POPULATION ECOLOGY – ORIGINAL RESEARCH

Spatial capture–recapture reveals age- and sex-specific survival and movement in stream amphibians

R. Ken Honeycutt[1] · Justin M. Garwood[2] · Winsor H. Lowe[3] · Blake R. Hossack[1]

Abstract

Life-history information sets the foundation for our understanding of ecology and conservation requirements. For many species, this information is lacking even for basic demographic rates such as survival and movement. When survival and movement estimates are available, they are often derived from mixed demographic groups and do not consider differences among life stages or sexes, which is critical, because life stages and sexes often contribute differentially to population dynamics. We used hierarchical models informed with spatial capture–mark–recapture data of *Ascaphus montanus* (Rocky Mountain tailed frog) in five streams and *A. truei* (coastal tailed frog) in one stream to estimate variation in survival and movement by sex and age, represented by size. By incorporating survival and movement into a single model, we were able to estimate both parameters with limited bias. Annual survival was similar between sexes of *A. montanus* [females = 0.885 (95% CI 0.614–1), males = 0.901 (0.657–1)], but was slightly higher for female *A. truei* [0.836 (0.560–0.993)] than for males [0.664 (0.354–0.962)]. Survival of *A. montanus* peaked at mid-age, suggesting that lower survival of young and actuarial senescence may influence population demographics. Our models suggest that younger *A. montanus* moved farther than older individuals, and that females moved farther than males in both species. Our results provide uncommon insight into age- and sex-specific rates of survival and movement that are crucial elements of life-history strategies and are important for modeling population growth and prescribing conservation actions.

Introduction

Survival and movement are processes central to the distribution and abundance of organisms (Wright 1949; Williams et al. 2002; Clobert et al. 2012). Understanding how survival and movement vary among demographic groups is

✉ R. Ken Honeycutt
rkenhoneycutt@gmail.com

1 U.S. Geological Survey, Northern Rocky Mountain Science Center, 800 E. Beckwith Avenue, Missoula, MT 59801, USA

2 California Department of Fish and Wildlife, 5341 Ericson Way, Arcata, CA 95521, USA

3 Division of Biological Sciences, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA

especially critical for conservation, because sexes and life stages often contribute differentially to population dynamics (Cole 1954; Caswell 2001). Although theory and practice demonstrate the importance of understanding how survival and movement differ for a range of life stages and sexes, unbiased estimates of these rates are still rare for many vertebrate groups, including amphibians, and often are limited to adults of a single sex (Gaillard et al. 2000; Smith and Green 2006).

Survival can vary tremendously among ages and between sexes within taxa and how it varies can be important for population dynamics (Crouse et al. 1987; Saether et al. 2013). For example, some long-lived species such as large mammals are expected to demonstrate actuarial senescence—the decline in the rate of survival with age (Jones et al. 2008). In systems where shorter life spans are expected, including most amphibians, ontogenescence—lower survival of young individuals compared to individuals of other ages in the population—is emphasized in demographic studies (Levitis 2011; Vitt and Caldwell 2013). In some species,

both ontogenescence and actuarial senescence are expected and curves representing survival over age are dome-shaped (Williams 1957; Caughley 1966; Gaillard et al. 2000), with survival increasing up to a prime age generally occurring shortly after reproductive maturity, and then decreasing as individuals age further (Medawar 1952; Levitis 2011). A U-shaped pattern results when mortality, the inverse of survival, is quantified for populations with both ontogenescence and actuarial senescence: individuals of prime age have the lowest mortality, while younger and older individuals have higher mortality (Pletcher 1999; Colchero and Clark 2012). Actuarial senescence has been widely demonstrated in wildlife populations (Jones et al. 2008); however, ontogenescence is seldom estimated alongside senescence (Levitis 2011). Hence, the overall dome-shaped survival pattern has rarely been resolved within a species (but see Frederiksen et al. 2004; Breton et al. 2014), and actuarial senescence in amphibians has rarely been studied (Miller et al. 2014). Furthermore, although differences in survival between sexes have been studied extensively in some taxa and attributed to environmental pressures incurred from sexual strategies (Toïgo and Gaillard 2003), little is known about sex-specific survival in amphibians.

Like survival, patterns of movement often vary among life stages and between sexes (Greenwood 1980; Lomnicki 1988; Gaines and Bertness 1993). Because decreased movement and colonization can cause populations to decline locally and at landscape scales (Campbell Grant et al. 2009; Hossack 2016), it is important to identify movement patterns to direct conservation, especially in human dominated landscapes (Mills and Allendorf 1996; Sala et al. 2000). Specifically, limitations on movement can affect local populations by cutting off potential rescue to populations at risk of extirpation (Brown and Kodric-Brown 1977). In many taxa, relatively long-distance movements are often assumed to occur primarily during the juvenile stage and in a particular sex (Gaines and Bertness 1993; Pittman et al. 2014). Sex-biased dispersal in the juvenile stage is hypothesized to have evolved in response to pressures such as mate availability, inbreeding avoidance, and conspecific competition for resources (Hamilton and May 1977; Greenwood 1980; Dobson 1982; Perrin and Mazalov 2000).

Patterns of sex-biased movement, which are often attributed more broadly to mating system dynamics, have been well documented among birds and mammals, with female-biased movement most common in birds and male-biased movement most common in mammals (Greenwood 1980; Pusey 1987; Lawson Handley and Perrin 2007). Results from amphibian studies have been less consistent, with male, female, and no bias in movement being reported, even though movement patterns are likely driven by similar processes to those in birds and mammals (Smith and Green 2006; Liebgold et al. 2011; Helfer et al. 2012). This lack of consistency may be a consequence of the small number of amphibian studies that have directly estimated movement for both sexes within a population (e.g., Muths et al. 2010, Liebgold et al. 2011, Helfer et al. 2012), as well as the fact that amphibians have more variation in mating systems and life-history strategies than other vertebrate classes (Duellman and Trueb 1986; Austin et al. 2003). Amphibians in systems where female-biased movements have been suggested—such as in the bullfrog (*Lithobates catesbeianus*), common frog (*Rana temporaria*), and coastal tailed frog (*Ascaphus truei*)—may be responding to unique pressures inherent to their mating systems, for example to resource defense by males or to limitations of other resources necessary for females to successfully reproduce, such as oviposition sites (Austin et al. 2003; Wahbe et al. 2004; Palo et al. 2004; Burkholder and Diller 2007).

