

Site-selection bias can drive apparent population declines in long-term studies

Auriel M.V. Fournier^{1,2}, Easton R. White^{3,4}, Stephen B. Heard⁵

¹Coastal Research and Extension Center, Mississippi State University, 1815 Popp's Ferry Road, Biloxi, MS 39532, USA

²Corresponding author. Present address: Forbes Biological Station–Bellrose Waterfowl Research Center, Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, Havana, Illinois 62644, USA; auriel@illinois.edu

³Center for Population Biology, University of California, One Shields Avenue, Davis, CA 95616, USA

⁴Present address: Department of Biology, University of Vermont, 63 Carrigan Drive, Burlington, VT 05405, USA; Easton.White@uvm.edu

⁵Department of Biology, University of New Brunswick, PO Box 4400, Fredericton, NB E3B 5A3, Canada; sheard@unb.ca

Abstract

Detecting population declines is a critical task for conservation biology. The spatiotemporal variability of populations, along with logistical difficulties in population estimation, makes this task difficult. Here we call attention to a possible bias in estimates of population decline: when study sites are chosen based on abundance of the focal species, for statistical reasons apparent declines are likely even without an underlying population trend. This “site-selection bias” has been mentioned in the literature but is not well known. We show using simulated and real population data that when site-selection biases are introduced, they have substantial impact on inferences about population trends. We use a left-censoring method to show patterns consistent with the operation of the site-selection bias in real population studies. The site-selection bias is, thus, an important consideration for conservation biologists, and we offer suggestions for minimizing or mitigating it in study design and analysis.

Keywords: Population Decline, Conservation, Abundance, Population Dynamics, Site Selection

Introduction

Few issues are more important in the field of conservation biology than determining which natural populations are declining, asking what drives these declines, and designing interventions by which declines can be arrested or reversed (Martin et al. 2014; Inger et al. 2015; Ceballos et al. 2017; Heldbjerg et al. 2018; White 2018; Brewster et al. 2018). Accurately determining which populations are declining, and how rapidly, is particularly critical: only if we know which populations are most threatened can we allocate resources appropriately to understand and deal with the problem (Joseph et al. 2009, Gerber 2016). Here we call attention to a simple but pervasive statistical problem that arises in efforts to detect population declines in time-series data: when study sites are initially identified or chosen based on the local abundance of the focal species, subsequent time series can show exaggerated or even illusory declines.

Accurately detecting and measuring population declines is a major challenge for several reasons. Studying population dynamics over time is labor intensive and expensive, and since total population censuses are rarely possible, such studies must deal with substantial measurement uncertainty (Baum & Blanchard 2010; Reynolds *et al.* 2011; d'Eon-Eggertson *et al.* 2015; Rueda-Cediel *et al.* 2018) especially for species with low or variable detection probabilities (Nichols et al. 2000; Bailey et al. 2004). Furthermore, populations are naturally variable, often with random fluctuations and temporally autocorrelated changes that can reflect complex underlying dynamics (d'Eon-Eggertson et al. 2015; Mosnier et al. 2015; Öst et al. 2016; McCain et al. 2016; Rueda-Cediel et al. 2018). Incorrect conclusions about monitored populations can arise from short time series (Krebs 1991; White 2018), inconsistent methods (Hayward et al. 2015), and non-random sampling (Yoccoz et al. 2001, and this is our focus here). It is, therefore, essential that we understand what we can infer from population time-series data, and what constraints and biases limit that inference.

One important kind of non-random sampling, the selection of study sites at which the focal species is relatively abundant, may be rather common (in part because of understandable concerns about research logistics). Unfortunately, this abundance bias interacts in a simple but important way with population dynamics, and has consequences for inferences about population trends. Imagine that we begin a long-term study on the ecology of the (fictional) purple-snouted crompus (*Crompus nasupurpurea*). Population dynamics might or might not be our primary focus, but in either case we're likely to estimate population densities and track them over time. But where will we choose to begin our study? Crompus populations vary over time (Fig. 1), and population densities across sites are imperfectly correlated, meaning that we'll have a choice of study sites where crompi are locally abundant and ones where they are scarce. For many reasons (including logistics and the need to convince granting agencies of feasibility), we're most likely to begin our work in a population with plenty of crompi. This means we are more likely to begin a study near a population peak than near a trough; and in the ensuing time series we are more likely to see crompus populations decline than rise. This is simply a form of regression to the mean (Barnett et al. 2004). If many ecologists make this kind of study-site choice, the result may be a systematic bias toward the detection (or exaggeration) of population declines (Pechmann et al. 1991; Palmer 1993). We refer to this bias here as the "site-selection bias", although we note that many other biases also arise from non-random site selection of various sorts.

