



Detecting population trends with historical data: Contributions of volatility, low detectability, and metapopulation turnover to potential sampling bias



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ARTICLE INFO

Article history:

Received 22 May 2017

Received in revised form 21 August 2017

Accepted 22 August 2017

Available online 30 August 2017

Keywords:

Sampling

Bias

Colonization

Extinction

Metapopulation

Detectability

Trend estimation

Turnover

ABSTRACT

In retrospective studies, discrete population units such as ponds may be resurveyed at a later time using only the set of initially occupied sites. There are possible confoundings that affect estimates of occupancy change under these conditions. For most possible parameter values for a metapopulation, simulations and analytical results show that turnover leads to a tendency to observe a decline in the proportion of initially occupied sites that are occupied at a later time even when the overall metapopulation is stable or increasing. For a given time interval, the spurious decline will be greater when metapopulation turnover is higher. If site-level detectability d is <1 , a single resurvey of only the initially occupied sites will show a decline of $1-d$ even if no change has taken place. Finally, volatile populations can be difficult to resurvey, especially if sample units are chosen based on having an abundance of the species at the earlier survey. All three issues can exist simultaneously and their influence on trend estimates can be difficult to distinguish based on samples at only two points in time. A sample of literature illustrates clear cases where these biases could exist, even though a variety of survey methods were used. Suggestions are made for improved sampling, including resampling the entire original set of sites and conducting multi-year resurveys.

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1. Introduction

A global decline of amphibian populations is a significant theme in the scientific literature of the last two decades. In addition, population decline is a key determinant for placing species on lists of conservation concern (see IUCN red list criteria). Likewise, management of species is strongly influenced by their trends. Marsh and Trenham (2008) found, based on a survey of population monitoring studies, that 62% of the studies were for purposes of conservation and 53% specifically sought to estimate trends (85% for the longest-duration studies). For abundant or intensely studied species, trend estimates may be reliable. For rare, poorly studied, or cryptic species, however, population estimates and trends may not be reliable.

There are two basic types of trends commonly estimated: population abundance and occupancy. Population trends require some sort of systematic estimate of numbers over time. An example is the North American Breeding Bird Survey (Sauer et al., 2017). In

the case of some surveys, of pond-breeding amphibians in particular (but other species as well), it can be more efficient to think in terms of trends in site occupancy. Ponds are often taken as a survey unit, and fewer occupied ponds over time may be interpreted as an indicator of decline. Concern over amphibian decline has led to numerous investigators revisiting old survey data to establish a baseline for evaluating historic occupancy and rate of decline (e.g., Cassani et al., 2015; Corser 2001; Drost and Fellers 1996; Fellers and Drost 1993; Fisher and Shaffer 1996; Graham et al., 2011; Highton 2005; Johnson et al., 2011; Marsh and Trenham 2008; Moskwik 2014; Palis 1997; Skelly et al., 2003). Such retrospective studies pose unique challenges for inference.

For long-term (temporal) surveys, guidelines do exist. It is recommended that resampling within a survey bout be conducted to enable detectability to be estimated (MacKenzie et al., 2003, 2009; MacKenzie and Royle 2005). In the case that discrete habitat patches or units (like ponds) are not identifiable, it is recommended that random locations be selected and visited on each sample date (MacKenzie et al., 2009). Detailed protocols exist for estimating occupancy or metapopulation colonization and extinction parameters (MacKenzie et al., 2003; MacKenzie and Royle 2005). However, colonization and extinction parameter estimation

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is labor-intensive and cannot be done from a single survey. While it is known that failure to follow these protocols will produce a bias in results, the nature and magnitude of this bias has not been elucidated or accounted for. For example, Grant (2015), Tingley and Beissinger (2009), and Walls (2014) only briefly mention potential biases. Articles promoting use of museum archives may not mention sampling difficulties at all (e.g., Shaffer et al., 1998).

Because pond-breeding amphibians are often surveyed at discrete units, we use this taxon to illustrate issues that arise with retrospective studies. Adult amphibians may be fossorial and cryptic, thus aquatic larvae or other juvenile stages are often targeted during population surveys. Compared to many terrestrial vertebrates, amphibians can be difficult to sample. First, amphibians have a short and temporally variable reproductive period which, in some cases, can lead to a survey missing the larval stage (Bevelhimer et al., 2008). Second, amphibians might not reproduce in a given year in a given pond (Semlitsch et al., 1996; Taylor et al., 2005). Third, if a local population is rare, it might simply be missed during a re-survey. Fourth, species can have highly variable population sizes (McCain et al., 2016), which means that detectability of pond occupancy may not be constant. Fifth, local colonization and extinction (site turnover) can give the appearance of local extirpations for any particular site. Finally, adults are known, in some cases, to actively move between or select ponds for mating (Crump 1991; Resetarits and Wilbur 1989, 1991; Spieler and Linsenmair 1998), violating the assumption that a pond corresponds to a fixed population sub-unit.