Accounting for the effect of movement on estimates of survival is critical because emigration and the presence of non-residents (i.e., transients) in populations can lead to survival estimates that are biased low, especially when study areas are small relative to movement rates (Pradel et al. 1997; Schmidt et al. 2007; Zimmerman et al. 2007; Schaub and Royle 2014). Non-residents and transients are individuals that move beyond the boundaries of the study area after being captured and marked as part of a study. Variation in movement rates and transience among demographic groups can bias sex- and age-specific estimates of survival. For example, sex-biased movement in some avian species directly affects sex-specific estimates of survival (Tavecchia et al. 2002; Schaub and Royle 2014). And for frogs and toads, it is common to be able to estimate survival for adult males but not for adult females, possibly due to differences in movement rates between the sexes. Also, high mortality often makes estimating survival for free-ranging juveniles difficult (i.e., those not constrained to experimental enclosures) (Biek et al. 2002; Muths et al. 2010; Schmidt et al. 2012).

Despite the huge expansion of research and advances in statistical methods in recent decades, basic information on survival and movement rates are still lacking for most species of amphibians. Furthermore, reliable estimates of demographic rates for amphibians often come from a small number of widely distributed species with predictable phenology or other characteristics that make them convenient to study (Funk et al. 2005; McCaffery and Maxell 2010; Muths et al. 2010). In particular, the life-history strategies of amphibians that are limited to small, cold streams often differ greatly from those of the pond-breeding species, which are the source of most vital rate estimates. Amphibians are generally assumed to have low initial survival that increases with age, but age-specific trends in survival have rarely been estimated, in part because survival of young juveniles is so low. As a result, models of population growth often have

to assume or borrow vital rate estimates (e.g., Biek et al. 2002). Dispersal of amphibians is also generally considered biased toward younger life stages, especially metamorphs (Breden 1987; Wells 2010, but see Smith and Green 2006), but few studies have examined sex- and age-specific survival and movement using methods that account for detection uncertainty.

We investigated how survival and movement of *A. montanus* (Rocky Mountain tailed frog) and *A. truei* (coastal tailed frog) vary with sex and age. Tailed frogs are the most ancestral of the extant frogs and have several unusual attributes that should require high survival, including larval periods that can exceed 4 years and delayed sexual maturity (up to 8 years) (Daugherty and Sheldon 1982a; Dodd 2013; Hayes and Quinn 2015). To generate estimates of survival and movement, we used Cormack–Jolly–Seber (CJS) models informed with one-dimensional spatial capture–mark–recapture (CMR) data from five streams for *A. montanus* and one stream for *A. truei*. We predicted that survival of juveniles would be lower than for adults and explored the potential for actuarial senescence in the *A. montanus* populations. We also predicted that movement would be juvenile-biased and that females would move farther than males.

Materials and methods

Study species and area

The family Ascaphidae is limited to northwestern North America and is comprised of only *A. montanus* and *A. truei*, which are isolated geographically by the arid Columbia River Basin. Tailed frogs reach peak abundances in small, cold streams with clean, coarse substrates, where tadpoles are the dominant grazers (Kiffney et al. 2001; Dodd 2013). Permanent streams are required for viable populations, because tadpoles can take up to 4 years to reach metamorphosis (Dodd 2013). Though tailed frogs tend to be concentrated in and along streams, movements into adjacent forest are common and individuals can be captured on land in forested landscapes (Corn and Bury 1991). Previous work has investigated aspects of movement, growth, and return rate of these species, but we are unaware of estimates for survival or movement that account for imperfect detection (Daugherty and Sheldon 1982a, b; Burkholder and Diller 2007; Hayes and Quinn 2015). The most detailed study of the movement ecology of tailed frogs suggested that younger *A. montanus* individuals were more likely to move long distances than older individuals (Daugherty and Sheldon 1982b).

We sampled five streams in the northern Rocky Mountains for *A. montanus* and one stream in northern California for *A. truei* (Fig. 1). The Rocky Mountain streams are on U.S. Forest Service lands dominated by mixed-conifer
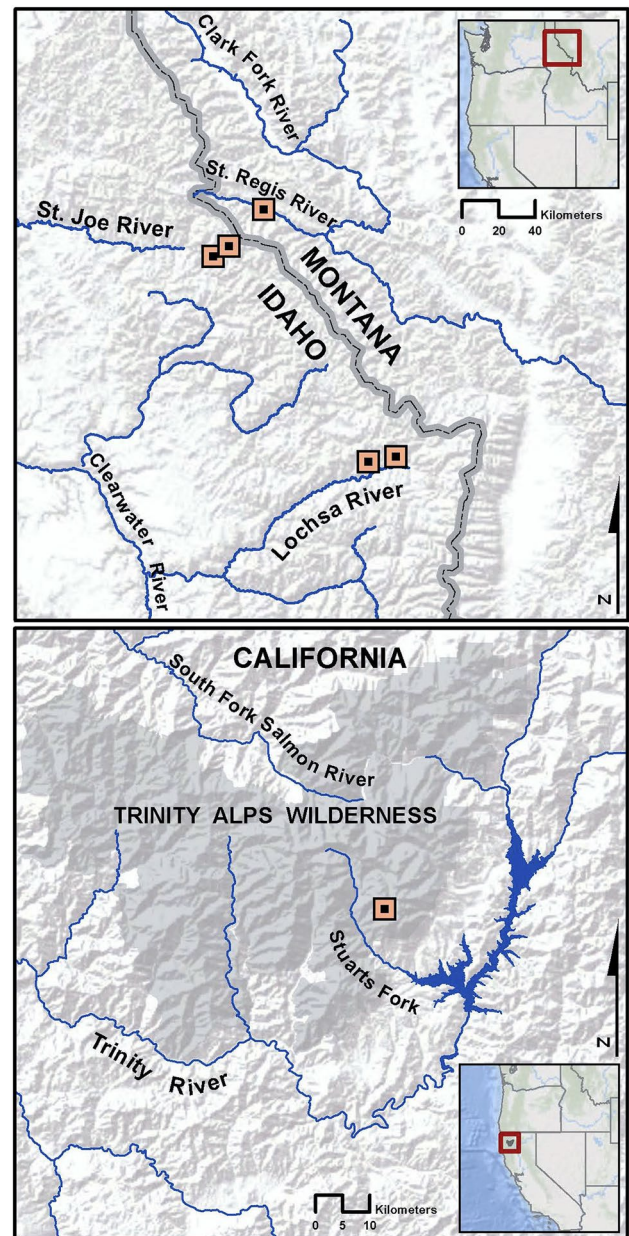
Fig. 1 Locations of six streams in the northern Rocky Mountains and California, USA, where we conducted capture–mark–recapture surveys of *Ascaphus montanus* and *A. truei* during 2012–2013 and 2004–2005, respectively. The color version of this figure is available online

forests and a long history of logging activity and road building. The stream in northern California is in a subalpine region in the Trinity Alps Wilderness surrounded by dry and rocky slopes. The reaches which we studied in the Rocky Mountain streams were portions of longer stretches of continuous habitat suitable for tailed frogs; the termini of the reach which we studied in California adjoined stream habitat likely not suitable for tailed frogs. The Rocky Mountain streams are locations where *A. montanus* were present

during a concurrent project examining survival and movement of the Idaho giant salamander (*Dicamptodon aterrimus*) in nine streams (Honeycutt et al. 2016). We chose the California stream due to its protected status and the absence of invasive salmonids or cattle grazing in the area. The midpoint elevation at the Rocky Mountain streams ranged from 1030 to 1224 m and was 2035 m at the California stream.

