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Growth, Age at Maturity, and Age-Specific Survival of the Arboreal Salamander (*Aneides lugubris*) on Southeast Farallon Island, California

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ABSTRACT.—Growth, age at maturity, and survival are life-history parameters that provide important information for understanding population dynamics. We modeled growth and age at maturity for an island population of Arboreal Salamanders, *Aneides lugubris*, using snout-vent length (SVL) growth intervals from a 4-yr capture-mark-recapture study fit to the von Bertalanffy growth interval model. We estimated annual survival as a function of SVL using a multistate open robust design model, and computed age-specific survival using results from the von Bertalanffy growth model. Arboreal Salamanders have indeterminate growth that slows with age from hatchling size (24.4-mm SVL) to the mean adult (asymptotic) size of 66.0-mm SVL. Age at maturity is 2.69 yr, and average adult age is 8–11 yr. Annual survival increased with age from 0.363 in age 0 to 0.783 in ages >4 yr. Our results provide the first estimates of life-history parameters for this species and indicate similarities to other terrestrial salamanders from low-elevation Mediterranean climates.

Quantifying life-history and demographic parameters enables ecologists to interpret and understand population dynamics of animals (Lebreton et al., 1992; Caswell, 2001). For example, growth rates, age at first reproduction, and age-specific survival are important parameters in life-history models (Cole, 1954; MacArthur and Wilson, 1967). Growth and survival depend on population density, competition, and health factors as well as environmental conditions such as food availability or climate (Schoener and Schoener, 1978; Morrison and Hero, 2003). Therefore, life-history characteristics can be used to make comparisons among populations and to examine effects of management activities (Morrison and Hero, 2003; Bruce, 2005). A larger proportion of amphibian species are at risk of extinction than of any other taxon (Wake and Vredenburg, 2008), yet few demographic studies of marked individuals have been conducted on salamanders (but see Tilley, 1980; Marvin, 2001; Waldron and Pauley, 2007). Most plethodontids are relatively long lived, slow to mature, and have lower fecundity than most anurans (Petranka, 1998), rendering them particularly sensitive to conditions that influence adult survival (Benton and Grant, 1996). The majority of recent work on demography of plethodontid salamanders has been focused on the southeastern United States (Waldron and Pauley, 2007). We present empirical data from the first 4 yr of a capture-mark-recapture (CMR) study to determine growth rates and demographic characteristics of an island-dwelling population of the plethodontid Arboreal Salamander (*Aneides lugubris*) from California, USA. The largest species of the genus *Aneides*, the Arboreal Salamander is a California near-endemic, occurring in coastal oak woodlands, conifer forests, and shrublands from Humboldt County to northern Baja California, Mexico, including the offshore islands of South Farallon, Los Coronados, Catalina, and Año Nuevo and several smaller islands in the San Francisco Bay (Stebbins, 1951; Anderson, 1960; Petranka, 1998). The Arboreal Salamander has no aquatic larval stage, eggs are laid in terrestrial nests, and hatchlings resemble miniature adults (Wake and Hanken, 1996). The Arboreal Salamander is the only herpetile inhabiting the South Farallon Islands, a set of offshore rocky islands situated on the edge of the continental shelf in the Pacific Ocean. Localized management activities at Southeast Farallon Island, such as eradication of invasive plants and mice, could adversely impact salamanders, particularly if chemicals are

used extensively, but such activities also could have positive effects by removing competitors. Baseline demographic data are critical to documenting effects of existing and future changes to salamander populations (Bailey et al., 2004). We initiated this long-term CMR study in 2006 to provide baseline data on growth rates, changes in growth with age and size, age at maturity, and age-specific survival of this unusual insular Arboreal Salamander population. Here, we report on data from 2006 to 2010.

MATERIALS AND METHODS

Study Area.—Southeast Farallon Island (37°42'N, 123°00'W) is located 44 km west of San Francisco, California, USA. Comprising 48 ha, it is an elevated portion of a granitic submarine ridge running southwest from Point Reyes (Hanna, 1951). The shoreline is deeply cut by surge channels. The upland portion of the island is a series of rocky crags, some with sheer cliffs dropping into the sea on one or two sides. Along the southwest side there is a broad marine terrace approximately 15 m above sea level. On the lower talus slopes and level terrace, guano-enriched soil is well-developed between rocks. Burrows of seabirds (petrels and auklets) occur over nearly the entire island and, together with the many rocks and crevices, provide abundant cover for salamanders. The dominant vegetation is the herbaceous annual maritime goldfields (*Lasthenia maritima*), although in some areas nearly pure stands of dense, low, invasive annual grasses (*Hordeum* sp., *Bromus* spp., *Poa* sp.) are found.

Temperature is moderate due to oceanic influence (1971–2009: mean = 12.9°C, SD = 1.6), with a Mediterranean climate of winter rains (1971–2009: mean = 49.1 cm, SD = 18.2) and dry but foggy summers and autumns (PRBO, unpublished data). The islands contain no standing or running fresh water with the exception of puddles and seepage areas during winter and spring (Anderson, 1960). During the summer and fall, the island becomes very dry and its appearance is almost desert-like.

Salamander Capture and Measurement.—Arboreal Salamanders are primarily nocturnal, foraging for small invertebrates such as spiders, beetles, isopods, larval lepidoptera, ants, sow bugs, caterpillars, and centipedes on the ground or on the trunks of trees (Stebbins, 1951; Holland and Goodman, 1998). During the day, they remain under rocks, boards, bark, and decaying logs; inside decaying stumps and logs; in Woodrat houses and rodent burrows; and in stone walls and crevices, making them easily captured using cover objects.

