Trap characteristics and species morphology explain size-biased sampling of two salamander species

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Abstract. Demographic studies often depend on sampling techniques providing representative samples from populations. However, the sequence of events leading up to a successful capture or detection is susceptible to biases introduced through individual-level behaviour or physiology. Passive sampling techniques may be especially prone to sampling bias caused by size-related phenomena (e.g., physical limitations on trap entrance). We tested for size-biased sampling among five types of passive traps using a 9-year data set for two species of aquatic salamanders that have a 20 and 61 fold change in length over their ontogeny (*Amphiuma means*, *Siren lacertina*). Size-biased trapping was evident for both species, with body size distributions (body length mean and SD) of captured individuals differing among sampling techniques. Because our two species differed in girth at similar lengths, we were able to show that size biases (in length) were most likely caused by girth limitations on trap entry rates, and potentially by differences in retention rates. Accounting for the biases of sampling techniques may be critical when assessing current population status and demographic change.

Keywords: *Amphiuma means*, body size, detection probability, inventory, passive trapping, population monitoring, sampling bias, *Siren lacertina*.

Introduction

Sampling every individual in a population is infeasible in most ecological studies. As a result, demographic studies often use samples of the population to make inferences about the population as a whole. These samples are often assumed to be unbiased and reflective of the general structure of the population of interest. However, non-random sampling of individuals may occur due to factors such as trap properties (Smith et al., 2004; Willson, Winne and Keck, 2008), observer differences (Cunningham et al., 1999; Diefenbach, Brauning and Mattice, 2003), individual behavior (Biro and Dingemanse, 2009), or weather conditions (Connette, Crawford and Peterman, 2015). In cases where sampling methods lead to non-random sampling of individuals with respect to body size, these inherent biases can potentially confound inference about true demographic processes in size-structured populations (Willson, Winne and Keck, 2008; Connette, Crawford and Peterman, 2015).

Passive trapping requires animals to encounter traps during the course of their natural movements and is used both for demographic studies and as an index of activity (Willson and Gibbons, 2010). Passive trap captures depend on a sequence of often unquantified processes (e.g., "removal" in Bravener and McLaughlin, 2013), each of which can introduce bias into the final sample (fig. 1). Size-dependent biases within any of these steps can potentially compromise the ability of the sample to be representative of the population as a whole. The first step in the capture sequence, availability for capture by passive traps, depends on whether or not an animal is moving and capturable during the trapping period (e.g., due to seasonal activity or microhabitat preference; Todd and Winne, 2006; Schalk, Luhring and Crawford, 2010). A subset of available individuals may

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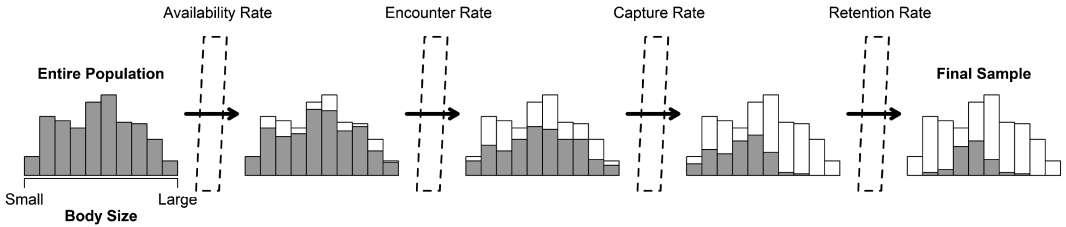*Corresponding author; e-mail: tomluhring@gmail.com

Figure 1. Theoretical illustration of the passive trapping process and the generation of a size-biased sample. Population size-frequency histograms are partially shaded to indicate the individuals remaining in a sample. Arrows indicate that a sample of individuals is filtered (dashed rectangle) to yield a particular subset at the next stage of the capture process. In the above example, availability and encounter rates are independent of size, but the capture process excludes large individuals, while the retention process allows small individuals to leave and selects for larger individuals in the final sample.

then be captured if they encounter, enter, and are retained by a trap prior to the observation at the end of the sampling interval (fig. 1). The first steps of this sequence are general to most sampling methodologies (e.g., count surveys, active capture techniques), as the inclusion of an individual in the final sample always requires that they are first available and successfully encountered. Samples generated by the physical capture of individuals may then be uniquely influenced by the remaining steps in the capture process: capture and retention of individuals.