We should address two important issues immediately. First, we are not suggesting that populations will decline because researchers are actively inflicting harm (although all studies should evaluate this possibility). Second, we do not doubt that many populations are indeed suffering declines, and that many of those declines are caused directly or indirectly by human activity (Møller et al. 2008; Ceballos et al. 2017; Butchart et al. 2018). The site-selection bias deserves attention not because it invalidates claims of population decline – it does not – but because conservation biologists need decline estimates to be as accurate as possible.

We are not the first to realize that site-selection bias might exist. Pechmann *et al.* (1991), clearly recognized the issue in a highly-cited paper on amphibian population fluctuations:

“Large populations may be more likely to be noticed or used by researchers. Anecdotal data may therefore be biased toward observing peak populations that eventually will decline, rather than the reverse.” (Pechmann *et al.* 1991:894)

Not long after, Palmer (1993) used simulations to suggest that non-declining species, monitored initially at sites with high abundance, would appear to be declining. Skelly *et al.* (2003) made a similar point, but for presence-absence resurvey data: when researchers revisit historically known populations but do not search for new populations, local extinctions can be documented but newly founded populations cannot. The result, again, is similar bias towards the detection of exaggerated declines. No study, however, has attempted to quantify the effects of this bias or to detect its operation in real population data.

Here, we ask three questions. First, are literature warnings of the site-selection bias well known? Second, does selection of study populations by their population size lead to distortions of time trends, when that non-random site selection is applied to either simulated or real data? Third, do real time series show patterns consistent with site-selection bias effects? We show that literature warnings have gone largely unheeded, that deliberately inflicted site-selection bias can have a strong influence on inferred population trends, and that patterns in real population time series are consistent with an important effect of site-selection bias. In short: some declines (but not, of course, all) inferred for real populations are likely overestimated, and some may even be illusory – and this threatens our ability to respond appropriately to widespread and genuine conservation problems.

Methods

Literature Review

Pechmann *et al.*'s 1991 paper represents the earliest warning of the site-selection bias in the literature. Although the warning was not positioned very prominently in the paper, it was crystal clear and obviously important. We asked whether this explanation of the site-selection bias, in a highly cited paper, had detectable impact in the scientific literature. We examined papers citing Pechmann *et al.*'s, located via a ScopusTM search executed on December 19, 2017, and asked how many of those citations referred to or built on this mention of the site-selection bias. We assigned each citation to one or more of 8 categories, of which one was reference to the site-selection bias. The other 7 categories, referencing other points made by Pechmann *et al.*

(1991), are detailed in Appendix S1. We similarly traced all peer-reviewed citations to Palmer (1993).

Inducing bias in simulated population data

We used simulated population time series data to measure the strength of the site-selection bias, given temporally varying populations and plausible study-site-choice behavior. This procedure is not intended to demonstrate the existence of the bias in real studies; rather, it asks how severely the bias affects population-decline inference, when it exists. We simulated population time series in R (Version 3.4.0, R Core Team 2017). Complete R code is provided in the Supplementary Material. We generated 10,000 simulations, each with a set of 20 plots (or, equivalently, subpopulations) from which we could later select plots either with or without a site-selection bias. We began each plot with a population size drawn from a normal distribution with mean 1000 individuals and coefficient of variation of 0.2. Individual populations fluctuated independently but with the same generating model, which imposed a (lag 1) autocorrelation of 0.5 and used variation drawn from a lognormal distribution (with standard deviation 0.198, to match the CV for initial population sizes). We use the lognormal so that population growth and decline have an exponential basis, but otherwise we are not attempting to match the mechanisms underlying population dynamics of any particular real species. Each population was simulated for 110 years, and then the first ten years were removed to reduce dependence on initial conditions. In our simulations, we assume we are modeling the actual population size, rather than an estimate. That is, our times series include process error (noise in population growth rates) but not observation error (uncertainty arising from mark-release-recapture, transect sampling, or other methods for estimating population sizes in nature). We are not implying that the site-selection bias applies only to data in which population sizes are known exactly; the logic of regression to the mean applies to any population time series, regardless of the method of estimation. We chose to demonstrate the effects of the site-selection bias for the simpler case of known (simulated) populations before asking if we can detect it in real data that includes observation error.