This long-term monitoring study was initiated during the rain year 2007 with the placement of 106 cover objects on

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TABLE 1. Summary of Arboreal Salamander (*Aneides lugubris*) surveys at Southeast Farallon Island, California. Rain year is defined as September–August and is referred to by the year in January–August, so rain year 2007 is from September 2006 to August 2007. $N\text{-hat}$ (\pm SE) is the estimate of superpopulation size, residence time (\pm SE) is the average number of surveys (\sim 2 weeks between surveys) a salamander remained at the surface, under a cover board each year. Residence and $N\text{-hat}$ were estimated from multistate open robust design capture–recapture model $\{S(e2+y+SVL) Psi out=in(zero) pent(y+srvy) Phi(y+srvy+SVL) p(y*srvy)\}$.

	Rain year			
	2007	2008	2009	2010
Begin date	15 Dec 2006	1 Nov 2007	1 Nov 2008	15 Sep 2009
End date	1 Mar 2007	1 May 2008	1 May 2009	15 Jul 2010
Rain (cm)	28.1	41.3	30.4	49.9
No. of records	186	601	385	653
Individuals marked	82	168	103	171
No. of recaptures	50	232	131	422
$N\text{-hat}$	141.4 \pm 14.0	303.2 \pm 22.0	344.4 \pm 30.2	287.6 \pm 7.8
Residence time	2.74 \pm 0.30	4.92 \pm 0.27	2.17 \pm 0.18	4.62 \pm 0.27

Southeast Farallon Island on 6 November 2006. A rain year is defined as September–August and is referred to by the year in January–August, so rain year 2007 is from September 2006 to August 2007. One hundred cover boards were redwood planks ($30 \times 30 \times 5$ cm) placed in pairs approximately every 600 cm (mean = 601 cm, SD = 270, range = 248–1,265) along a path from the north to the south side of the island. Five cover boards were irregularly sized plywood cover boards (1 cm in thickness, 2×300 cm², $3 \times 8,000$ cm²), and one was 3 planks joined into a cover board ($150 \times 150 \times 2$ cm). Boards were placed directly on soil along a trail that curves around Little Lighthouse Hill from North Landing to near Corm Blind Hill. Ninety-six cover boards were placed in talus slope and cliff habitat, and 10 cover boards were on the marine terrace. The larger boards were placed haphazardly near the main cover board trail (mean distance from larger boards to cover board trail = 936 cm, range = 113–1,905).

PRBO biologists checked for the presence of salamanders during the day under 106 cover boards on the day 1 and 15 of the month (or nearest possible day) from approximately 1 November to 1 May, the period of greatest surface activity for this species in rain years 2007–2010. Checks usually started in the morning and took from 2 to 10 h. Protocol was to continue sampling on days 1 and 15 of each month until no more salamanders are captured during a given occasion. Logistical constraints shortened the sampling season in the first year of the study, and sampling was extended in 2010 due to a particularly wet season (Table 1). Captured animals were measured from snout to posterior end of vent (SVL) to the nearest 1 mm, weighed to the nearest 0.1 g, and sexed (when eggs or mental gland were present). From December 2006 to December 2009, a subsample of captured animals was individually identified with toe clips in a unique identification code (Wake scheme in Donnelly et al., 1994), digital photographs of lateral spot patterns, or both (Table 1). The marked subsample was typically the first 10–30 unmarked individuals >35-mm SVL captured each survey, with the number dependent upon survey time constraints. In rain year 2007, toe clips were the dominant method used for identification, with few photos taken. From November 2008 to December 2009, toe clips and photos were taken of newly marked animals, and photos taken of recaptured toe-clipped animals. Beginning December 2009, we photographed every captured salamander for photo identification. Using toe clips for verification, we determined that spot patterns did not change appreciably between years and we could identify individuals based on spot patterns more reliably than from toes that could regenerate within 12 months. We developed a photo database of captured salamanders >35 mm for long-term mark–recapture monitoring. Salamander capture, handling, and marking procedures followed the guidelines for use of live

amphibians and reptiles in field research of the American Society of Ichthyologists and Herpetologists, The Herpetologists' League, and the Society for the Study of Amphibians and Reptiles. We collected data on temperature and rainfall by checking a permanent thermometer three to five times per day and a permanent rain gauge every day at noon.

Detectability, Emigration, and Survival.—Plethodontids are found at the surface during the moist season of the year, but they retreat into crevices and burrows during dry weather, as well as intermittently during wet seasons. They are territorial, have very small home ranges (Petranka, 1998), and aggressively defend high-quality cover items (Smith and Pough, 1994). Terrestrial salamander populations are largely subterranean, with only some individuals near the surface and available for capture (detection) on a given sampling occasion (Taub, 1961; Heatwole, 1962; Petranka and Murray, 2001). Site-specific habitat characteristics, environmental conditions, or seasonal behavioral patterns can influence whether animals are available for capture. Estimating detection probability of salamanders has several components. A salamander is in the "superpopulation" if it ever occupies a cover board as part of its home range during any survey. A salamander in the superpopulation may be unavailable for capture during a given survey because it is underground or at the surface but not under a cover board (Bailey et al., 2004). In addition, detection probabilities of plethodontids vary temporally and can have a transient, or trap-shy age-like structure (Stewart and Bellis, 1970; Semlitsch, 1980; Howard, 1987; Smith and Petranka, 2000; Bailey et al., 2004). Trap shyness means higher initial capture probabilities than recapture probabilities.

