

OPINION

Please don't misuse the museum: 'declines' may be statistical

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Abstract

Detecting declines in populations at broad spatial scales takes enormous effort, and long-term data are often more sparse than is desired for estimating trends, identifying drivers for population changes, framing conservation decisions, or taking management actions. Museum records and historic data can be available at large scales across multiple decades, and are therefore an attractive source of information on the comparative status of populations. However, changes in populations may be real (e.g. in response to environmental covariates) or resulting from variation in our ability to observe the true population response (also possibly related to environmental covariates). This is a (statistical) nuisance in understanding the true status of a population. Evaluating statistical hypotheses alongside more interesting ecological ones is important in the appropriate use of museum data. Two statistical considerations are generally applicable to use of museum records: first without initial random sampling, comparison with contemporary results cannot provide inference to the entire range of a species, and second the availability of only some individuals in a population may respond to environmental changes. Changes in the availability of individuals may reduce the proportion of the population that is present and able to be counted on a given survey event, resulting in an apparent decline even when population size is stable.

Keywords: availability, declines, detection probability, historic resurveys, museum data, shrinking salamanders, temporary emigration

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Museum data aren't 'free'

Museum records and other historical datasets can be rich sources of ecological information (Shaffer *et al.*, 1998; Swetnam *et al.*, 1999; Graham *et al.*, 2004; Lips, 2011); indeed the development of software that simplifies complex statistical modeling has allowed researchers to more frequently utilize these datasets. Study objectives, site selection inclusion probabilities, sampling protocols, and collection effort are typically not associated with museum records, so these data are typically reduced to 'known presences' when at least one specimen is recorded at a geographic location. For example, scientists analyze 'presence-only' data to estimate species' distributions and the relationship of species occurrence to covariates (Phillips *et al.*, 2006). However, these methods, like all statistical tests and approaches, can be easily misapplied (Yackulic *et al.*, 2012), leading to biased inference (Royle *et al.*, 2012), and ultimately may suggest inappropriate management actions. The limitations on the potential value of

museum data depend on the way in which data were collected and stored, and require careful evaluation of the potential biases in each dataset (Tingley & Beissinger, 2009).

When information about changes in population abundance is desired, it is common to assume a correlation between range size (from spatially referenced museum records) and population size (Bonebrake *et al.*, 2010). However, estimating range size from museum data may be biased, as populations at range margins may be harder to detect due to lower abundances (Lawton, 1993) and higher turnover (Doherty *et al.*, 2003), or simply due to nonrandom sampling of the landscape (Kadmon *et al.*, 2014).

An analogous problem is in the arrival dates of birds or the dates of first flowering (e.g. Primack & Miller-Rushing, 2012); detection of the earliest arrival or flowering (conditional on the event actually occurring) is increasingly likely as the frequency, synchrony, or effort expended to detect the event increases. Phenological events are therefore subject to the same analysis challenges as spatial ranges, with similar cautions in estimating differences in arrival times, flowering frequencies, and other events from museum records

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where the detection process may confound observation of the true occurrence of a phenological event (Tingley & Beissinger, 2009). Further, mixtures of individuals with different phenologies (e.g. migration behavior; Both, 2007) is an alternative hypothesis for variation in recorded event dates, highlighting the difficulty in assigning cause to an incompletely observed processes.

When such heterogeneity results in variation in the availability of some individuals for detection at each sampling occasion, individuals that are unavailable are 'temporary emigrants' from the population (Kendall & Bjorkland, 2001). While this temporary emigration may result from nuisance processes (e.g. home ranges only partially overlap sampling locations), other reasons are more ecologically meaningful [e.g. only individuals in breeding condition are available for detection in a given year (Bailey *et al.*, 2004a)].

This individual heterogeneity in detection probabilities is a pernicious problem (Kendall & Nichols, 1995), and when availability of individuals is not accommodated for during sampling, individual metrics like body size (e.g. Eastman *et al.*, 2012), morphology (e.g. Pergams & Lawler, 2009), coloration (e.g. Doucet & Hill, 2009; Özgo & Schilthuizen, 2012), or phenology (e.g. Menzel *et al.*, 2006; Kearney *et al.*, 2010) characterized through museum records may not be truly representative of the entire population of interest. Individual heterogeneity may arise simply from differences in weather among sampling occasions (G. M. Connette, J. A. Crawford, W. E. Peterman, In revision), or from individual traits (which may also be of direct interest). For example, Doucet & Hill (2009) recognizes that in museum specimens of manakin birds, 'In addition to individual variation, plumage coloration varies by time of year, which, along with temporal degradation, may contribute to bias in accurately assessing change in population-level characteristics'. Attempts to correct for bias in museum records may address one component of the detection process (e.g. effort), as Kearney *et al.* (2010) report: 'While the use of opportunistically collected data probably adds considerable noise to any signal of phenological shift, we accounted for any chronological bias by including the number of museum records as a covariate in the analysis of the trend through time'. However, any inference to the true pattern may still be obscured by individual heterogeneity; correcting for effort still assumes the population is sampled randomly, with all individuals having an equal chance of being included as a museum record.

