Patterns of Growth and Movements in a Population of *Ensatina eschscholtzii platensis* (Caudata: Plethodontidae) in the Sierra Nevada, California

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ABSTRACT. — Movements and growth in a population of the terrestrial plethodontid salamander *Ensatina eschscholtzii platensis* were investigated using mark–recapture methods over a period of 1946 days at a mid-elevation site in the central Sierra Nevada of California. The study site included two plots of equal size, totaling 3.0 ha, in an old-growth pine-fir-incense cedar forest. Our sample included 925 captures, and 14% of the animals were recaptured at least once. Males were more active than females; recapture rates were significantly higher for males than for females, despite a 1:1 sex ratio. Variance in distance traveled was significantly greater for males than for females, and most long-range movements were by males, but mean distance traveled did not differ significantly between sexes. The maximum distance moved for males and females was 120.4 m and 60.6 m, respectively. These movement differences between sexes may explain differences in patterns of mtDNA and allozyme variation within the *Ensatina* species complex. We suggest that terrestrial plethodontids routinely travel distances >10 m and caution against calculating home-range sizes from studies conducted only on plots of small size.

Ensatina eschscholtzii is a terrestrial plethodontid salamander that is widespread in mesic western North America. It passes its entire life cycle on land; there is no breeding migration, and salamanders avoid standing or flowing water. Systematics and biogeography of the *Ensatina* complex have been under study (cf. Wake and Yanev, 1986; Moritz et al., 1992; Jackman and Wake, 1994), and ecological data are needed for estimating extent of gene flow and other population genetic parameters.

In September, 1985, we initiated a long-term study of movement patterns in *Ensatina eschscholtzii platensis*. Prior ecological studies had been conducted only for populations of *E. e. eschscholtzii* in southern California and *E. e. xanthoptica* in the East Bay Region of central coastal California (Stebbins, 1954). These taxa differ substantially in allozymes and mitochondrial DNA from the population studied (Wake and Yanev, 1986; Moritz et al., 1992). The primary goal of our study was to compare movement patterns of males and females, and estimate home range size. In addition, growth rates and longevity were determined.

MATERIALS AND METHODS

The study site is in old growth forest of ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*) and black oak (*Quercus kelloggii*) in Calaveras Big Trees State Park, Calaveras Co., California, at an average elevation of 1400 m (see Fig. 1 in Wake et al., 1989). Two 1.5 ha study plots were established on either side of Moran Creek, a small permanent stream. Each plot extended along the creek for 100 m, and up the respective creek bank for 150 m. Grid lines from the plot perimeter were laid every 10 m and numbered stations were established at sites of intersecting lines. At each of these sites a pitfall trap was established within 1 m of the point of intersection (trees, logs, and rocks were avoided). Pitfall traps were used to minimize the amount of disturbance to the habitat (e.g., log turning). Traps were far more effective than day-time or night-time searches for salamanders (unpubl data). The traps were round cans 18 cm deep and 16 cm in diameter. Each trap was provided with drain holes and a bed of wet wood shavings and covered with either a log or piece of bark. There were 176 traps per plot. On the south plot an additional pitfall trap was installed within 1 m of the center of each 10 × 10 m section. Thus, the south plot contained 150 more traps than the north plot. The north plot was flatter and received more sun than the south plot; the south plot was more densely vegetated at ground level. Both plots had nearly full canopy cover from towering old growth trees.

The central Sierra Nevada experiences sharp seasonality in climate that affects salamander movements. Feeding and courting are restricted

to periods when the ground surface is moist (Stebbins, 1954). This site receives on average 1500 mm precipitation per year, and rainfall occurs primarily from September or October through early May. Surface conditions become progressively drier from mid-April through the summer, and the habitat is too dry for surface activity for 4–5 mo. Snow falls on the site every year, usually between December and February, but the amount is highly variable. Snow cover persists for more than a month on only limited parts of the site.

Traps were monitored every 1–4 wk during the wet season, from September, 1985, through March, 1988. Spacing of visits was dependent on weather and was more frequent when conditions were judged to be suitable for activity. A few specimens (<1% of the total) may have spent as long as 4 wk in a trap, but only during the coldest time of the year. Occasionally it was impossible to check all traps because of heavy snow. Tree falls necessitated the minor relocation of a few traps. 1988 was a year of severe drought and surface salamander movements ceased by mid-March. The study was then suspended in anticipation of a controlled burn. However, the burn was not conducted and monitoring was reinitiated from early November, 1990, to January, 1991.