We next subset our simulated populations in two ways, to simulate ecologists choosing among available study populations. First, to simulate the site-selection bias, we took the two plots with the largest populations in year 1. Choosing the largest and next-largest populations makes our conclusions somewhat conservative (vs. choosing only the single largest), because the second population should dampen the effect of the first. Second, as a control we took two plots at random. In each case, we estimated population trends for each selected plot over 2, 5, 10, 15, 20, 50 and 100 years via linear regression (of log-transformed population size) using the `lm()` function in R, with the regression slope being our estimate of population trend. We recognize that the assumption that populations are near a peak in population in year 1 (the implication of choosing the two highest populations) is a strong one, which is why we have also included situations where we look at the sites with the 5 and 10 (out of 20) highest population sizes in year 1. Results were nearly identical to the 2-population case, and we do not discuss the 5- and 10-population cases further.

We note two potential complications with our regression-slope estimates. First, in time series with temporal autocorrelation, significance tests would be inappropriate without

adjustment. However, nothing in our analysis depends on significance tests for single regression slopes. We analyse only patterns in large samples of such slopes, and regression slopes are unbiased in the presence of autocorrelation (Baltagi 2011:224). Second, regression assumptions are challenged for time series data including a mix of process and observation error (our simulations include only the former, but our real-world data include both). Fortunately, Humbert et al. (2009) showed that simple regressions yield unbiased slope estimates regardless of error types. Confidence intervals on single slopes may be either over- or underestimated depending on the mix of error types (Humbert et al. 2009), but at no point do we interpret such confidence intervals (again, we analyse only patterns in large samples of slope estimates). We therefore adopt the regression-slope approach, for both simulation and real-world datasets, because it is simple, and because it is the approach most commonly applied in the population-decline literature. There is, of course, a bewildering variety of alternative methods (Thomas 1996), which we do not explore here.

To test for effects of the site-selection bias, we compared trend estimates between the two largest populations and two random populations in a generalized linear model with a normal link function, including an interaction with length of the sampling period (2-100 years). We hypothesized that the site-selection bias would lead to significantly larger declines (i.e. more negative slope estimates) in the initially most abundant plots.

Real population data (Portal Project)

Our simulations use a simple population-dynamic model that may not strictly apply to any real-world species. Therefore, we applied a similar site-selection algorithm to a real data set that includes multiple subpopulations. We examined data from the Portal Project, which involves long-term monitoring of a Chihuahuan Desert ecosystem near Portal, Arizona, USA (Ernest et al. 2009). Since 1977, 8 replicate control plots have been sampled, with population size estimates for ants, plants, and rodents (Ernest *et al.* 2009; we did not work with data from the study's treatment plots). Control plots were assigned at random from a larger set of plots within an overall site selected because of its high rodent diversity. From this large dataset, we selected the seven most common rodent species among those sampled in the first year of the census. Using the abundance time series for those seven species, we first artificially induced the site-selection bias to examine its potential strength, and then tested for a signature of the bias in unmodified data.

To examine the potential strength of the site-selection bias, we worked with the four rodent species that showed apparent declines (log-transformed regression slope less than zero, whether significantly so or not, for all eight subpopulations summed). We chose among the eight available subpopulations (i.e. plots, in the Portal project) based on population sizes in year 1, exactly as we did for our simulated data. We compared regression slopes for two subsets of data: the two plots with the largest populations in year 1, and as a control, randomly chosen pairs of plots.

To test for the actual occurrence of a site-selection bias in the Portal data, we examined the effect of removing the first five years of data, after plot selection but before calculation of trend estimates. If time-series datasets tend to begin in high-population years (as a result of site-selection bias), this clipping will reduce the estimate of population decline; but absent a site-

selection effect, clipping should not affect the trend. To control for time-series length, we compared years 1977 through 2012 to the left-truncated dataset of years 1982 through 2017.

We note that our use of the Portal dataset to explore ideas about site-selection bias should not be taken as a critique of the fine work of the team that has produced and curated it. They graciously engaged with us about using their data in this way.

Real population data (worldwide vertebrate populations)

While the Portal data connects our simulations to real population data, it represents only a single study of a few species in one area. Therefore, we sought to simulate the site-selection bias, and detect its occurrence, using a much larger set of real population time series. We worked with a compilation of population-dynamics data by Keith *et al.* (2015), using sources including the Global Population Dynamics Database (NERC Centre for Population Biology, Imperial College 2010). From Keith *et al.*'s (2015) database, we selected population time series with 35+ years of data to ensure adequate statistical power for detecting trends (White 2018). We were left with time series data for two populations of elasmobranchs (class Chondrichthyes), nine of mammals (Mammalia), 98 of fish (Actinopterygii), and 857 of birds (Aves).