As variation in response to regional climatic conditions and local environmental conditions is expected in multispecies communities (Parmesan & Yohe, 2003), on

any given sampling occasion, one may fail to detect a species [or individuals of a species which may have one set of traits, e.g. flowering time; Cleland *et al.* (2006)] even as another species (or other individuals of a species with different traits) is available for detection. This may be additionally influenced by interactions among species, which may bias the estimation of population changes (Bailey *et al.*, 2009). When not accommodated explicitly in an analysis, the assumptions of equal availability for every individual in a population and equal collection effort is made when using museum records, though an assessment of violation of these assumptions is not typically tested (Tingley & Beissinger, 2009; Boakes *et al.*, 2010).

One recent example is the treatment of museum data to infer changes in population-level metrics in eastern *Plethodon* salamanders (Caruso *et al.*, 2014), which help to highlight the potential pitfalls of relying on museum records for inference to population changes in time.

Evidence for eastern *Plethodon* declines

Highton (2005) collected extensive data on the occurrence of *Plethodon* species across the Appalachian mountains, USA, from the 1950s to the 1990s, reporting that these data suggest large-scale declines during the 1980s. Declines on this scale would represent a potentially serious change in the structure and functioning of the Appalachian forest ecosystem, and identifying the consequences of environmental changes to *Plethodon* populations is potentially useful in developing conservation actions.

To investigate the causes and consequences of these reported declines, Caruso & Lips, (2012) resurveyed Highton's sites in the Great Smokey Mountains National Park and concluded that declines have continued. More recently, Caruso *et al.* (2014) posited a link between average population body size and climate warming based on resurveys of a larger number of sites and historic museum records. These studies, while presenting interesting hypotheses with potential support in the data, do not account for the known problem of individual variation in detection probability and false-absences (Link & Nichols, 1994).

Alternative hypotheses for reported range-wide declines in *Plethodon* populations

Unfortunately, evaluating the evidence for declines based on historical data is not straightforward (Skelly *et al.*, 2003; Moritz *et al.*, 2008; Thompson & La Sorte, 2008; Tingley & Beissinger, 2009). I describe two competing classes of hypotheses (one ecological, which is of primary interest, and one statistical, which is important

for unbiased inference to the true population process) for observed changes in eastern *Plethodon* populations:

1. A set of ecological mechanisms which may drive changes in population size that are reflected in counts, and
2. A statistical mechanism whereby changes in counts of individuals or occupied sites may be the result of an only partially observed process.

In this way, one may specify multiple mechanisms for the observed changes in relative abundance, occupancy, and body size at the set of study sites which were established and revisited by Highton (2005) for his natural history studies of *Plethodon* salamanders, and resurveyed by Caruso & Lips (2012) and Caruso *et al.* (2014).

1. Salamander populations may have exhibited systematic declines across the study sites in response to environmental factors, or
2. Changes in the availability of individuals may reduce the proportion of the population which is available to be counted on a given survey event, resulting in an apparent decline even when population size is stable (which may also be related to environmental factors).

These two hypotheses are not mutually exclusive, and in fact, should be evaluated simultaneously. Ignoring the second (process) component can lead to bias and misidentification of the ecological (pattern) components. The first hypothesis was partially evaluated by Caruso & Lips, (2012) and Caruso *et al.* (2014); here I focus on the second.