Detectability is estimated as conditional detection probability (p), or the probability that an animal is alive, at the surface, and under a cover board where it can be captured during sampling occasion j ($j = 1, 2, \dots, J$, where J is the total number of sampling occasions). We used multistate open robust design (MSORD) mark–recapture analysis to estimate detectability and other parameters. MSORD models are derived from Kendall and Bjorkland (2001) and Kendall and Nichols (2002), based on the design first described by Schwarz and Stobo (1997).

The MSORD models are a combination of several mark–recapture model types. The robust design aspect means multiple capture occasions occur between survival intervals, for multiple secondary capture occasions (j) within each primary sampling period (t). The multistate aspect includes an explicitly unobservable state that marked animals can move into and out of to produce survival and detectability estimates unbiased by temporary emigration from the sampling area (cover boards). We defined animal states as observable (o) and not observable (n). The open aspect means the model does not make the unrealistic assumption of demographic closure (no births, deaths, immigration, or emigration) between secondary

TABLE 2. Model selection results for multistate open robust design modeling of Arboreal Salamander capture–recapture data from Southeast Farallon Island, California, 2006–2010. *S*, survival; *Psi*, movement (temporary emigration); *pent*, entry probability; *Phi*, residence probability; *p*, capture probability; *e2*, 2 encounter classes; *y*, year; *srvy*, survey.

No.	Model	AIC _c	ΔAIC _c	AIC _c weight	Model likelihood	Num. Par.	Deviance
5	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y+srvy</i>) <i>Phi</i> (<i>y+srvy+SVL</i>) <i>p</i> (<i>y*srvy</i>) }	6370.3	0	0.99	1	81	6197.6
7	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y</i>) <i>Phi</i> (<i>y+srvy+SVL</i>) <i>p</i> (<i>y*srvy</i>) }	6380.7	10.5	0.01	0.01	69	6235.1
17	{ <i>S</i> (<i>e2+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y+srvy</i>) <i>Phi</i> (<i>y+srvy+SVL</i>) <i>p</i> (<i>y*srvy</i>) }	6383.9	13.6	0	0	79	6215.8
4	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y+srvy</i>) <i>Phi</i> (<i>y*srvy+SVL</i>) <i>p</i> (<i>y*srvy</i>) }	6390.9	20.6	0	0	102	6169.7
15	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y+srvy</i>) <i>Phi</i> (<i>y+srvy+SVL</i>) <i>p</i> (<i>srvy</i>) }	6401.6	31.3	0	0	54	6288.9
11	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y+srvy</i>) <i>Phi</i> (<i>srvy+SVL</i>) <i>p</i> (<i>y*srvy</i>) }	6404.2	33.9	0	0	78	6238.3
13	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y+srvy</i>) <i>Phi</i> (<i>y+srvy+SVL</i>) <i>p</i> (<i>y+srvy</i>) }	6406.0	35.7	0	0	57	6286.8
6	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y+srvy</i>) <i>Phi</i> (<i>y+srvy+SVL</i>) <i>p</i> (<i>y+srvy</i>) }	6409.8	39.5	0	0	57	6290.6
9	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (.) <i>Phi</i> (<i>y+srvy+SVL</i>) <i>p</i> (<i>y*srvy</i>) }	6436.6	66.3	0	0	66	6297.6
3	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y*srvy+SVL</i>) <i>Phi</i> (<i>y*srvy+SVL</i>) <i>p</i> (<i>y*srvy+SVL</i>) }	6440.1	69.9	0	0	125	6164.0
2	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(<i>e2+yr+SVL</i>) <i>pent</i> (<i>y*srvy+SVL</i>) <i>Phi</i> (<i>y*srvy+SVL</i>) <i>p</i> (<i>y*srvy+SVL</i>) }	6449.9	79.6	0	0	129	6164.0
8	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>srvy</i>) <i>Phi</i> (<i>y+srvy+SVL</i>) <i>p</i> (<i>y*srvy</i>) }	6464.7	94.4	0	0	78	6298.8
1	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=(<i>e2+yr+SVL</i>) in(<i>e2+yr+SVL</i>) <i>pent</i> (<i>y*srvy+SVL</i>) <i>Phi</i> (<i>y*srvy+SVL</i>) <i>p</i> (<i>y*srvy+SVL</i>) }	6477.7	107.5	0	0	133	6181.9
14	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y+srvy</i>) <i>Phi</i> (<i>y+srvy+SVL</i>) <i>p</i> (<i>y</i>) }	6507.5	137.2	0	0	44	6416.4
12	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y+srvy</i>) <i>Phi</i> (<i>SVL</i>) <i>p</i> (<i>y*srvy</i>) }	6511.1	140.8	0	0	66	6372.1
16	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y+srvy</i>) <i>Phi</i> (<i>y+srvy+SVL</i>) <i>p</i> (.) }	6531.9	161.6	0	0	41	6447.2
10	{ <i>S</i> (<i>e2+y+SVL</i>) <i>Psi</i> out=in(zero) <i>pent</i> (<i>y+srvy</i>) <i>Phi</i> (<i>y+SVL</i>) <i>p</i> (<i>y*srvy</i>) }	6535.9	165.7	0	0	69	6390.3

sampling periods. The following parameters are found in the MSORD data type in program MARK: *S*(*o t*) = survival, survival from primary period *t* to *t* + 1 for those animals occupying state *o* during period *t*; *Psi*(*o-n t*) = movement, probability an individual in state *o* in primary period *t* moves to state *n* in primary period *t* + 1, given it survives to period *t* + 1; *pent*(*o t*) = entry, probability that an individual in state *o* in primary period *t* is a new arrival (within that primary period) to the study area for that state at capture occasion *j*; *Phi*(*o t j a*) = residence, probability that an individual in the study area associated with state *o* at capture occasion *j*, and who first arrived in the study area *a* during previous capture occasions, is still in the study area at capture occasion *j* + 1; and *p*(*o j*) = detectability, probability of capturing an individual in the study area in state *o* at capture occasion *j*.