We began by asking whether we could induce and then detect a site-selection bias. Since the worldwide data lack the replicate-plot nature of our simulated data, we could not select among plots based on abundance. Instead, we used a time-for-space substitution. We contrasted estimates of population trends (regression slopes) for subsets of the worldwide time series: 1) data for 15 years starting at the time series high point, and 2) data for 15 years centered on the time series high point (seven years before and after). We executed this analysis for the 202 times series that included at least 7 years' data before and after the high point. We repeated this analysis using a random starting point rather than a high-centred series as the control; results did not differ, and we do not report them here. We note that this high-point analysis is a deliberate worst-case scenario (involving omniscient selection of the highest point in the entire time series), intended to put an upper limit on the seriousness of the site-selection bias.

For our real-world data, whether regression on raw or log-transformed population sizes is a more appropriate measurement of trend depends on whether any decline (or increase) reflects population dynamics (fundamentally exponential) or change in environment (plausibly linear), so we conducted analyses both ways. Nothing in the interpretation differed, so we report results from the log-transformed regressions for consistency with our simulations.

Next, we asked whether trimming the initial years (up to 15) of a time series reduced the tendency to detect declines, as it should if site-selection bias is making population times series disproportionately likely to begin in high years. We contrasted the estimated trends between data subsets for years 1-15, 2-16, 3-17, and so forth, conducting the analysis for each species that showed an overall decline ($n=346$). To assess the apparent strength of the site-selection bias, we chose trimming of the initial 10 years, and calculated the relative change in the trend estimate (time-series slope). The 10-year trim is an arbitrary choice that seeks to trim enough years to mitigate the bias while retaining enough of the time series for a good estimate of trend.

Results

Literature Review

We located 478 citations of Pechmann *et al.* (1991) in ScopusTM (after removing 11 apparent database errors that did not actually cite the paper). Just one (Wicknick *et al.* 2005) referred to Pechmann *et al.*'s (1991) observations about the site-selection bias. Wicknick *et al.* (2005) accurately summarized Pechmann *et al.*'s (1991) observation, but did not engage further with the issue. The other 477 citing papers mostly referred to Pechmann *et al.* (1991) to support assertions that amphibian populations are dynamic or that multiple factors can cause amphibian populations to fluctuate (see Appendix S1: Figure S1). Interestingly, 43 papers cited Pechmann *et al.* (1991) to support statements that amphibian populations are in decline, or that such declines are worrisome; none of these mentioned the possibility of the site-selection bias. Palmer's (1993) paper, which warned of the site-selection bias more prominently, has not been heavily cited. Of 26 peer-reviewed citations, we located just two that clearly and accurately referred to the possibility of the site-selection bias in estimates of population trends (Vilella & Smith 2005; Britton *et al.* 2009). Neither made any change to methodology or analysis to correct for the possible bias. We located no papers that tested for evidence of the problem in real data.

Inducing bias in simulated population data

Analysis of simulated time series data indicated that the site-selection bias can be detected, and can be strong, when deliberately induced. When the two largest (in year 1) populations are selected for study, more declines than increases were estimated – even for time series as long as 100 years (Fig. 2, top left). Apparent declines were more frequent and steeper for shorter time series (Fig. 2, bottom left). In contrast, time series for randomly chosen populations show slope distributions centered on zero, as expected (Fig. 2, right). Slope differences between random and site-selection-biased simulations were significant, as was the interaction between site selection and time-series length (Table 1).

Real population data (Portal Project)

Four Portal rodents showed apparent declines, although the decline was very weak for two of the four. For both species with substantial declines (*Dipodomys spectabilis* and *Onychomys leucogaster*), sampling populations based on year-1 abundance produced stronger estimates of the decline (Fig. 3 and Fig. S2; dashed red line to the left of solid black line), indicating that imposing a site-selection bias has the predicted effect. Furthermore, for both species, trimming the first 5 years' data reduces the estimated strength of decline (solid black line is further right in panel c), and this effect was significant (t-test on distribution of slopes; *D. spectabilis* $t_{(78.2)} = -12.5$, $P < 2 \times 10^{-16}$; *O. leucogaster*, $t_{(69.3)} = -5.4$, $P < 8.2 \times 10^{-7}$). Neither of these patterns held for the two species with very slight declines (*Dipodomys merriami* and *Perognathus flavus*; Fig. S3 and S4).

Real population data (worldwide vertebrate populations)

Starting analyses of time series at their high points (a time-for-space analogy of the site-selection bias) produced apparent declines, with regression slopes for the 15 years following a high point typically much more negative than those for the 15 years centered on the high point (Fig. 4). Potential explanatory variables (e.g. taxonomic class, variance in population size, autocorrelation generation length) did not strongly predict which time series were more likely to be affected by biased sampling (Appendix S1: Figure S5).

