



## Temporal correlations in population trends: Conservation implications from time-series analysis of diverse animal taxa



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### ABSTRACT

Population trends play a large role in species risk assessments and conservation planning, and species are often considered threatened if their recent rate of decline meets certain thresholds, regardless how large the population is. But how reliable an indicator of extinction risk is a single estimate of population trend? Given the integral role this decline-based approach has played in setting conservation priorities, it is surprising that it has undergone little empirical scrutiny. We compile an extensive global dataset of time series of abundance data for over 1300 vertebrate populations to provide the first major test of the predictability of population growth rates in nature. We divided each time series into assessment and response periods and examined the correlation between growth rates in the two time periods. In birds, population declines tended to be followed by further declines, but mammals, salmon, and other bony fishes showed the opposite pattern: past declines were associated with subsequent population increases, and vice versa. Furthermore, in these taxa subsequent growth rates were higher when initial declines were more severe. These patterns agreed with data simulated under a null model for a dynamically stable population experiencing density dependence. However, this type of result could also occur if conservation actions positively affected the population following initial declines—a scenario that our data were too limited to rigorously evaluate. This ambiguity emphasizes the importance of understanding the underlying causes of population trajectories in drawing inferences about rates of decline in abundance.

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### 1. Introduction

A central problem in conservation biology is the difficulty of identifying which species are currently at risk of extinction or are likely to be at risk in the near future. The framework developed by the International Union for Conservation of Nature (IUCN) is the most widely used for risk assessments. The IUCN Red List categories and criteria (IUCN, 2001; [www.iucnredlist.org](http://www.iucnredlist.org)) have been used to assess extinction risk of over 70,000 species of animals, plants, and fungi. The five IUCN risk criteria reflect consideration of both the small-population paradigm (Soule and Wilcox, 1980; Frankel and Soule, 1981) and the declining-population paradigm (Caughley, 1994). Under the IUCN framework,

the Red List category (ranging from Least Concern to Extinct) is assigned based on the criterion that produces the highest estimated risk. This means that species can be listed based entirely on a rate of decline (Criterion A), regardless how large the census size ( $N$ ) is. For example, a taxon that has declined >30% over ten years or three generations (whichever is longer) qualifies as Vulnerable under criterion A2, even if  $N$  is very large. According to the IUCN (2014), a 'Vulnerable' classification means that the species is "considered to be facing a high risk of extinction in the wild."

This decline-based approach can be effective for early detection of at-risk species that would not likely be flagged by other methods (Stanton, 2014). Caughley (1994) argued that the declining population paradigm is relevant to most problems in conservation, and few would disagree with the following premise: if a population that has recently declined continues to decline in the future, it will eventually be at risk

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of extinction. Theory shows that if a population has a negative growth rate, then in the absence of density dependence, the expected time to extinction depends more strongly on the rate of decline than on initial  $N$  (Lande et al., 2003). In addition, for many species  $N$  is more difficult to estimate than rate of decline, which can be based on an index rather than estimates of absolute abundance (Mace et al., 2008). Numerous examples exist of species that were once very numerous ( $N > 10^6$ ) but have since gone extinct (passenger pigeon, *Ectopistes migratorius*; great auk, *Pinguinus impennis*; Galapagos damselfish, *Azurina eupalama*) or nearly so (American bison, *Bison bison*). If conservation actions are not initiated until a population reaches levels that trigger concern because of small population size, recovery options become more costly and less likely to succeed (Wilcove and Chen, 1998; Drechsler et al., 2011; Hutchings et al., 2012). Finally, populations that remain large after being reduced to a fraction of their historical size can be at substantial risk, particularly if their reduction has altered ecosystem functioning in ways that promote negative feedback loops or other Allee effects (Courchamp et al., 1999; Swain and Chouinard, 2008; Swain and Benoit, 2015).

Nevertheless, using rate of decline as an indicator of risk independent of census size remains controversial (Godfrey and Godley, 2008). Trends in abundance are challenging to evaluate in a conservation context for two major reasons. First, trends are typically estimated from a limited number of data points that are subject to measurement error, and this reduces precision and introduces potential biases (Holmes, 2001; Holmes et al., 2007; Connors et al., 2014). Second, a wide range of natural and anthropogenic factors can influence population trajectories, creating the challenge of distinguishing long-term trends from short-term fluctuations. Examples include random demographic stochasticity and environmental fluctuations (such as weather patterns and regime shifts; Coulson et al., 2001; Chavez et al., 2003; Lindenmayer et al., 2010), long-term environmental change related to climate (Anderson et al., 2015), and indirect effects due to changes in community interactions (Borrvall and Ebenman, 2006). A range of anthropogenic factors such as threats from habitat loss, invasive species, and exploitation could accelerate population declines or slow recovery, while implementation of conservation actions could have a positive influence on population trajectories (Hoffmann et al., 2010; Donald et al., 2007; Butchart et al., 2005). The interplay of all of these factors complicates interpretation and makes it more challenging to set priorities for conservation and management.