Survival (*S*) is identical for both states. This necessary constraint is a reasonable assumption given that salamanders in both states are essentially a single pool of animals that may or may not be available for capture. Movement between states (*Psi*) is similar to temporary emigration (gamma) parameters in Pollock's robust design (Kendall et al., 1997). *Psi*(*o-n*) is temporary emigration away from the cover boards so the animal is not available for capture. *Psi*(*n-o*) is migration back to the cover boards where the animal is available for capture. If the 2 *Psi* parameters are equal, emigration is random, resulting in less precise but unbiased survival estimates. If the 2 *Psi* parameters are unique, emigration is Markovian, resulting in biased survival and detection estimates. Zero temporary emigration also results in unbiased estimates of survival and recapture. We modeled *Psi* as Markovian, random, and zero in the fully parameterized model (models 1–3 in Table 2), and we used Akaike's Information Criterion (AIC) model selection to indicate the most parsimonious structure of *Psi* (Akaike, 1985). For animals in the unobservable state *n*, *pent*(*n*), *Phi*(*n*), and *p*(*n*) are fixed at zero. For animals in the observable state *o*, *pent*(*o*), *Phi*(*o*), and *p*(*o*) were modeled as fully time dependent within and between years in the global model and simplified where AIC model selection indicated more parsimonious fit to the data.

The RELEASE goodness-of-fit procedure in program MARK on individual years of data showed that survival probability of newly observed and previously observed individuals differed, indicating a large portion of the newly observed individuals were present for only one observation period. This may be due

to handling effects (Brownie et al., 1978), transients in the population (Pradel et al., 1997), or observation heterogeneity (Prévot-Julliard et al., 1998). Whatever the cause, individuals with a zero probability of survival after their initial capture (hereafter called transients) will bias survival and emigration estimates. Presence of large numbers of transients required age-like encounter class structure to be added to survival {*S*(*e2*)} and transition {*Psi*(*e2*)} models to account for this extreme form of heterogeneity. In these model structures, the first encounter class is a mixture of residents and transients, with subsequent encounter classes made up solely of residents. In addition to encounter class, we modeled survival and emigration as year dependent in the fully parameterized model. We simplified survival and emigration to time constant where AIC model selection indicated a more parsimonious model of the data. SVL is positively correlated with age (Halliday and Verrell, 1988), so we also modeled *S*, *Psi*, *pent*, *Phi*, and *p* as a function of the individual covariate SVL to examine age-specific effects on parameters. We removed SVL from parameter model structure where the 95% confidence interval (CI) of the beta coefficient included zero.

Model Selection.—Our a priori model set is presented in Table 2. We started with the fully parameterized “global” model with Markovian temporary emigration (model 1). In the global model, *S* has 2 encounter classes to control for transients, annual variation, and variation as a function of SVL (a proxy for true age); *Psi* is Markovian ($Psi^{o-n} \neq Psi^{n-o}$), has 2 encounter classes to control for transients, annual variation, and variation as a function of SVL; and *pent*, *Phi*, and *p* vary in every survey and as a function of SVL. When we found a most parsimonious structure for a given parameter, that parameter kept its most parsimonious model structure as other parameters were evaluated for their most parsimonious structure (Burnham and Anderson, 2002).

We first tested for the most appropriate model of *Psi* that would determine what form of temporary emigration was present. Model 2 was the random temporary emigration model, and model 3 was zero temporary emigration. Next, we examined the beta coefficients of all SVL functions in the top-ranked model of *Psi* and removed all whose 95% CI included zero. Models 4–6 removed the interaction term from *p*, *Phi*, and *pent*. Models 7–16 simplified the temporal variation in *p*, *Phi*, and *pent* to find the most parsimonious form. Model 17 removed annual variation from *S* to model constant survival.

We used the logit link function for all parameters except *pent*. Values of *pent* for all surveys within a year must sum to 1.0, so for *pent* we used unique mlogit link functions in each year. Two additional derived estimates from the MSORD models are $N\text{-hat}$, the population size, and *residence time*, the average number of surveys that individuals spent available for capture in the study area (i.e., at the surface and under a cover board).

Size and Growth.—Arboreal salamanders are the largest species of *Aneides*; mature individuals reportedly range in size from 65- to 100-cm SVL (Staub and Wake, 2005). Age-size relationships suggest that 3 years is required to reach maturity and the minimum size of sexual maturity was 34-mm SVL for females (Anderson, 1960), although this size may be small for typical females reaching sexual maturity (Staub and Wake, 2005). However, size-frequency extrapolation can be problematic because of the assumption that age and size are statistically correlated and because it requires knowledge of adult growth rates and age-specific variation in body size (Gibbons, 1976; Halliday and Verrell, 1988). We modeled growth and estimated age at reproductive maturity for this insular population using mark-recapture data.

