viridescens*) in permanent lakes of the Laurentian Shield, Quebec. *Copeia* 1996:866–874.
- CASTANET, J., H. FRANCILLON-VIEILLOT, AND R. C. BRUCE. 1996. Age estimation in Desmognathine salamanders assessed by skeletochronology. *Herpetologica* 52:160–171.
- DOWNES, F. L. 1989. *Ambystoma maculatum* (Shaw), Spotted Salamander. In R. A. Pflingsten and F. L. Downes (eds.), *Salamanders of Ohio*, pp. 108–124. Bulletin of the Ohio Biological Survey, Columbus.
- DUCELLMAN, W. E., AND L. TRUEB. 1986. *Biology of Amphibians*. Johns Hopkins Univ. Press, London.
- FITCH, H. S. 1956. A field study of the Kansas ant-eating frog, *Gastrophryne olivacea*. Univ. of Kansas Publications of the Museum of Natural History 8:275–307.
- FLAGEOLE, S., AND R. LECLAIR JR. 1992. Étude démographique d'une population de salamanders (*Ambystoma maculatum*) à l'aide de la méthode squelette-chronologique. *Canadian Journal of Zoology* 70:740–749.
- GADGIL, M., AND W. BOSSERT. 1970. Life historical consequences of natural selection. *American Naturalist* 104:1–24.
- GEORGE, I. D. 1940. A Study of the Bullfrog, *Rana catesbeiana*, at Baton Rouge, Louisiana. Unpubl. Ph.D. diss., Univ. of Michigan, Ann Arbor.
- HOMAN, R. N., J. V. REGOSIN, D. M. RODRIGUES, J. M. REED, B. S. WINDMILLER, AND L. M. ROMERO. 2003. Impacts of varying habitat quality on the physiological stress of Spotted Salamanders (*Ambystoma maculatum*). *Animal Conservation* 6:11–18.
- HOWARD, R. D. 1988. Reproductive success in two species of anurans. In T. H. Clutton-Brock (ed), *Reproductive Success*, pp. 99–113. Univ. of Chicago Press, Chicago.
- KELLNER, A., AND D. M. GREEN. 1995. Age structure and age at maturity in Fowler's Toads, *Bufo woodhousii fowleri*, at their northern range limit. *Journal of Herpetology* 29:485–489.
- LOWCOCK, L. A., H. GRIFFITH, AND R. W. MURPHY. 1992. Size in relation to sex, hybridity, ploidy, and breeding dynamics in central Ontario populations of the *Ambystoma laterale-jeffersonianum* complex. *Journal of Herpetology* 26:46–53.
- MARTOF, B. S. 1953. Territoriality in the green frog *Rana clamitans*. *Ecology* 34:165–174.
- MARTOF, B. S. 1956. Growth and development of the Green Frog, *Rana clamitans*, under natural conditions. *American Midland Naturalist* 55:101–117.
- PEARSON, P. G. 1955. Population ecology of the Spadefoot Toad, *Scaphiopus h. holbrooki* (Harlan). *Ecological Monographs* 25:233–267.
- PERRIN, N., AND R. SIBLY. 1993. Dynamic models of energy allocation and investment. *Annual Review of Ecology and Systematics* 24:379–410.
- PETRANKA, J. W. 1989. Density-dependent growth and survival of larval *Ambystoma*: evidence from whole pond manipulations. *Ecology* 70:1752–1767.
- RANEY, E. S., AND W. M. INGRAM. 1941. Growth of tagged frogs (*Rana catesbeiana* Shaw and *Rana clamitans* Daudin) under natural conditions. *American Midland Naturalist* 26:201–206.
- REGOSIN, J. V., B. S. WINDMILLER, AND J. M. REED. In Press. Burrow occupancy and spacing behavior of Spotted Salamanders (*Ambystoma maculatum*). *Copeia*.
- RICHARDS, C. M. 1958. The inhibition of growth in crowded *Rana pipiens* tadpoles. *Physiological Zoology* 31:138–151.
- ROSE, S. M. 1960. A feedback mechanism of growth control in tadpoles. *Ecology* 41:188–199.
- RUSSELL, A. P., G. L. LAWRENCE, AND D. R. HALL. 1996. Growth and age of Alberta Long-Toed Salamanders (*Ambystoma macrodactylum krausei*): a comparison of two methods of estimation. *Canadian Journal of Zoology* 74:397–412.
- RYAN, R. A. 1953. Growth rates of some ranids under natural conditions. *Copeia* 1953:73–80.
- SCOTT, D. E. 1990. Effects of larval density in *Ambystoma opacum*: an experiment in large-scale field enclosures. *Ecology* 71:296–306.
- . 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. *Ecology* 75:1383–1396.
- 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.
- THOMPSON, D. A. W. 1942. *On Growth and Form*. Cambridge Univ. Press, Cambridge.
- TINSLEY, R. C., AND K. TOCQUE. 1995. The population dynamics of a desert anuran, *Scaphiopus couchii*. *Australian Journal of Ecology* 20:376–384.
- TURNER, F. B. 1957. The Ecology and Morphology of *Rana pretiosa pretiosa* in Yellowstone Park, Wyoming. Unpubl. Ph.D. diss., Univ. of California, Berkeley.
- . 1960. Postmetamorphic growth in anurans. *American Midland Naturalist* 64:327–338.
- VAN BUSKIRK, J., AND D. C. SMITH. 1991. Density-dependent population regulation in a salamander. *Ecology* 72:1747–1756.
- WAKE, D. B., AND J. CASTANET. 1995. A skeletochronological study of growth and age in relation to adult