Use of historic data gathered over time, as in museum records or multiple literature records, has unique challenges. If the sites were occupied at different times, an aggregate list of all observations would tend to overestimate average historical occupancy (Loehle and Sleep 2015). Museum records may also reflect different sampling intensities, sampling methods, and surveyor skill (see Loehle and Sleep 2015). For these and other reasons, such data may not represent a valid baseline for estimating trends.

For all of the above reasons, any set of survey locations for detecting occupancy trends that are based simply on the species having been observed there in the past (i.e., not a random survey), as documented by Walls (2014) and Cruickshank et al. (2016), will risk confounding (Fig. 1). We here evaluate the nature and implications of such possible confounding for retrospective surveys. We focus on three factors that may influence population trend estimates: metapopulation processes (Hanski and Ovaskainen 2003); detectability; and population volatility. Note that these issues do not occur for species that are abundant, are easily detected, or for which metapopulation dynamics can be ruled out.

2. Methods

We explored three lines of evidence related to metapopulation processes, detectability, and volatility using pond-breeding amphibians as our model organism.

2.1. Metapopulation processes

The implications of confounding due to metapopulation processes were explored using population models and sampling theory. The context is site (e.g., pond) occupancy of pond-breeding amphibian species for a single resurvey of only previously occupied sites. We evaluated the process of surveying metapopulation units using patch occupancy models (Hanski and Ovaskainen 2003). This approach assumes that all patches are the same quality and have the same connectivity across unsuitable habitat. The model consists simply of a list of sites which may be either occupied or not and have a fixed probability of transitioning between these two states in

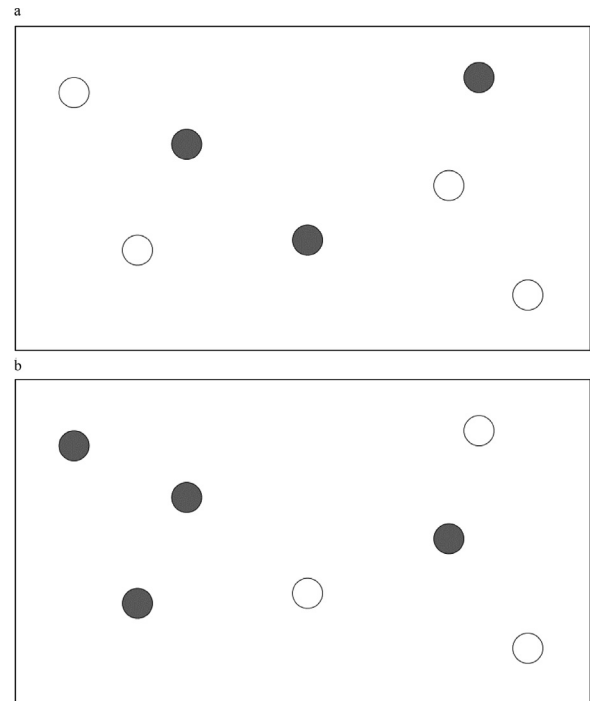


Fig. 1. Illustration of the effects of metapopulation dynamics on resampling bias. For a collection of sites (e.g., ponds) at time 1 (a) three are occupied (solid circles). At a later time (b), four are occupied, but only one of the original three.

either direction. Only occupancy was modeled, not population size. This is appropriate for sampling regimes based on assessing species status by revisiting historically occupied sites. Given a metapopulation structure with all sites equal in quality and equally likely to be colonized (the simplest case), the equilibrium number of patches can be estimated when extinctions equal colonizations. For total patches N , and occupied patches N_o , we have

$$c * (N - N_o) = e * N_o \tag{1}$$

giving equilibrium patch number

$$N_o = c * N / (c + e) \tag{2}$$

where c and e are per year patch colonization and extinction probabilities, respectively.

We took example colonization and extinction values for networks of ponds occupied by amphibians from Marsh and Trenham (2001, their Table 2), using their total number of suitable ponds and occupied ponds (total suitable ponds = 200 for *Rana lessonae* and 1500 for *Hyla arborea*). The system was simulated as deterministic to eliminate stochastic effects. We modeled the actual population before consideration of detectability. The population of initially occupied sites, N_o , over time was

$$N_{o_{t+1}} = N_{o_t} - e * N_{o_t} + c * N'_{o_t} \tag{3}$$

$$N'_{o_{t+1}} = N'_{o_t} + e * N_{o_t} - c * N'_{o_t} \tag{4}$$

where N_{o_t} is the set of originally occupied sites unoccupied at time t and N'_{o_t} is the set of originally occupied sites unoccupied at time t . Similarly, the originally unoccupied sites, N_u , were modeled by

$$N_{u_{t+1}} = N_{u_t} - e * N_{u_t} + c * N'_{u_t} \tag{5}$$

$$N'_{u_{t+1}} = N'_{u_t} + e * N_{u_t} - c * N'_{u_t} \tag{6}$$

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