We calculated annual growth rates of known individuals as the percentage of change in SVL from one rain year to the next. Because sex was difficult to determine, we pooled all individuals for growth analyses. We used growth interval forms of the von Bertalanffy equation to model annual growth (Fabens, 1965),

$$L_2 = a - (a - L_1)e^{-kd}, \quad (1)$$

where L_1 is the length at first capture, L_2 is the length at recapture, d is the time between capture and recapture (i.e., number of growing seasons, always = 1 in these data), e is the base of the natural logarithms, a is the asymptotic size, and k is the characteristic growth parameter (Fabens, 1965; Schoener and Schoener, 1978; Frazer and Ehrhart, 1985; Aresco and Guyer, 1999). Asymptotic size represents the mean size at which growth essentially stops. We used nonlinear least squares regression (command `nl`, STATA version 10.0; StataCorp LP, College Station, TX) to fit the recapture data to equation 1 and to estimate asymptotic SVL (a) and the characteristic growth parameter (k).

We estimated mean age at reproductive maturity using modeling procedures outlined by Frazer and Ehrhart (1985) with the general von Bertalanffy equation,

$$L = a(1 - be^{-rt}), \quad (2)$$

where t is age, a is the asymptotic size, r is the characteristic growth parameter, and e is the base of the natural logarithms. Because equation 2 requires knowledge of age, we solved for t by calculating parameter b using the estimates of a and k obtained from equation 1 (Frazer and Ehrhart, 1985). Mean hatchling SVL (h) of Arboreal Salamanders was 24.4 mm (SD = 1.73), which was based on the measurements of newly hatched individuals ($n = 44$ hatchling-size individuals) found in the study area. From equation 2, we solved for b ,

$$b = 1 - (h/a),$$

where h is the average SVL for hatchlings and a is asymptotic size.

Thus, the model we used was as follows:

$$L = 66.0(1 - 0.63e^{-0.30t}). \quad (3)$$

We solved for t at given values of $L = L_m$, that is, an estimate of the mean size at reproductive maturity (Frazer and Ehrhart, 1985), in which the average SVL of the adult males and females in the population (i.e., mean = 60.9, SE = 6.5) was used as the

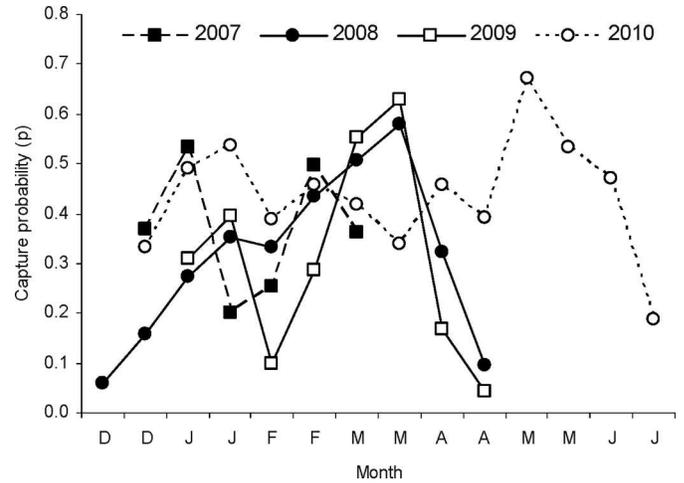


FIG. 1. Capture probability (p) estimates by survey for Arboreal Salamanders (*Aneides lugubris*) on Southeast Farallon Island, California. Two surveys were conducted each month. Estimates from multistate open robust design capture-recapture model $\{S(e2+y+SVL) \text{ Psi out} = \text{in}(\text{zero}) \text{ pent}(y+srvy) \text{ Phi}(y+srvy+SVL) \text{ p}(y*srvy)\}$.

upper limit for L_m , and the smallest recorded SVL of a salamander with sexually dimorphic characters (i.e., 43.0) was used as the lower limit for L_m (Waldron and Pauley, 2007). We also examined a frequency distribution of SVL to determine number of year classes between hatchling and adult size.

We estimated monthly within-rain-year growth in SVL and change in condition (mass) by calculating changes in SVL and mass for adult individuals that were captured and measured more than once within a rain year. Hatchlings were not individually identifiable, so we estimated within-rain-year growth rate of hatchling-size individuals. We calculated average SVL for all hatchling-size animals captured under a cover board pair during a given survey and then computed percentage of change and absolute change between surveys for each cover board pair that included hatchlings. Hatchlings have been defined as animals of 15–30-mm SVL (Anderson, 1960), or 26–32-mm tail length (Storer, 1925; Stebbins, 1951). We defined hatchlings as individuals <30-mm SVL, subadults as 30–45-mm SVL, and adults as >45-mm SVL.

RESULTS

We obtained 1,833 records of captured salamanders from cover board surveys between 16 December 2006 and 1 August 2010. Of these, 520 individuals were marked, with 265 individuals captured more than one time. Years 2007 to 2009 were below-average rainfall years and 2010 was above average (Table 1). $N\text{-hat}$ was stable (Table 1), and the first estimate in 2007 is biased low by the presence of significant numbers of transients.

Detectability, Emigration, and Survival.—The most parsimonious model in the set was model 5 (Table 2): S with encounter class structure, annual variation, and as a function of SVL [$S(e2+\text{year}+SVL)$], zero temporary emigration [$\text{Psi}(\text{zero})$], probability of entry with additive model structure varying by survey and year [$\text{pent}(\text{year} + \text{survey})$], residence probability with additive model structure varying by survey and year and as a function of SVL [$\text{Phi}(\text{year} + \text{survey} + SVL)$], and detectability with multiplicative model structure varying by survey and year [$\text{p}(\text{year} * \text{survey})$]. This model was far superior to other models in the set, 100 times more likely than the next highest-ranked model to be the best in the set. Because the top-ranked model was so superior, we report parameter estimates only from model 5 and did not use model averaging.