Changes in availability or detection may obscure ecologically interesting patterns

Under this second class of hypotheses, changes to habitat or environment (e.g. forest cover or climate change) may reduce the portion of a population available for detection at a given site. These changes may differentially affect individuals depending on age, sex, or other characteristics. Here, I make the distinction between population abundance and observed counts of individuals, which can be related by the canonical equation $E(C) = N/p$, where E denotes expectation, C is the count obtained during a survey event, N is the true population size (either of individuals when abundance is of primary interest, or of number of sites with at least one individual of a species when an estimate of site-occupancy is desired), and p is the probability a member of the population (of individuals or occupied sites) is present and available for detection during a survey event (e.g. Williams *et al.*, 2002). It is important to note that the probability of detecting an

individual is not equivalent to the probability of detecting *at least one individual* of a species, unless the species is territorial and sample units are scaled to a single individual territory or home range (Mackenzie & Nichols, 2004). For each survey occasion, counts can reference the number of individuals encountered (sometimes referred to as an 'index' to abundance), the number of individuals in classes defined by individual characteristics (such as age, size, or sex), or the number of sites in which >1 individual of a species is detected (i.e. site-occupancy). When a sampling design includes information permitting inference about p , then estimation proceeds via maximum likelihood or Markov chain Monte Carlo (e.g. Williams *et al.*, 2002; MacKenzie *et al.*, 2006; Royle & Dorazio, 2008).

One may further decompose the detection probability, p , into the component probabilities that the individual is available (i.e. present on the forest floor) for detection p_a , and that, conditional on availability, it is counted during a survey, p_d (Pollock *et al.*, 2004; Nichols *et al.*, 2009). When a portion of the population is unavailable for detection during a survey, the resulting counts reflect both availability and detection probability (i.e. the product $p_a * p_d$) for individuals in the population. These detection probabilities may underlie observed changes in frequencies of classes defined by, e.g. morphology (Gibbs & Karraker, 2006), body size (Caruso *et al.*, 2014), phenology (Bailey *et al.*, 2004b), or other characteristics such as age or sex.

When inferences are based on raw counts (no effort to deal with detection issues), the assumption underlying any comparison (e.g. over time, space) is that (i) the relationship between C and the expected population size, N , is approximately linear; or (ii) the detection probability, p , is constant, or at least is drawn from a stationary distribution. Violations of these assumptions can result in decreasing counts or changing size frequencies over time. This can be demonstrated using a simple set of scenarios. In these scenarios, I simulated observations for each of two groups using the R code [`rbinom(n = 1000, size = 50, p = a * d)`]; where a and d are the availability and detection parameters, respectively. I simulated observations of individuals for two time periods, with different a or d parameters (Fig. 1a–c). These scenarios demonstrate that, given a constant population size of two groups (say, small or big individuals), it is possible to observe changes in the relative proportion of groups between two time periods even when no difference exists (Fig. 1a–c). Alternatively, variation in the availability parameter may fail to detect true population changes (Fig. 1d), leading to erroneous inference. In this scenario, the population of small individuals remains

constant ($N = 50$), while the population of big individuals initially is the same but doubles in the second time period ($N = \{50, 100\}$).

Returning to the *Plethodon* survey data (Highton, 2005; Caruso & Lips, 2012), while the counts from multiple sites showed some level of decline across time, this is not sufficient evidence that declines are widespread in *Plethodon* populations. Similarly, observed declines

in body size cannot be presumed to characterize the entire population (Caruso *et al.*, 2014) without accounting for variable detection among individuals of different sizes. It is possible that only the surface (and observable) component of the population has changed in size frequency, and that the observed surface population is a function of sampling design and local environmental conditions.