Removing initial years from the vertebrate time series reduced the tendency toward population declines. This effect is illustrated for a single exemplar time series in Figs. 5a and 5b. Removing initial years from each time series reduced the strength of apparent decline for most populations (Fig. 5c): 63% of populations showed a lesser decline after trimming, far from the null expectation of 50%. Starting at year 11 (removing the initial ten years) makes trends less negative for most datasets (65%; Fig. 5d), and the effect of this trimming can be quite large, with 14% of datasets showing at least a 2-fold change in estimated slope and 5% showing a 3-fold change.

Discussion

We were able to establish three important things about the site-selection bias. First, despite its occasional appearance in the literature (Pechmann *et al.* 1991; Palmer 1993; Wicknick *et al.* 2005; Villella & Smith 2005; Britton *et al.* 2009), the problem does not seem to be widely appreciated; or at least, warnings appear to have had little if any impact on practice. This is somewhat surprising, because the site-selection bias is simply a manifestation of regression to the mean, a very well understood phenomenon (Barnett *et al.* 2005). Second, simulated non-random selection of study populations can have dramatic effects on estimates of population trends. Third, at least some real population data show features consistent with an influence of the site-selection bias on our view of population declines in nature.

We traced what appears to be the first clear mention of the site-selection bias in the literature: Pechmann *et al.* (1991), a paper that appeared in *Science* at a time when amphibian declines were beginning to be front-page news. While that paper has been highly cited, its warning of the site-selection bias went almost entirely unheeded: only one of 478 papers cited Pechmann *et al.* (1991) for that aspect of their argument. Citations using Pechmann *et al.* (1991) to support statements that amphibian populations are in decline were over 40 times more common – even though the paper explicitly argued that such inferences are not straightforward. (We note again that we do not dispute that many populations truly are in decline – including, importantly, many amphibian populations.) A slightly later but clearer mention (Palmer 1993) has not been well cited (26 citations, with only two explicitly referring to the bias).

We were able to demonstrate clear effects of simulated site-selection bias on apparent population trends, in simulated population data and in two real datasets. This is not surprising, of course: we deliberately manipulated data to induce site-selection biases, and it would have been shocking if they did not have detectable effects. What is important, though, is that those effects were strong, and that biased site selection could artificially inflate the magnitude of estimated

declines or create apparent declines where there are none. When site-selection bias is severe, its effects on estimates of population trends are very strong.

Our simulations do not establish any influence of the site-selection bias on trend estimates from real datasets. That, of course, depends on the degree to which site selection is *actually* non-random with respect to population size – something that is seldom reported and difficult to reconstruct from information in the literature. However, we reasoned that the signature of biased site selection would be detectable as an easing of apparent declines for time series trimmed of their first few years of data. The pattern in the Portal rodent data is consistent with this same signature, but because we had only four declining species (and for two of those, the decline was very weak) we can't be sure that this pattern is really due to site selection. After all, even in the absence of the site-selection bias, *some* declines will be moderated by a left-censoring procedure like ours. (The random assignment of control plots within the Portal site should also have blunted the impact of any sensitivity of site selection to rodent abundance in addition to diversity.) The worldwide vertebrate dataset gives us ample power to identify the signature of site selection, though, and the bias was strong enough to significantly impact our inferences about population trends: trimming 10 years from the beginning of each declining time series decreased the magnitude of decline for 65% of populations (Fig. 5d). This suggests that the site-selection bias is pervasive and of significant strength in real-world population data. We note that there is a possible alternative explanation, although it is difficult to test. About 90% of the time series we examined started in the 1960s, and if the 1960s and 1970s featured more severe environmental impacts than following decades, trimming the initial 10 years could remove the time of steepest actual decline. However, we know of no reason to suspect that environmental impacts have moderated significantly since the 1970s for such a wide array of species.

We expect that effects of the site-selection bias will vary among populations, but other than a coarse breakdown by major taxon, we did not explore predictors of bias strength. We might hypothesize, for example, that the bias might decay more slowly in species with longer generation times; or that the bias might be weaker where local populations are more open to emigration and immigration (which should weaken spatial asynchrony and reduce the risk of selecting a single population near peak). Future analyses along these lines would be valuable, although they will likely require more intensive analysis of a smaller ensemble of datasets, because they will require more information about each.

