

THE POPULATION DYNAMICS OF LAG PHASES AND COLLAPSES

by

KEVIN JOSEPH AAGAARD

A Dissertation submitted to the  
Graduate School-New Brunswick  
Rutgers, The State University of New Jersey  
In partial fulfillment of the requirements

For the degree

Doctor of Philosophy

Graduate Program in Ecology and Evolution

Written under the direction of

Dr. Julie L. Lockwood

And approved by

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New Brunswick, New Jersey

October, 2014

## ABSTRACT OF THE DISSERTATION

The population dynamics of lag phases and collapses

By KEVIN JOSEPH AAGAARD

Dissertation Director:

Julie L. Lockwood

Exotic species and collapses of native species pose equivalently severe threats to global biodiversity and ecological health. Much work has been done to improve our understanding of the patterns and processes associated with biological invasions and population declines. However, due to the complexity of the issues posed to conservation and management, we still lack fundamental knowledge about their population dynamics. Early-action is often recommended to deal with both situations, which, as has been argued, requires minimal detail about the population biology of the target species. While this holds true in many cases, it does not justify ignoring population biology as a whole. Indeed, by analyzing data about past events we can greatly improve our ability to manage future ones. Furthermore, applying powerful tools and concepts from other disciplines can help develop expectations for general trends across taxa and systems.

In this dissertation I explore statistical methods to identify and describe poorly explained population growth patterns, using both exotic and native species. I used a large,

uncommonly complete database of citizen-collected data and developed efficient, robust methods to quantify population lag phases and collapses. I found lags—periods of low population growth rates relative to future growth—to be common in exotic birds in Hawaii. I found seemingly spontaneous population collapses— $\geq 90\%$  declines in abundance within a specified timeframe—in nearly half of the populations investigated. I expand on the details of the method I developed for collapses to account for variation about important portions of any population's growth patterns; specifically estimated maximum abundances and the duration of observed declines. I applied this method to endemic Hawaiian forest birds to display its utility and assess limitations.

These results have important implications for conservation management, and yield novel conclusions about the population biology of exotic and native species. By establishing methods to classify populations experiencing lags or collapses, we can begin to develop models to anticipate their occurrence prescribe well prepared management actions and conservation strategies. With more knowledge of the spatial dynamics of exotic populations we can strategically apply targeted control measures in efficient, cost-effective ways.

## **Acknowledgements**

I am very grateful to Julie Lockwood for advising me and helping me every step of the way. Her patience with me as I learn the art and science of research and publication has been invaluable. She has provided me with discerning comments and critiques that have helped rescue distorted manuscripts.

I also must thank my committee, and those who have served on past committees of mine: Ed Green—for not laughing at my statistical naiveté, Dan Simberloff—for providing unsurprisingly brilliant insights and not holding it against me when I couldn't deliver donuts, Nina Fefferman—for lending modeling expertise, Peter Morin—for letting me badger him, and Dina Fonseca—for teaching me about grant writing. I am especially appreciative of Peter Smouse for helping facilitate my grad school career at Rutgers and encouraging me throughout my dissertation. I am also grateful to those who helped me along my way in less conspicuous roles, whether with various side project field studies or unsuccessful generations of my dissertation chapters.

Finally, I must thank my wife for accepting and listening to what she does not care about, and my parents for showing me how to work hard, endeavor to persevere, and hold my silverware properly.

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## **Introduction**

In the last decade the field of population biology has been heavily integrated with invasion ecology to explore core ecological principles and provide sound management advice (Sakai et al 2001). Management options for invasive species include eradication, exclusion, and control efforts (Courchamp et al. 2003). Eradication involves the most effort, requiring the complete reduction of a target population so that none remain. Exclusion can be enacted on a smaller scale, in an attempt to preserve targeted management areas, but is less practical on a regional scale. Control is less accurately defined (Courchamp et al. 2003), but involves physical (e.g., barriers) or biological (e.g., predators) mechanisms. Either control option is best implemented with an intimate knowledge of the population biology of the species targeted for control. Some authors have raised questions about the goal of management, whether it should be used to reduce the number of invaders or to reduce their negative effects (Lodge and Shrader-Frechette 2003, Lodge et al. 2006). However, for the most part, reducing effects of invaders can be accomplished by reducing their numbers (100 individuals of a species can do less harm than 1,000).

In many ways, invasion ecology represents the polar opposite perspective from conservation management (Lockwood et al. 2013); while the former is aimed at limiting growth and spread, the latter is aimed at enhancing those very things. Thus, pursuits to increase our understanding of the population biology of exotic species often have a great deal of overlap with pursuits aimed at improving our understanding of the population biology of threatened species. For instance, the most parsimonious approach to managing invasive species is to eradicate them as early as possible, which does not require any

consideration of population biology (Simberloff 2003, Allendorf and Lundquist 2003). Similarly, conservation strategies aimed at preventing a collapse from leading to an extinction can be successful without incorporating knowledge of the targeted species' population biology. Despite this, information aiding in the prediction of invasive (and native) species' population dynamics and which populations may become invasive (or collapse) can only benefit management efforts. For instance, while eradication without regard to population biology may be possible, eradication cannot be implemented if the target species is below its detection threshold (i.e., cannot eradicate what cannot be found). Similarly, conservation actions may be prematurely halted once a species declines below this detection threshold, if it assumed to be extinct. A better understanding of a species' population biology will better prepare us to deal with very rare populations when they are detectable, but before they have become so pervasive that it makes management much more difficult, and will improve our ability to protect even common (but variably abundant) species.

My work will contribute to the fields of conservation and invasive species population biology by exploring complex population dynamics and relate these to management goals. My research uses exotic and native species abundance data extensively, which—in the case of exotics—is directly related to impacts (Parker et al. 1999, Thomsen et al. 2011), as in the density-impact curves presented by Yokomizo et al. (2009). These density-impact relationships depend on species-level characteristics—life history traits, for example. Some populations can have large impacts at low abundances, while others produce noticeable impacts only at high abundance. This is captured by three basic curve shapes: logarithmic (curve I), with high species impact at all but the lowest densities;

sigmoidal (curve II), with increasing impact at intermediate density; and exponential (curve IV), with high impacts only at high abundances. Each of these curves is distinguished from curve III, a simple linear increase of impact with density (Yokomizo et al. 2009). The impact in each of these curves is in terms of economic cost, but can easily be extended to ecological impacts (Lockwood et al. 2013).

Density-impact curves establish expectations about management practices and timing in employing these practices. My results provide insight regarding when these impacts may occur and how long they may last. For instance, prolonged lag phases in population growth will lead to extended delays in appreciable impact for invasive species. Furthermore, if a population experiences a collapse, it may quickly and dramatically decline to such low abundances that it displays little impact. The three chapters of my dissertation are designed to help answer these questions using statistical models and the rich data sources associated with the birds of Hawaii.