At each step in the capture process, trap design has potential to bias the characteristics of animals represented in the observed population sample. The final steps of the passive trapping process (e.g., from encounter to retention) can be affected (and thus manipulated) by differences in trap properties. Encounter probability can be manipulated by the size of the trap entrance (Koivula et al., 2003) or by structures that redirect animals towards the trap entrance (e.g., drift fences with pitfall or associated funnel traps, Ryan et al., 2002). Entrance rate is affected by the number and smallest diameter of the entrances (Stuecheli, 1991; Greenberg, Neary and Harris, 1994; Shoup et al., 2003; Willson, Winne and Keck, 2008; Farallo, Brown and Forstner, 2010). Once an animal is in the trap, retention rate is affected by the size and design of possible exits (Fronzuto and Verrell, 2000; Willson, Winne and Fedewa, 2005; Willson, Winne and Keck, 2008; Halstead, Wylie and Casazza, 2013).

We expect species with larger breadth of intraspecific body sizes to be more likely to demonstrate size-bias in trapping because they are more likely to reach sizes that interfere with their capturability. Although behaviour and environmental factors may affect likelihood of trap entrance, we expect physical constraints imposed by trap characteristics to produce predictable and invariable effects on sampled body size distributions – namely the maximum size of animal that can enter a trap. Furthermore, we predict that the size and accessibility of potential trap exits directly affects the probability that an animal is retained.

We used length and mass data from a 9-year demographic study to test for trapping-induced size bias in two species of large aquatic salamanders that undergo considerable growth during ontogeny (*Amphiuma means*, *Siren lacertina*). Aquatic traps used in this study utilized funnels as entrances, but differed considerably in characteristics expected to influence entrance (smallest diameter of funnel: 25-150 mm) and retention rates (mesh size: 4-38 mm) (table 1; see online supplementary fig. S1). Body length and mass are commonly used metrics for testing for size-biases, however, we believe size-bias would be caused primarily by limitations of entrance and mesh size on the girth (diameter) of animals being able to enter and readily exit the trap. After testing for the effects of trap type on body size distributions of captured animals, we explored the potential effect of girth as a mechanism for size-biased capture

Table 1. Trap types and predicted limitations of entrance and retention effects on capture sizes. Entrance size limits the maximum girth of animal catchable by that trap, whereas mesh size determines the smallest animal that can be retained once inside the trap. Maximum and minimum lengths of expected *Siren lacertina* and *Amphiuma means* caught are calculated from a girth to SVL regression (see methods).

Trap	Entrance: funnel opening diameter (mm)	Predicted maximum SVL (mm) enterable		Retention: mesh size (mm)	Predicted minimum SVL (mm) retainable	
		S. lacertina	*A. means*		*S. lacertina*	*A. means*
Plastic minnow	25	217	382	4	42	101
Steel minnow	45	384	650	6	58	128
Trashcan	45	384	650	6	58	128
Fyke net	150	no upper limit		6	58	128
Hoop net	150	no upper limit		38	326	556

rates. To do this, we estimated girth to length relationships for each species, used funnel and mesh size as predictors of maximum and minimum girths of capturable individuals for each species, and then calculated a predicted range of lengths that we expected to see sampled by each trap type. We predicted that trap entrance size would create size-dependent entrance rates by excluding larger animals and that mesh size would affect size-dependent retention rates by enabling smaller animals to readily escape. We then compared field-sampled body length distributions among traps types and examined them for evidence of size bias consistent with predicted girth limitations.

Materials and methods

Study species

Greater siren (*Siren lacertina*) and two-toed Amphiuma (*Amphiuma means*) are large, primarily aquatic salamanders (Petranka, 1998; Schalk and Luhring, 2010). We expect *A. means* and *S. lacertina* to be particularly sensitive to size-biased sampling as they grow 20-fold (hatchling-maximum adult total length; 57-1162 mm) and 61-fold (16 to 978 mm), respectively in length during their lifetime (Goin, 1947; Conant and Collins, 1998; Gunzburger, 2003). We expect captures of *S. lacertina* to demonstrate truncated distributions of capture sizes in aquatic traps at smaller body lengths than *A. means* because *S. lacertina* are heavier per unit of length (Luhring, 2008; fig. 2) and appear to increase in girth faster than *A. means* (fig. 2). This higher girth at smaller sizes would cause *S. lacertina* to approach maximum girth at a smaller body length for traps than *A. means*.