While we have confirmed that the site-selection bias is an important worry for population-dynamic studies, we can make recommendations for study design and data analysis. First, long-term studies should always report site selection criteria (for an analogous argument, see Coppolillo et al. (2004)). Second, where possible, researchers should consider random sampling of suitable habitat as a means of choosing study populations, or formally consider the spatial variability of population trends (Vos et al. 2000; Yoccoz et al. 2001, Weiser et al. 2018). Of course, there are perfectly sensible reasons why researchers may choose to begin work where their study organisms are abundant, and many inferences are not affected by such decisions – but estimates of population trends are. When non-random site selection is justified, researchers should consider the possibility of pairing their non-random sites with additional sites chosen randomly from suitable habitat (Ponchon et al. (2018) have recently demonstrated the utility of

this approach in the tangentially related case of mark-recapture survival estimation). Rotational survey designs, where a subset of the sites are replaced each year, could also be useful (Skalski 1990). Third, site-selection biases should be greatly reduced in multi-species studies, because even if sites are selected based on the abundance of one species, the time series for other species in the same plots should be much less affected. Therefore, even when a single species is of focal interest, gathering and recording data for *other* species in the same plots should be considered. Fourth, data analysis should consider the possibility of site-selection biases whenever possible. The comparative analysis of raw and left-censored time series provides a simple way of diagnosing possible site-selection biases and estimating their strength, although we acknowledge that there is a trade-off between data quality and quantity and that many time series are too short for analysis following substantial left-censoring. Ideally, statistical methods might be developed to estimate and account for site-selection bias without left-censoring data, as has been done for a number of other challenges in estimation of trends (Thomas 1996). We hope that this paper might spur the development and testing of such methods. Finally, researchers working with long-term datasets – especially via meta-analysis – should recognize that site-selection biases are possible and may be especially likely in datasets arising from studies begun for reasons other than detection of population trends.

Site-selection bias may have similar, but opposite, effects in the case of rare species. Discovery that a species is rare may motivate the beginning of a long-term population study (Palmer 1993; Campbell et al. 2002). Such a reverse site-selection bias might result in the frequent observation of population increases simply because studies start in population troughs. This is, of course, the same regression-to-the-mean phenomenon that drives apparent declines from high population densities, operating from the opposite extreme (although it may be complicated by the absorbing lower boundary at population size zero). Observed recoveries, therefore, should not be uncritically accepted as evidence of conservation success or improved conditions for the imperiled species (Palmer 1993). Left-truncation of such rare-starting time series should shed light on the strength of this effect, as it did for the apparent declines in the data we examined. We note a further complication for rare species, though: once a species is detected as rare (and especially if it is red-listed), this very observation may provoke increased search effort (Jeppsson *et al.* 2010) and thus increasing population size estimates. Measures of, and correction for, search effort will be important in assessing population trends for species that begin in rarity. More generally, regression-to-the-mean effects, including those arising from non-random site selection, can affect any metric – a point occasionally made in the literature on long-term monitoring of biodiversity (Zobel et al. 1994; Wesche et al. 2012).

Bias in our ability to detect and measure population decline when it is occurring – or worse, the possibility of false positives in the detection of declines – has serious implications for conservation biology (Vos et al. 2000; Yoccoz et al. 2001). Ecosystems are under a wide suite of natural and anthropogenic pressures, and the result is undoubtedly real declines for many species. Documented extinctions, of course, provide irrefutable evidence that declines can be real and threaten biodiversity (Ceballos et al. 2015). Accurate detection and estimation of declines is a vital first step allowing conservation biologists and managers to prioritize available effort and financial resources in support of the populations that need it most.

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Table 1. Generalized linear model comparing slope values between two random populations and two highest populations, including an interaction for the length in years of the sampling period. Slopes are more negative for time series starting in the highest populations; length of the time series had a modest effect.

Variable	Beta	Std. Error	t-value	p-value
Intercept	-106.3	0.45	-233.0	<0.001
2 random	106.7	0.64	142.9	<0.001
years	1.39	0.009	165.3	<0.001
2 random * years	-1.404	0.013	-101.4	<0.001

Figure Legends

Figure 1. Population time series for two populations of purple-snouted crompi. Each shows varying population densities with some temporal autocorrelation. At time zero, a researcher can choose either of the two plots in which to begin a long-term study tracking population density (whether or not that is the main motivation). For logistical reasons, a researcher is more likely to begin work where there are more crompi (top panel; open circle), and the result is a tendency to detect population decline regardless of when the time series is stopped. A study in the plot represented by the bottom panel would likely detect population increases but is less likely to be initiated.