Pyšek et al. (2008) review the biases in geographic and taxonomic focus of invasion ecology. They found that the ecological impact of an invasive species is the main predictor of whether a species is targeted for investigation; a logical finding given that more attention is expected to be paid to more troublesome species. Similarly, there is a preponderance of studies involving invasions in North America and Europe; disproportionately more than Oceania (Australia and Pacific islands) when numbers of naturalized exotics are considered (Pyšek et al. 2008). This bias stems from the number of academic researchers working in North America and Europe. Other reviews have found a lack of adequate temporal variety in studies of invasive species (Strayer et al. 2006). Because evolutionary processes occur on the timescale of biological invasions, the



need for the inclusion of long time-scales when exploring biological invasions is even greater (Whitham et al. 2006), especially considering the ever-changing status of an invasive species' measured impact (Yokomizo et al. 2009). Together, these reviews call for more research of all invaders (whether currently exhibiting impacts or not), in areas with high numbers of naturalized exotic species (especially islands), and with long term considerations to increase predictability of exotic species impacts. The research I present in this preliminary proposal fills these voids.

### *Objectives*

- Measure the occurrence and characteristics of lags in the population growth rate of exotic birds on Hawaii.
- Develop a method to accurately quantify uncertainty about critical aspects of population dynamics to standardize determinations of collapsed populations.
- Detect and describe unexpected declines in abundance among exotic birds on Hawaii, labeling those of certain intensity as collapses.

### *Lags*

Lags are a widely acknowledged but seldom quantified property of most biological invasions (Crooks 2005). Part of the trouble with assessing the prevalence and mechanisms of lag phases is the lack of a quantitative definition. This definition issue was addressed recently by Aikio et al. (2010) and Larkin (2012). Based on their work, I define a lag as a discrete stage in population growth that has a clearly distinguishable end point after which the population transitions into a phase of rapid growth. Thus, I established a single stage process of exponential growth as the default expectation, and classified populations that diverge from this expectation (i.e., those that are best

explained by two separate processes) as having lag phases. I found evidence for the occurrence of lag phases in 14 out of 17 exotic avian populations on the Hawaiian Islands. Results suggest that management officials cannot afford to delay management actions for exotic species that have existed in low numbers for a long time, as their rarity may not continue indefinitely.

This chapter is formatted for *Diversity and Distributions* and was published there (Aagaard and Lockwood, 2014).

### *Collapses*

Detecting population collapses is of considerable importance within many applied biological fields. Collapses are broadly defined as rapid declines in abundance. I develop a Bayesian approach to quantify uncertainty in observed maximum abundance, a critical step when defining collapses as a percentage drop from this value. I translate this uncertainty into confidence limits around the magnitude of decline that should be considered a collapse. Finally, I use three different statistical functions—linear, exponential, and a LOESS curve— to assess the period of collapses. I show that four of 12 native bird populations on Hawaii have declined by >90% over the span of 10 years. The method we present here helps fill the missing gaps of systematic tools for assessing uncertainty and can be readily applied to any system with sufficient time series of abundance data.

This chapter is formatted for *Methods in Ecology and Evolution* and will be submitted there (Aagaard and Lockwood, *in prep*).

### *Population collapses in exotic species*

Following establishment, some exotic species exhibit spontaneous population collapses, occasionally all the way to extinction (Simberloff and Gibbons 2004). Collapses are another population phenomenon, in addition to lags, that is thought to be somewhat common, but are not well-defined either empirically or quantitatively. Here, I rely on the IUCN (World Conservation Union 2001) criteria of a population collapse as my quantitative definition. This definition states that a collapse is a decline in abundance of  $\geq 90\%$  within 10 years or three generations, whichever is longer. I use statistical models to determine the 90% reduction (or, a decline to below 10% of previous abundance), using Bayesian hierarchical models to identify the appropriate ‘previous abundance’ with which to establish the lower-bound threshold. I found collapses in 14 of 33 established populations with sufficient data. I have shown the clear utility of these methods for the identification and description of collapses, which may be a more common feature of exotic species’ population dynamics than previously anticipated.

This chapter is formatted for *Methods in Ecology and Evolution* and will be submitted there (Aagaard and Lockwood, *in prep*).

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## **Chapter 1: Exotic birds show lags in population growth**

Article Type: Original Article

Kevin Aagaard\*, Julie Lockwood

Graduate Program in Ecology & Evolution, and Department of Ecology, Evolution, &  
Natural Resources, Rutgers University, New Brunswick, NJ 08901 USA

\*Corresponding author: [aagaard@scarletmail.rutgers.edu](mailto:aagaard@scarletmail.rutgers.edu), (telephone) 848-932-3213,  
(fax) 732-932-8746

JLL email: [lockwood@aesop.rutgers.edu](mailto:lockwood@aesop.rutgers.edu)

## ABSTRACT

**Aim** A key aspect of the ecology and management of biological invasions is the prevalence and duration of lag phases in population growth. We explore the occurrence of lag phases in exotic bird populations using Audubon Christmas Bird Count data.

**Location** Hawaiian Island archipelago.

**Methods** We expand on the use of piece-wise model fitting techniques to detect lags in exotic bird populations on Hawaii. We searched for explanations as to the occurrence of these lags using five possible mechanisms (body size, niche breadth, propagule pressure, length of record, and lag phase growth rate).

**Results** We found evidence of lag phases for 14 of 17 species we evaluated (range: 10 - 38 years, mean using observed data =  $16 \pm 12$ ), and we discovered very rapid growth to maximum abundance following the end of the lag phase (mean using observed data =  $8 \pm 6$  years). We found no evidence for any association between the possible mechanisms influencing the occurrence and duration of the lag phases.

**Main Conclusions** Our results are the first to rigorously quantify lags in exotic animal populations; most existing evidence comes from plants. We show that lags are as common in birds as in plants, although we provide preliminary evidence that the duration of lags in birds is shorter than in plants. We highlight the need for continued efforts to elucidate lag phase occurrence and duration in biological invasions, and we demonstrate the expanded utility of piecewise model fitting approaches to quantify these lags using count data.