Data collection

Sampling occurred on the United States Department of Energy's Savannah River Site in Aiken County, South Car-
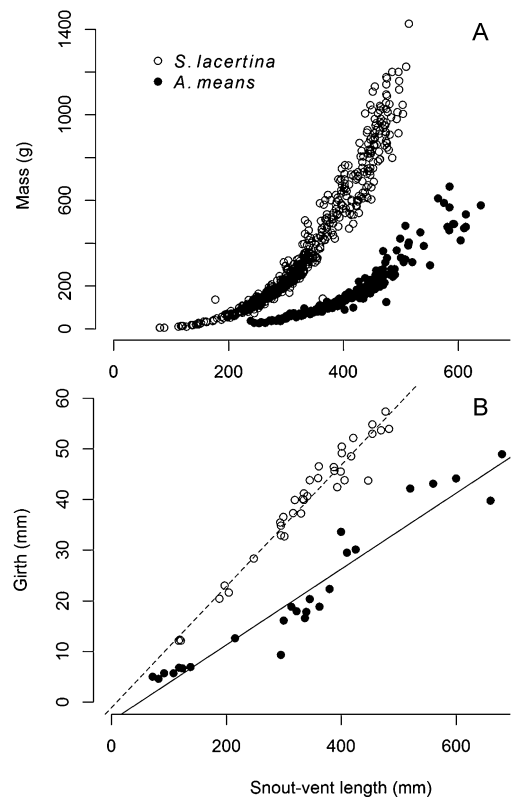

Figure 2. Relationship between snout-vent length (SVL) and mass (A) and girth (B) for *S. lacertina* (open circles) and *A. means* (closed circles). Length-mass relationships for both species and length-girth relationships for *S. lacertina* are taken from live animals in the study population. Length-girth relationships for *A. means* were collected from museum specimens (see methods). Girth and snout-vent length were strongly correlated for *S. lacertina* (girth = 0.12 × SVL − 0.10; Adjusted R^2 = 0.96) and *A. means* (girth = 0.07 × SVL − 0.36; Adjusted R^2 = 0.92).

olina, USA at a 5-ha isolated Carolina bay wetland (Dry Bay; 33°15′0.30″N 81°44′46.07″W) from September 2006 through January 2014 (Luhring, 2008). Animals were captured in five types of passive-sampling traps, 1) plastic minnow traps, 2) modified steel minnow traps, 3) trashcan minnow-traps, 4) hoop nets, and 5) fyke net (Vogt, 1980; Luhring and Jennison, 2008; Willson, Winne and Keck, 2008; Luhring, 2009). Traps varied in funnel opening diameter and mesh size (table 1; fig. S1A-E), which we predicted would affect size-dependent entry and retention rates, respectively.

Traps within Dry Bay were arranged into 4-6 arrays during each of 19 10-day sampling periods (once monthly September 2006-September 2007, July and August 2008, January 2009 and 2010, June 2011, February 2014). Locations of arrays and the traps within in them were repeatedly used across sampling efforts (Luhring, 2008; see online supplementary fig. S2) with a trashcan trap (length × diameter; 70 × 55 cm, non-mesh rubber walls and 4 wire mesh funnels; Luhring and Jennison, 2008; fig. S1C), plastic minnow trap (43 × 16 cm, plastic mesh walls; fig. S1E), and steel minnow trap (42 × 19 cm, plastic-coated wire mesh walls; fig. S1D) placed together at one of 5 sampling stations per array. Each array also received 3-5 hoop nets (183 × 76 cm, 3 hoops with knotted nylon netting mesh walls; fig. S1B) (identical number for each array within a sampling period) and 1 array received a double-throated fyke net (approximately 360 cm in length with a large square front hoop 150 × 150 cm, followed by 5 120 × 120 cm square hoops, cloth mesh walls; fig. S1A). Although steel minnow traps, plastic minnow traps, and trashcan traps were placed within 1 m of each other, trashcan traps generally were set in deeper water (e.g., fig. S1D) at the edges of thick stands of panic grass (*Panicum* sp.) whereas the steel and plastic minnow traps were set inside and along the edges of these stands. No traps were completely submerged in order to prevent drowning target species and bycatch (e.g., snakes). Hoop nets and the fyke net were set between trapping stations within arrays.

