Conservation Biology

Contributed Paper

Site-selection bias and apparent population declines in long-term studies

Auriel M.V. Fournier [1]*, Easton R. White [2]† and Stephen B. Heard[3]

[1]Coastal Research and Extension Center, Mississippi State University, 1815 Popp's Ferry Road, Biloxi, MS 39532, U.S.A.
[2]Center for Population Biology, University of California, One Shields Avenue, Davis, CA 95616, U.S.A.
[3]Department of Biology, University of New Brunswick, P.O. Box 4400, Fredericton, NB, E3B 5A3, Canada

Abstract: *Detecting population declines is a critical task for conservation biology. Logistical difficulties and the spatiotemporal variability of populations make estimation of population declines difficult. For statistical reasons, estimates of population decline may be biased when study sites are chosen based on abundance of the focal species. In this situation, apparent population declines are likely to be detected even if there is no decline. This site-selection bias is mentioned in the literature but is not well known. We used simulations and real population data to examine the effects of site-selection biases on inferences about population trends. We used a left-censoring method to detect population-size patterns consistent with site-selection bias. The site-selection bias is an important consideration for conservation biologists, and we offer suggestions for minimizing or mitigating it in study design and analysis.*

Keywords: abundance, population dynamics, site selection

Sesgos en la Selección de Sitios y las Declinaciones Poblacionales Aparentes en los Estudios a Largo Plazo

Resumen: *La detección de las declinaciones poblacionales es una tarea muy importante para la biología de la conservación. Las dificultades logísticas y la variabilidad espacio-temporal de las poblaciones complican la estimación de las declinaciones poblacionales. Por razones estadísticas, las estimaciones de las declinaciones poblacionales pueden estar sesgadas cuando se eligen los sitios de estudio con base en la abundancia de la especie focal. En esta situación, las declinaciones poblacionales aparentes probablemente sean detectadas sin que exista dicha declinación. Este sesgo en la selección del sitio está mencionado en la literatura, pero sabe poco sobre él. Usamos simulaciones y datos de poblaciones reales para examinar los efectos que tienen los sesgos en la selección de sitio sobre las inferencias que se tienen sobre las tendencias poblacionales. Usamos un método censurado por la izquierda para detectar los patrones en el tamaño poblacional consistentes con el sesgo en la selección de sitios. Este sesgo es una consideración importante para los biólogos de la conservación y ofrecemos sugerencias para minimizarlo o mitigarlo en el análisis y diseño de los estudios.*

Palabras Clave: abundancia, dinámica poblacional, selección de sitio

摘要: *监测种群下降是保护生物学中的一项重要任务。然而, 监测的组织实施难度和种群的时空差异导致种群下降难以估计。由于统计学原因, 基于目标物种的丰度来选择研究位点可能会引起对种群下降的估计发生偏差。在这种情况下, 即使种群没有下降, 也可能探测到明显的下降趋势。这样的位点选择偏差在文献中有所提及但尚不清楚。因此, 我们用模拟的和真实的种群数据估计了位点选择偏差对种群趋势推断的影响, 并用左截尾方法分析了与位点选择偏差相一致的种群大小格局。结果显示, 位点选择偏差是保护生物学家需要重点考虑的问题; 本研究为在实验设计和分析中最大程度减少和控制这一影响提供了建议和思考。* **【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 丰度, 种群动态, 位点选择

*email auriel@illinois.edu
†Current address: Department of Biology, University of Vermont, 63 Carrigan Drive, Burlington, VT 05405, U.S.A.
Article impact statement: *Estimates of population declines are biased if studies begin in large populations, and time-series data show a signature of such an effect.*
Paper submitted January 30, 2019; revised manuscript accepted May 2, 2019.

Conservation Biology, Volume 00, No. 0, 1–10

DOI: 10.1111/cobi.13371

Introduction

Few issues are more important in the field of conservation science than determining which natural populations are declining, asking what drives these declines, and designing interventions by which declines can be arrested or reversed (Ceballos et al. 2017; Brewster et al. 2018; Heldbjerg et al. 2018; White 2019). Accurately determining which populations are declining and how rapidly is critical to conservation because only if one knows which populations are most threatened can resources be allocated appropriately to examine and address the problem (Joseph et al. 2009; Gerber 2016). An important statistical problem arises in efforts to detect population declines: when study sites are chosen based on the local abundance of the focal species (site-selection bias), subsequent time-series data may show exaggerated or 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 because total population censuses are rarely possible, biologists must deal with substantial measurement uncertainty (e.g., 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 often fluctuate randomly, exhibit temporally autocorrelated changes, or both, and such phenomena reflect complex underlying dynamics (e.g., Mosnier et al. 2015; McCain et al. 2016; Öst et al. 2016). Incorrect conclusions about monitored populations can arise from short time series (Krebs 1991; White 2019); inconsistent methods (Hayward et al. 2015); and nonrandom sampling (Yoccoz et al. 2001), which is our focus here. Understanding what can be inferred from population time-series data and what constraints and biases limit that inference is essential.