**KEYWORDS:** *Audubon Christmas Bird Counts, biological invasions, exotic birds, lag phases, piecewise models, population dynamics*

## INTRODUCTION

Population lag phases have been defined as a period of slow population growth followed by a marked increase in rate of growth (Crooks 2005, Aikio et al. 2010). The occurrence of lag phases within exotic populations is seen as a serious complicating factor in our ability to predict and manage invasive species (Crooks 2005, Larkin 2012). Their existence suggests that currently rare exotic species may later explode in numbers and geographic extent. Therefore, there is practical interest in predicting the prevalence of lag phases and how long they may last, as well as understanding which elements of a species' life history and the invaded habitat (or both) might allow predictions of the extent and type of lag phase (Crooks 2005). This effort is hindered by the inconsistency of definitions applied to lag phases across studies, and statistical limitations associated with lag detection resulting from low population abundances characteristic of slow growth rates (Crooks and Soulé 1999, Aikio et al. 2010). The few authors who have quantified lag phases have done so for plants, and their results suggest that lags are common and can regularly last over 50 years (e.g., Kowarik 1995, Aikio et al. 2010, Larkin 2012). Here we expand on the methods of Aikio et al. (2010) to produce what is to our knowledge the first rigorous, quantitative survey of lag phases in exotic animals, which can have equally pernicious effects as exotic plants on native ecosystems (Clout and Williams 2009).

Early work on lag phases included anecdotal compilations of case studies that applied inconsistent definitions of 'exotic' and 'lags' (Crooks and Soulé 1999). A primary issue was whether observed lag phases were congruous with basic population models such as the exponential or logistic (Crooks and Soulé 1999, Crooks 2005). These models produce

initial phases of slow growth followed by rapid increases (Figure 1). Crooks (2005) defined the slow-growth phases of such models as ‘inherent’ lags and suggested that they should be distinguished from ‘unexpected’ lags, which he defines as a period of slow population growth that differs in length from what one should expect from exponential models (Figure 1). Here, we focus on this latter class of lag phases.

Aikio et al. (2010) refined the difference between inherent and unexpected lags by categorizing lag phases that can be modeled using only one mathematical expression (e.g., linear, exponential, logistic) as one-stage processes, whereas unexpected lags require the incorporation of two distinct expressions (e.g., two separate models). This definition is a clear step forward in the effort to identify and understand lag phases, in part because it sets a one-stage process as a null expectation, leaving any deviation from this (specifically, a two-stage process) as a phenomenon that requires further biological explanation (Aikio et al. 2010). These methods provide a robust way to analyze population time series for evidence of lag phases, and we apply it here to abundance records for 17 populations of exotic birds in Hawaii.

In part due to the observed high prevalence of lag phases in plants (e.g., Kowarik 1995) much interest was generated into uncovering consistent mechanisms for their production (Crooks 2005). The mechanisms that can produce lag phases include—among others—Allee effects, post-establishment evolution, shifts in environmental factors, and genetic impoverishment (Crooks 2005, Lockwood et al. 2013). Thus far, there is no consensus on the importance of suggested mechanisms; all of them have at least some empirical support (Crooks 2005, Lockwood et al. 2013). In addition it is unclear whether animals, which are more vagile than plants, should exhibit a similarly high prevalence or



duration of lags (e.g., Kowarik 1995, Aikio et al. 2010, Essl et al. 2011, Larkin 2012).

For example, we may expect that exotic animals will overcome Allee effects (i.e., mean individual fitness increases with abundance) more readily than plants through their ability to actively search for and associate with intraspecific individuals. Similarly, animals can actively choose habitat and ‘escape’ the confines of marginal habitat into which they may have been initially released. Plants on the other hand must grow in place and may take longer to ‘find’ more suitable habitat. While plants can ‘search’ for mates and ‘find’ habitat surprisingly well via seed/pollen dispersal, these mechanisms are only applicable during times of reproduction or with animal facilitation. Without exploring lag phases and their causes across broad taxonomic groups, all potential mechanistic differences will remain speculative. This is an especially important gap in knowledge given how unlike the causes of lag phases across different taxa are likely to be. We begin to fill this gap here.

We tested five mechanisms that might have produced the lag phases we see in exotic Hawaiian birds. First, we expect lags to last relatively longer (as compared to other birds) for species that have life histories typified by low reproductive rates and long generation times, here indexed as high body mass following Bennett and Owens (2002). Such slow life history species tend to have heightened vulnerability to environmental and demographic stochasticity (Blackburn et al. 2009). Second, we expect species with broader niches to be less constrained by environmental factors at the location of their initial release and therefore exhibit shorter lag phases. Populations of these species will increase in numbers quickly, relative to those with narrow niche requirements. Third, we expect that species that were introduced in very small initial numbers (i.e., low propagule

size) are more likely to show longer lag phases than those with higher propagule sizes. Species founded by few individuals may have strong genetic founder effects and bottlenecks, and thus may suffer from inbreeding depression that inhibits their population growth (Crooks 2005). Low propagule pressure will also subject populations to Allee effects, which will tend to create periods of slow or no population growth after initial introduction (Courchamp et al. 2008). Next, we expect that lags will be detected more readily in species in which the length of the lag is short relative to the length of residence on Hawaii. Essentially, longer time series provide more data points for fitting regression lines, and thus greater statistical power to differentiate between one and two-stage processes. Finally, we expect to find faster growth rates associated with shorter lag phases, since fast growth rates would allow for a lag to occur in a shorter amount of time allowing us to more easily detect it in time series with limited data points.

## METHODS

To identify species that exhibit lag phases, we assembled time series of abundance counts for 17 species of birds introduced to the Hawaiian Islands (Table 1—with scientific names for each population, also see Figure S1 in Supporting Information for full time series). Abundance records were taken from the Audubon Christmas Bird Count (CBC; National Audubon Society 2010), which began in Hawaii in 1938. We included counts conducted up to and including 2010 (the most recent available reported year, at the time of data acquisition). Many fundamental sampling biases are accounted for within CBC records by scaling reported count numbers by survey effort (party hours), by standardizing the time of year and location of counts, and by standardizing methodology.

Furthermore, we used the methods of Link et al. (2006, 2008) for scaling the counts according to effort variation and to ensure proper comparability among count circles.

While we have taken these precautions for the proper use and application of our data, the time series we analyzed here are still best thought of as estimates of relative abundance.

For 14 of 17 species, the CBC records encompass the entire residence time on the Hawaiian Islands, sometimes spanning over 40 years. The date of introduction preceded CBC records for the remaining three species: house sparrows (*Passer domesticus*); hwamei (*Garrulax canorus*); and nutmeg mannikin (*Lonchura punctulata*) (Pyle and Pyle 2009). We included these three species because historical records indicated that their populations were extremely low up to 1938 (Pyle and Pyle 2009), so we have some confidence that the early counts in the CBC record are indicative of the status of that population from the time of its initial introduction. For these three species our determination of lag presence will be conservative (i.e., tending toward concluding no lag), similarly the estimation of lag phase duration, if detected, will be conservatively short. Our dataset consists of one species (cattle egret, *Bulbulcus ibis*) that likely colonized Hawaii naturally; five species (hwamei; red avadavat, *Amandava amandava*; red-vented bulbul, *Pycnonotus cafer*; red-whiskered bulbul, *Pycnonotus jocosus*; yellow-fronted canary, *Serinus mozambicus*) that were accidentally introduced (cage escapees); with the rest being intentionally introduced.