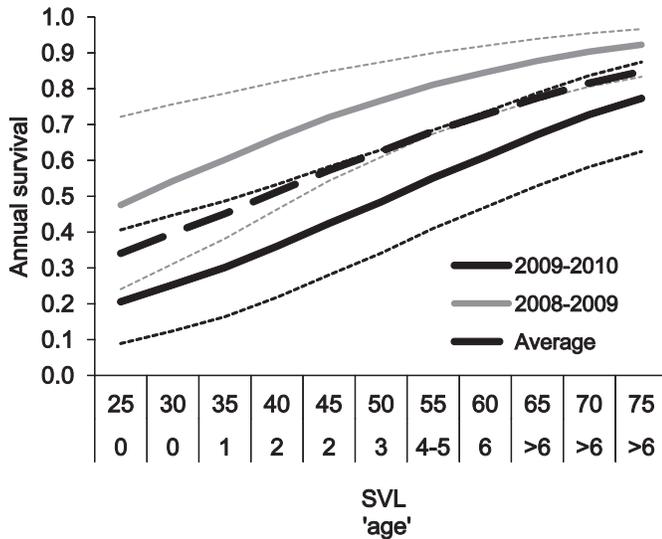


FIG. 2. Survival as a function of SVL and "age" (determined from growth models) for Arboreal Salamanders (*Aneides lugubris*) on Southeast Farallon Island, California, 2007–2010. Solid lines are year-specific survival estimates, and dotted lines are 95% CI, dashed line is average survival. Estimates from multistate open robust design capture–recapture model $\{S(e^{2+y+SVL}) \Psi_i \text{ out} = \text{in}(\text{zero}) \text{ pent}(y+\text{srvy}) \Phi_i(y+\text{srvy}+SVL) p(y^*\text{srvy})\}$.

Annual temporary emigration (Ψ_i ; probability of not being under any cover board during surveys for a season) was zero. Zero temporary emigration indicates the absence of temporary emigration between years in this population, and the estimates of survival and detectability are unbiased.

Detectability varied by survey and year with a survey * year interaction effect, meaning every survey had a unique estimate of capture probability (p ; Fig. 1). Overall average estimate of p was 0.377 (SD = 0.168, range = 0.047–0.692). Residence probability varied by year and survey but overall averaged 0.719 (SD = 0.221, range = 0.248–0.972). Overall average residence time (average number of surveys an animal spent under a cover board) was 3.6 surveys (~7 weeks), but this parameter also varied annually (Table 1).

The S value of salamanders during the first interval after marking was biased by large numbers of animals never recaptured (transients); so, results are given only for the second encounter class. We found significant annual variation in apparent survival. Average annual survival from 2008 to 2009 was 0.808 ± 0.058 (95% CI = 0.669–0.897) and from 2009 to 2010 survival was 0.546 ± 0.072 (95% CI = 0.405–0.680). Average annual survival of the second encounter class for both years was 0.677. Survival was significantly related to SVL at capture (Fig. 2). We used results from our growth models to assign age-specific survival to animals based on SVL (Table 3). Average hatchling, subadult, and adult survival probabilities

TABLE 3. Age-specific annual survival and fecundity estimates used in matrix population models for Arboreal Salamanders (*Aneides lugubris*) of Southeast Farallon Island, California.

Age (yr)	Avg. survival	2008–2009 survival	Fertility
0–1	0.363	0.494	0
1–2	0.450	0.590	0
2–3	0.552	0.693	0
3–4	0.625	0.757	1
4–5	0.668	0.793	1.5
5+	0.783	0.875	2
Avg. adult age	8	11	
Lambda	0.928	1.093	

indicate an average of 9% of a given cohort would reach maturity and 1% would reach age 10 yr old. Two matrix population models using parameters from Table 3 computed the average age of adults to be 8–11 yr old (Poptools 3.1; Hood, 2009).

Size and Growth.—Our recapture data included hatchling, subadult, and adult salamanders, as required for accurate von Bertalanffy growth curve modeling (Frazer et al., 1990). Size-frequency distribution of all capture records shows a right-skewed distribution, with an overall peak between 50 and 65 mm. Average SVL for all records was 52.9 mm (SE = 0.28, range = 20–79). Females (mean = 62.5-mm SVL, SE = 0.78, range = 48–73) were larger than males (mean = 59.8, SE = 0.9, range = 43–77; $t_{110} = 3.04$, $P = 0.003$).

Annual growth rates of subadults and adults ($N = 122$) slowed with increasing size, from 23%/yr (8.3 mm) for animals 36-mm SVL to 0.3%/yr (0.2 mm) at 65-mm SVL (Fig. 3). Growth rate of hatchling-size animals ($N = 10$) was 5.0%/month (1.1 mm) for animals 24-mm SVL (42%/yr; 10.1 mm/yr assuming growth for 9 months/yr). According to Frazer et al. (1990), the estimate of mean asymptotic SVL should be slightly larger than the average size of the largest individuals in the population. Following Waldron and Pauley (2007), we used SVL >61.1, the mean SVL of 112 reproductively mature marked adults, as our cut-off to determine the average size of the largest individuals. The average SVL of the largest (>61.1-mm SVL) reproductively mature individuals in our study population ($N = 29$ males, 31 females) was 65.6 (SD = 3.5). Asymptotic SVL (a) from the von Bertalanffy growth model (equation 1) was 66.0 (95% CI = 40.6–109.1). The characteristic k was 0.30 (95% CI = 0.21–0.40). The von Bertalanffy growth curve fit the data well ($r^2 = 0.91$). Age at reproductive maturity was 2.69 yr (SE = 0.41; 95% CI = 1.84–3.54).