- size in *Batrachoseps attenuatus*. *Journal of Herpetology* 29:60–65.
- WEST, L. B. 1960. The nature of growth inhibitory material from crowded *Rana pipiens* tadpoles. *Physiological Zoology* 33:232–239.
- WILBUR, H. M. 1977. Propagule size, number, and dispersion pattern in *Ambystoma* and *Asclepias*. *American Naturalist* 111:43–68.
- WINDMILLER, B. S. 1996. The Pond, the Forest, and the City: Spotted Salamander Ecology and Conservation in a Human-Dominated Landscape. Unpubl. Ph.D. diss., Tufts Univ., Boston, MA.
- WOODWARD, B. D. 1982. Local intraspecific variation in clutch parameters in the spotted salamander (*Ambystoma maculatum*). *Copeia* 1982:157–160.

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### Response of Mountain Yellow-Legged Frogs, *Rana muscosa*, to Short Distance Translocation

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**ABSTRACT.**—To determine the response of Mountain Yellow-Legged Frogs to short distance translocations, I placed transmitters on 20 adult frogs and moved them short distances from 144–630 m and monitored their responses for up to 30 days. Of the 20 translocated frogs, seven frogs returned to their original capture site, four frogs moved in the direction of their capture site but had not returned by the end of the study, and nine frogs did not return and were found at the translocation site. Apparently, displacing frogs was stressful, and translocated frogs lost body mass during the study period. Eighteen translocated frogs that were weighed at the beginning and end of the study lost body mass (mean loss was –1.2 g) compared to a group of 18 randomly selected PIT tagged frogs also weighed during the same tracking period (mean gain in body mass = 2.5 g) at our Kings Canyon study site. Translocation of adult *Rana muscosa* as a conservation tool may not be effective because some would simply attempt to return to their original capture site, and their homing may be stressful to an already declining frog population.

The process of reestablishing threatened and endangered species by relocation, repatriation, and translocation (RRT) has become increasingly used as a wildlife management technique for a variety of animals including birds, mammals (Ralls et al., 1992), and more recently, amphibians, and reptiles (Griffith et al., 1989). Although there is much discussion over the proper definitions, Griffith et al. (1989) define translocation as “the intentional release of animals to the wild in an attempt to establish, reestablish, or augment a population . . .” As species decline, there is considerable interest in moving them from favorable habitats where they may still thrive, to habitats where populations need to be restored. Dodd and Seigel (1991), however, cast doubt on the effectiveness of RRT as conservation strategies for reptiles and amphibians because there are few documented successes (Reinert, 1991). In some studies, there was no way to determine success because no baseline information existed from which researchers could determine whether or not the translocations were successful. Another problem with translocation studies is there is sometimes no post study monitoring. Therefore, Dodd and Seigel (1991) urged caution in the use of RRT and asked that researchers carefully document the studies and monitor the results for several years

to determine whether the recovery efforts were successful.