Capture–mark–recapture survey sessions

In the Rocky Mountain streams, we conducted CMR surveys during three primary survey periods in 2012 (20 Jun–09 Sep) and again in 2013 (30 Jun–04 Sep). Our survey design for the Rocky Mountain streams was originally based on a robust design framework with multiple secondary surveys within each primary survey period (Pollock 1982), but we collapsed all secondary sessions within each primary period to fit within the framework of simpler CJS models. Henceforth, a survey period refers to the collapsed secondary survey sessions within each primary period. Within years, intervals between survey periods ranged from 14 to 27 days. During the first survey period at each stream, we surveyed 100 m of stream. To recapture individuals that may have emigrated from these initial 100-m reaches, we extended both the upstream and downstream termini of reaches by 10 m in each of the second, third, and fourth survey periods. We maintained reach lengths at 160 m for the fifth and sixth survey periods because of logistical constraints associated with larger survey areas (Honeycutt et al. 2016). We marked all new frogs encountered in these extended sections. The Rocky Mountain streams were surveyed during the day by a three-observer crew with a Smith-Root LR-24 backpack electrofishing unit, which is an effective method for detecting tailed frogs (Cossel et al. 2012). For *A. montanus*, we sampled only within the water and its immediate edge.

In the California stream, we conducted six surveys in 2004 (16 Jul–25 Sep) and three surveys in 2005 (29 Jul–24 Aug). The survey design for the California stream did not include a robust design, so collapsing these surveys was not necessary. Within years, intervals between surveys ranged from 9 to 22 days. In this stream, we searched the same 203-m reach during each survey. In addition to searching the water for *A. truei*, we included approximately 2 m of the riparian area along both banks of the stream in our search, where frogs were generally found near the water (mean = 0.29 m). Surveys were conducted at night between 21:00 and 02:00 h by two observers using sealed beam flashlights to detect eye shine.

In both regions, we assigned unique marks to individuals at first capture with visible implantable elastomer (VIE; Northwest Marine Technologies, Shaw Island, WA, USA), recorded each individual's location along the study reach

with a meter tape (± 1 m), measured snout-vent length (SVL), determined sex, and examined the VIE marks of recaptures using ultra-violet light. During surveys, we placed frogs in individual plastic bags with water and retained them for batch processing once a stream section had been completely searched. Prior to marking with elastomer, new captures from the Rocky Mountain streams were anesthetized with approximately 150-mg/L buffered solution of MS-222 or 0.025-mL/L solution of benzocaine. Anesthetized individuals were held until they regained full mobility. Captures from the northern California stream were marked without the use of an anesthetic. All individuals were released at their point of capture.

Statistical analysis

We investigated survival and movement using spatial CJS models implemented in JAGS with the R package R2jags (Plummer 2003; Kéry and Schaub 2012; Su and Yajim 2014). The spatial CJS differs from traditional CJS models by incorporating information on locations of individuals relative to the dimensions of study areas (Schaub and Royle 2014). The model contains two state processes modeling (1) survival and (2) the locations of individuals, and an observation process. Survival from one occasion to the next is modeled as the product of the latent state (i.e., the suspected true condition; alive [$z_{i,t} = 1$] or dead [$z_{i,t} = 0$]) at the previous occasion and the true survival probability ($s_{i,t}$):

$$z_{i,t+1}|z_{i,t} \sim \text{Bernoulli}\left(z_{i,t}s_{i,t}\right). \tag{1}$$

Movements by individuals and, therefore, their changes in location (G) between the previous occasion ($G_{i,t}$) and the next ($G_{i,t+1}$) are modeled from a t distribution with $G_{i,t}$ as the mean, variance in movement (σ_G^2), and degrees of freedom (df) that describe the tail of the distribution:

$$G_{i,t+1} \sim t\left(G_{i,t}, \sigma_G^2, df\right). \tag{2}$$

The model describes movement as random walk where movement is independent between time steps and each individual may move either upstream or downstream during each time step. Mean movement distance (move) is modeled from the variance in movement under a t distribution with mean of 0, variance in movement (σ_G^2), and degrees of freedom (df) as: move $\sim t\left(0, \sigma_G^2, df\right)$. The observation process is the product of three conditions during a sampling occasion (t) for an individual (i): (1) alive ($Z_{i,t} = 1$) or dead ($Z_{i,t} = 0$), (2) inside ($r_{i,t} = 1$) or outside ($r_{i,t} = 0$) the study area, and (3) the recapture probability ($p_{i,t}$) of the individual at that time. The capture history ($y_{i,t}$) of an individual is assumed to be a function of this Bernoulli observation process where the individual is recorded as either captured ($y_{i,t} = 1$) or not ($y_{i,t} = 0$):

$$y_{i,t}|z_{i,t}, r_{i,t} \sim \text{Bernoulli}\left(z_{i,t}r_{i,t}p_{i,t}\right). \tag{3}$$

Including these state processes in the model allows for estimation of survival as well as permanent emigration from the study area, whereas, in the traditional CJS, these values are confounded. Therefore, estimates of survival are less biased by emigration than those from models lacking spatial information (Schaub and Royle 2014).

We used a one-dimensional version of the model to represent our study space as a line, where only movement along the length of the stream was measured and bank-to-bank movement was ignored (Honeycutt et al. 2016). Our model is built directly from the two-dimensional spatial CJS model presented by Schaub and Royle (2014), differing only in that movement is considered one-dimensional rather than two-dimensional. Because tailed frogs can leave streams (Corn and Bury 1991), the spatial information which we gathered accounts for only a portion of possible movement and emigration from the study area. Specifically, the spatial portion of our model only accounts for emigration along the stream channel (i.e., beyond the ends of study reaches), not for emigration away from streams. Hence, estimates of survival from our model fall somewhere between true and apparent survival, but certainly closer to true survival than estimates from non-spatial capture–mark–recapture models. Likewise, estimates of movement distance in our model represent movement only along the stream, and we do not distinguish local movements of residents from actual dispersal events. We assume, however, that movement distances in our study reflect, at least in part, the dispersal patterns of the focal species. The analyses for each species were conducted separately.