More fundamentally, to be effective conservation tools, analyses of time-series data must provide useful insights into the likely future status of a species, based on data from an assessment period that provides baseline information on population trends. This raises an important question: How reliable an indicator of conservation status is a single estimate of population trend? If a population has recently declined, is it reasonable to expect that it will continue to decline in the future? Curiously, given the widespread inclusion of population-decline criteria in assessments of extinction risk (IUCN, 2001; Waples et al., 2013), there has been little empirical evaluation of this crucial topic (but see Porszt et al., 2012 for an example for one species of Pacific salmon). That is not to say that evaluations of population trends have been lacking: risk has been assessed using unstructured (Dennis et al., 1991) and structured (Brook et al., 2000) population models, and causes of population change have been inferred based on the pattern of decline (Wolf and Mangel, 2008; Sugihara et al., 2012; Di Fonzo et al., 2013; Shoemaker and Akçakaya, 2015). However, although temporal changes in abundance trends have been examined for some marine fishes (Hutchings et al., 2010), a detailed empirical evaluation of the temporal consistency of trends in natural populations within and among different taxonomic groups has not been undertaken.

In this paper, we make a first attempt to fill this information gap. To better understand the predictability of population trajectories, we compiled an extensive global dataset of time series of abundance data for over 1300 vertebrate populations from four major groups: birds, mammals, salmon, and other bony fishes. We split each time series

into assessment and response periods of equal duration and asked the following questions: (1) Does the per-capita population growth rate ( $r$ ) in the assessment period predict the growth rate in the response period? (2) Does the relationship between growth rates in the two time periods depend on (a) the taxon, (b) the type of threats affecting the species, or (c) implementation of conservation actions? (3) For populations that declined substantially in the assessment period, does the subsequent trajectory depend on the magnitude of the previous decline? Question 1 allows an empirical evaluation of the assumption that population declines will be followed by continued declines. Question 2 asks whether patterns of population trajectories are taxon-specific or can be related to specific anthropogenic factors. Question 3 asks whether severity of decline can be used as a reliable early-warning sign (a 'red flag') of compromised recovery potential (Hutchings et al., 2012).

To provide context for interpreting results for actual populations, we also simulated time-series data to characterize how temporal patterns of population trajectories change under three simple null models that do not involve any long-term population trend:

- 1) A true random walk, with population growth rate chosen randomly and independently at each time period;
- 2) A random walk with temporal autocorrelation, whereby growth rate is affected by the previous time period; and
- 3) A population with random fluctuations constrained by density dependence.

Null model #1 is unlikely to be realistic for any natural population but provides a useful point of reference. Null model #2 captures some aspects of environmental forcing. Null model #3 reflects the reality that long-term growth rates must be close to 0 for populations that persist for any appreciable length of time (Peterman, 1981).

## 2. Methods

### 2.1. Data sources

We compiled time series of abundance data (estimates of absolute abundance or indices of relative abundance) for individual populations from several large global databases (for detailed information about the sources for abundance and metadata, see Supplementary material). We only used populations for which estimates were available for at least 20 years or 6 generations, whichever was greater; this provided sufficient data for analysis of population trends in two consecutive time periods of duration comparable to that relevant to the IUCN Red List criterion A (the longer of 10 years or 3 generations). After applying this filter, we had sufficient data to conduct separate analyses for four different groups of species: birds ( $n = 800$ ), mammals ( $n = 51$ ), salmon ( $n = 343$ ) and other bony fish ( $n = 121$ ) (Table 1). These data were compiled at a variety of geographic scales, from global to local (Table 2). We analyzed data for salmonids and other bony fishes separately because most salmonids are anadromous and semelparous (or nearly so), which means typical measures of abundance include only adults maturing in a single year (as opposed to all adults in iteroparous species).

**Table 1**

Number of populations for which we obtained sufficiently long time series of abundance data to use in the analyses described in this paper. Data sources are described in Supplementary material. LPI = Living Planet Index (Loh et al., 2005; Collen et al., 2009); SCC = Species of Conservation Concern (Holmes et al., 2007); NABBS = North American Breeding Bird Survey.

Source	Birds	Mammals	Salmon	Other bony fish	Elasmobranchs	Total
LPI	442	48	79	120	4	693
SCC	11	3	–	1	–	15
NABBS	347	–	–	–	–	347
Holmes et al. (2005)	–	–	264	–	–	264
Totals	800	51	343	121	4	1319

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