All populations we considered show very small initial abundances, with a few then reaching and sustaining higher numbers by the end of their period of record (see Figure S1 in Supporting Information). Most populations evinced complex dynamics after their initial increase phase, occasionally showing a marked drop in population size during the

later years of the record. No population shows a population trajectory that can clearly be labeled as either exponential or logistic growth (Figure S1), which is perhaps unsurprising given that the CBC annual count data (as well as all count data) must be influenced by environmental and demographic stochasticity as well as count error (beyond what is already acknowledged and accounted for; see above).

The complexity of these population time series presented us with two inter-related methodological issues. The first issue is as much related to the definition of a lag phase, as it is methodological. By definition a lag is a marked change in population growth rate that characterizes how an exotic species establishes itself after initial colonization (Crooks 2005, Aikio et al. 2010). Based on this definition, the longer-term dynamics of the exotic population are not of interest. We could certainly fit complex, non-linear statistical models to the full population growth trajectories of our 17 species. However, providing a good over-all fit is not our objective and such complex non-linear models, by design, will obscure the details of growth associated with any particular piece that function; which for our purposes is the dynamics of early population growth. Nevertheless, complex longer-term dynamics statistically make it difficult to identify when a population may have realized a true increase in growth rate. For example, how do we know that a few years of high abundance reflect a real change in underlying demographic rates (i.e. higher fecundity and survival) rather than a few years in which counts were biased high? This insight raises the second issue: how to distinguish true and lasting changes in growth rates from the occasional stochastic bumps in demographic rates or biases in counts.

In recognition of these issues, we extracted and analyzed only the portion of each population's time series from the date of first record—or establishment, as above—to the maximum abundance estimate observed within the record. This truncation allowed us to carefully characterize the early colonization dynamics of our focal species. We then created a distribution of possible maximum abundance values that reflected the overall variance in the annual counts across the entire record, with the observed maximum servings as the initial mean of that distribution (Figure S2). To do this, we fit a Bayesian model of the following form:

$$Y[i] \sim N(\mu[i], \sigma^2),$$

$$\mu[i+1] = \mu[i] * \lambda[i],$$

$$\lambda[i] \sim N(\lambda, \tau),$$

$$\tau \sim \text{Unif}(0, 10),$$

$$\sigma^2 \sim \text{Unif}(0, 100),$$

where  $Y$  is the time series for each target population, with  $i$  representing each year's count within the time series,  $\mu$  is the estimated maximum abundance for each population (assuming year to year exponential growth, with the mean growth rate =  $\lambda$  and variance  $\tau$ ), and  $\sigma^2$  is the variance about the annual estimates, at first unknown and therefore given an uninformative prior. We allowed this model to run for 10,000 iterations, with a burn-in of 1,000 to allow for convergence (achieved quickly with this simple model). After all iterations are complete, the resulting posterior distribution can be thought of as a collection of all likely maximum abundances, given the observed maximum and year-to-year variance in counts for that species. Thus, if a species' population time series shows little year-to-year differences in counts, then the range of likely maximum abundances

will be small; and vice versa. This method effectively allows the entire population time series to inform our belief that the observed maximum abundance is due to a factor other than stochasticity or count error. It is important to note that since the abundance data (y-axis on Figure S2) we use here have been corrected for observer effort, they are continuous and not discrete making the use of a normal rather than Poisson prior distribution appropriate.

To identify which species a two-stage process best represented we fit three classes of models to each species' population growth trajectory. We first fit a single linear model. Populations grow in a near-linear fashion during a lag phase (Crooks 2005; Figure 1). It is possible that the populations we analyzed were introduced recently enough that they have not yet emerged from a lag phase, and thus, a linear model alone may provide the best fit for these populations. We fit a linear model of the form  $N_t = r*t + N_0$ ; where  $N_t$  is the size of the population at a given time,  $N_0$  is the size of the initial population,  $t$  is time, and  $r$  is the population growth rate.

We next fit an exponential model, which we used to approximate a non-linear growth trajectory. The exponential curve has widespread use in modeling the growth of biological systems and is the classic expectation for population growth after initial colonization (Crooks and Soulé 1999, Crooks 2005). We fit an exponential model with the following form:  $N_t = N_0 * e^{(r*t)}$ ; where  $N_t$  represents population size at a given time,  $N_0$  is the size of the initial population,  $e$  is base of the natural logarithm,  $r$  represents the growth rate, and  $t$  represents time. Note that fitting a logistic model to the full time series is not warranted because we truncate the data at the maximum observed value and

therefore such a model will always fit less well than an exponential because of the extra parameter (an asymptote,  $k$ ) to be estimated.

For the third class of model, we followed the methods of Aikio et al. (2010) and fit a piecewise model consisting of multiple combinations of two separate models applied sequentially, which may be disconnected as time here is discrete (we have no data on abundance estimates between CBC records). We fit only a linear model to the early portions of all time series following the logic of Aikio et al. (2010). We fit a linear and exponential model to the second portion of each time series. However, the linear model consistently out-performed the exponential across all species and all estimates of maximum abundance (Table S2-A). We therefore only report the results from fitting two linear models henceforth. We bounded the piecewise model so that there were always at least four points with which to fit each portion. That is to say, for a population with  $J$  total years of data we fit the first linear model to the first  $x$  years of data, and then fit the second linear model to the remaining  $J - x$  years of data, for all  $x = \text{years}$ . The piecewise model fitting resulted in 3 – 32 representations of population growth per species, with the number of models for each species determined by the length of its count record. To determine which piecewise model best fit the empirical abundance estimates per species, we used least squares linear regression. We selected the model with the lowest sum of the squared error (SSE) as the most parsimonious of the set of candidate linear-piecewise models.

We compared the most parsimonious piecewise model to the single linear and single exponential models using AICc, which penalizes models for extra parameters, to select the best model of the three candidates. With this procedure we were able to account for

differences in scale among the target populations and avoid selecting a model with a low SSE value that is attributable to small differences in abundance estimates (i.e. some populations had maximum abundances of less than one individual observed per party hour, while others were observed in abundances greater than 40 per party hour).