We make several assumptions common to CJS models. We assumed that death, birth, immigration, and emigration could occur between, but not within, survey periods. We assumed recapture probability and survival of individuals come from a random Bernoulli process, that there was no spatial variation in survival of frogs within streams, and that we identified individuals and their locations without error (Lebreton et al. 1992; Schaub and Royle 2014). We also assumed no individual heterogeneity in survival probabilities, and that frogs could have been captured anywhere along the study reaches (Schaub and Royle 2014).

When *A. montanus* were captured more than once during a survey period, the average distance of their captures along the stream was used to inform the model (Vignieri 2007; Liebgold et al. 2011). To scale our estimates to annual survival, we included a term in all models indicating the length of time between capture periods. Also, because *A. montanus* were sampled across five streams and analyzed together, we accounted for variation in interval lengths between capture periods among streams by weighting the average of the interval lengths between capture periods from all streams by the cumulative number of individuals released from each stream prior to the interval. We did not explicitly define ages in our study and assume that size increases with age. Though size is not always a reliable indicator of amphibian age (Halliday and Verrell 1988), a long-term mark–recapture study of *A. montanus* indicated that size is a precise indicator of age for tailed frogs for several years after metamorphosis, beyond which growth slows and determining age based on size may be less reliable (Daugherty 1979). We used SVL at first capture to inform our models.

Prior to investigating movement and survival, we evaluated the structure of recapture probability for each species. For both species, we included standardized SVL, a quadratic effect of standardized SVL, and sex in the recapture portion of our models to account for potential effects of these parameters on sex- and size-specific estimates of survival and movement. We also included a random effect of survey period to allow for flexibility in recapture probability among survey periods. For the *A. montanus* analysis, we included a random effect of stream, because differences in substrate among streams could have added variation in recapture probability. We standardized SVL using the mean and standard deviation of each sex in each species, because size ranges differed between males and females (and unsexed individuals), which agrees with previous findings (Burkholder and Diller 2007; Dodd 2013). For both species, we used a stepwise procedure to eliminate model terms for which the 95% credible intervals of estimated coefficients widely overlapped 0. We found that recapture probability for *A. montanus* was best described by an additive structure including time as a random variable for each stream, an effect of sex, and a linear and quadratic effect of SVL. For *A. truei*, we found recapture probability varied as a random process among sampling sessions, where females were more likely to be captured than males.

We predicted that mean movement varied among sexes and sizes and, therefore, included sex, SVL, and an interaction between sex and SVL as covariates on movement. To accomplish this, we included SVL and sex as covariates in a linear statement using the log link. JAGS uses precision (values between 0 and 1) to estimate variance and, therefore, the log of precision results in negative input values. Therefore, a positive coefficient indicates a negative relationship with movement variance and hence with movement distance and covariates. For example, a positive coefficient representing the effect of increasing SVL on movement would indicate that movement decreases with size. For the Rocky Mountain streams, we accounted for increasing lengths of study reaches between survey periods in the spatial CJS model (Honeycutt et al. 2016). Tests for differences in movement distances among time intervals indicated little difference despite the high variation in the lengths of the intervals.

We further investigated the movement patterns of tailed frogs by deriving movement kernels from the models, which illustrate the likelihood of movement to different distances

during the study periods by individuals in the different demographic groups. For each individual captured during the study, we estimated the distance which it moved between the first location where it was captured ($G_{i,t.\text{first}}$) and the last location where it was modeled to be alive ($G_{i,t.\text{last.alive}}$) during the study, where the last occasion of life is modeled from Eq. (1). Only when an individual was recaptured on the final sampling occasion of the study period is the true value known for movement distance of that individual during the study; otherwise, the distance is an estimate from the model.

A mixture of transient and resident individuals in populations studied with CMR data can cause poor fitting models and biased survival estimates (Pradel et al. 1997). We used the global test in program U-CARE to assess the goodness of fit of our data to standard CJS models and Test3. SR to test for transients in the populations (Choquet et al. 2009). The global test indicated that the *A. montanus* data set was overdispersed (c-hat = 2.98) and one-sided Test3. SR for transients indicated presence of transients among both males ($p < 0.0001$) and females ($p < 0.0001$). Removal of the first capture from each individual resulted in better fit (c-hat = 1.44) and elimination of male transients (males $p = 0.19$), but not female transients ($p = 0.0027$). The *A. truei* data were underdispersed (c-hat = 0.30) and transients were unlikely for males ($p = 0.59$) or females ($p = 0.24$).

We accounted for the high number of transients in *A. montanus* populations by estimating survival conditioned on the third capture and beyond. Captures prior to the third for each individual and individuals captured fewer than three times remained in the data set to inform the portion of the model describing movement, and were described by different survival parameters than those for individuals captured three or more times. This is similar to using a time-since-marking (TSM) framework where survival during the interval after an individual is initially released (and after the second release in our model) is treated separately from survival over intervals following subsequent releases (Pradel et al. 1997; Grant et al. 2010). We used this method within the spatial CJS model, because the spatial portion of our model only considered movement in one dimension along the stream, not movement away from the stream. Without accounting for transience or movement away from the stream, our estimates of survival would be biased low. Here, we treated the effects of female and male transience equally, which could bias survival estimates of males high as U-CARE Test3. SR indicated that there were likely more female than male transients. For *A. truei*, we conditioned survival upon first capture and used the entire data set, because Test3.SR did not indicate the presence of transients for this population.

For *A. montanus*, we tested for differences in survival based on sex and size with continuous linear and quadratic functions of SVL, because we predicted survival to vary between sexes and among sizes. Using size as a proxy for

age, this allowed us to investigate patterns of ontogenescence and actuarial senescence that, if present, would result in a dome-shaped survival curve with size as the dependent variable (Frederiksen et al. 2004; Breton et al. 2014; Bleu et al. 2015). We chose this method over others described for measuring age-related survival, such as Gompertz curves and life tables, because our method allowed us to account for movement (Pletcher 1999; Colchero and Clark 2012; Jones et al. 2014). Accounting for movement is important, because, if rates of movement—and potential emigration from the study area—vary by age, it could bias age-dependent estimates of survival. For *A. truei*, we did not test the effect of SVL on survival, because it caused problems with model convergence.