One important kind of nonrandom sampling, the selection of study sites at which the focal species is relatively abundant, may be common—in part due to research logistics. This abundance bias interacts with population dynamics and affects inferences about population trends. Consider, for example, a long-term study on the ecology of the (fictional) purple-snouted crompus (*Crompus nasupurpurea*). Whether or not population dynamics are the primary focus, a researcher is likely to estimate population densities and track them over time. But where will the researcher choose to begin the study? Crompus populations vary over time (Fig. 1), with imperfect correlation, presenting a choice of study sites where crompi are locally abundant and ones where they are scarce. For logistical and feasibility reasons, among others, a researcher is most likely to begin work in a population with plenty of crompi. This means the study is more likely to begin near a population peak than near a trough, and the ensuing time series is more likely to show crompus populations declining than increasing. This is simply a form of regression to the mean (Barnett et al. 2005). If many researchers 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 should address 2 important issues immediately. We are not suggesting populations will decline because researchers are actively inflicting harm and we do not doubt that many populations are declining 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).

We are not the first to recognize the existence or implications of site-selection bias. Pechmann et al. (1991), in an article on amphibian population fluctuations, recognized the potential for nonrandom site selection to exaggerate population declines. Palmer (1993) used simulations to suggest that nondeclining species, monitored initially at sites with high abundance, could appear to be declining. Skelly et al. (2003) made a similar point, but for presence-absence resurvey data. They pointed out that 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 a bias toward the detection of exaggerated declines. No one, however, has attempted to quantify

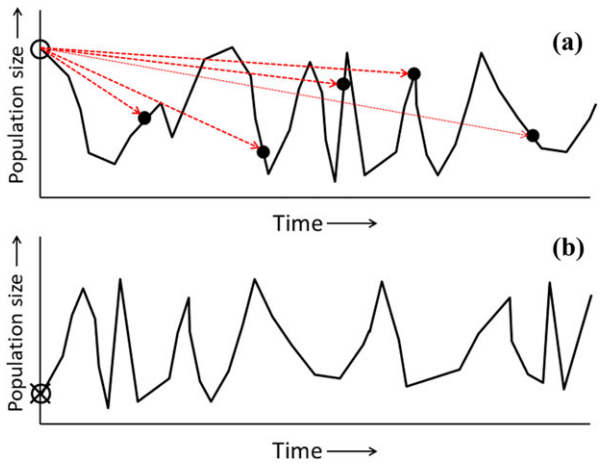

Figure 1. Population time-series data for 2 hypothetical populations of the same species with independent population fluctuations. At time zero, a researcher chooses either of the 2 populations in which to begin a long-term study tracking population density. Researchers may be more likely to choose the population that begins (a) at high density (open circle) than the one that begins (b) at low density (circle with X). Given the choice of the population in (a), for nearly any study end point (closed circles), the inferred population trend is a decline (dashed arrows).

the effects of this bias or to detect its existence in real population data.

We asked 3 questions. Are warnings of the site-selection bias well known? Does selection of study populations based on population size lead to distortions of time trends when that nonrandom site selection is applied to simulated or real data? Do real time-series data show patterns consistent with effects of site-selection bias?

Methods

Literature Review

Pechmann et al. (1991) represents the earliest warning of the site-selection bias in the literature. We asked whether their clear explanation of site-selection bias, in a highly cited article, had a detectable impact in the scientific literature. We located (Scopus search on 19 December 2017) articles that cite Pechmann et al. (1991) and determined how many referred to or built on the mention of site-selection bias. We assigned each citation to one or more of 8 categories, of which one was reference to site-selection bias. The other 7 categories pertained to other points made by Pechmann et al. (1991) (details in Supporting Information) We similarly traced all peer-reviewed articles that cite 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 was not intended to demonstrate the existence of the bias in real studies. Rather, we sought to determine how severely the bias, when it exists, affects population-decline inference. We simulated population time-series data in R (version 3.4.0; R Core Team 2019). Complete R code is in Supporting Information. We generated 10,000 simulations, each with a set of 20 plots (or, equivalently, subpopulations) from which we could select plots either with or without a site-selection bias. Each plot was assigned a time-zero population size drawn from a normal distribution with a mean of 1,000 individuals and coefficient of variation of 0.2. Individual populations fluctuated independently and had the same generating model. The model imposed a lag-1 autocorrelation of 0.5 and used variation drawn from a lognormal distribution (SD 0.198 to match the coefficient of variation for initial population sizes). We used the lognormal so that population growth and decline would have an exponential basis, but otherwise we were not attempting to match the mechanisms underlying population dynamics of any particular real species.

Each population was simulated for 110 years. We removed the first 10 years to reduce dependence on initial conditions. In our simulations, we assumed we were modeling the actual population size, rather than an estimate. That is, our times series included 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 sets 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 examined the effects of site-selection bias for the simpler case of known (simulated) populations before determining whether we could detect it in real data that include observation error.