To account for uncertainty in the maximum abundance value, we extracted the lower (2.5%) and upper (97.5%) confidence interval (CI) estimates of the posterior maximum abundance distribution (see above). We then re-ran the above procedure replacing the observed maximum with the upper CI estimate of maximum abundance, and then again with the lower CI estimate (Figure S2). We noted when either of these two alternative maximum values resulted in a different model being ranked as the best fit by AICc, and when such differences occurred, we also noted the resulting estimate of lag length. We label species as having ‘true lags’ when the two-piece model provided the best fit regardless of the uncertainty in the maximum abundance observed. We labeled species as exhibiting ‘probable lags’ when the best-fit model was not always the two-piece (i.e. when there was disagreement in results when allowing the maximum to vary). Species which had population time series that were always best described by either a linear or exponential model alone were considered to show no lag. When lags were observed, the differences in estimated lag lengths provide us with a range of lag durations; thus reflecting our uncertainty over the true value of the maximum abundance.

Finally, we used least squares regression to explore the relationship between duration of lags (duration of lag = 0 if not detected) and our five explanatory variables. We used Sibley (2009) to determine the body mass of each of the 17 species we considered. Niche breadth was quantified following Cassey (2002). Briefly, we assigned each species all



applicable food (eight total, e.g., seed/grain, insects, vegetation/fruit) and habitat categories (eight total, e.g., grassland, urban, lowland woods) and scored the species with a maximum of 16 ‘niches’. Those species with a larger available diet or broader habitat range were considered to have wider niche breadths. We calculated propagule pressure by summing the propagule sizes of all reported introduction events for each species, determined by reviewing historical records presented in Pyle and Pyle (2009). Any species with nebulous or poorly defined propagule sizes were excluded from this particular analysis (e.g., species with reports of “many” introduced individuals rather than a specific number were ignored). We tallied the number of years each species was recorded in the CBC as our measure of the length of abundance record. Lastly, we correlated the growth rate in the lag phase of each species’ population growth trajectory with both the duration of the lag phase and the growth rate in the increase phase (see Table S1). All analyses were conducted in R v. 2.15.0 (R Development Core Team 2012).

## RESULTS

Time series for the 17 species we examined showed that nine species showed evidence of a true lag, while an additional three species showed evidence of probable lags (Table 1, see also Table S2). The average lag phase duration was  $15.6 \pm 11.6$  years when using the observed maximum abundance estimate;  $15.1 \pm 12.3$  when using the upper bound of the 95% CI of the maximum abundance estimate; and  $11.5 \pm 10.6$  when using the lower bound of the 95% CI of the maximum abundance estimate. Six species experienced lag phases  $\geq 20$  years under all estimates of maximum abundance. The only

species that did not display a lag phase using any maximum abundance estimates were the northern cardinal (*Cardinalis cardinalis*), the house sparrow, and the chestnut manikin (*Lonchura atricapilla*). These results highlight our inability to distinguish between cases in which a population has either not yet exited its lag phase (as is a possibility with the northern cardinal and house sparrow), is showing an inherent lag (as is likely with the chestnut manikin), or simply does not exhibit a lag phase. The years in which lagged populations began to increase in abundance ranged from 1955 to 2008 (lengths ranging from 10 to 38 years) with no obvious year in which all populations transitioned to more rapid growth (Figure 2). The average time between the end of the lag phase and the year of maximum abundance was  $7.7 \pm 6.3$  years using the observed value,  $8.2 \pm 6.5$  using the upper bound of the 95% CI, and  $11.8 \pm 9.7$  years using the lower bound of the 95% CI. Twelve species reached their maximum abundances in  $\leq$  five years following the end of their lag phase using the observed maximum abundance estimate; 11 using the upper bound of the 95% CI, and seven using the lower bound of the 95% CI.

We found no evidence that any of the five potential mechanisms we tested dictated lag duration. First, we found no evidence that longer lags for species with low reproductive rates and long generation times (using body mass as a proxy;  $R^2 = 0.062$ ). Second, we did not find shorter lags for species with broader niches ( $R^2 = 0.037$ ). Third, we posited low propagule size would lead to longer lags, however, it showed no relationship ( $R^2 = 0.147$ ). Fourth, we expected that longer time series would provide greater statistical power to differentiate between one and two-stage processes, and perhaps produce longer lag phases; however we found no evidence for such a relationship ( $R^2 = 0.083$ ). Our final hypothesis was that we would find faster growth rates associated

with shorter lag phases overall; but we again found no evidence for such a relationship ( $R^2 = 0.232$ ). Given the lack of results provided by these analysis, we correlated the lag phase and increase phase growth rates, but still found no relationship ( $R^2 = 0.368$ ).

## DISCUSSION

Exotic birds show a high prevalence of lag phases in population growth, similar to results found for exotic plants (e.g., Aikio et al. 2010). Although the existence of lag phases has been recognized for quite some time (e.g., Hobbs and Humphries 1995), the few quantitative surveys for lags have been conducted exclusively on plants. Our methods represent a refinement of the approach of Aikio et al. (2010) for use with small datasets and count data, and our results extend evidence for the prevalence of lags to birds specifically and vertebrates more broadly. Deliberate eradication of exotic vertebrates is becoming more common as logistical and technological advances are made (Howald et al. 2007). However, published information on management of exotic vertebrates has largely ignored the issue of population lag phases and what that might mean for allocation of limited capital for eradication campaigns. Our results suggest that it is not prudent for managers to assume that exotic vertebrates that have existed in low numbers for a long period will remain rare into the future.

We show that the exotic birds of Hawaii had average lags of 11 to 15 years, with some lasting  $> 20$  years. Based on similar methods and definitions as we use here, Aikio et al. (2010) show that exotic plants of New Zealand have lag phases averaging 20 – 30 years, with a small fraction lasting for over 40 years. Similarly, Larkin (2012) demonstrates that exotic plants in the upper-Midwest US have lags averaging just under

50 years, with an upper limit of 140 years. This comparison suggests that exotic birds experience lag phases of shorter duration than do plants, perhaps due to inherent differences in vagility between the two groups. However, absent more quantitative analyses of other taxa besides birds and plants, this conclusion is tentative.

All existing mechanistic explanations for lag phases assume the newly established exotic population emerges from a lag via a marked increase in demographic rates (Crooks 2005). Detecting such a rate change is statistically challenging, especially when the underlying data is based on empirical counts instead of accumulations of records. Count data are inherently noisy since they reflect environmental and demographic stochasticity and myriad sources of count error (Link et al. 2006, Link et al. 2008). Our approach to explicitly account for this uncertainty represents a novel extension of the methods in Aikio et al. (2010) and should prove useful to others when using count-based records of exotic population growth to detect lags. Using this approach we were able to highlight species for which we were uncertain about the presence of a lag. For example, we could not be certain of lags in species that existed at abundances near their observed maximum for only brief periods of time (e.g., nutmeg mannikin); those with generally low abundance for the duration of their time series (e.g., rose-ringed parakeet); or those with ‘spikes’ in abundance of only minor degree (e.g., northern cardinal). Accounting for this uncertainty allows us a more nuanced view of the prevalence of lags, and perhaps also into the suite of mechanisms that produce such lags.