Average within-wet-season (December–June) growth in SVL for 1,136 repeat measurements of 265 adult individuals was 2.06 mm (SE = 0.45, SD = 2.91). The average between-rain-year (annual) growth in SVL for 281 repeat measurements on 122 adult individuals was 1.73 mm (SE = 0.33, SD = 3.16). Because some portion of the variance in SVL growth estimates is due to measurement error, we estimated maximal annual subadult and adult growth rate as mean + 3*SE. Average annual growth in SVL of adults was 1.7 mm, with a maximum of 2.9 mm. At 3 yr to reach maturity (~46-mm SVL) and average adult growth rate of 1.7 mm/yr, estimated age of a 66-mm (asymptotic SVL) individual is 15 yr or at 2.9 mm/yr estimated age is 10 yr.

Young animals grow quickly so younger year classes should be separated by distinct SVL differences. The size-frequency distribution of 520 marked individuals revealed year classes that corresponded with estimates of year-class mean SVL from the growth model (Fig. 4).

DISCUSSION

Basic life-history information, especially from capture–recapture studies, is key to evaluating hypotheses about life-history strategies and evolution, and these types of data are rare for amphibians in general. We found that the Farallon Arboreal Salamander exhibits indeterminate growth, in which individuals continue to grow beyond the size at which they reach reproductive maturity. Important life-history predictions have been proposed for iteroparous species with indeterminate growth (Czarnoleski and Kozłowski, 1998). The smallest reproductive individual was 46.0-mm SVL, but the asymptotic size from the von Bertalanffy growth model was 66.0 mm. Growth rate during the first year of life was similar to the 10–21-mm/yr range reported for other terrestrial plethodontids (Houck, 1982; Hairston, 1983). Our estimate of age at reproductive maturity (3 yr old) was also similar to other terrestrial

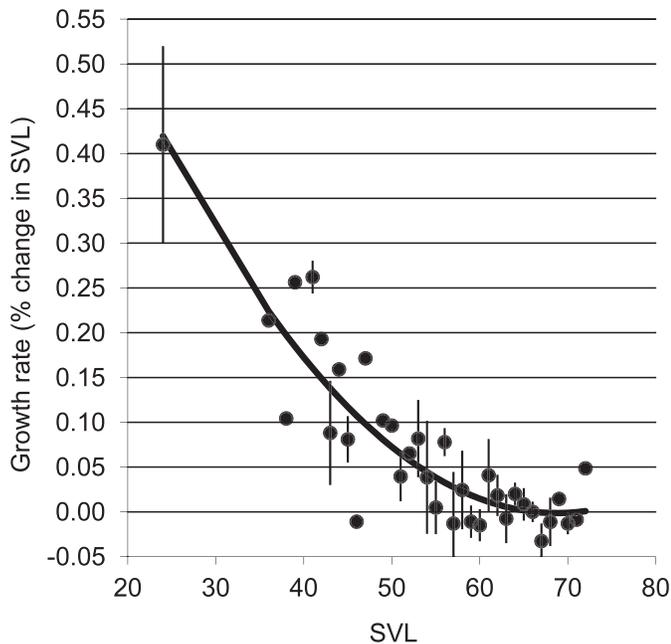


FIG. 3. Annual growth rate plotted against initial SVL data for Arboreal Salamanders (*Aneides lugubris*) on Southeast Farallon Island, California. Growth rates are percentage of change in SVL (mm) between rain years.

plethodontids (Marvin, 1996). Reported age at maturity for other *Aneides* ranges from 2 to 4 yr using size-frequency histograms (Pauley and Watson, 2005; Ramotnik, 2005; Staub and Wake, 2005) and up to 8 yr using growth models (Waldron and Pauley, 2007). Histograms can be unreliable because of individual variation in growth rate, but our growth model results were identical to our histogram results, and both agreed with earlier reports for age at maturity of Arboreal Salamanders from histograms (Anderson, 1960). In many plethodontid species, females begin reproducing later and at larger body sizes than males (Marvin, 1996). Because we pooled sexes for growth analyses, we probably underestimated age and size at maturity for females and overestimated age for males. Also, because females guard eggs for approximately 3 months each year, growth may differ between sexes after maturation.

Growth and age at maturity are amphibian life-history characteristics that can vary with environmental conditions (Hamelaar, 1988; Miaud et al., 2001; Ashton, 2002; Morrison and Hero, 2003; Waldron and Pauley, 2007) or have a genetic basis (Berven, 1982; Bernardo, 1993). Farallon Arboreal Salamanders have smaller maximal sizes (SVL) and mature at smaller size than Arboreal Salamanders on the mainland (Anderson, 1960; Staub and Wake, 2005). Dwarfism on islands is a well-known phenomenon in terrestrial vertebrates related to smaller prey size (Case, 1978; Boback, 2003). Our population is located in an oceanic, Mediterranean climate that potentially could support year-round growth and early maturity due to mild year-round temperatures, diverse invertebrate prey, and abundant fog or precipitation during the dry season. Furthermore, this population is insular, with no other herpetofauna competitors. The only other terrestrial vertebrate species on the island that might compete with Arboreal Salamanders for resources is the House Mouse (*Mus musculus*). Farallon Arboreal Salamander survival, age at maturity, and size at maturity are similar to other terrestrial salamanders in lowland Mediterranean climates (Olgun et al., 2001). The Farallon population provides an interesting situation for future investigations into environmental variation and competition.