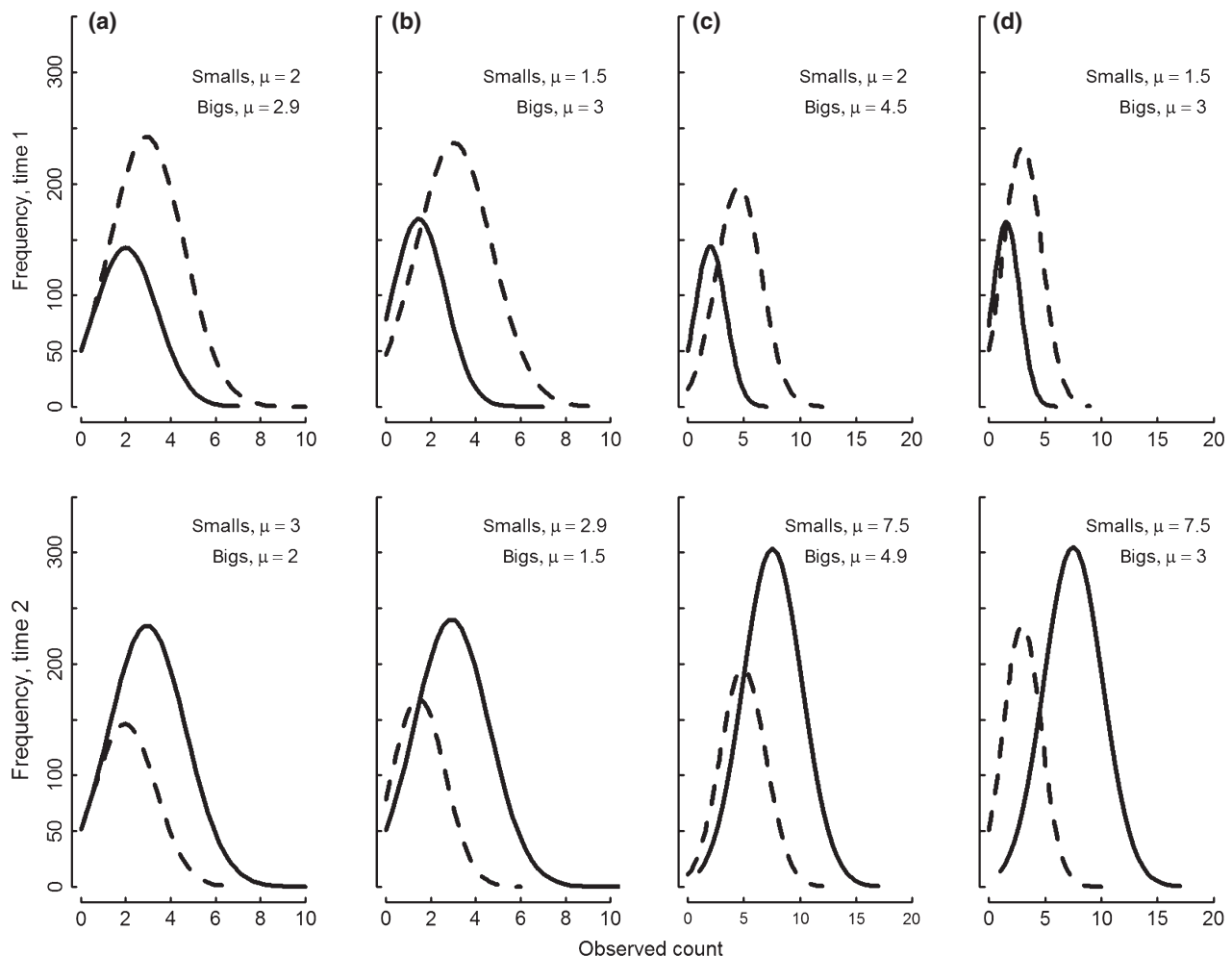


Fig. 1 The expected variation in counts of individuals for 1000 repeated samples and different scenarios for combinations of detection and availability probabilities, which differ between a hypothetical time period 1 (top panels) and time period 2 (bottom panels). Solid lines are the frequency distribution of counts of small individuals, dashed lines are for big individuals; the means of the sample distribution (i.e. the expected count) are reported for each group. Based on the observed data, one would conclude that proportion of small individuals increased in the population under each of the scenarios. In (a–c), the true population size is constant in the two time periods, with $N = 100$ ($N_{\text{small}} = N_{\text{big}} = 50$). In (a), only detection differs between time periods ($d_{\text{small}} = \{0.2, 0.3\}$; $d_{\text{big}} = \{0.3, 0.2\}$); the availability is constant and equal ($a_{\text{small}} = a_{\text{big}} = 0.2$). In (b) only availability differs between time periods ($a_{\text{small}} = \{0.1, 0.3\}$; $a_{\text{big}} = \{0.3, 0.1\}$); detection probabilities are constant and equal ($d_{\text{small}} = d_{\text{big}} = 0.2$). In (c) both availability ($a_{\text{small}} = \{0.2, 0.3\}$; $a_{\text{big}} = \{0.3, 0.2\}$) and detection probability ($d_{\text{small}} = \{0.2, 0.5\}$; $d_{\text{big}} = \{0.3, 0.5\}$) vary; applying contemporary detection probabilities to historic data would lead to erroneous inference in this scenario. Panel (d) is the most complex scenario considered here, where detection is constant among groups and time periods ($d_{\text{small}} = d_{\text{big}} = 0.3$), availability varies in time ($a_{\text{small}} = \{0.1, 0.5\}$; $a_{\text{big}} = \{0.2, 0.1\}$), and population size for big individuals doubles from time 1 to time 2 ($N_{\text{big}} = \{50, 100\}$); population size for small individuals is constant ($N_{\text{small}} = 50$) in both time periods.