Many examples of potential problems with actual translocations have been discussed (Dodd and Seigel, 1991; Reinert, 1991), including the possibility that animals move once they are translocated or are moved into low quality habitat, or habitat that still harbors problems that contributed to the original decline. If animals home (return to their capture site), then translocation to reestablish a population would be unsuccessful. Another potential problem is that translocations may be stressful and animals may spend valuable foraging or breeding time searching for their home site.

Recent studies have documented that the once-common Mountain Yellow-Legged Frog, *Rana muscosa*, has declined in the Sierra Nevada mountains of western North America in large part because of the introduction of nonnative trout (Bradford, 1989; Bradford et al., 1993; Knapp and Matthews, 2000). Despite the fact that its habitat has been protected in national parks and federal wilderness areas for the past 30–80 yr, *R. muscosa* is now extirpated from at least 50% of historic localities (Bradford et al., 1994; Drost and Fellers, 1996; Jennings, 1996). Because *R. muscosa* is declining and has been petitioned for federal listing, there is interest in trans-

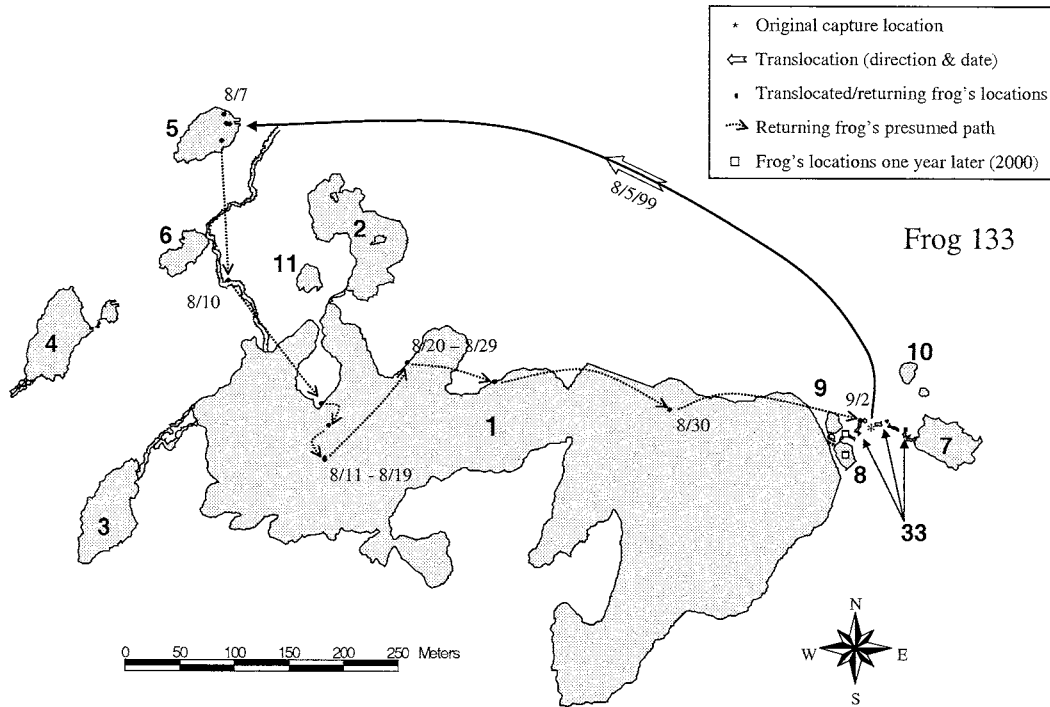


FIG. 1. Map of tagged frog 133 that returned home after relocation during August and September 1999. Asterisks indicate the original capture site and the solid line with arrow indicates the translocation direction and distance. The circles show the locations after relocation, and dotted lines show the assumed return path to the original capture site. The highlighted boxes show frog 133's locations in PIT surveys during 2000. Lake and stream numbers are in bold.