We sampled from our simulated populations in 2 ways to simulate ecologists choosing among study populations. First, to simulate the site-selection bias, we chose the 2 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 chose 2 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) with the lm() function in R. The regression slope was our estimate of population trend. The assumption that populations are near a peak in population size in year 1 (the implication of choosing the 2 highest populations) is a strict one, so we also included sampling of the 5 and 10 (out of 20) highest population sizes in year 1. Results were nearly identical to the 2-population case, so we do not discuss the 5- and 10-population cases further.

There are 2 potential complications with our regression-slope estimates. First, in time-series data with temporal autocorrelation, significance tests would be inappropriate without adjustment. However, nothing in our analysis depends on significance tests for single regression slopes. We analyzed only patterns in large samples of such slopes, and regression slopes are unbiased in the presence of autocorrelation (Baltagi 2011). Second, regression assumptions are challenged for time-series data that include a mix of process and observation error (our simulations included only the former, but our real-world data included 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 we did not interpret such confidence intervals. We therefore adopted the regression-slope approach for both simulation and real-world data sets because it is simple and it is the approach most commonly applied in population-decline studies.

To test for effects of the site-selection bias, we compared trend estimates between the 2 largest populations and 2 random populations in a generalized linear model with a normal link function, including an interaction with length of 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 from the Portal Project

In our simulations, we used 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 (U.S.A.) (Ernest et al. 2009). Since 1977, 8 replicate control plots have been sampled to generate 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 data set, we selected the 7 most common rodent species among those sampled in the first year of the census. Using the abundance time series for those 7 species, we artificially induced the site-selection bias to examine its potential strength and tested for a signature of the bias in unmodified data.

To examine the potential strength of the site-selection bias, we worked with the 4 rodent species that showed apparent declines (log-transformed regression slope <0 for all 8 subpopulations summed). We chose among the 8 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 2 subsets of data: the 2 plots with the largest populations in year 1 and, as a control, randomly chosen pairs of plots.

To test for the actual (not simulated) occurrence of a site-selection bias in the Portal data, we examined the effect of removing the first 5 years of data after plot selection but before calculation of trend estimates. If time-series data sets tend to begin in high-population years (as a result of site-selection bias), this clipping would reduce the estimate of population decline. Absent a site-selection effect, clipping would not affect the trend. To control for