Individual *E. e. platensis* have a distinctive color pattern, consisting of reddish orange dorsal spots or blotches on a gray-brown background. Salamanders retrieved from pitfall traps were photographed in color using a camera with a fixed focal length. Each salamander was sexed (juvenile, male, or female) and photographed against a centimeter grid with a label indicating date, capture site, and the sequential number of each captured salamander. Salamanders were returned to cover objects within 1 m of their site of capture. Following each trapping episode photographs were compared to all previous prints to identify recaptures using individual spotting patterns. From photographs, body size (tip of snout to tail base constriction, to nearest mm) was measured for individuals with multiple captures and tail length (tail base constriction to tip, to nearest mm) was measured for recaptured animals with regenerating tails. Body size and tail regeneration growth rates were calculated using these measurements. We believe the measurements from photographs were accurate to within 1 mm, based on direct comparisons, for salamanders that were straight, but some inaccuracy may have arisen from measuring bent animals.

The Mann-Whitney U test was used to compare recapture interval, m moved/day, m moved/episode, cumulative m moved, and final m from original capture site. The Kolmogorov-Smirnov test compared the distributions for m moved/day and cumulative m moved between males and females. The chi-square test was used to compare the number of captures and recaptures between the north and south plots and the frequency of movements >20 m between males and females. We also tested the sex ratio of captures and recaptures using the chi-square test. Statview 512+ was used for the above comparisons. We also tested for differences between sexes in the variance of cumulative distance moved (log transformed) (Sokal and Rohlf, 1981). Individuals that matured during the study were excluded from analyses unless otherwise noted.

RESULTS

Trapping Success.—A total of 925 living salamanders (including recaptures) were captured during the study (30 dead salamanders [nearly all drowned] and 12 tails without bodies were also found in the traps). Successful traps typically contained one animal, but from two to seven (a unique event) salamanders were found in a single trap. On 26–27 October 1985, 155 animals were captured (389 empty traps, 90 with one animal, 17 with two, four with three, one with four and one with seven). The second most successful trapping produced 77 animals (30 November 1990). On several trapping occasions no animals were found in any of the 502 traps. We caught a lower proportion of juveniles than observed by Stebbins (1954) for a population of *E. e. xanthoptica*. In the laboratory we found that juveniles placed in traps are able to climb out, while adults do so rarely. Thus, we suspect that juveniles escape traps more readily than do adults.

One hundred eleven animals were recaptured at least once (14% of total), including 25 females, 65 males, six juveniles, and 15 small animals that we could not sex. One adult male was recaptured seven times over a period of 902 d, while 93 (84%) of the animals were recaptured only once. While two females and 12 males were recaptured twice, only males were recaptured three times or more. Recapture interval varied from 14–1754 d (mean 197 ± 37.6 d). There was no significant difference in recapture interval between males and females (Mann-Whitney U = 758.5, P = 0.63 for individuals (65 males, 25 females); Mann-Whitney U = 981, P = 0.20 per episode (male episodes = 87, female episodes = 27)).

Trap density was 0.012 traps per m² on the north plot and 0.022 traps per m² on the south plot. Assuming equal densities of salamanders on both plots we expected the number of captures to be proportional to trap density. Although we captured more salamanders on the

south plot than the north plot, numbers were more numerous than expected on the north plot and less numerous on the south (north: 372 captures, south: 437 captures; $\chi^2 = 42.0, P = 0.0001$). We expected higher recapture rates on the south because of higher trap density, and this was the case (north: 53 recaptures, south: 83 recaptures) ($\chi^2 = 0.907, P = 0.34$).

Because trap density was greater on the south plot, shorter movement distances were expected. Mean distance per episode (males and females combined) was significantly different between the two plots (south: 19.7 ± 1.54 m, N = 64; north: 26.5 ± 2.68 m; N = 51; Mann-Whitney U = 1222.5, $P = 0.02$) but total distance traveled did not differ between the plots (south: 27.4 ± 3.6 m, N = 46; north: 30.7 ± 3.9 m, N = 44; Mann-Whitney U = 856.5, $P = 0.21$).

Males and females were present in equal proportions in the total sample (discounting all recaptures: 246 males, 243 adult females; $\chi^2 = 0.02$, $P = 0.89$). In contrast we recaptured significantly more males (65) than females (25); ($\chi^2 = 17.8, P = 0.0001$).