locations. Translocations have been used successfully by European researchers to reestablish populations of the *Rana temporaria* (Cooke and Oldham, 1995), but recent translocations of *R. muscosa* were not successful (G. M. Fellers unpubl. data; R. A. Knapp, unpubl. data). I suspected that adult *R. muscosa* may not be good candidates for translocation because they have high site fidelity and move short distances to relocate previously used breeding and feeding sites (Pope and Matthews, 2001; K. R. Matthews, unpubl. data). This study was conducted to determine the response of *R. muscosa* to short distance (144–630 m) translocations. I used radio-transmitters to monitor the movements of *R. muscosa* after they were translocated to determine whether they returned to their original sites of capture. In addition, I assessed frog stress by comparing their masses at the beginning and end of the tracking period to determine whether loss in mass occurred. Then, I compared these changes in masses to randomly selected frogs in the same study area that had not been translocated.

#### MATERIALS AND METHODS

**Study Area.**—My study was conducted in upper Dusy Basin, Kings Canyon National Park, California (37°5'40"N, 118°33'45"W) at an elevation of 3470 m (Fig. 1; additional maps of the study area are found in Matthews and Pope, 1999; Pope and Matthews, 2001). The site supports a large population (several thousand

of *R. muscosa* of varying age classes. This glacially formed, granite basin supports alpine fell field vegetation with low-growing herbaceous plants, dwarf shrubs and few krummholzed white-bark pines (Holland and Keil, 1995). There is a series of streams, lakes, and ponds in the basin that are fed by snowmelt. The study area covers approximately 0.35 km<sup>2</sup>. This study focused on 11 lakes and ponds and the adjacent creeks in Dusy Basin (Fig. 1). Only lakes 1 and 3 (all water bodies being considered lakes) support self-sustaining populations of trout. Fish were also found in some creeks that connect between lakes. Lakes ranged in area from 114 m<sup>2</sup> to 5.3 ha and were 0.25–10 m deep. All lakes and streams within the study area have been numbered and mapped using a Trimble Pro XRS (with real-time satellite differential correction) GPS system accurate to < 1 m.

**Field Techniques.**—On 4 August 1999 I attached radio transmitters (Holohil Systems Ltd.; BD-2 transmitters; 15 × 7 × 4 mm) to 20 *R. muscosa* (snout–vent length, SVL > 55 mm) and allowed at least a 24-h recovery period after transmitter attachment before frogs were moved (Appendix 1). I chose frogs larger than 55 mm (SVL) to reduce possible adverse effects of transmitter weight on the health of frogs.

To attach radio transmitters, a waist-belt made of aluminum ball or beaded chain was used (Matthews and Pope, 1999). Total weight of transmitter and belt was approximately 1.5 g (ranged from 4–8% of body

mass for frogs in this study) with a battery life of one month. Frogs were hand-captured, weighed, measured, tagged with both a radiotransmitter and a Passive Integrated Transponder (PIT) tag, and then released at the capture site. Sex was determined by the enlarged nuptial pad at the base of the inner-most finger found in adult males (Stebbins, 1985).

On 5 August 1999, I moved tagged frogs from their capture site to other lakes and ponds and followed their movements to determine whether they remained stationary or returned to their capture sites. I attempted to remove transmitters and belts just before the battery expired (about one month). After frogs were tagged they were located on an almost daily basis and sometimes twice daily using an Advanced Telemetry Systems (ATS, Isanti, Minnesota) Challenger 4000 receiver and a hand-held three-element Yagi antenna. I monitored transmitters for the predicted life of the battery (up to 30 days). When frogs were located, I recorded their position (using GPS with real-time differential correction) and air temperature. Water temperature data were collected every five minutes for the duration of the study using Onset optic stowaway and tidbit water temperature loggers.