Exotic birds show a very stark difference between the slow growth rates indicative of being in a lag and the rapid growth rates after a lag. Statistically we see that the difference in how well an exponential versus a two-piece model fits the empirical data is

extreme, with the latter often holding nearly 100% of the weight of evidence (see Table S2). In terms of management, the order of magnitude increase in population growth rate for a population after emerging from a lag not only suggests that exotic populations may grow slowly for long periods of time only to increase later, but also that this increase can be extremely rapid. This places a high premium on controlling or eradicating an exotic population early while still in a lag phase. Biologically, this sudden shift between low and fast growth rates suggests a near point-in-time mechanism that allows an exotic population to markedly increase in fitness. The degree to which all exotic populations show the same stark transition in growth rates is an open question, but one that certainly increases the dividend for searching for lags within other taxonomic groups or geographical locations.

Our failure to find evidence in favor of any of our tested mechanisms underlying variability in lag duration is consistent with results reported by Larkin (2012), who found only weak support for the factors he evaluated. In our case, we may have found no association because of the (i) inherent uncertainty associated with using historical information; (ii) low statistical power associated with our dataset ( $N \leq 17$ ), or (iii) influence of these factors was truly weak. Larkin (2012) suggests that the mechanisms producing lag phases almost certainly interact with one another, making statistical associations difficult to detect and prediction nearly impossible. Our results reinforce this conclusion, leading us to suggest that the search for broadly consistent cross-species explanations for lags may be quixotic. A more fruitful next step may be to explore, via observation, experimentation, or simulation, the mechanisms behind any single empirical example of an exotic population that demonstrates a lag phase; of which there are now

many stemming from our work and that of Aikio et al. (2010) and Larkin (2012). The mechanisms producing lags likely vary across species, and perhaps across populations of the same species. It is through exploration of several detailed case studies that we are more likely to generate predictive insights. The growth in the number of quantitative surveys for lag phases similar to ours will improve our ability to predict and interpret the dynamics of lags, and the mechanisms that produce them.

#### ACKNOWLEDGEMENTS

We thank W. Link, P. Cassey, and T. Blackburn for input early in this work. We also thank E. Green, D. Fonseca, D. Simberloff, P. Morin, P. Smouse, J. C. Burkhalter, O. Robinson, J. Avery, the Morin Lab, and anonymous reviewers for their feedback on various drafts of this manuscript. The authors report no conflict of interest.

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#### BIOSKETCH

The authors' interests lay in the fields of invasion ecology and population dynamics. We use models to inform predictions about the processes of established exotic species.

Author contributions: K.A. and J.L.L. conceived the ideas and wrote the manuscript jointly.



Table 1. Here we show the estimated length of lag phases for the three datasets used; 1) using the upper bound of the 95% confidence interval (CI) of the observed maximum abundance (“Upper bound”), 2) using the observed maximum abundance itself (“Observed”, and 3) using the lower bound of the 95% CI of the observed maximum abundance (“Lower bound”). For species with not lag phase detected, we report the best fitting model (whether “Exponential” or “Linear”), or we report that no model was clearly better fit to the data (“None”).

<b>Common Name</b> <i>Species name</i>	<b>Estimated lag phase length</b>		
	<b>Upper bound</b>	<b>Observed</b>	<b>Lower bound</b>
Cattle Egret <i>Bubulcis ibis</i>	<b>Exponential</b>	<b>None</b>	<b>14</b>
Chestnut Mannikin <i>Lonchura atricapilla</i>	<b>Exponential</b>	<b>Exponential</b>	<b>Exponential</b>
Common Waxbill <i>Estrilda astrild</i>	<b>38</b>	<b>37</b>	<b>23</b>
House Sparrow <i>Passer domesticus</i>	<b>None</b>	<b>None</b>	<b>None</b>
Japanese Bush-Warbler <i>Cettia diphone</i>	<b>19</b>	<b>18</b>	<b>19</b>
Java Sparrow <i>Padda oryzivora</i>	<b>19</b>	<b>19</b>	<b>19</b>
Lavender Waxbill <sup>†</sup> <i>Estrilda caerulescens</i>	<b>24</b>	<b>24</b>	<b>22</b>

Hwamei <i>Garrulax canorus</i>	<b>13</b>	<b>13</b>	<b>13</b>
Northern Cardinal <i>Cardinalis cardinalis</i>	<b>None</b>	<b>None</b>	<b>None</b>
Nutmeg Mannikin <sup>†</sup> <i>Lonchura punctulata</i>	<b>None</b>	<b>10</b>	<b>None</b>
Red Avadavat <sup>†</sup> <i>Amandava amandava</i>	<b>22</b>	<b>22</b>	<b>22</b>
Red-vented Bulbul <i>Pycnonotus cafer</i>	<b>12</b>	<b>12</b>	<b>Linear</b>
Red-whiskered Bulbul <i>Pycnonotus jocosus</i>	<b>13</b>	<b>13</b>	<b>13</b>
Rose-ringed Parakeet <sup>†</sup> <i>Psittacula krameri</i>	<b>34</b>	<b>34</b>	<b>None</b>
Saffron Finch <sup>†</sup> <i>Sicalis flaveola</i>	<b>22</b>	<b>22</b>	<b>22</b>
White-rumped Shama <sup>†</sup> <i>Copsychus malabaricus</i>	<b>13</b>	<b>13</b>	<b>None</b>
Yellow-fronted Canary <i>Serinus mozambicus</i>	<b>28</b>	<b>28</b>	<b>28</b>

## FIGURE LEGENDS

Figure 1. All exotic populations grow slowly, starting from initially small numbers, as exemplified by an exponential model. Such populations show inherent lags between the time they are introduced ( $t_0$ ) and the time when the number of individuals accelerates. Populations that exhibit periods of linear growth rate (to  $t_{lag}$ ), followed by non-linear growth, show lag phases that are best approximated using piecewise models.

Figure 2. Here we present the duration of lag phases across all species, with the symbols representing the year in which the lag phase ended for each population as estimated using the observed maximum abundance estimate ( $\bullet$ ), and the lower ( $\square$ ) and upper ( $\Delta$ ) bounds of the 95% confidence interval about the maximum abundance estimate. The left and right hash marks represent the year of first record and the year of maximum abundance in the CBC, respectively. Any symbol on the left hash mark represents the absence of a lag phase.

Figure 1.