One common class of factors affecting detection probabilities are observer effects, and observer experience is a known factor influencing detection rates (Kendall *et al.*, 1996). When collections were made by the same observers, decline in ability to detect or capture a species across time is a plausible (though uncomfortable) hypothesis (Emlen & Dejong, 1991). Alternatively, observers may improve with experience; for example, Highton (2005) reports: 'I became familiar with the patterns of seasonal activity and relative abundance at sites throughout the range of each species', which may have resulted in an unconscious improvement in detecting species, ages, or size classes of interest to the original study objectives.

Can counts be useful?

Detection probabilities are low and variable for *Plethodon* salamanders (Bailey *et al.*, 2004b), and are often found to be related to site-level and temporally varying covariates such as season, temperature, moisture, species, age and sex (Mazerolle *et al.*, 2007). For any dataset, adjusting historical surveys with contemporary detection rates is appealing, but assumptions must be acknowledged, including:

1. Detection probabilities are equal (or not systematically different) across the dimension of comparison (e.g. among sites, species, individuals, or time periods),
2. There is a constant relationship between measured covariates and detection probability over time,
3. The portion of the population which is available for capture is constant over time.

In the case of Caruso & Lips (2012) and Caruso *et al.* (2014), it is unclear that these assumptions were considered and dealt with directly in making inference to all eastern *Plethodon* populations – though they must be, to ensure unbiased conclusions and proper inference.

The potential for bias in using museum or historic records isn't restricted to *Plethodon* salamanders; for example bias in availability may result from variation in phenology [e.g. the arrival of migratory birds to breeding sites (Cotton, 2003); flowering dates (Caradonna *et al.*, 2014)], especially if this is related to age class or other individual covariates. For species of *Plethodon*, because of their largely underground existence, the chance that an individual is present on the surface (and therefore subject to measurement) is small, and is related to environmental conditions such as site disturbance, elevation, and species [e.g. Bailey *et al.* (2004b); Price *et al.* (2012)]. This should induce increased vigilance for violations of the assumptions of equal catchability, constant relationship with environmental covariates, and constant availability.

Nonrandom selection of populations results in bias toward detecting declines

Finally, I note that even if one could demonstrate that the count data are proportional to abundance across visits, the data from Highton (2005) represent a set of populations that were not selected at random, and thus one cannot make inference to the entire range of eastern *Plethodon* salamanders. Sites were chosen as focal sites for comparative studies of *Plethodon* species where it was easy to obtain large numbers of individuals [Highton (2005):35], thus population abundances for one or more of the target species may have been higher than average. When populations fluctuate around some equilibrium size because of demographic stochasticity, they are expected to exhibit stationary distributions. If a population happens to be sampled at a time when abundance is large relative to the equilibrium population size, then abundances at subsequent visits will on average be smaller. The same kind of phenomenon is true for the analogous situation in patch-occupancy problems where an investigator selects mostly or only historically occupied patches for resurvey efforts. Proportion of occupied patches can never increase above 100%. If patch extinction and colonization probabilities remain unchanged over the course of surveys, the proportion of occupied patches is expected to decline toward equilibrium values. So whenever sites of high abundance or occupancy are selected for resurvey efforts, we expect to find decreases as a result of chance alone. Historic data on occupied sites (presence-only data) are most appropriate for estimating factors affecting extinction (Karanth *et al.*, 2010), not to demonstrate declines.

Conclusion: be careful with counts

Observations of changes in surface-active salamanders by Caruso and colleagues (Caruso & Lips, 2012; Caruso *et al.*, 2014) suggest a potential response of eastern *Plethodon*, which is correlated with increased temperatures. Caruso *et al.* (2014) present an interesting hypothesis, that some of the surface-active portion of the populations chosen by (Highton (2005) for his life-history studies have changed in size. The important distinction is twofold; first these results cannot provide inference to the entire eastern *Plethodon* range, and second only the surface-active portions of the population may be affected. If individuals are more likely to spend more time below ground as the temperature increases, and this affects age or size classes differentially, then Caruso *et al.* (2014) do not observe a shift in average population body size, rather a shift in average body size of the surface-active population. The true

average population body size is confounded by observation error.

Conservation success may require acting sooner than later when a problem is identified, even with imperfect information (Martin *et al.*, 2012). The general sense is that the rate of amphibian declines has increased in recent history (McCallum, 2007), though causes of declines are often elusive (Stuart *et al.*, 2004). It is tempting to look to historic data to draw inferences about declines and describe changes in populations. In so doing, it is essential to make unbiased inferences, by putting forward multiple hypotheses for observed changes, and acknowledging the potential for observation processes to influence the support for these ecological hypotheses.

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