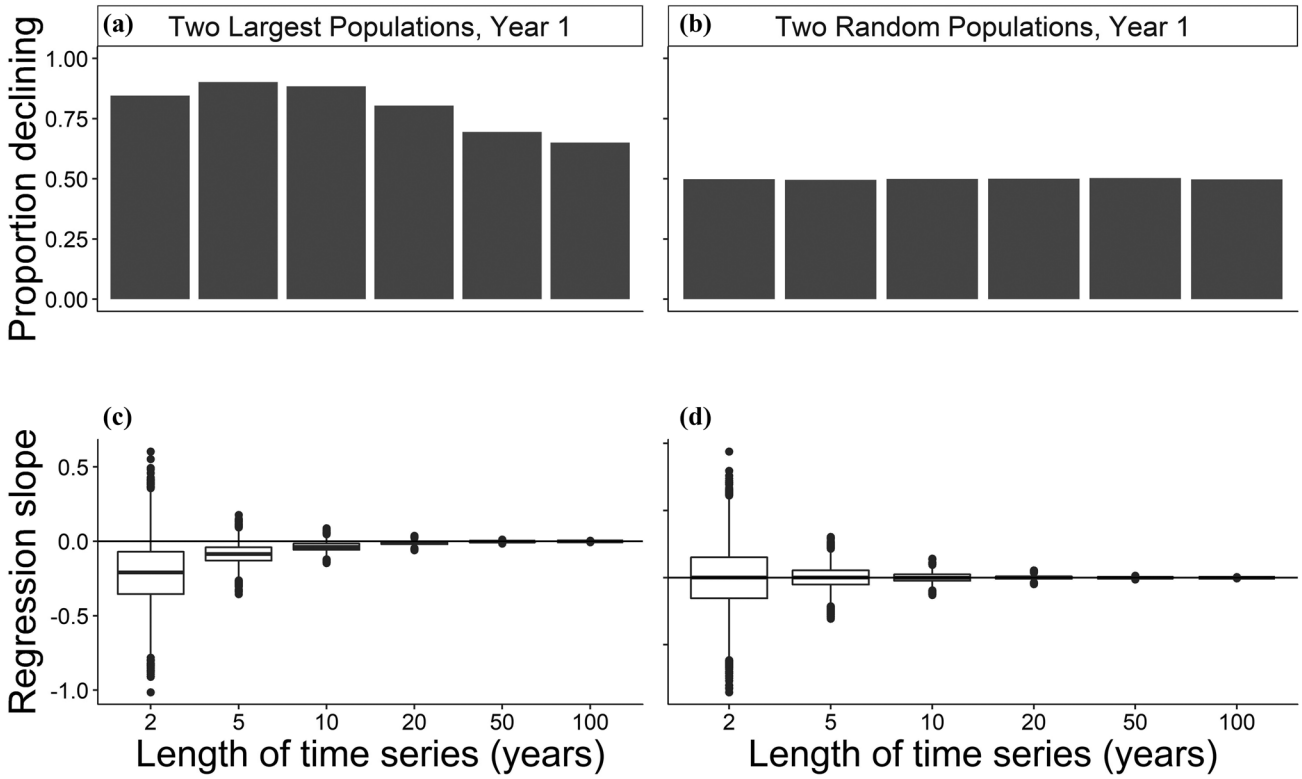

Figure 2. (a) Proportion of simulated time series for which the population-trend estimate is negative (declining population) when the 2 largest (of 20) populations of a species are selected for study in year 1 (left) or when 2 random populations are selected (right). (b) Distributions of regression slopes for time series as selected in (a) (boxes, 25th and 75th percentiles; whiskers, first and third quartiles ±1.5 times the inner quartile range, respectively).

time-series length, we compared years 1977–2012 with the left-truncated data set of years 1982–2017.

Our use of the Portal data set to explore ideas about site-selection bias is not a critique of the fine work of the team that produced and curates it. They graciously engaged with us about using their data in this way.

Real Population Data from Worldwide Vertebrate Populations

Although 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 worked with population-dynamics data compiled by Keith et al. (2015); they used sources including the Global Population Dynamics Database (NERC Centre for Population Biology 2010). From Keith et al.'s (2015) database, we selected population time series with over 35 years of data to ensure adequate statistical power for detecting trends (White 2019). We were left with time-series data for 2 populations of elasmobranchs, 9 of mammals, 98 of fish, and 857 of birds.

We asked whether we could induce and then detect a site-selection bias. Because 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: data for 15 years starting at the time series population high point, and data for 15 years centered on the time series population high point (7 years before and after). We executed this analysis for the 202 times series that included at least 7 years of data before and after the high point. We repeated this analysis with a random starting point rather than a high-centered series as the control. Results did not differ, so we do not report them here. This high-point analysis is a deliberate worst-case scenario (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 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.

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

Results

Literature Review

We found 478 citations of Pechmann et al. (1991). Just 1 (Wicknick et al. 2005) referred to Pechmann et al.'s (1991) observations about the site-selection bias; they accurately summarized Pechmann et al.'s (1991) observation, but did not consider the issue further. The other 477 citing articles 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 (Supporting Information). Forty-three articles 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) article has not been heavily cited. Of 26 peer-reviewed citations, we located just 2 that clearly and accurately referred to the possibility of the site-selection bias in estimates of population trends (Villella & Smith 2005; Britton et al. 2009). Neither made any methodological or analytical change to correct for the possible bias. We found no articles that tested for evidence of the problem in real data.

Inducing Bias in Simulated Population Data

Site-selection was detected, and was sometimes strong, when deliberately induced. When the 2 largest (in year 1) populations were selected for study, more declines than increases were estimated—even for time series as long as 100 years (Fig. 2). Apparent declines were more frequent and steeper for shorter time series (Fig. 2). In contrast, time series for randomly chosen populations had slope distributions centered on zero, as expected (Fig. 2). 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 from the Portal Project

Four Portal rodents showed apparent declines, although the decline was weak for 2 of the 4. For both species with substantial declines (*Dipodomys spectabilis* and *Onychomys leucogaster*), sampling populations based on year-1 abundance produced larger estimates of the

Table 1. Generalized linear model comparing slope values between 2 random populations and the 2 largest populations, including an interaction for the length in years of the sampling period.*

Variable	*Beta*	*SE*	*t*	*p*
Intercept	−106.3	0.45	−233.0	<0.001
2 random populations	106.7	0.64	142.9	<0.001
Years	1.39	0.009	165.3	<0.001
2 random populations years	−1.404	0.013	−101.4	<0.001

* *Slopes are more negative for time series starting in the largest populations than time series that do not start with the largest populations. Length of the time series had a modest effect.*

decline (Fig. 3 & Supporting Information), indicating that imposing a site-selection bias had the predicted effect. Furthermore, for both species, trimming the first 5 years of data reduced the estimated strength of decline (Fig. 3c), and this effect was significant (*D. spectabilis*, $t = -12.5$, df = 78.2, $p < 2 \times 10^{-16}$; *O. leucogaster*, $t = -5.4$, df = 69.3, $p < 8.2 \times 10^{-7}$). Neither of these patterns held for the 2 species with slight declines (*D. merriami* and *Perognathus flavus*) (Supporting Information).

Real Population Data from Worldwide Vertebrate Populations

Starting analyses of time series at the population high point (a time-for-space analogy of the site-selection bias) produced apparent declines: regression slopes for the 15 years following a high point were 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.