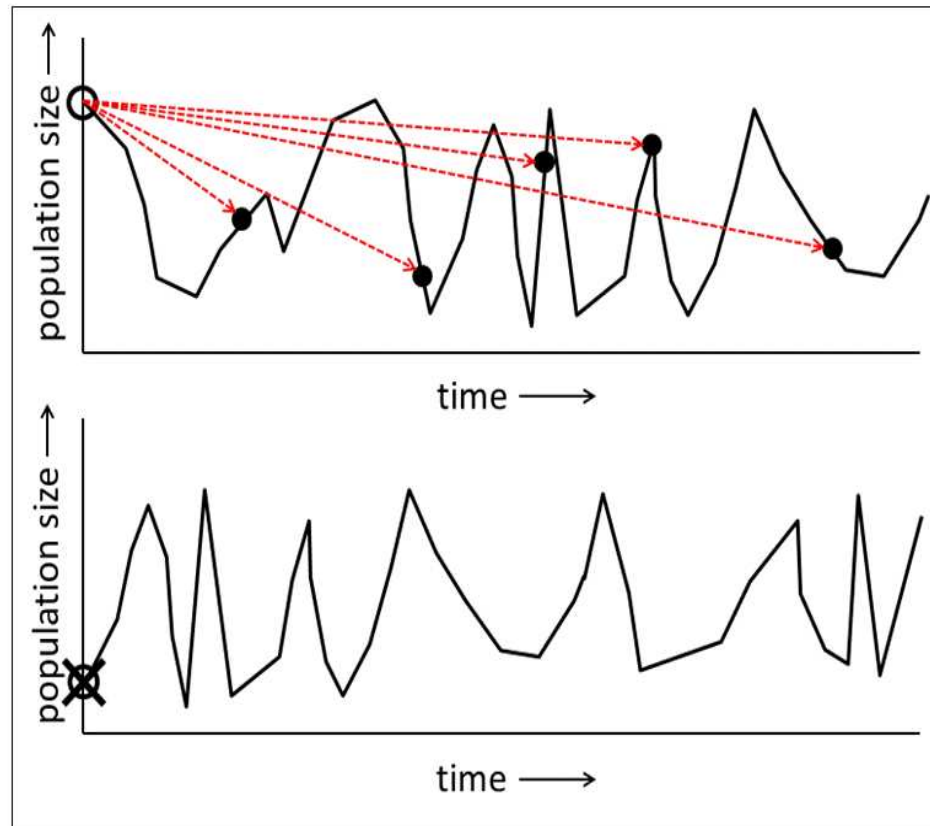
Figure 2. Top: Fraction of 20,000 simulated time series for which the trend estimate was negative (the population was declining). Declines are in the majority given selection of the two populations (per set of 20) with highest year-1 densities (left), but not given selection of two random populations per set (right). Bottom: Distributions of regression slopes for time series, as in top panel. Boxes represent 25th and 75th percentiles; whiskers represent the first and third quantiles minus or plus 1.5 times the inner quartile range respectively.

Figure 3. Analysis of time series for *Dipodomys spectabilis* from the Portal Project. (a) Log counts in eight subpopulations (plots), 1977-2017. (b) Trend estimates (log-transformed regressions slopes) for subsets of two plots, 1977-2012. The curve is the distribution for randomly chosen pairs of plots, the solid black line is the mean slope for randomly chosen pairs of plots, and the dashed red line is the slope for the two plots with highest year-1 densities. (c) Same as panel (b), but using data for 1982-2017. Corresponding plots for *Dipodomys merriami*, *Onychomys leucogaster*, and *Perognathus flavus* appear in the Supplemental Materials.

Figure 4. Trend estimates for the worldwide vertebrate population dataset, from linear regressions conducted for the 15 years following the time-series high point (vertical axis) vs. 15 years centered on the high point (horizontal axis). Points below the identity line are those where the slope starting from the high point was more negative; that is, where abundance-biased sampling led to the hypothesized effect. This analysis includes the 202-time series for which the high point fell at least 8 years from either end of the series.

Figure 5. (a) Example time series from the Global Population Dynamics Database, for a population of the Western meadowlark, *Sturnella neglecta* (Pardieck et al. 2017). (b) The trend in population size (i.e. the estimated slope coefficient) for different numbers of initial years removed from the data in panel (a). In other words, we estimate the trend in abundance from years 1 through 15, then 2 through 16, and so forth. (c) Frequency of the slopes estimated to fit data in (b) for each species for which an overall decline was detected ($n = 346$). A positive value indicates that the estimated trend in abundance over time becomes less negative with the removal of initial years. (d) Impact of the bias, measured as the relative effect on trend estimates of removing the initial 10 years of data. For example, a bias of 2.5 would indicate that the slope is 2.5 times greater with, vs. without, the first 10 years' data; a bias less than one indicates that