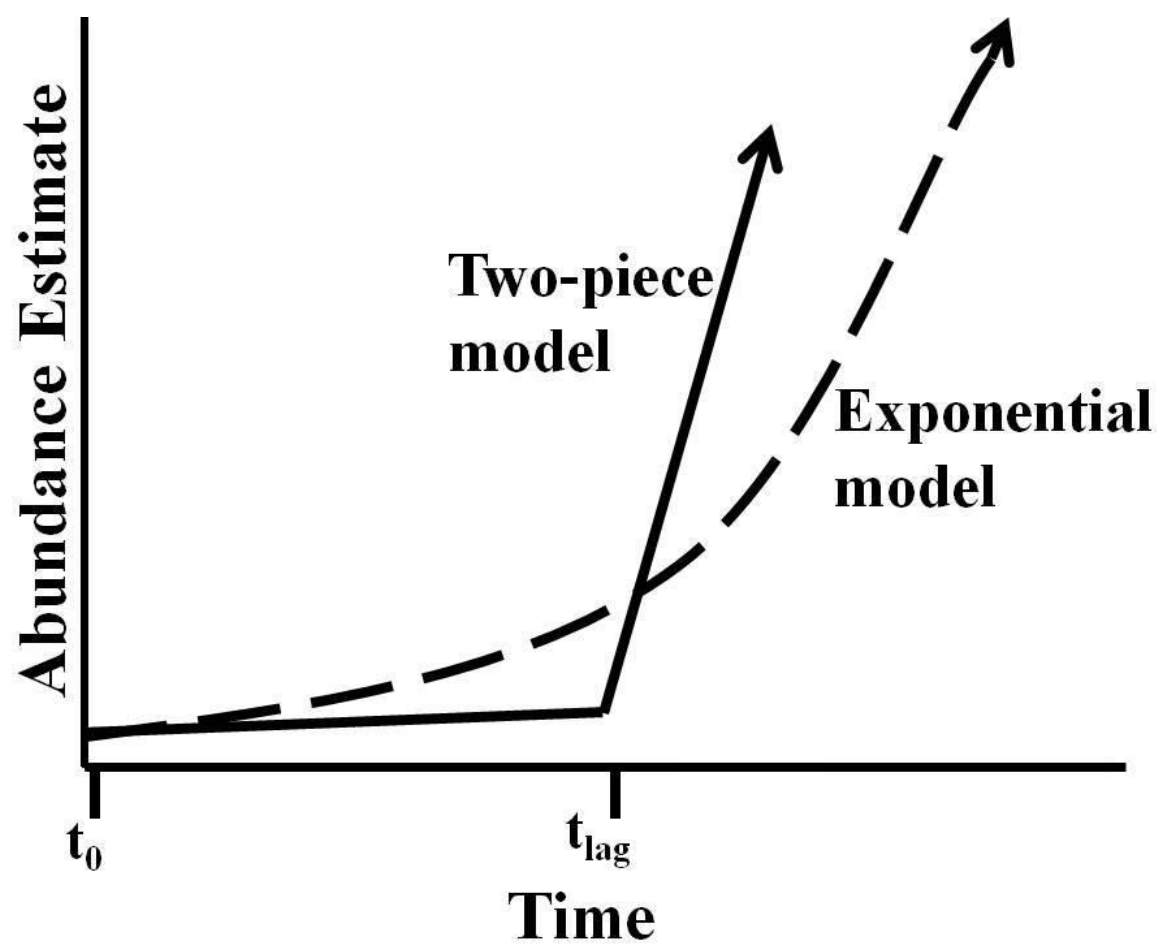
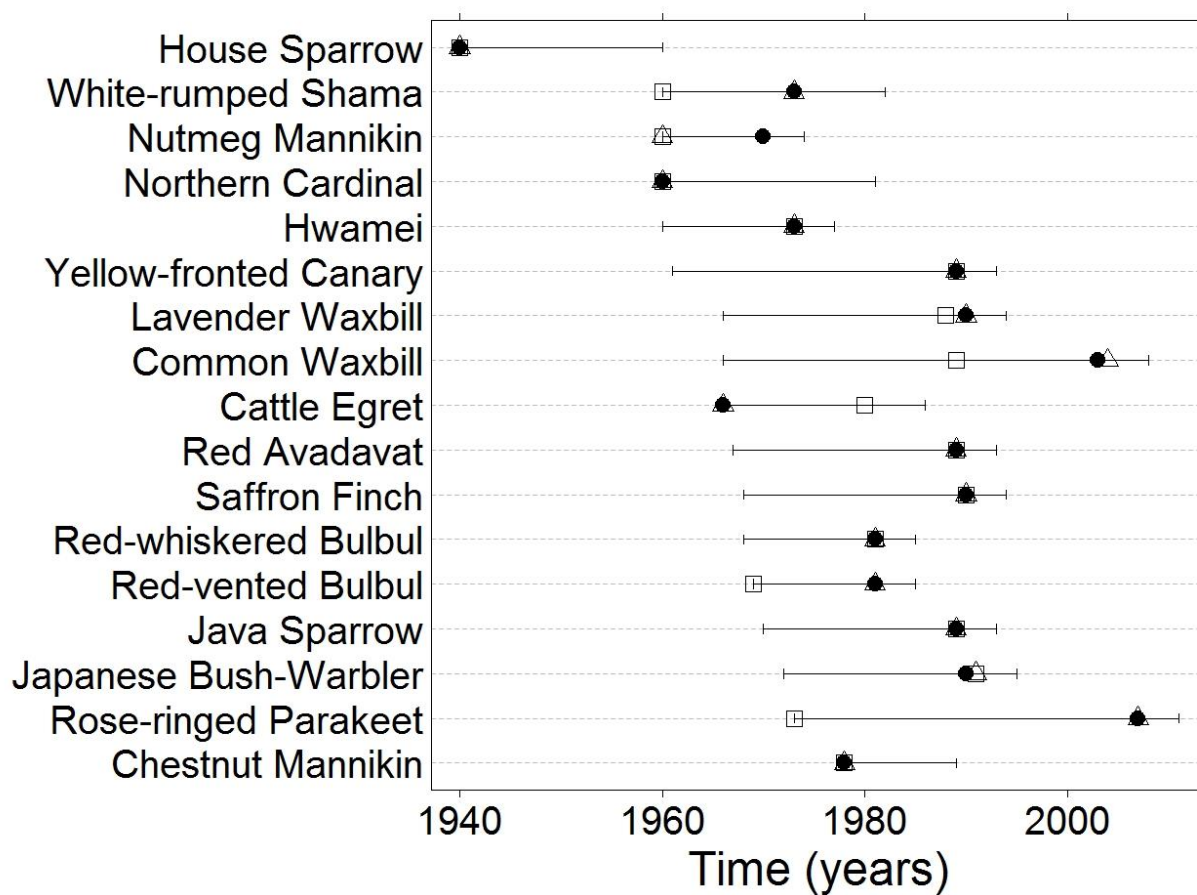


Figure 2



## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1. Parameter estimates for the target species, denoted with their common name.