Removing initial years from the vertebrate time series reduced the tendency toward population decline. This effect is illustrated for a single exemplar time series in Fig. 5a and b. 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 10 years) made trends less negative for most data sets (65%) (Fig. 5d). The effect of this trimming was often large; 14% of data sets showed at least a 2-fold change in estimated slope and 5% showed a 3-fold change.

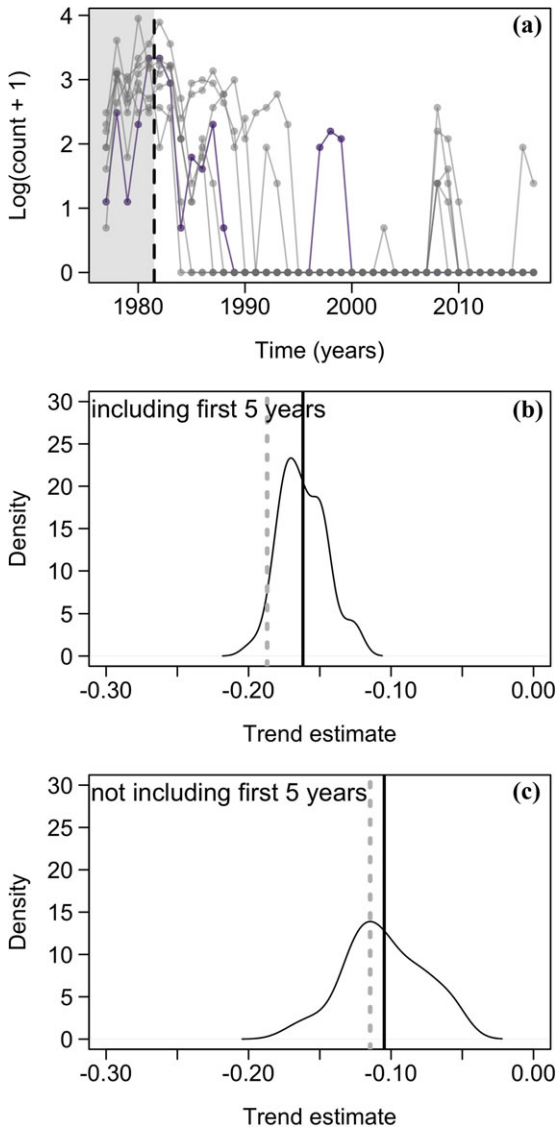

Figure 3. Results of time-series analysis of Dipodomys spectabilis *from the Portal Project: (a) log counts in 8 subpopulations (plots), 1977–2017 (dashed line, divider between first 5 years and rest of the data; shaded area, first 5 years on surveys), (b) population trend estimates (log-transformed regressions slopes) for subsets of 2 plots, 1977–2012 (curve, distribution for randomly chosen pairs of plots; solid line, mean slope for randomly chosen pairs of plots; dashed line, slope for the 2 plots with highest year-1 densities), (c) as in (b) except with data for 1982–2017. Plots for* Dipodomys merriami, Onychomys leucogaster, *and* Perognathus flavus *are in Supporting Information.*

Discussion

We established 3 important things about the site-selection bias. First, despite its occasional appearance in the literature (Pechmann et al. 1991; Palmer 1993; Villella & Smith 2005; Wicknick et al. 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

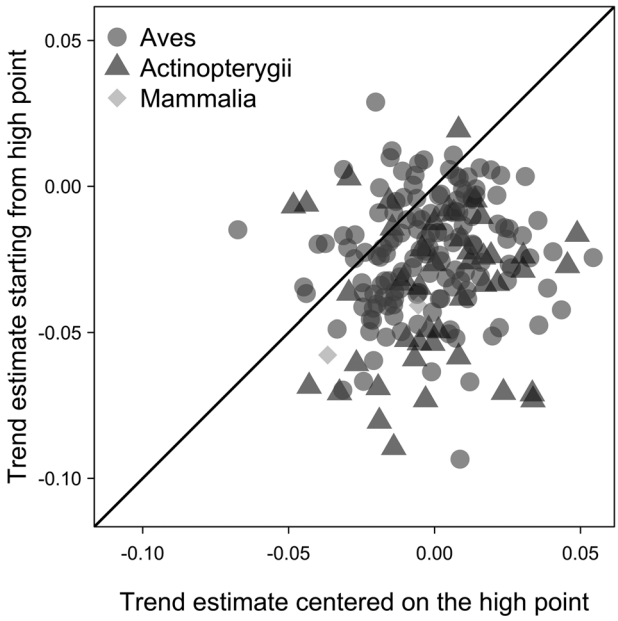

Figure 4. Population trend estimates from a worldwide vertebrate population data set based on linear regressions conducted for the 15 years following the population high point versus linear regressions conducted for the 15 years centered on the high point. Points below the diagonal line are those where the slope starting from the high point was more negative; that is, where abundance-biased sampling led to a more negative trend then if random sampling had taken place. The 202 time series for which the population high point fell at least 8 years from either end of the series are included.

the mean, a well-understood phenomenon (Barnett et al. 2005). Second, simulated nonrandom 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). Although that article has been highly cited, its warning of the site-selection bias went almost entirely unheeded. Only 1 of 478 articles 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 article explicitly argued that such inferences are not straightforward. (We do not dispute that many populations truly are in decline—including many amphibian populations.) A slightly later but clearer mention (Palmer 1993) has not been well cited (2 of 26 citations explicitly referring to the bias).