Frogs were moved distances from 144–630 m from one water body (lake or stream) to another water body. To reduce stress on frogs, I attempted to recapture them and return them to their original capture site if they had not returned by the end of the study. Because most translocated frogs (except frog 289) had a PIT tag inserted in 1999, I could search for frogs not recaptured in the summer of 1999 in subsequent PIT surveys (Pope and Matthews, 2001). The study was conducted primarily in August when frogs are generally less mobile and remain within average home ranges of 385 m<sup>2</sup> compared to September when frogs move more and home ranges increase to 5336 m<sup>2</sup> (Matthews and Pope, 1999). Frogs were moved from one water body to another water body that is not typically used, in an attempt to simulate a reintroduction. The longer translocations (> 400 m) would have placed frogs well outside of their maximum home ranges in September (around 5000 m<sup>2</sup>; Matthews and Pope, 1999) and possibly into unfamiliar areas.

To determine whether relocating frogs stressed them and resulted in a loss of body mass, I weighed frogs at the beginning and end of the study. I knew from previous work with tagged frogs (Matthews and Pope, 1999) that the effect of the transmitter was minimal and during summer tracking periods frogs with transmitters increased body mass during the study. Eighteen frogs were recaptured at the end of the 1999 tracking period and their transmitter removed; I was unable to relocate two transmittered frogs at the end of 1999. From these 18 frogs I collected body mass data at the beginning of the study and at the end of the tracking (days tracked ranged from 17–30 for these frogs). I determined whether the change in mass over the tracking period differed between the group of translocated frogs and 18 randomly selected PIT tagged frogs from the same study area weighed over the same time period. I also compared the mass changes of the translocated frogs to weight changes of frogs from another study that were transmittered but not translocated (Matthews and Pope, 1999).

## RESULTS

Of the 20 translocated frogs, seven returned to their original capture site (within a few meters), four moved in the direction of their capture site but had not returned by the end of the study, and nine did not return and were found at the translocation site (Appendix 1). During the tracking period from 5 August through 4 September 1999, five translocated frogs returned to their original capture site within 11–30 days (Appendix 1). Distance of translocation for these five frogs ranged from 206–485 m. Two additional translocated frogs (115 and 217) were not relocated by the end of 1999 but were found in the summer of 2000 during PIT surveys at their original capture lake (Pope and Matthews, 2001), indicating that they had returned either later in 1999 or in 2000. These two frogs were moved longer distances of 478 and 630 m. One frog (289) was lost during the study period; it was moved from lake 5 to lake 2, followed for 14 days and then its radio signal could not be located.

Frogs that returned within the study period generally stayed at the release site for several days and then took a fairly direct path back to their original capture sites (Fig. 1). For example, frog 133 was moved 485 m from stream 33 (Fig. 1), stayed at the release site for four days and, within 29 days, returned to its original capture site following a fairly direct path using water bodies. Similarly, frog 275 was moved 225 m where it stayed in the same water body for 13 days and was found at its capture site in less than 16 days. All frog relocations were subsequently found closer to the capture site than to the release site, and the frogs were never found moving further away from the release site.

Four frogs did not return to their original capture site by the end of the study period but were found closer to their capture sites (Appendix 1). Frog 350 (Fig. 2) was originally captured in lake 1 and was moved into lake 5 where it stayed for seven days. After seven more days it was found in the stream adjacent to lake 1, and subsequently it moved into the lake 2 where it remained for the study period. Frog 429 exhibited a similar response to translocation as frog 350. After it was moved from lake 1 into lake 7 (430 m), it remained for six days. Subsequently it moved back into lake 1 and more than half way back to its original capture site by the end of the study but was still about 150 m away from its original capture site. Frogs 535 and 615 were moved 595 m and 205 m, respectively, and both were over halfway back to their capture sites by the end of the study.

Frogs that returned during the 30-day tracking period in 1999 were originally translocated a mean distance of 267.6 m (206–485 m). The two transmittered frogs that were moved in 1999 but not found until 2000 were originally moved longer distances of 478 and 630 m.

Nine frogs stayed in the lake where they were translocated (150–615 m) during the study period (Appendix 1). Frog 217 had moved back to stream 33 by 2000 when found in the PIT surveys. Frog 409 was moved from lake 4 to lake 7 and it remained in lake 7 for the entire study. At the end of the study period, I could not find one frog (frog 409, Appendix 1) that had remained at the translocation site; thus, I was not able to return it to its capture site. Frog 409 was still located at the translocation site during the 2000 and 2001 PIT surveys.