While the minimal distance moved was zero for both males and females, nearly all individuals moved between recaptures. Distance moved did not increase with duration of recapture interval for males or females (males $r^2 = 0.001$, $P = 0.74$; females $r^2 = 0.15$, $P = 0.05$ [b = −0.01]).

Individuals were recaptured in the same trap on only three occasions. An adult female, captured twice, was found in the same trap on dates separated by 1754 d (4.8 yr). An adult male was found at its original site after having been recaptured 14.1 m away 29 d earlier. Another adult male was found in the same trap 70 d after its first capture, but was recaptured three more times in three different traps, the most distant being 25.5 m from the site of first capture.

Final distance from original site of capture varied from 0 m (one male and one female) to 120.4 m (a male). Mean final distance for males was 21.7 ± 2.1 m and for females was 22.2 ± 2.8 m, with no significant difference between the means (Mann-Whitney U = 766.5, $P = 0.68$). Final distances for seven juveniles ranged from 10–86.3 m, including two stream crossings.

The greatest cumulative movement was 150.4 m over a 902 d period by the adult male recaptured seven times; however, this individual ended only 7.1 m (the minimal measurable distance) from the site of initial capture. The greatest cumulative movement by an adult female was a single movement of 60.8 m, and the next greatest distance was 56.6 m. The mean cumulative distance traveled for males was 31.2 ± 3.5 m; for females, 23.3 ± 2.9 m. The means and distributions did not differ between the sexes (Mann-Whitney U = 674, $P = 0.21$; Kolmogorov-
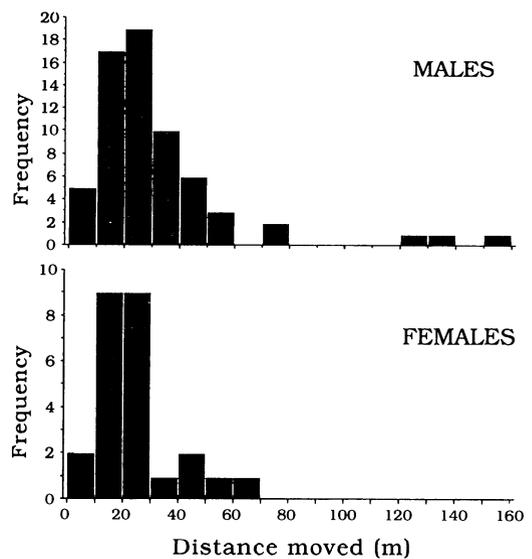

FIG. 1. Frequency histogram of cumulative distance moved by recaptured individuals. There was no statistical difference between sexes in the percentage of individuals that moved more than 20 m per episode.

Smirnov D = 0.23, $P = 0.33$), but males had a greater variance (test for equality of variances, $P < 0.05$).

The mean distance traveled per day did not differ significantly between sexes (by individual: males = 0.33 ± 0.05 m/day; females = 0.21 ± 0.04 m/day; Mann-Whitney U = 774, $P = 0.54$). Furthermore, there was no significant difference between the distributions of the values between sexes (Kolmogorov-Smirnov D = 0.18, $P = 0.43$).

The maximal movement per recapture episode was 120.4 m (406 d interval) by a mature male and 60.8 m (147 d interval) by a mature female. One individual that was a juvenile at first capture but an adult female at the time of recapture moved 82.5 m (218 d interval). Episode distance did not differ significantly between sexes (Mann Whitney U = 1128, $P = 0.76$). Furthermore, there was no significant difference between the percentages of males and females that moved greater than 20 m (recapture episode: $\chi^2 = 0.35$, $P = 0.55$; individual: $\chi^2 = 0.82$, $P = 0.37$) (Fig. 1).