We demonstrated clear effects of simulated site-selection bias on apparent population trends, in simulated population data and in 2 real data sets. This is not surprising because we deliberately manipulated data to induce site-selection biases, and it would have been surprising if they did not have detectable effects. What is important 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 strong.

Our simulations do not establish any influence of the site-selection bias on trend estimates from real data sets. That depends on the degree to which, in real studies, site selection is nonrandom 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 was consistent with this signature, but because we had only 4 declining species (and for 2 of those, the decline was weak), we could not be sure this pattern was 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 worldwide vertebrate data set yielded 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 the site-selection bias is pervasive and of significant strength in real-world population data. 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 hypothesize, for example, that the bias is stronger for species with longer generation times (Supporting Information) and that the bias is 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 data sets because they will require more information about each.

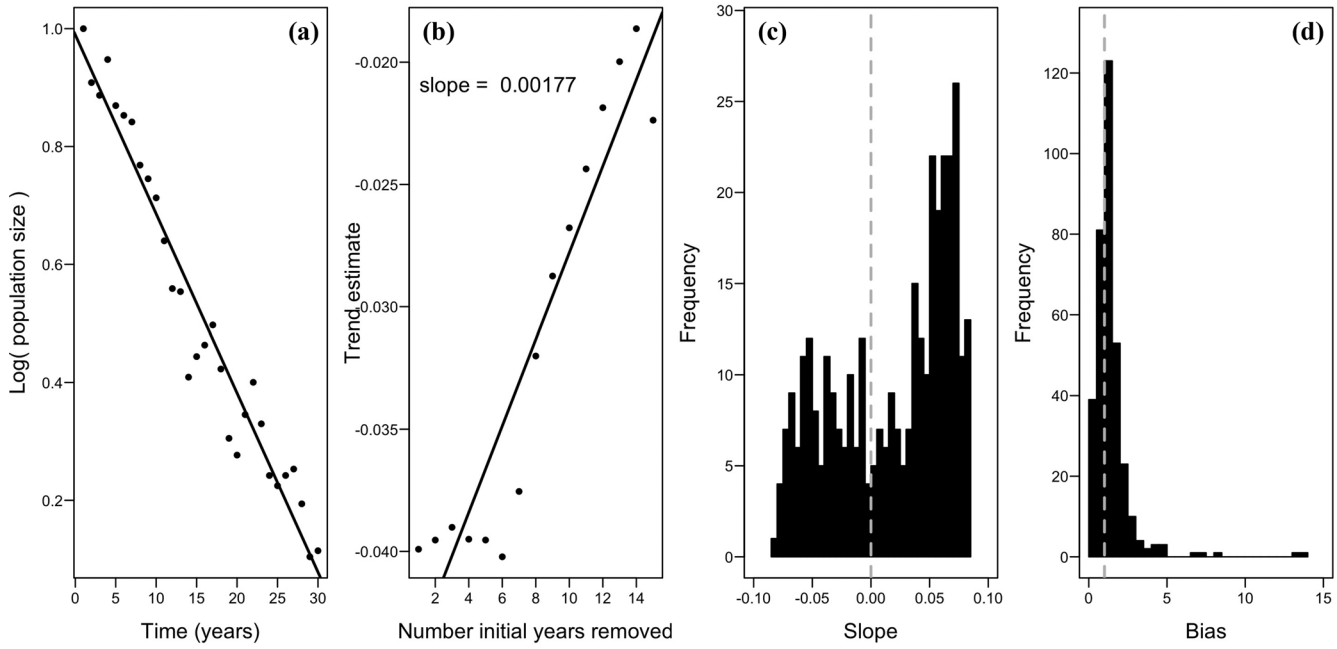

*Figure 5. (a) Example population time series from the Global Population Dynamics Database for a population of the Western Meadowlark (*Sturnella neglecta*) (Pardieck et al. 2017) (diagonal line, line of best fit). (b) The trend in population size (i.e., estimated slope coefficient) for Western Meadowlark after left truncation (removal of initial years) of the data set in (a) (i.e., trend in abundance from years 1–15, then 2–16, 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) (vertical dashed line, slope of zero; positive value, estimated trend in abundance over time becomes less negative with the removal of initial years). (d) Impact of site-selection bias measured as the relative effect on trend estimates of removing the initial 10 years of data (dashed line, bias = 1, no change in slope estimate). A bias of 2.5 indicates slope is 2.5 times greater with, vs. without, the first 10 years of data; a bias <1 indicates slope is smaller with, vs. without, the first 10 years of data.*