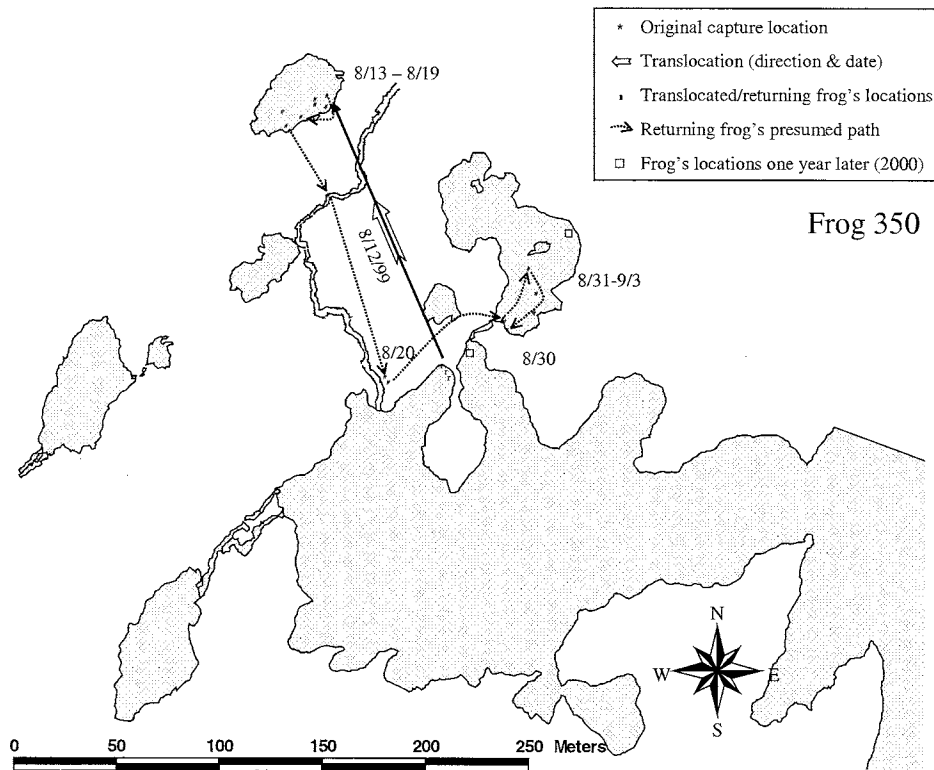


FIG. 2. Map of tagged frog 350 that moved toward its capture site after relocation during August and September 1999. Asterisks indicate the original capture site, and the solid line with arrow indicates the translocation direction and distance. The circles show the locations after relocation, and dotted lines show the assumed return path. Frog 350 was also found in lakes 1 and 2 during PIT surveys in 2000 (highlighted box).

The 18 frogs weighed at the beginning and end of the study lost body mass during the tracking (mean loss of body mass =  $-1.2$  g) compared to a group of 18 randomly selected PIT tagged frogs also weighed during the same tracking period in our Dusy Basin study area (mean gain of body mass =  $2.6$  g;  $t$ -test,  $P < 0.001$ , normality test passed).

The water temperatures in the lakes ranged from  $10$ – $20^{\circ}\text{C}$  during the study period. These are similar to temperatures encountered during other years in Dusy Basin (Pope, 1999) and suggests that 1999 conditions were similar to previous years.

#### DISCUSSION

To my knowledge, this is the first published study of *R. muscosa* translocations, and it appears that at least some translocated frogs will return to their initial capture sites. Site fidelity and homing has been demonstrated in several amphibians (Sinsch, 1990, 1992). *Bufo bufo* successfully returned from 3-km displacements (Hueser, 1969), and *Pseudacris regilla* homed from short distance displacements (275 m) but not from longer (914 m) ones (Jameson, 1957). Site fidelity and returning to previously used breeding and feeding areas have been documented in *R. muscosa* (Pope and Matthews, 2001) and is presumably an important factor in their successful relocation of

previously used important habitats. Therefore, it is not surprising that some *R. muscosa* returned to their capture sites, especially since they use different water bodies throughout their active season for breeding, feeding, and overwintering (Matthews and Pope, 1999; Pope and Matthews, 2001). Unfortunately, little is known about the extent to which ranids home or what mechanisms (e.g., olfaction, site recognition, etc.) may be involved (Sinsch, 1990). Possibly, Mountain Yellow-Legged Frogs were familiar with the areas into which they were translocated since over the active summer period their home ranges may be up to  $5000\text{ m}^2$ , although they did not move much in August in a previous study (Matthews and Pope, 1999).