Traps were checked each morning and all animals were removed. All *S. lacertina* and *A. means* were returned to the lab, weighed, measured (body length), marked, and released at the point of capture within 24-hours. Because our demographic study was focused on *S. lacertina*, all individuals of this species were photographed dorsally. Both species were weighed to the nearest 0.1 g on a Mettler PC 440 electronic scale (Mettler Instrument Corporation, Highstown, NJ). *Amphiuma means* were measured in a squeeze box (see Sorensen, 2004) and *S. lacertina* were measured on a meterstick (both to the nearest 1.0 mm). We injected passive integrated transponder (PIT) tags (12 mm tags, AVID Marketing Incorporated, Norco, California, USA) into the tail of *S. lacertina* (minimum size: ∼180 mm SVL) and *A. means* (minimum size: ∼300 mm SVL) (see Luhring, 2008, 2009) to permanently mark individuals as this has been shown to be an effective and safe approach for marking large aquatic salamanders (Sorensen, 2003; Winandy and Denoël, 2011). Because the trapping effort was part of a robust design mark-recapture study (Luhring, 2008), each individual was transported from the field to the lab, measured, marked,

photographed (*S. lacertina*) and returned to the point of capture within a trapping day. To minimize handling time and because time constraints associated with anesthetization and recovery would prevent the return of large numbers of animals to the field on their capture day, neither species was anesthetized prior to PIT-tagging (Luhring, 2008). Photographs were collected with a Nikon D200 (model#25235) camera with a Nikon 18-70 mm (model#2149) lens mounted to a Bogen TC-2 copy stand (Bogen Imaging Incorporated, Ramsey, NJ) 0.5 m above the siren. An index card with PIT-tag ID and a 15 mm vinyl ruler (Carolina Biological Supply, Burlington, NC, USA) used were placed on the wetted surface below the camera to provide an ID and size reference in each picture.

Girth to length relationships

After finding patterns of size-bias in our data, we used girth to predict upper and lower bounds of captureability for each species-trap combination and compared them to observed distributions of body length. To do this, we established length to girth relationships for each species based on available data from the study site (photographs of *S. lacertina*) and museum specimens (*A. means*). A subset of 37 photos from different sirens (verified by PIT tag number) were used to measure girth with ImageJ (Schneider, Rasband and Eliceiri, 2012) by measuring across the widest part of the body when viewed dorsally (hereafter "girth"). Because photos were not taken of *A. means* as a part of the demographic study, girth measurements of *A. means* were taken from 25 museum specimens (see list as online supplement S3) by using digital callipers to measure across the widest part of the body when viewed dorsally. *Siren lacertina* used for girth measurements ranged from 117 to 483 mm SVL (snout-vent length, measured from tip of snout to anterior edge of cloaca) (mean 336 mm) and *A. means* ranged from 72 to 680 mm SVL (mean 328 mm). Girth to snout-vent length regressions (fig. 2) were then used to predict species-specific SVL's captureable by each trap type. Captureable size (SVL) for each species was predicted to range between a maximum SVL where we predicted girth to be equal to trap entrance diameter (maximum size that can enter the trap) and a minimum SVL where we predicted girth to be equal to mesh diameter (minimum size retainable) (table 1).

Data analysis

To test our prediction that different trap types effectively sample salamanders of different body size ranges, we treated individual SVL measurements as our response variable with trap type as a categorical predictor of body size (mm SVL) for an Analysis of Variance (ANOVA). Because body size measurements were obtained from a 9-year study, we simply estimated the long-term mean body size sampled by each trap type without considering temporal variation in body size distributions. We first performed a Bartlett Test of Homogeneity of Variances, which indicated that variance in sampled body lengths differed in relation to trap type for both *S. lacertina* and *A. means*. As a result, we fit