We confirmed that site-selection bias is a worry for population-dynamic studies, and we recommend the following to address the problem. 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 available 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. 2019). 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 nonrandom site selection is justified, researchers should consider the possibility of pairing their nonrandom sites with additional sites chosen randomly from available habitat (Ponchon et al. [2018]; 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 multispecies 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 this article spurs the development and testing of such methods. Finally, researchers working with long-term data sets—especially via meta-analysis—should recognize that site-selection biases are possible and may be especially likely in data sets 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. A further complication for rare species is that once a species is detected as rare (and especially if it is red listed), this observation may provoke increased search effort (Jeppsson et al. 2010) and thus increase 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 nonrandom site selection, can affect any metric—a point occasionally made in the literature on long-term monitoring of biodiversity (e.g., Wesche et al. 2012).

Bias in the 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 science (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 that allows conservation scientists and managers to prioritize available effort and financial resources in support of the populations that need it most.

Acknowledgments

We thank M. Giasson for her work on the citation analysis and T. Lucas for being involved in early discussions about our simulations. D. Skelly, S. Anderson, and T. Branch were involved in early discussions and pilot analyses for the work reported here. M. Ernest supplied data from the Portal project and advised us on its structure. We further acknowledge all the ecologists involved, over the years, in building both the Portal data set and the much larger compilation of population-size records in the worldwide vertebrate population data set. B. Wintle, J. Myers, and a remarkable number of anonymous reviewers made helpful comments on the manuscript. Finally, S.B. Heard thanks readers of his blog, *Scientist Sees Squirrel*, for vigorous discussion of the blog post that led to this article. This research was funded by the Natural Sciences and Engineering Research Council of Canada, Discovery Grant to S.B. Heard.

Supporting Information

The R code for the generation and analyses of simulated and empirical population data (Appendix S1); citation analysis of Pechman et al. (Appendix S2); time-series analysis of *Onychomys leucogaster* (Appendix S3), *Dipodomys merriami* (Appendix S4), and *Perognathus flavus* from the Portal Project (Appendix S5); and correlates of site-selection bias (Appendix S6) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Bailey LL, Simons TR, Pollock KH. 2004. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. Ecological Applications **14:**692–702.

Baltagi BH. 2011. Econometrics. 5th edition. Springer Verlag, Berlin.

Barnett AG, van der Pols JC, Dobson AJ. 2005. Regression to the mean: what it is and how to deal with it. International Journal of Epidemiology **34:**215–220.

Brewster CL, Beaupre SJ, Willson JD. 2018. Habitat loss and local extinction: linking population declines of eastern collared lizards (*Crotaphytus collaris*) to habitat degradation in ozark glades. Journal of Herpetology **52:**352–361.

Britton AJ, Beale CM, Towers W, Hewison RL. 2009. Biodiversity gains and losses: evidence for homogenisation of Scottish alpine vegetation. Biological Conservation **142:**1728–1739.

Butchart SHM, Lowe S, Martin RW, Symes A, Westrip JRS, Wheatley H. 2018. Which bird species have gone extinct? A novel quantitative classification approach. Biological Conservation **227:** 9–18.

Campbell SP, Clark JA, Crampton LH, Guerry AD, Hatch LT, Hosseini PR, Lawler JJ, O'Connor RJ. 2002. An assessment of monitoring efforts in endangered species recovery plans. Ecological Applications **12:**674–681.

Ceballos G, Ehrlich PR, Barnosky AD, Garcia A, Pringle RM, Palmer TM. 2015. Accelerated modern human–induced species losses: entering the sixth mass extinction. Science Advances **1:**e1400253.

Ceballos G, Ehrlich PR, Dirzo R. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences **114:**r6089–e6096.

Coppolillo P, Gomez H, Maisels F, Wallace R. 2004. Selection criteria for suites of landscape species as a basis for site-based conservation. Biological Conservation **115:**419–430.

d'Eon-Eggertson F, Dulvy NK, Peterman RM. 2015. Reliable identification of declining populations in an uncertain world. Conservation Letters **8:**86–96.

Ernest SKM, Valone TJ, Brown JH. 2009. Long-term monitoring and experimental manipulation of a Chihuahuan Desert ecosystem

near Portal, Arizona, USA Ecological Archives E090-118. Ecology **90:**1708–1708.

Gerber LR. 2016. Conservation triage or injurious neglect in endangered species recovery. Proceedings of the National Academy of Sciences **113:**3563–3566.

Hayward MW, Boitani L, Burrows ND, Funston PJ, Karanth KU, MacKenzie DI, Pollock KH, Yarnell RW. 2015. FORUM: ecologists need robust survey designs, sampling and analytical methods. Journal of Applied Ecology **52:**286–290.

Heldbjerg H, Sunde P, Fox AD. 2018. Continuous population declines for specialist farmland birds 1987–2014 in Denmark indicates no halt in biodiversity loss in agricultural habitats. Bird Conservation International **28:**278–292.