Apparently, translocations were stressful and translocated frogs lost body mass during the study period compared to other frogs not translocated but in the same Dusy Basin study area. Also, in a study of frogs transmitters but not translocated, Matthews and Pope (1999) found that 10 of 14 transmitters gained weight during the 8–31 days of tracking. Thus, it appears that the relocation and not the transmitters caused the frogs to lose weight. This loss of body mass and possible stress needs to be considered in the risk assessment of doing translocations, especially considering that condition of *R. muscosa* depends on maximizing feeding during the short summer season at high elevations (Pope and Matthews, 2002). Possibly, the

additional four frogs that moved toward their capture site but did not return, may have returned if the study had been longer. However, a longer study may have further stressed the frogs.

The results of this study suggest that, given sufficient time, frogs can return to their capture site following short distance translocations and that translocations cause enough stress to result in loss of body mass. Thus, translocations may not be a viable option for adult *R. muscosa*. In addition, there are genetic issues regarding moving frogs from different areas because recent work suggests that the Sierra Nevada may have several different subspecies of *R. muscosa* (Macey et al., 2001). It may be valuable to know whether frogs will also home from longer distance translocations; however, longer movements may cause harm. Translocating egg masses or tadpoles are other possibilities that should be evaluated, as homing would presumably not be a concern.

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## LITERATURE CITED

- BRADFORD, D. F. 1989. Allotopic distribution of native frogs and introduced fishes in high Sierra Nevada lakes of California: implication of the negative effect of fish introductions. *Copeia* 1989:775–778.
- BRADFORD, D. F., F. TABATABAI, AND D. M. GRABER. 1993. Isolation of remaining populations of the native frog, *Rana muscosa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. *Conservation Biology* 7:882–888.
- BRADFORD, D. F., D. M. GRABER, AND F. TABATABAI. 1994. Population declines of the native frog, *Rana muscosa*, in Sequoia and Kings Canyon National Parks, California. *Southwestern Naturalist* 39:323–327.
- COOKE, A. S., AND R. S. OLDFHAM. 1995. Establishment of populations of the Common Frog, *Rana temporaria*, and Common Toad, *Bufo bufo*, in a newly created reserve following translocation. *Herpetological Journal* 5:173–180.
- DODD JR., C. K., AND R. A. SEIGEL. 1991. Relocation, repatriation and translocation of amphibians and reptiles: are they conservation strategies that work? *Herpetologica* 47:336–350.
- DROST, C. M., AND G. M. FELLERS. 1996. Collapse of a regional frog fauna in the Yosemite area of the California. *Conservation Biology* 10:414–425.
- GRIFFITH, B., J. M. SCOTT, J. W. CARPENTER, AND C. REED. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477–480.
- HEUSSER, H. 1969. Die Lebensweise der Erdkrote (*Bufo bufo* L): Das Orientierungsproblem. *Review Suisse Zoology* 76:444–517.
- HOLLAND, V. L., AND D. J. KEIL. 1995. California Vegetation. Kendall/Hunt Publishing Co., Dubuque, IA.
- JAMESON, D. L. 1957. Population structure and homing responses in the Pacific tree frog. *Copeia* 1957:221–228.
- JENNINGS, M. R. 1996. Status of amphibians. In *Sierra Nevada Ecosystem Project: Final Report to Congress*. Vol. II, pp. 921–944. Centers for Water and Wildland Resources, Univ. of California, Davis (available online at [ceres.ca.gov/snep/pubs](http://ceres.ca.gov/snep/pubs)).
- KNAPP, R. A., AND K. R. MATTHEWS. 2000. Non-native fish introductions and the decline of the Mountain Yellow-Legged Frog from within protected areas. *Conservation Biology* 14:28–438.
- MACEY, J. R., J. L. STRASBURG, J. A. BRISSON, V. T. VREDENBURG, M. JENNINGS, AND A. LARSON. 2001. Molecular phylogenetics of western North American frogs of the *Rana boylei* species group. *Molecular Phylogenetics and Evolution* 19:131–143.
- MATTHEWS, K. R., AND K. L. POPE. 1999. A telemetric study of the movement patterns and habitat use of *Rana muscosa*, Mountain Yellow-Legged Frog, in a high elevation basin in Kings Canyon National Park, California. *Journal of Herpetology* 33:615–623.
- POPE, K. L. 1999. Mountain Yellow-Legged Frog Habitat Use and Movement Patterns in a High Elevation Basin in Kings Canyon National Park. Unpubl. master's thesis, California Polytechnic Univ., San Luis Obispo.
- POPE, K. L., AND K. R. MATTHEWS. 2001. Movement ecology and seasonal distribution of Mountain Yellow-Legged Frogs, *Rana muscosa*, in a high-elevation Sierra Nevada basin. *Copeia* 3:787–793.
- . 2002. Influence of anuran prey on the condition and distribution of *Rana muscosa* in the Sierra Nevada. *Herpetologica* 58:354–363.
- RALLS, K., D. B. SINIFF, A. DOROFF, AND A. MERCURE. 1992. Movements of sea otters relocated along the California coast. *Marine Mammal Science* 8:178–184.
- REINERT, H. K. 1991. Translocation as a conservation strategy for amphibians and reptiles: some comments, concerns, and observations. *Herpetologica* 47:357–363.
- SINSCH, U. 1990. Migration and orientation in anuran amphibians. *Ethology Ecology and Evolution* 2:65–79.
- . 1992. Amphibians. In F. Papi. (ed.), *Animal Homing*, pp. 213–233. Chapman and Hall, London.
- STEBBINS, R. C. 1985. *Western Reptiles and Amphibians*. Houghton Mifflin Co, New York.