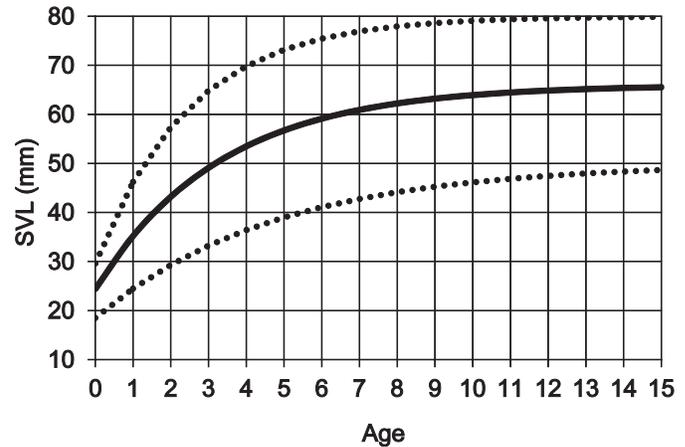


FIG. 4. Predicted curve for growth in SVL (solid line) for Arboreal Salamanders (*Aneides lugubris*) of Southeast Farallon Island, California, from von Bertalanffy growth interval equation. Dotted lines are 95% CI of curve.

Our estimates of annual survival for Arboreal Salamanders are the first for any *Aneides* species. Our survival estimates should be considered conservative, because there is reason to believe they are biased low (see below). Staub and Wake (2005) reported that Black Salamanders, *A. flavipunctatus*, can live up to 20 yr in captivity. Green Salamander (*A. aeneus*) mark-recapture intervals have been as great as 13 yr in Kentucky, USA (Waldron and Pauley, 2007). A conservative estimate of Green Salamander longevity based on growth models is 11 yr (Waldron and Pauley, 2007). *Plethodon kentucki* and *Ensatina eschscholtzii* reach sexual maturity at 3 yr but are known to live as long as 15 yr (Staub et al., 1995; Marvin, 1996, 2001). Reported observations on the longevity of other plethodontids are slightly lower (e.g., 6–15 yr for *Desmognathus quadramaculatus*, Castanet et al., 1996; Bruce et al., 2002; 5–11 yr for *D. ochrophaeus*, Houck and Francillon-Vieillot, 1988; 3–10 yr for *Plethodon metcalfi*, Ash et al., 2003). It is reasonable that the largest species in the genus also should have the longest life span (Stearns, 1992).

The CMR models we used for detectability, emigration, and survival estimation assume the following: 1) all animals present in the population at time t are equally likely to be captured, 2) every marked animal present in the population at time t has the same probability of surviving from time t to time $t + 1$, and 3) marks are not lost or overlooked by the observer (Pollock et al., 1990). We expect that all three of these assumptions could have been violated to some extent in this study, but our model structure controlled for some of these violations. We know from our goodness-of-fit results that a significant number of transients were present, thus violating assumption 1, but we controlled for this with encounter class structure in S and Psi . We also know that there was individual heterogeneity in survival based on size or age as evidenced by the significant SVL covariate, thus assumption 2 was violated but controlled for with the individual covariate SVL. Other sources of individual heterogeneity, such as sex, may exist for which we did not control. Assumption 3 is the most difficult as there may be animals that were marked but later overlooked for several reasons. Overlooked toe-clips, toe-clips that regrew before recapture, and illegible photographs are some possible means whereby assumption 3 was violated. These violations would result in underestimates of detectability and survival and overestimates of temporary emigration as permanently lost marks would be confused with mortality, and temporarily overlooked animals could negatively bias p and positively bias Psi . Thus, our estimates should be considered potentially

biased low in survival and detectability and biased high in temporary emigration. However, our MSORD model structures successfully controlled for the potentially biasing effects of temporary emigration, temporal variation in recapture probability, temporal- and SVL-related variation in residence probability, and the presence of large numbers of transients.

We found that transience was much reduced in rain year 2010 when toe clipping was reduced and photographic records made of all captured salamanders. In the first 3 yr, the proportion of transients (animals seen only once) was 0.55 ± 0.045 (mean \pm SE), whereas in rain year 2010 the proportion of transients was 0.23 ± 0.034 . The reduction in transients in 2010 could be due to a mortality or permanent emigration effect from toe clipping, an increase in recapture probability due to comprehensive photographic records for all captured animals, or a combination of the two effects. Toe clipping captive salamanders caused no mortality effects but reduced weight gain relative to controls (Ott and Scott, 1999; Davis and Ovaska, 2001). Salamanders released into the wild after toe clipping have lower return rates than controls, but it is unclear whether this is due to changes in local survival or recapture probabilities (Davis and Ovaska, 2001; McCarthy et al., 2009).

Populations of plethodontid salamanders exhibit surprising stability over time in undisturbed environments (Welsh and Droege, 2001). Therefore, evidence of population declines or reduced adult survival could indicate some alteration in environmental conditions that may have serious, negative, long-term consequences, particularly for such a long-lived species that is relatively slow to mature as the Arboreal Salamander (Benton and Grant, 1996). Long-term CMR studies supply critical baseline data to investigate impacts of localized management activities, and facilitate life-history comparisons among populations.

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