Although Moran Creek is permanent, it is small (1 m or less in width), and even during times of high water there are at least 12 places in the 100 m stretch included in our study area that appeared to be suitable (large logs or piled stones cross the creek) for crossing by terrestrial salamanders. Yet, only three individuals were known to cross the stream, and two of these were juveniles.
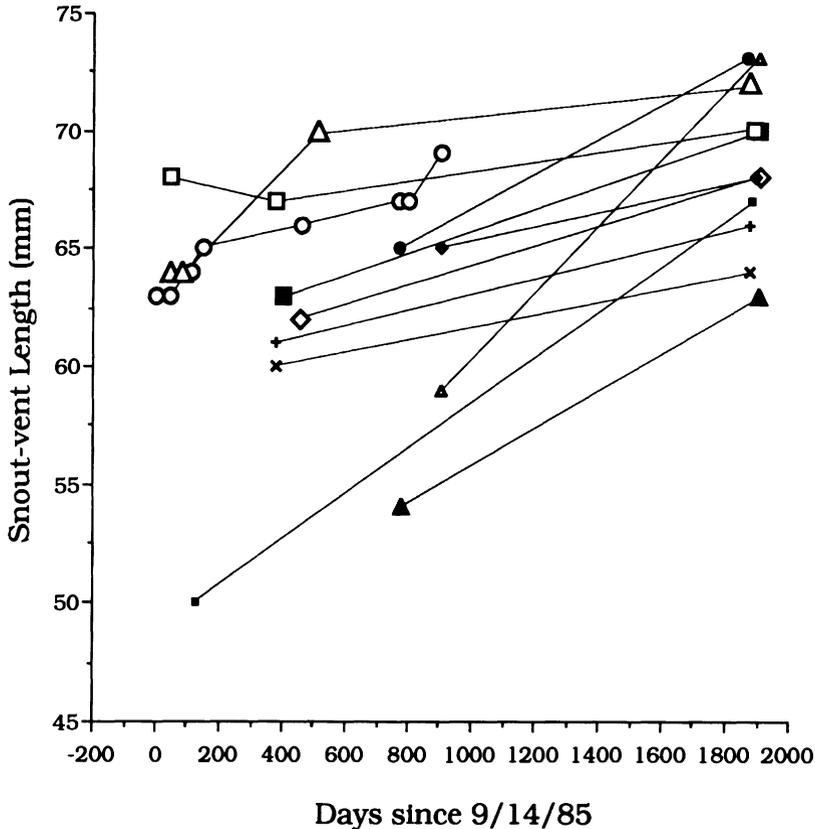
FIG. 2. Measured growth of individual salamanders between recaptures. Only individuals with total recapture intervals >1000 d were used.

Growth and Longevity.—Individual growth patterns for animals with >1000 d recapture intervals are presented in Fig. 2. Mean growth rates for males and females varied greatly (males: 0.005 ± 0.0049 mm/day; females: 0.092 ± 0.0071 mm/day). Growth rates were computed without taking into account seasonal differences in activity. Thus, if salamanders experienced no growth during part of the year, the growth rate would be higher during periods of activity. Overall, growth rates decreased with increasing body size (log growth rate in mm/day = 1.6–4.3 (log mean SVL in cm); $P = 0.02$; $r^2 = 0.10$).

The tail was lost by 5.4% (N = 6) of recaptured animals during our study and several animals had no tail when initially captured. The tail was regrown by 9% (N = 10) of recaptures during the study. Rates of tail regeneration were variable (3 females: 0.0047 mm/day ± 0.0023; 6 males: 0.0037 mm/day ± 0.0009; 1 juvenile: 0.0012 mm/day). We recaptured one animal frequently enough (N = 5) to document complete tail regeneration. The tail grew from 0.3 mm to 52 mm in 2 yr.