If the sex of an individual could not be determined in the field on its first capture, it was coded as unsexed for the duration of the study, even if sex could be determined upon subsequent captures. We did this to avoid any bias in recapture probability among sexes that assigning sex beyond first capture (i.e., at second capture or beyond) might cause. Unsexed individuals represented the smallest individuals from both species, as sex of young juveniles can be difficult to determine based on external characteristics. For the *A. truei* analysis, we removed the 6 unsexed individuals; 160 unsexed individuals remained in the *A. montanus* analysis and were treated separately from known males ($n = 577$) and females ($n = 807$). We retained these 160 individuals in the analysis, because they provided information regarding movement and survival from the smallest individuals in the populations. This allowed us to explore the relationship of movement and survival across the continuum of sizes of tailed frogs that we encountered.

Our global model for describing survival and movement for both species had the following structure: $s(\text{TSM} \times \text{Sex} + \text{SVL} \times \text{SVL}^2)$, p(stream (each with random time) + Sex + SVL × SVL^2), move(Sex × SVL), with exceptions of the terms for TSM in the survival, and stream in the recapture portions, being absent for *A. truei*. Our final model structure for estimating survival and movement of *A. montanus* was: $s(\text{TSM} + \text{Sex} + \text{SVL} + \text{SVL}^2)$, p(stream (each with random time) + Sex + SVL + SVL^2), move(Sex × SVL). We chose this model structure, because it allowed us to explore all of our predictions regarding sex- and age-specific survival and movement in a single model. Models including a three-way interaction among s, Sex, and linear and quadratic terms for SVL resulted in poor precision and were not included. For *A. truei*, our final model was s(Sex), p(random time + Sex), move(Sex); more complex models provided poor precision. In our models, the time scale of movement is the average length of intervals between survey periods for each species, which was approximately 3 weeks for *A. montanus* and 1.5 weeks for *A. truei*.

We used uninformative priors for all model parameters including $N(0, sd = 5)$ on the logit scale for survival and recapture probability, $N(0, sd = 10)$ on the logit scale for the coefficients representing effects of Sex and SVL, and a uniform distribution from 0 to 1000 for the movement parameter. We ran three Markov chains for each model, each with 150,000 iterations including a burn-in period of 50,000 iterations, and thinned chains by excluding every other iteration. We confirmed sufficient iterations in Markov chains with the Gelman–Rubin test and assumed that chain convergence was reached if scale reduction factors for parameters were < 1.1 (Gelman and Rubin 1992). The programming script which we used to execute these models is provided in Electronic Supplementary Material 1 along with our data for *A. montanus* individuals (Electronic Supplementary Material 2).

Results

In total, 1544 *A. montanus* individuals were marked in the study streams and included in the analysis; 330 *A. montanus* were captured more than once. Recapture probability varied among streams from a low of 0.194 (95% CI 0.076–0.351) to a high of 0.457 (0.303–0.627) for males; recapture probabilities were slightly lower for females [logit scale coefficient: −0.205 (−0.472 to 0.061)] and higher for unsexed individuals [logit scale coefficient: 0.182 (−0.652 to 1.254)], though confidence intervals broadly overlapped 0. Mean annual survival of *A. montanus* resident females was similar to males [females = 0.885 (0.614–1), males = 0.901 (0.657–1)]. The survival of unsexed individuals was lower than for individuals of known sex and was poorly estimated [0.772 (0.253–1)]. Average-sized *A. montanus* had higher survival than smaller and larger individuals did, though the estimates of the coefficients slightly overlapped 0 [logit scale coefficient SVL: 0.266 (−0.113 to 0.642), logit scale coefficient SVL^2: −0.283 (−0.561 to 0.027)], resulting in dome-shaped survival curves (Fig. 2).