an ANOVA model for each species with unequal variances assumed among trap types (e.g., Rice and Gaines, 1989). This resulted in an estimated mean body length, μ, and standard deviation, σ, for each trap type to characterize the body length range sampled. We fit this model in a Bayesian framework using Markov Chain Monte Carlo (MCMC) simulation with uninformative priors assumed for all model parameters. We used the program JAGS v. 3.4.0 (Plummer, 2003) to run three parallel chains for a total of 10 000 iterations each, discarded the first 5000 iterations as burn-in, and thinned the remainder at a rate of 1:10 to obtain 1500 samples from the joint posterior distribution. This resulted in acceptable model convergence ($\hat{R} < 1.01$ for all parameters; Gelman and Hill, 2007). To make pairwise comparisons of body size distributions among trap types, we computed the difference in the estimated mean body size for each combination of trap types and their corresponding 95% credible intervals (CRIs). We interpreted differences among trap types to be significant in cases where these 95% CRIs did not include zero.

Results

We recorded 729 captures of *S. lacertina* and 168 captures of *A. means* between 2006 and 2014. *Siren lacertina* averaged mean $\pm$ SD = 330 $\pm$ 85 mm SVL, with an observed range of 80 to 514 mm. *Amphiuma means* averaged mean $\pm$ SD = 419 $\pm$ 84 mm SVL, with an observed range of 239 to 639 mm. Hatchlings of *S. lacertina* and *A. means* were not effectively sampled by any trap type. Snout-vent length (SVL) distributions varied among trap types (figs 3, 4). For both species, the mean size of captured individuals was smallest for plastic minnow traps. Steel minnow traps and trashcan traps had the next largest expected capture sizes but were not statistically distinguishable from each other; the percent difference between $\mu_{Steel\ Minnow}$ and $\mu_{Trashcan}$ (mean SVL of captures) was estimated at 3.52% (95% CRI: −0.9-8.0%) for *S. lacertina* and 2.3% (95% CRI: −4.9-12.1%) for *A. means*. Individuals captured in fyke nets had the largest mean size for *A. means* and the second largest for *S. lacertina*, surpassed only by hoop nets. Hoop nets had the largest mesh and failed to catch *S. lacertina* less than 322 mm or any *A. means*.

We also found differences in the range, or breadth, of body sizes sampled by various trap types (fig. 4). For *S. lacertina*, point estimates
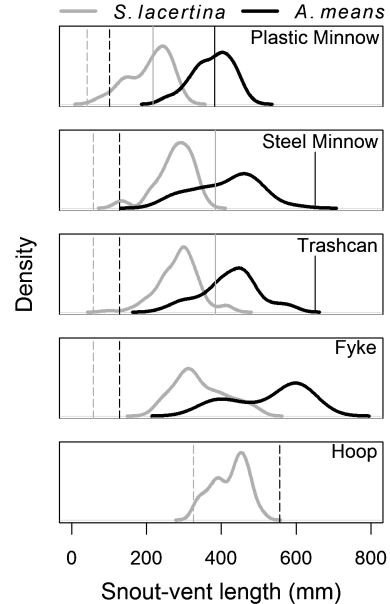

Figure 3. Capture density plots (proportion of individuals captured across a range of SVL) for *Siren lacertina* (grey line) and *Amphiuma means* (black line) from 2006-2014. Also shown are predicted maximum (solid vertical line) and minimum (dashed vertical line) sizes capturable for plastic minnow traps, steel minnow traps, trashcan minnow traps, fyke net, and hoop nets. Fyke and hoop net maxima are absent because they exceed the maximum sizes recorded for both species. No *A. means* were captured in hoop nets.

[posterior means] for the standard deviation of observed capture sizes ranged from 47.1 mm (σ_{Hoop}) to 69.6 mm (σ_{Fyke}). For *A. means*, plastic minnow traps sampled the smallest range of body sizes ($\sigma_{Plastic\ Minnow}$ = 52.9 mm), while fyke nets sampled the largest range of body sizes (σ_{Fyke} = 104.7 mm) but were statistically indistinguishable in capture size breadth from steel minnow and trashcan traps.