Humbert J-Y, Mills LS, Horne JS, Dennis B. 2009. A better way to estimate population trends. Oikos **118:**1940–1946.

Jeppsson T, Lindhe A, Gärdenfors U, Forslund P. 2010. The use of historical collections to estimate population trends: a case study using Swedish longhorn beetles (Coleoptera: Cerambycidae). Biological Conservation **143:**1940–1950.

Joseph LN, Maloney RF, Possingham HP. 2009. Optimal allocation of resources among threatened species: A project prioritization protocol. Conservation Biology **23:**328–338.

Keith D, et al. 2015. Temporal correlations in population trends: conservation implications from time-series analysis of diverse animal taxa. Biological Conservation **192:**247–257.

Krebs CJ. 1991. The experimental paradigm and long-term population studies. Ibis **133:**3–8.

McCain C, Szewczyk T, Bracy Knight K. 2016. Population variability complicates the accurate detection of climate change responses. Global Change Biology **22:**2081–2093.

Møller AP, Rubolini D, Lehikoinen E. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences. **42:**16195–16200.

Mosnier A, Doniol-Valcroze T, Gosselin J-F, Lesage V, Measures LN, Hammill MO. 2015. Insights into processes of population decline using an integrated population model: the case of the St. Lawrence Estuary beluga (*Delphinapterus leucas*). Ecological Modelling **314:** 15–31.

NERC (National Environment Research Council) Centre for Population Biology. 2010. The global population dynamics database. Version 2. NERC Centre for Population Biology, Imperial College, London. Available from http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html (accessed November 2018).

Nichols JD, Hines JE, Sauer JR, Fallon FW, Fallon JE, Heglund PJ. 2000. A double-observer approach for estimating detection probability and abundance from point counts. The Auk **117:**393–408.

Öst M, Ramula S, Lindén A, Karell P, Kilpi M. 2016. Small-scale spatial and temporal variation in the demographic processes underlying the large-scale decline of eiders in the Baltic Sea. Population Ecology **58:**121–133.

Palmer MW. 1993. Potential biases in site and species selection for ecological monitoring. Environmental Monitoring and Assessment **26:**277–282.

Pardieck KL, Ziolkowski DJ, Lutmerding M, Campbell K, Hudson M-AR. 2017. North American Breeding Bird Survey Dataset 1966–2016, version 2016.0. U.S. Geological Survey, Laurel, Maryland.

Pechmann JH, Scott DE, Semlitsch RD, Caldwell JP, Vitt LJ, Gibbons JW. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science **253:**892–895.

Ponchon A, Choquet R, Tornos J, McCoy KD, Tveraa T, Boulinier T. 2018. Survival estimates strongly depend on capture–recapture designs in a disturbed environment inducing dispersal. Ecography **41:**2055–2066.

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from http://www.r-project.org/ (accessed January 2019).

Reynolds JH, Thompson WL, Russell B. 2011. Planning for success: Identifying effective and efficient survey designs for monitoring. Biological Conservation **144:**1278–1284.

Rueda-Cediel P, Anderson KE, Regan TJ, Regan HM. 2018. Effects of uncertainty and variability on population declines and IUCN Red List classifications. Conservation Biology **32:**916–925.

Skalski JR. 1990. A design for long-term status and trends monitoring. Journal of Environmental Management **30:**139–144.

Skelly DK, Yurewicz KL, Werner EE, Relyea RA. 2003. Estimating decline and distributional change in amphibians. Conservation Biology **17:**744–751.

Thomas L. 1996. Monitoring long-term population change: Why are there so many analysis methods? Ecology **77:**49–58.

Villella RF, Smith DR. 2005. Two-phase sampling to estimate river-wide populations of freshwater mussels. Freshwater Science **24:**357–369.

Vos P, Meelis E, Ter Keurs WJ. 2000. A framework for the design of ecological monitoring programs as a tool for environmental and nature management. Environmental Monitoring and Assessment **61:**317–344.

Weiser EL, Diffendorfer JE, López-Hoffman L, Semmens D, Thogmartin WE. 2019. Consequences of ignoring spatial variation in population trend when conducting a power analysis. Ecography **42:**836–844.

Wesche K, Krause B, Culmsee H, Leuschner C. 2012. Fifty years of change in Central European grassland vegetation: large losses in species richness and animal-pollinated plants. Biological Conservation **150:**76–85.

White ER. 2019. Minimum time required to detect population trends: the need for long-term monitoring programs. BioScience **69:**40–46.

Wicknick JA, Anthony CD, Reblin JS. 2005. An amphibian survey of Killbuck Marsh Wildlife Area, Ohio. Ohio Journal of Science **105:** 2–7.

Yoccoz NG, Nichols JD, Boulinier T. 2001. Monitoring of biological diversity in space and time. Trends in Ecology & Evolution **16:**446–453.