Female movement of *A. montanus* varied more than male movement [log scale coefficient: −1.220 (−1.774 to −0.678)], suggesting that females moved farther along the stream between capture occasions than males, though the credible limits of the values overlapped [females = 30.2 m per 3-week period (0.8–132.7), males = 16.4 m per 3-week period (0.4–72.3)]. Mean movement of unsexed individuals between capture occasions was similar to that of males [13.0 m per 3-week period (0.2–67.3)]. Movement kernels estimated from the models indicated that females tended to move longer total distances during the study than did males (females: median = 38 m, sd = 27.7 m, range = 0–189 m; males: median = 21 m, sd = 19.7 m, range = 0–155 m); but unsexed individuals were estimated to have the longest movements during the study period (median = 120 m, sd = 227.0 m, range = 0–2567 m). However, only 27% of
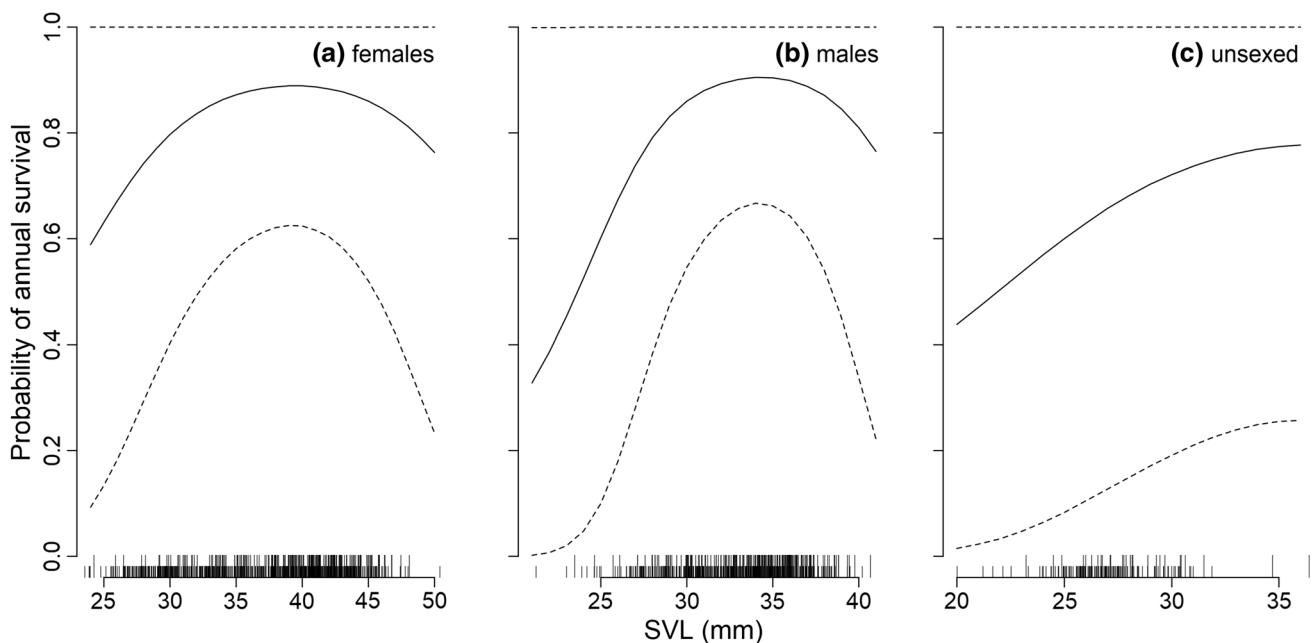
Fig. 2 Estimated mean survival of male, female, and unsexed *A. montanus* in five streams in the Rocky Mountains, USA. Solid lines represent mean values of survival and the dashed lines represent the 95% credible intervals. The rug plot along the *x*-axis indicates the relative density of sizes of individuals marked during the study. Taller tick marks represent individuals captured more than once and shorter tick marks indicate individuals captured only once. The difference in the range of values displayed in each panel corresponds to different size ranges of **a** females (24–50 mm), **b** males (21–41 mm), and **c** unsexed (20–36 mm)
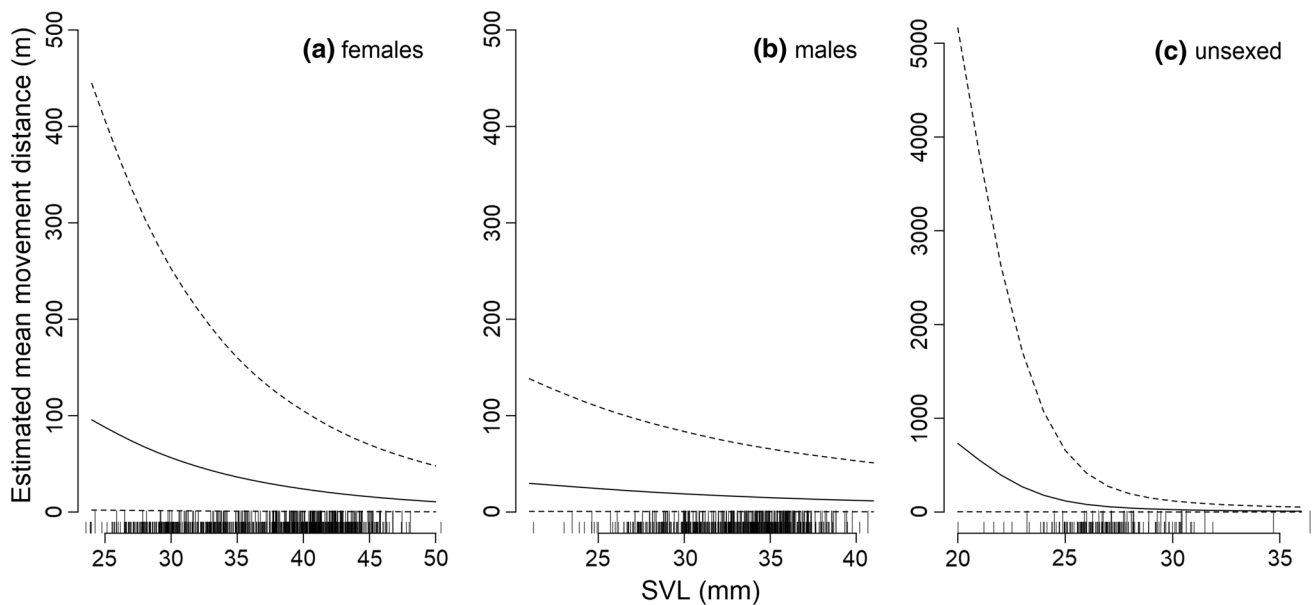
Fig. 3 Expected mean movement distances for *A. montanus* from populations in the Rocky Mountains, USA. Mean movement for each sex is represented by solid lines and 95% credible intervals by dashed lines. The rug plot along the *x*-axis indicates the relative density of sizes of individuals marked during the study. Taller tick marks represent individuals captured more than once and shorter tick marks indicate individuals captured once. The time scale of movement is the average length of intervals between survey periods, approximately 3 weeks. The difference in the range of values displayed in each panel corresponds to different size ranges of **a** females (24–50 mm), **b** males (21–41 mm), and **c** unsexed (20–36 mm)

estimated movements during the study for unsexed individuals fully converged during MCMC runs (i.e., scale reduction factors for the estimated values < 1.1), while the convergence rates were 92 and 93% for females and males, respectively.

Overall, smaller *A. montanus* had higher variance in movement distance than larger frogs [log scale coefficient: 0.305 (−0.033 to 0.66)], suggesting that movement distance decreased with size (Fig. 3). Movement variance tended to decline more sharply with increasing SVL in females [log scale coefficient: 0.633 (0.048–1.233)]—and to an even larger degree in unsexed individuals [log scale coefficient: 2.523 (−0.634 to 5.344)]—than in males; suggesting that movement of males was more stable across sizes than for females and unsexed individuals (Fig. 3). All movement estimates for *A. montanus* are based on a single *t* distribution with estimated sd = 11.7 and *df* = 2.0.

In total, 79 *A. truei* individuals were marked in the California study stream and included in the analysis, with 41 individuals captured more than once. Recapture probability was slightly higher for females [0.230 (0.156–0.319)] than for males [(0.179 (0.113–0.262)]. Estimated annual survival of females [0.836 (95% CI 0.560–0.993)] was higher than that of males [0.664 (0.354–0.962)], though CIs broadly overlapped. The coefficient for the effect of sex on movement variance only slightly overlapped 0 (log scale coefficient: −1.112 [−2.414–0.194]), indicating that *A. truei* females likely had higher movement rates than males. The mean movement distance along the stream by female *A. truei* was nearly double that of males, although the credible intervals for these values overlapped [females = 13.6 m per 1.5-week period (0.3–59.5), males = 7.8 m per 1.5-week period (0.2–34.0)]. Movement kernels estimated from the models indicated that female *A. truei* tended to move longer total distances during the study than did males (females: median = 23 m, sd = 24.9 m, range = 0–121 m; males: median = 14 m, sd = 13.7 m, range = 1–92 m) (Fig. 4); 95% of these estimated movements fully converged during MCMC runs. Movement estimates of *A. truei* are based on a single *t* distribution with estimated sd = 6.0 and *df* = 2.2.