Because the variance around estimated growth rates decreased with longer recapture intervals (Fig. 3), we used animals with recapture intervals >1000 d to estimate age. The longest recapture interval (which includes two recaptures) was 1859 d (5.09 yr). This adult male was 68 mm SVL at first capture and 70 mm SVL at final recapture (growth rate 0.0011 mm/d). This recapture interval was not unusual; there were 13 recapture intervals >1000 d (N = 11 males, 2 females; x̄ = 1367 ± 320 d). Ages of these salamanders were calculated using estimated age at sexual maturity (Stebbins, 1954), average growth rates, and length of recapture interval. For example, a conservative age estimate for the animal recaptured after 1859 d is 15.2 yr (3 yr to 55 mm (Stebbins, 1954), 7.12 yr to 68 mm (using average male growth rate of 0.005 mm/d), and 5.09 yr to 70 mm (actual recapture interval)). The actual growth rate of this individual was only 0.0011 mm/d, but we assumed the faster average rate from sexual maturity to time of first capture, and thus our age estimate is conservative. Conservative age estimates for
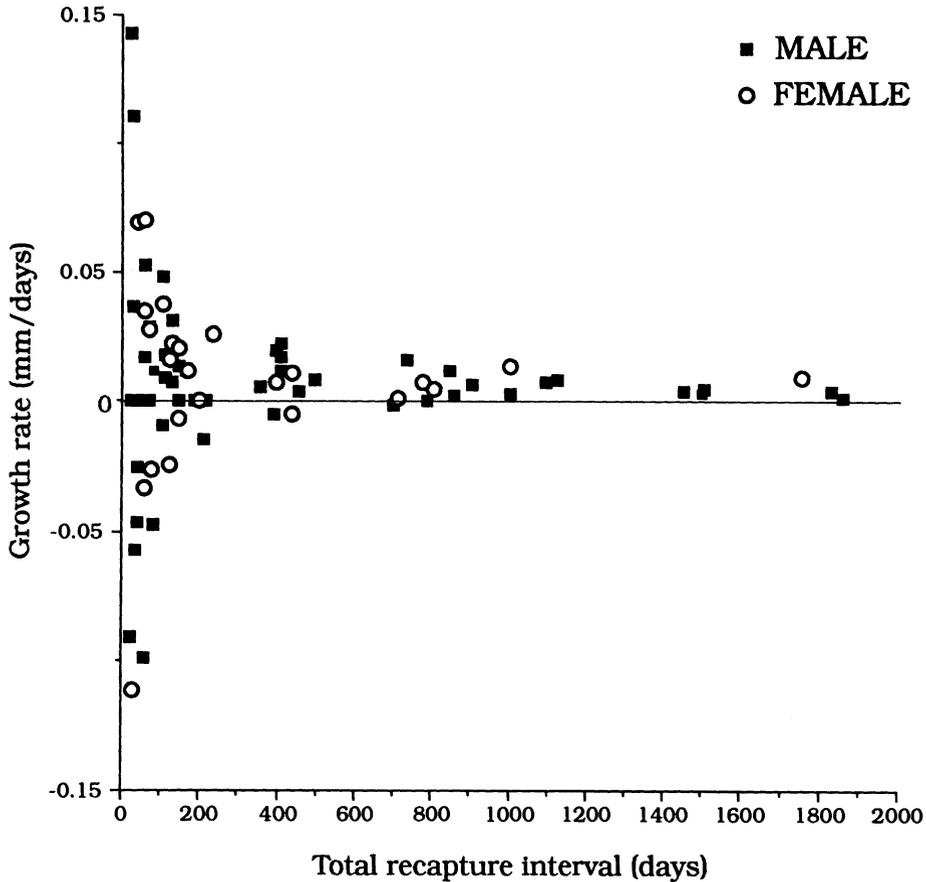
Fig. 3. Estimated growth rate plotted as a function of the interval from first to last capture. Variance around the estimates decreases as recapture interval increases. Thus, only salamanders with a total recapture interval >1000 d were used in age calculations.

those with >1000 d recapture intervals (N = 13) ranged from 5.5 yr to 14.9 yr (age: $\bar{x}$ = 9.6 ± 2.8 yr, size: $\bar{x}$ = 67.8 ± 3.6 mm).

DISCUSSION

Movement Patterns.—Because some males traveled greater distances than females, the variance in total distance moved was significantly greater in males than females. Consequently, over hundreds and thousands of years, males as a group disperse more than females, thus contributing disproportionately to gene flow. Stebbins' (1954) studies on a different subspecies support this conclusion; female *E. e. eschscholtzii* were more sedentary than males. A difference in movement patterns between males and females has been observed in *Plethodon glutinosus* as well (Merchant, 1972).

This result offers a possible explanation for differences in patterns of allozyme and mtDNA variation in *E. eschscholtzii.* Evidence from al-

lozymes was interpreted as a northward dispersal of southern *E. e. platensis,* but the contact zones with northern populations for allozymes and for mtDNA did not correspond (Jackman and Wake, 1994; Schneider and Wake, unpubl. data). The allozymes, carried by both sexes, had spread much farther than had the mtDNA, which is transmitted only by the relatively sedentary females.

Recapture Rates.—Because males and females were present in equal numbers in the total sample, we expected equal numbers of recaptures. The higher recapture rate for males has several possible interpretations: (1) females move off the plot more than males; (2) males have lower mortality rate than females; (3) females are better at avoiding traps after being caught once; (4) males are more active on the surface than females. Hypothesis 1 predicts higher vagility for females than for males and our movement data do not support this prediction. Hypothesis

TABLE 1. Plot size, home range size, and maximum distance traveled for terrestrial plethodontine salamanders, listed in order of increasing plot size. Note that home range estimates increase as plot size increases. N.A. = not available.