As seen with mass (fig. 2A), *S. lacertina* increased in girth faster with respect to body length than *A. means* (fig. 2B). Entrance constraints (funnel opening) and maximum length of *S. lacertina* and *A. means* captured by each trap type generally corresponded with predicted limitations caused by girth (fig. 3) and girth ranges were similar for both species for each trap type (fig. 5). Only hoop net captures of *S. lacertina* showed an absence of smaller captureable animals from capture records.
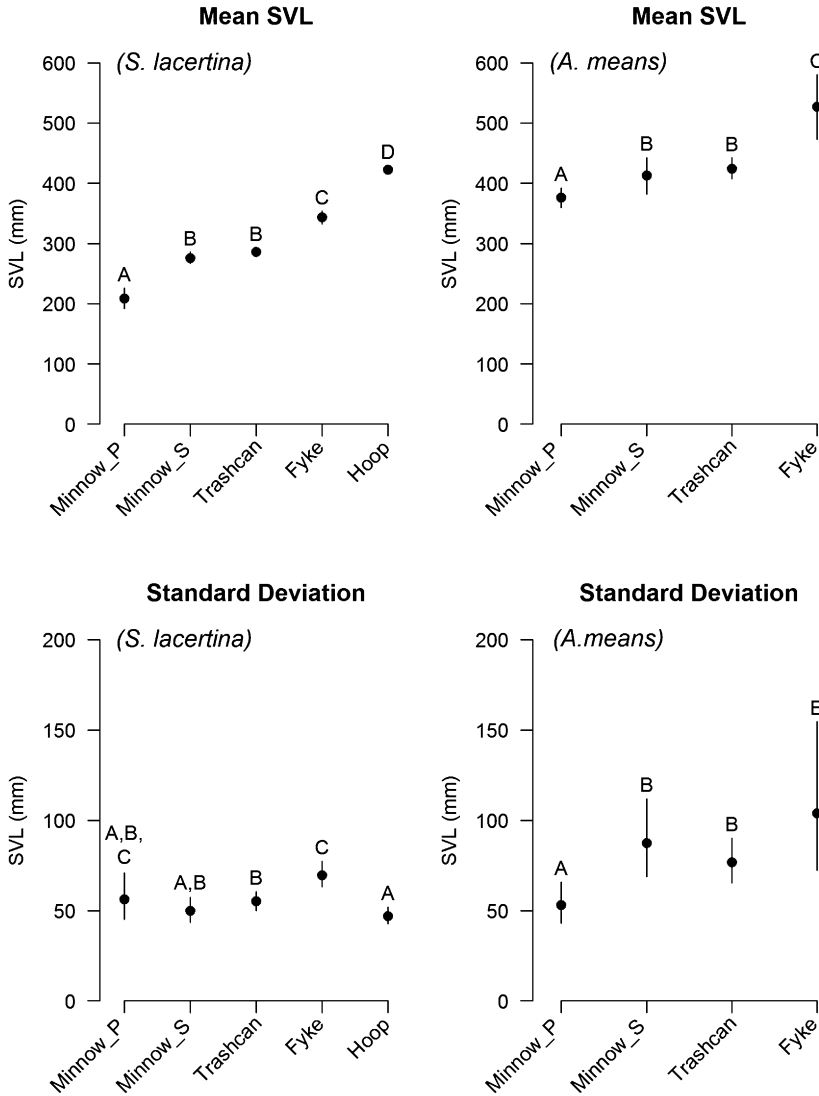
Figure 4. Estimated mean and standard deviation for snout-vent length of captured *Siren lacertina* and *Amphiuma means* for each trap type. Dots indicate point estimates (posterior means) for each parameter while vertical bars depict 95% credible intervals. Different letters among parameter estimates indicate that the 95% CRI for the difference between those parameters (within species) does not overlap zero.

Discussion

We found clear evidence that the use of different trap types resulted in size-related sampling bias. These biases were consistent with size-dependent effects of body size (namely girth) on trap entrance and retention rates. In our study, most trap types differed in the mean size of captured individuals, while some trap types also differed in the observed breadth of body sizes

they effectively sampled. Thus, rather than sampling individuals at random from the population, different traps selectively sampled particular size-classes and varied in the range of body sizes sampled.