Discussion

Our study provides rare evidence of age-specific survival and age- and sex-specific movement from free-ranging amphibians (Miller et al. 2014; Jones et al. 2014). Though estimates of survival and movement are available for many vertebrates, sex- and age-specific estimates that account for survival, movement, and capture probability within single models are uncommon (Schaub and Royle 2014). These estimates are important for determining baseline demographic information for species and for prescribing conservation actions.
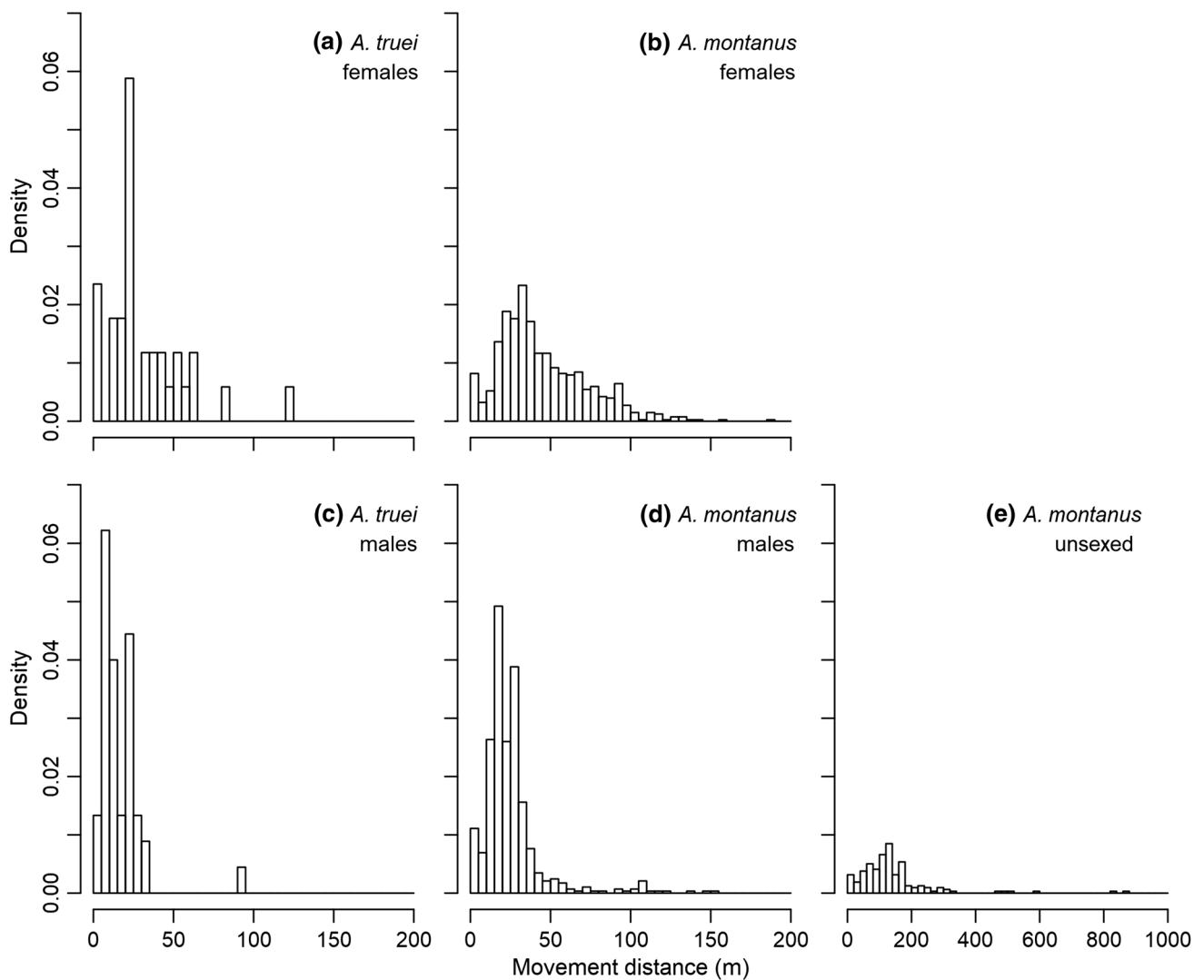
Fig. 4 Densities of estimated movement distances by tailed frogs in five streams in the Rocky Mountains (*Ascaphus montanus*) and one stream in California (*A. truei*), USA. The time scale of movement for each individual spans from the first occasion which it was captured until the last occasion which it was modeled to be alive. True values of movement during the study period were available when the individual was recaptured on the final sampling occasion. We omitted one estimated movement of 2567 m by an unsexed *A. montanus* from panel **e** to maintain clarity in the figure

Though our point estimates lack precision, the high rates of survival of average-sized *A. montanus* (female = 0.885, male = 0.901) and female *A. truei* (0.836) were in line with expectations for a long-lived amphibian that has delayed maturity, low fecundity, and lack of parental care (Dodd 2013). However, the estimate for male *A. truei* (0.664) was lower than we expected. Though the credible intervals for the survival estimates of the two species overlap, the pattern of lower survival for *A. truei* compared to *A. montanus* could be attributed to the *A. truei* population being at a higher elevation (nearly 1000 m higher than *A. montanus*) where frogs likely encounter harsher environmental conditions such as lower temperatures, lower winter oxygen levels, and less productive waters than in lower elevation locations

(Bradford 1983). The lower survival of *A. truei* males in this population is unlikely due to unmodeled transience as we found no evidence of transience from the U-CARE test, and the propensity for transient behavior was likely limited by the survey reach being bounded by habitat unsuitable for tailed frogs. However, overland movement and emigration by *A. montanus* that was not accounted for by the spatial CJS likely contributed to reducing the precision of our survival estimates for that species.

Our results support a pattern of both ontogenescence and senescence in *A. montanus*, as indicated by the effects of size on survival [coefficient SVL: 0.266 (−0.113 to 0.642), coefficient SVL^2: −0.283 (−0.561 to 0.027)]. Although our assessment is based on size rather than age, the two are

closely related in tailed frogs until at least approximately age 7 (Daugherty 1979), and are likely positively correlated in our populations. For tailed frogs and other amphibians, ontogenescence is generally ascribed only to the earliest or larval stages of populations (Petranka 1985). However, our results suggest that ontogenescence continues into the early juvenile period as well, which may be related to timing and size of individuals at metamorphosis (Schmidt et al. 2012). Notably, the survival rates which we estimated for adult tailed frogs are similar to those of other long-lived, pond-breeding anurans in the region that are much more fecund than tailed frogs (McCaffery and Maxell 2010; Muths et al. 2010). The similar survival rates among adults of these species suggest that ontogenescence in the highly fecund species is likely much stronger than for species such as tailed frogs that lay comparably few eggs.