Plot size (m)	Average home range (m²)	Max. dis. traveled (m)	Sex	Species	Reference
3 × 3	0.163	N.A.	male	P. cinereus	Mathis, 1991
3 × 3	0.162	N.A.	female	P. cinereus	Mathis, 1991
10 × 10	0.49	N.A.	male	P. teyahalee	Nishikawa, 1990
10 × 10	1.03	N.A.	female	P. teyahalee	Nishikawa, 1990
10 × 10	0.6*	N.A.	N.A.	P. hubrichti	Kramer et al., 1993
10 × 10	5.04	N.A.	male	P. jordani	Nishikawa, 1990
10 × 10	1.87	N.A.	female	P. jordani	Nishikawa, 1990
30.5 × 15.2	37.6	N.A.	male	P. jordani	Merchant, 1972
30.5 × 15.2	9.2	N.A.	female	P. jordani	Merchant, 1972
30.5 × 15.2	47.2	N.A.	male	P. glutinosus	Merchant, 1972
30.5 × 15.2	21.4	N.A.	female	P. glutinosus	Merchant, 1972
4.6 ha	10.78	N.A.	male	P. cinereus	Kleeberger and Werner, 1982
4.6 ha	19.85	N.A.	female	P. cinereus	Kleeberger and Werner, 1982
3.2 ha	N.A.	91.5	N.A.	P. glutinosus	Wells and Wells, 1976
1.5 ha	N.A.	120.4	male	E. eschscholtzii	present study
1.5 ha	N.A.	60	female	E. eschscholtzii	present study

* Median size.

2 receives no support from our recapture data; there is no significant difference between male and female recapture intervals. We have no behavioral data to address hypothesis 3, but it seems unlikely. Hypothesis 4 is indirectly supported by movement data—the variation in cumulative distance traveled was greater for males than for females, suggesting that some males move more often than females. Consequently, more males than females are recaptured.

Home Range and Territory Size.—Because of the difficulty in observing free-ranging terrestrial salamanders without degrading habitat or interfering with behavior, few studies have examined movement patterns (but see Nishikawa, 1990; Mathis, 1991). Our study focused on large scale movements (smallest measurable non-zero distance was 7.1 m) so we did not attempt to estimate home range or territory size. Our movement data suggest that distance traveled (and thus home range or territory size) may well be correlated with size of the study plot (Table 1).

Estimated home range sizes for *Plethodon cinereus* range from 0.162 (Mathis, 1991) to 19.85 m² (Kleeberger and Werner, 1982) for plots ranging from 9 m² to 4.6 ha. Studies using small plots may yield small home range sizes because large movements are not detected. For example, had we used a 10 by 10 m grid, the male we recaptured 7 times would have been recaptured within the 10 × 10 plot over the course of the study, but movements to more distant pitfall traps would not have been detected.

There are a few reports of relatively long-range movements in other terrestrial salamanders. Kleeberger and Werner (1982) suspected that some individuals of *P. cinereus* on their study site had moved off-site and later returned. An individual *Plethodon glutinosus* moved 91.5 m (Wells and Wells, 1976), and some *P. jordani* display homing behavior over a displacement distance as great as 150 m (Madison, 1969). Our data suggest that such long range movements occur regularly in *Ensatina*.

A study on small scale movements of *Ensatina*, comparable to the studies on *Plethodon*, would yield valuable data regarding differences in movement patterns and territory use. Furthermore, studying the effects of season on movement patterns may reveal that long range movements only occur at certain times of the year. For example, Mathis' (1991) study focused on movement patterns only in the non-breeding season in order to avoid spacing or movement patterns related to breeding activity.

Capture disrupts normal activity patterns (possibly leading to loss of territory in some cases). A few individuals spent up to four weeks in the cans (always during the coldest time of the year when surface activity was minimal). Some long range movement might have been induced. Photography was an additional interference, but we assumed that the effects were short-lived.

Growth and Longevity.—Based on growth data as well as time intervals between recaptures, we estimate that animals approximately 68 mm

SVL are 9.6 yr old. Our estimates are slightly greater than those of Stebbins (1954), who estimated the oldest marked individual (size of 72 mm) in his study population to be at least 8½ yr old. Growth rates for tail regeneration were consistent with Stebbins' (1954) estimates of approximately 2 yr for complete regeneration.

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