Siren lacertina and *A. means* differed in body length captured in each trap type (SVL; figs 3, 4), but generally overlapped in girth (fig. 5). This is consistent with girth being the primary influence on size of animal entering and being
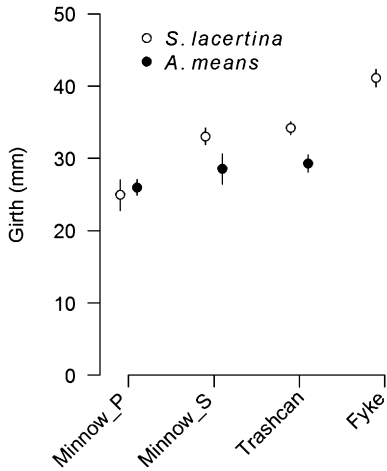
Figure 5. Converted values of girth for expected means and standard deviations from fig. 4 using length-girth regression equations. Data plotted for visual reference but not analysed because girth was estimated from girth-length relationships and not directly measured from each individual.

retained by traps. However, this was not a precise predictor for some traps (e.g., upper limit of plastic minnow traps fig. 3). This may be because girth (the maximum transverse width of the body) is a measurement of soft malleable tissue. When head width was used for *S. lacertina*, the maximum catchable size in plastic minnow traps is predicted to be 242 mm SVL (see online supplementary fig. S4) which is closer to the actual upper limit of plastic minnow trap captures. Although girth may be less precise than head width for smaller animals, girth increasingly exceeds head width with increased body size and becomes more of a limiting factor (e.g., several large sirens were able to push their head through hoop net mesh but were unable to pull the rest of their body through) (fig. S4). Shrinkage caused by the preservation process may have caused estimates of *A. means* girth to be smaller than that of living animals (Verrell, 1985; Colleoni et al., 2014) and led to the lowered estimated values of girth captured in each trap relative to *S. lacertina* (fig. 5). If shrinkage led to underestimated *A. means* girths in our study, then distributions of estimated girth measurements for *A. means* and *S. lacertina* (fig. 5) would likely be even more strongly aligned across trap types.

Although some shrinkage may have occurred in *A. means* specimens prior to measurement, our mass to SVL relationships suggest that *S. lacertina* increase in girth faster with respect to body length than *A. means* (fig. 2A) and this led to smaller *S. lacertina* (body length) sampled among trap types (figs 3, 4). Upper bounds on body size distributions among minnow traps (plastic, steel, trashcan) appear to be strongly limited by entrance size (most evident for *S. lacertina*) (fig. 3).

Retention rate did not appear to be as rigidly tied to trap characteristics. Despite four of five trap types being predicted to sample some of the smallest individuals, we failed to capture the smallest size classes, as reported previously with passive trapping of snakes (Willson, Winne and Keck, 2008). We attribute this to size-biased availability, encounter or retention rate of the smallest size class. Size-biased availability or trap encounter rates might result from habitat preference or behavioural avoidance of the trapped areas by smaller individuals because sirens and amphiumas readily consume smaller salamanders (Luhring, 2007a; Schalk, Crawford and Luhring, 2009; Montaña, Ceneviva-Bastos and Schalk, 2014). Differences between minnow trap capture size distributions (figs 3, 4) appeared to be related to differences in entrance diameter (identical for trashcan and steel minnow trap) rather than for microhabitat (plastic and steel minnow traps placed in shallower water than trashcan minnow traps). Hoop nets were the only trap type that appeared to capture individuals approaching the predicted minimum retainable size (hoop net – predicted minimum: 326 mm, smallest captured *S. lacertina*: 322 mm SVL; fig. 3), suggesting the occurrence of size-biased retention. As opposed to the missing lower end of size distributions seen with other trap types (e.g., minnow traps), smaller *S. lacertina* were capturable as evidenced by their capture by other nearby traps. Thus, trap characteristics influencing size-biased retention rate appear to be observed only in cases where previous steps in the trapping sequence have not al-

ready truncated the size distribution (e.g., size-biased availability).

Although body length is a commonly used measurement of animals, other characteristics such as girth may interact with trap properties to determine sample bias. The strongest patterns of size-biased sampling (with respect to range of body lengths captured by each trap type) were observed in the species with the larger increase in girth per unit length (*S. lacertina*), not in the species with the larger range in body length (*A. means*) (figs 2, 3, 4). Predicted size limits on trap entry appeared to largely hold for both species based on predicted girth and trap entrance size (fig. 3). Although girth constraints are theoretically identical for both species, *S. lacertina* approach girth constraints at smaller body lengths than *A. means* (table 1), thus creating more tightly constrained ranges of body length distributions for *S. lacertina* (fig. 3). This is consistent with our hypothesis that girth limitations on entry rates introduced size-bias at a crucial step in the sampling process. While post hoc detection of size-biased sampling is fairly straightforward when traps yield different body size distributions, it is critical to understand the mechanism(s) causing the bias to determine if demographic patterns seen in the sample are representative of the population. For instance, in cases where a trap type has an upper or lower size limit on captures, the potential magnitude of observable size shifts in a population is truncated. Furthermore, when capture depends on activity of individuals, a change in capture rate or size distributions could reflect changes in size-dependent activity levels or true shifts in body size distributions.