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APPENDIX 1. A summary of tagged frog information including transmitter number, distance relocated, water body origin, sex, start weight, length, relocation lake number, whether frog returned during study, whether frog was moved back by hand in 1999, PIT location in 2000, end weight, start location tracking, and number of days tracked.

	Trans #	Distance relocated (m)	Water body origin	Sex	Start weight (g)	Length (mm)	Relocation lake	Returned during study	Moved back by hand 99	PIT location 2000	End weight (g)	Start relocation tracking	# days tracked
Returned during study	133	485	33	M	24	60	5	y	n	33	20	8/5/1999	11
	275	225	1	F	31	70	4	y	n	2	28	8/5/1999	17
	477	206	2	F	29	67	4	y	n	1, 2	25	8/5/1999	20
	515	215	2	F	38	73	4	y	n	2	n/a	8/5/1999	30
	556	207	2	F	35	73	4	y	n	2	37	8/5/1999	28
Returned by 2000	115	630	4	F	29	67	7	n	n	4	29	8/5/1999	30
	217	478	33	F	33	63	5	n	n	33	27	8/5/1999	28
	350	144	1	M	23	60	5	n	y	2	23	8/11/1999	22
Moved toward capture site	429	430	1	F	24	63	7	n	y	n/a	22	8/5/1999	28
	535	595	4	F	39	75	4	n	y	4	45	8/5/1999	28
	615	205	2	M	22	61	4	n	y	1	21	8/5/1999	28
	76	600	4	F	34	70	7	n	y	4	35	8/5/1999	28
	95	435	1	M	16	58	7	n	y	n/a	16	8/5/1999	23
Stayed in relocation site	176	485	33	F	23	62	5	n	y	33	19	8/5/1999	30
	250	150	5	F	21	60	2	n	y	n/a	17	8/5/1999	28
	289	160	5	F	25	64	2	n	n	n/a	n/a	8/5/1999	14
	369	615	4	F	22	62	7	n	y	n/a	22	8/5/1999	28
	385	436	1	F	18	56	7	n	y	1	16	8/5/1999	28
	636	165	5	F	22	62	2	n	y	n/a	22	8/5/1999	28
	409	615	4	M	18	56	7	n	n	7	17	8/5/1999	28