Senescence was once thought to be rare in wild populations (Medawar 1952), but there is increasing evidence it is common among vertebrates (Jones et al. 2008; Nussey et al. 2013). Despite these new lines of evidence, senescence is generally not considered an aspect of amphibian life history, likely owing to the difficulty in detecting this pattern in wild populations (but see Pearson 1955; Miller et al. 2014). If we extrapolate the sizes of individual *A. montanus* to ages based on Daugherty and Sheldon (1982a), the onset of senescence in our populations follows the prediction demonstrated by Jones et al. (2008), where the onset of senescence correlates positively with generation time. Also, the decline in survival occurs at sizes near the onset of sexual maturity (Daugherty and Sheldon 1982a), which is consistent with other predictions of senescence patterns (Williams 1957; but see Jones et al. 2008). In addition to classical explanations for senescence, which emphasize weak selection later in the lives of individuals (Williams 1957), variation in survival among ages may result from increased sensitivity of those age classes to environmental pressures such as predation (Bleu et al. 2015). Our study was shorter term than is typical for assessing senescence in wild populations; longer term data sets can provide estimates that are more precise and allow for deeper exploration of the shape of the senescence curve with higher order models. We confirmed the pattern of senescence in *A. montanus* with an additional analysis using Bayesian Survival Trajectory Analysis (BaSTA); however, this a posteriori analysis did not support ontogenescence in *A. montanus* (Colchero et al. 2012) (Electronic Supplementary Material 3).

Our data suggest that female tailed frogs not only move farther on average than males, but also that they may be more likely than males to make long-distance movements. For example, the top 5% of female and male *A. montanus* movements were estimated to be > 95 m and > 57 m during the study period, respectively (Fig. 4). For *A. truei*,

the pattern was similar between sexes with the top 5% of female and male movements > 81 m and > 30 m, respectively. This pattern of female-biased movement has previously been reported for *A. truei* but not *A. montanus* (Burkholder and Diller 2007; Daugherty and Sheldon 1982b). Sex-biased movement is commonly linked with mating strategies, where intense male–male competition for mates (the local mate competition hypothesis) is associated with male-biased movement, and competition for resources (local resource competition hypothesis) is associated with female-biased movement (Greenwood 1980; Dobson 1982; Pusey 1987; Gros et al. 2008). We suspect the trend of female-biased movement in tailed frogs is partially driven by the species' peculiar reproductive strategies. Breeding occurs from spring through autumn, perhaps, because females can store sperm for several months and then fertilize and oviposit eggs when conditions are suitable (Dodd 2013). During this time, females may move long distances in search of suitable oviposition sites and evidence suggests that they may breed only every other year (Metter 1964; Burkholder and Diller 2007), which may encourage females to move in and out of breeding areas while males remain relatively philopatric (Wahbe et al. 2004). Pressure for this behavior may have been stronger in the Rocky Mountain streams where sex ratios were female-biased. Furthermore, male tailed frogs do not call, and we are unaware of competition for mates in this genus. In total, this mating strategy would seem to favor male philopatry to streams, whereas females are free to optimize resource acquisition, increasing their probability of movement.

Our movement estimates from *A. montanus* support the long-standing assumption in the amphibian literature that juveniles are more likely to disperse than adults (Dole 1971; Wells 2010). This assumption was challenged by a comprehensive study of Fowler's toads (*Bufo fowleri*) which suggested that the perception of greater per-capita movement by juveniles was simply a product of their greater abundance compared to adults (Smith and Green 2006). In contrast to Smith and Green (2006), we found that small *A. montanus* likely moved farther than large individuals, and evidence for this pattern was stronger for females than males. For example, the longest 5% of estimated movements of unsexed *A. montanus* individuals—who generally represented the smallest among *A. montanus* captured—were > 340 m. And across all *A. montanus*, movement decreased as size increased. We did not detect this pattern in *A. truei*, perhaps due to the smaller sample size for this species, though previous evidence suggests that juveniles may make more significant terrestrial movements than adults (Bury and Corn 1987; Wahbe et al. 2004; Matsuda and Richardson 2005). Although prior studies have shown juvenile-biased movement in amphibians, to our knowledge, no other studies have accounted for

the potential confounding effects of survival and recapture probability in these estimates.

Even in spatial models where movement and emigration are accounted for in survival estimates, uncertainty in emigration and movement still affects the estimates of survival. Uncertainty in these estimates increases as the length of movements of animals increase relative to the dimension of the study area; uncertainty further increases as recapture probabilities decline (Schaub and Royle 2014). In our study, low recapture probabilities and higher than expected movement rates along with movement away from the streams likely limited the precision of both our survival and movement estimates, though this was less likely a problem in the California reach. Specifically, the uncertainty in mean movement rates in our study, especially for juveniles, could not be completely untangled from the uncertainty of the survival estimates. This result is similar to that from Daugherty and Sheldon (1982b) where questions about the role of mortality and emigration in local population dynamics remained, because none of the youngest individuals released were ever recaptured. Our movement estimates lack precision, in part, because we were not able to account for overland movement which was more likely in the *A. montanus* populations than in the *A. truei* population. This is because the Rocky Mountain streams were surrounded by forests with abundant cover, which likely promotes overland movement as opposed to more xeric conditions surrounding the California stream. With the exception of estimated movements by smaller unsexed *A. montanus*, the lengths of our reaches generally encompassed the range of estimated movement distances in both species. However, even though the boundaries of the study area are explicitly accounted for in the spatial CJS model, individuals that are released near and make relatively long-distance movements towards the boundaries of study areas potentially have a negative effect on the precision of demographic estimates. Therefore, longer stream reaches with buffers where no new individuals are marked would likely provide parameter estimates that are more precise; but longer reaches and larger study areas are costly in terms of resources expended.

In our study, we chose to spread capture effort across five separate populations of *A. montanus* instead of focusing on a single-study site. This choice allowed our estimates to better represent the demographic patterns of the species as a whole—rather than the pattern of a single population—although with the cost of acquiring less information at any one stream. These issues underscore the fundamental challenge of demographic studies of wild populations, where sampling logistics inevitably constrain the accuracy and precision of results (Williams et al. 2002). This is especially true when planning the extent of a study area, which must be balanced between being large enough to encapsulate a large majority of the movement patterns of the focal species and within the resources available to investigate the question of interest.

Intraspecific differences in survival and movement are thought to be common in vertebrates and to have important population consequences (Hutchings 1993; Funk et al. 2005). However, to provide unbiased baseline estimates of these vital rates, researchers must not only separate rates into age- and sex-specific components, but also explicitly account for recapture probability, survival, and movement. Our evidence of age- and sex-specific survival and movement in tailed frogs adds to mounting evidence that complex demographic processes occur in many vertebrates (Medawar 1952; Nussey et al. 2013). More fundamentally, these estimates are crucial for models of population growth and for conservation planning.

Compliance with ethical standards

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