Size-biased sampling can have important implications for many studies of animal populations. In addition to confounding basic assessments of the relative frequencies of different size- or age-classes, size-biases in capture rates can lead to an inability to detect entire life stages (e.g., juveniles; Willson, Winne and Keck, 2008, this study) or track changes in population size structure. Furthermore, many

mark-recapture models for estimating population parameters such as abundance, density, or demographic rates assume that there is no un-modelled heterogeneity in capture or resighting probabilities either among all marked individuals or between marked and un-marked individuals (Williams, Nichols and Conroy, 2002). Although violation of this assumption likely results in small bias to survival estimates, the potential effects on population size estimates can be considerable (Cormack, 1972; Carothers, 1973). For instance, in extreme cases where capture probability of unmarked individuals is considerably less than for marked individuals (e.g., ineffectively sampled age classes), estimated population sizes or densities may be severely under-estimated. Furthermore, the applicability of estimated demographic parameters to under-sampled size or age classes may remain unknown.

Demographic studies examining size-dependent selection events (e.g., Wikelski and Trillmich, 1997; Brown and Brown, 1998; Winne, Willson and Gibbons, 2010; Luhring and Holdo, 2015) are also dependent on being able to distinguish between observed patterns body size due to sampling bias and those caused by real demographic shifts (e.g., Connette, Crawford and Peterman, 2015; Grant, 2015). In our study population, for example, three droughts from the 1990's to 2010's created size-class gaps by extirpating the smallest *S. lacertina* (size-dependent drought mortality; Luhring and Holdo, 2015). Initial surveys showed gaps between size classes, however, multiple surveys over several years with individually-marked animals were required to determine that this gap was caused by natural phenomena and not size-biases in passive sampling techniques (Luhring, 2008, 2009; Luhring and Holdo, 2015).

One can attempt to avoid or at least ameliorate sampling bias through the "potpourri approach" whereby a multitude of sampling measures are employed to maximize probability of detection across all size classes and buffer against detection biases of any one technique

(Gibbons et al., 1997; Layman and Smith, 2001; Luhring, 2007b). Although this approach may reduce the likelihood of having serious problems with size-biased detection, it does not guarantee that size-biases are absent or unimportant (Willson, Winne and Keck, 2008). Size-biased capture rates should be especially problematic for trap types that capture animals at either end of a size distribution. One extreme example was seen at our study site following a major drought which extirpated smaller *S. lacertina* from the population (Luhring and Holdo, 2015). Following the drought at this site mostly large *S. lacertina* (mean 388 mm SVL) were present and all *S. lacertina* captures ($n = 31$) were in trap types with entrances 45 mm or larger. Only 1 post-drought recruit (rarely-captured size class) would have been able to physically enter plastic minnow traps which selectively sample smaller animals. Thus, size-dependent selection had removed most capturable individuals for one trap type, which would have been unlikely to detect species presence despite the persistence of a robust adult population.

In passive trapping, sampling bias is a procedural artefact that can be introduced at any of the four stages of the trapping process (fig. 1). Due to the potential for size- or age-biased sampling to misrepresent demographic processes through non-random sampling of populations, accurate interpretation of demographic data may depend on understanding and accounting for non-random sampling of individuals. In cases where such biases are not understood or easily accounted for, careful consideration must be given to how demographic inferences are made, and how they might change if sampled individuals are not representative of the population as a whole.

Although we used a post hoc analysis of size bias in our trapping design, passive trap designs can be decided a priori with pilot studies, data from previous studies, or by measuring museum specimens. Investigators should carefully consider how each step of the trapping process

works with regard to morphology (including allometric trajectories during ontogeny), animal behaviour, physiology, and how they can potentially result in non-random sampling (bias). With the two species we studied, trap entrance size ultimately determines the upper girth limit of captures whereas mesh size potentially sets the lower girth limit of retention of captured animals.

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