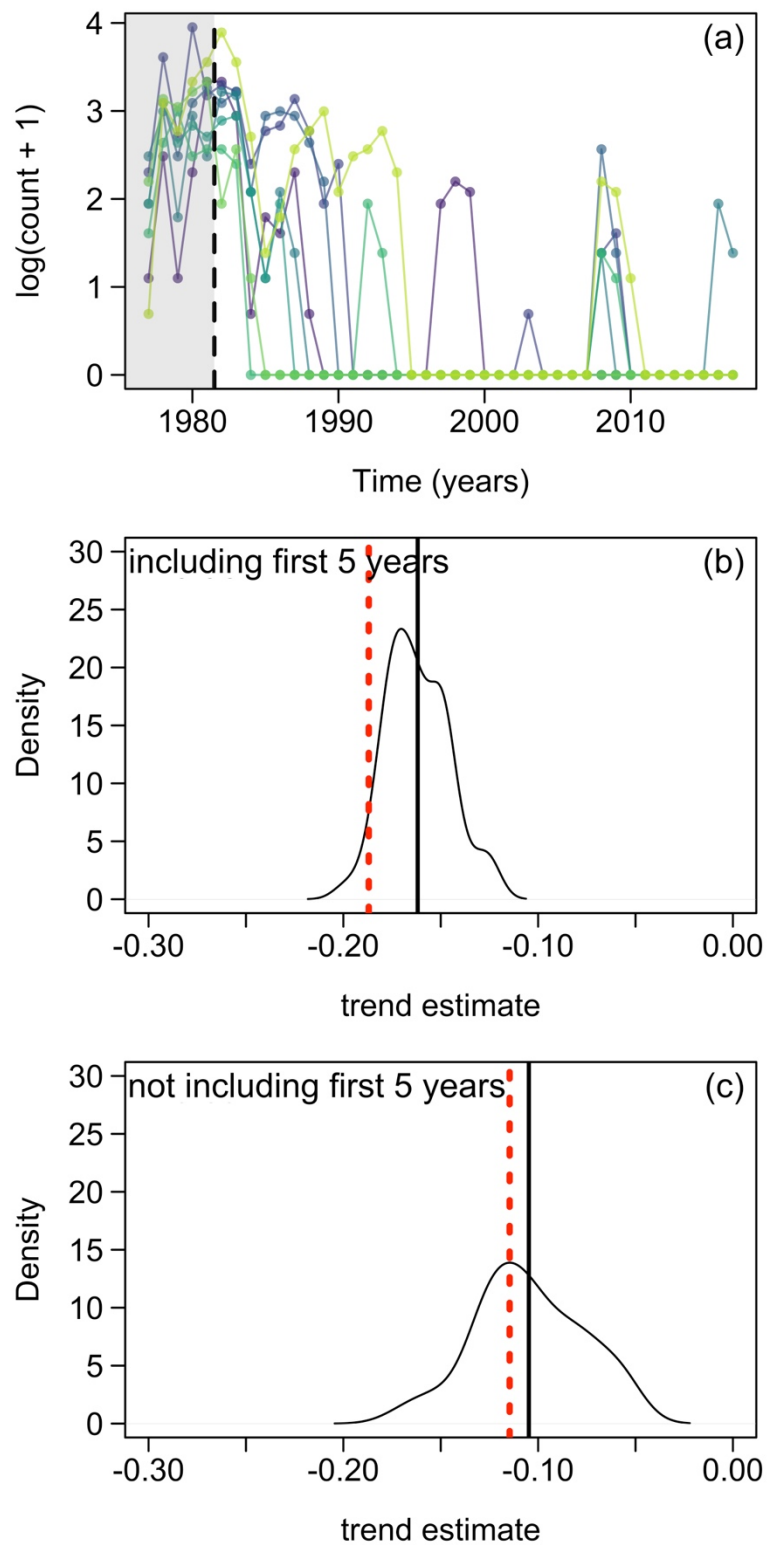
slope is smaller with, vs. without, the first 10 years' data. Dashed line: bias = 1 (no change in slope estimate).



Series (years)

Figure 2

Figure 3



~ ~ ~

Figure 4

Figure 5

Supplementary Material - R code for population simulations

R code for the generation and analysis of simulated population data is provided (as five text files separate from this document)

File 1. 01_sims.R Code to generate temporally autocorrelated population data for multiple sites, and then estimate the temporal trend for (a) the two sites with highest year-1 population density, and (b) two randomly chosen sites.

File 2. 02_percent_trend_negative.R Code to compile fractions of negative trend estimates (population declines), for Figure 5, top panel.

File 3. 03_create_csv_files.R Code to compile trend estimates (regression slopes) for Figure 2, bottom panel.

File 4. 04_compare_random_and_highest.R Code for statistical analysis of simulated time series with and without site-selection bias, for Table 1.

File 5. 05_sim_fig_1.R Code to create Figure 5