‘ $r_{\text{lag}}$ ’ is the growth rate for the first linear model; ‘ $r_{\text{increase}}$ ’ is the growth rate for the second linear model; ‘ $r_{\text{exponential}}$ ’ is the growth rate for the exponential model; and ‘ $\Delta (r_{\text{lag}} - r_{\text{increase}})$ ’ is the difference between the growth rates of the two linear models, when applicable (i.e., a growth rate change from negative to positive does not yield a meaningful % increase result). For some species, like the northern cardinal, the data was not more accurately estimated by either the exponential or single linear model.

Common Name	Parameter Estimates				
	$r_{\text{lag}}$	$r_{\text{increase}}$	$r_{\text{exponential}}$	$\Delta (r_{\text{lag}} - r_{\text{increase}})$	% increase
Cattle Egret	NA	NA	NA	NA	NA
Chestnut Mannikin	NA	NA	0.22	NA	NA
Common Waxbill	0.07	0.63	NA	0.56	822
House Sparrow	NA	NA	NA	NA	NA
Japanese Bush-Warbler	0.01	0.11	NA	0.10	865
Java Sparrow	0.06	1.25	NA	1.19	1970
Lavender Waxbill	-0.006	0.06	NA	0.06	NA
Hwamei	0.02	0.07	NA	0.06	324
Northern Cardinal	NA	NA	NA	NA	NA
Nutmeg Mannikin	-0.23	16	NA	16	NA
Red Avadavat	0.02	0.21	NA	0.20	1311
Red-vented Bulbul	0.11	0.83	NA	0.73	693

Red-whiskered Bulbul	0.003	0.13	NA	0.13	4903
Rose-ringed Parakeet	0.0002	0.02	NA	0.02	8596
Saffron Finch	-0.003	0.64	NA	0.65	NA
White-rumped Shama	-0.006	0.08	NA	0.09	NA
Yellow-fronted Canary	-0.003	0.69	NA	0.69	NA

Table S2. Here we show AIC<sub>c</sub> weights for each population and each model, using different values for the maximum abundance estimate. ‘Upper bound’ represents the outcome of applying our models to each time series using the upper bound of the 95% confidence interval (CI) about the maximum abundance estimates. ‘Observed’ represents the outcome of applying our models to each time series using the observed value of the maximum abundance estimate. ‘Lower bound’ represents the outcome of applying our models to the lower bound of the 95% CI about the maximum abundance estimate. If a two-piece model best fit the observed count data, we listed the length of the lag in last column (Lag). If the exponential or linear model provided the best fit, we indicated this in the Lag column. If we could not distinguish a best-fit model amongst the candidate set, the ‘Lag’ column is labelled as ‘None’. (A) shows AIC<sub>c</sub> weights when the piecewise exponential model was included in the analysis; (B) shows the AIC<sub>c</sub> weights when the piecewise exponential model was not included.

(A)

Species	Upper bound				
	Linear	Exponential	Piecewise	Piecewise	Lag
			Linear	Exponential	
Cattle Egret	2%	<b>95%</b>	2%	1%	<b>Exponential</b>
Chestnut Mannikin	16%	<b>83%</b>	1%	0.09%	<b>Exponential</b>
Common Waxbill	0%	0%	<b>100%</b>	0%	<b>38</b>
House Sparrow	7%	30%	61%	1%	<b>None</b>
Japanese Bush-Warbler	0.11%	0%	<b>99%</b>	0%	<b>19</b>
Java Sparrow	0.38%	0.40%	<b>99%</b>	0%	<b>19</b>



Lavender Waxbill	0%	0%	<b>100%</b>	0%	<b>24</b>
Hwamei	0.03%	0%	<b>99%</b>	0%	<b>13</b>
Northern Cardinal	46%	47%	7%	0%	<b>None</b>
Nutmeg Mannikin	0.37%	47%	53%	0.49%	<b>None</b>
Red Avadavat	6%	0%	<b>94%</b>	0%	<b>22</b>
Red-vented Bulbul	3%	0.02%	<b>97%</b>	0%	<b>12</b>
Red-whiskered Bulbul	0.14%	0%	<b>99%</b>	0%	<b>13</b>
Rose-ringed Parakeet	0%	0%	<b>100%</b>	0%	<b>34</b>
Saffron Finch	0%	0%	<b>100%</b>	0%	<b>22</b>
White-rumped Shama	3%	0%	<b>97%</b>	0%	<b>13</b>
Yellow-fronted Canary	0%	0%	<b>100%</b>	0%	<b>28</b>
<b>Species</b>	<b>Observed maximum abundance</b>				
	<b>Linear</b>	<b>Exponential</b>	<b>Piecewise</b>	<b>Piecewise</b>	<b>Lag</b>
			<b>Linear</b>	<b>Exponential</b>	
Cattle Egret	21%	39%	40%	0.22%	<b>None</b>
Chestnut Mannikin	20%	<b>78%</b>	2%	0.04%	<b>Exponential</b>
Common Waxbill	0.27%	0%	<b>99%</b>	0%	<b>37</b>
House Sparrow	10%	34%	55%	1%	<b>None</b>
Japanese Bush-Warbler	0.04%	0%	<b>99%</b>	0%	<b>18</b>
Java Sparrow	0.17%	0.01%	<b>99%</b>	0%	<b>19</b>
Lavender Waxbill	0%	0%	<b>100%</b>	0%	<b>24</b>
Hwamei	0.01%	0%	<b>99%</b>	0%	<b>13</b>
Northern Cardinal	46%	47%	7%	0%	<b>None</b>

Nutmeg Mannikin	0.29%	29.84%	<b>69.51%</b>	0.36%	<b>10</b>
Red Avadavat	14%	0%	<b>86%</b>	0%	<b>22</b>
Red-vented Bulbul	3%	0.02%	<b>97%</b>	0%	<b>12</b>
Red-whiskered Bulbul	0.01%	0%	<b>99%</b>	0%	<b>13</b>
Rose-ringed Parakeet	19%	0%	<b>81%</b>	0%	<b>34</b>
Saffron Finch	0%	0%	<b>100%</b>	0%	<b>22</b>
White-rumped Shama	3%	0%	<b>97%</b>	0%	<b>13</b>
Yellow-fronted Canary	0%	0%	<b>100%</b>	0%	<b>28</b>
<b>Species</b>	<b>Lower bound maximum abundance</b>				
	<b>Linear</b>	<b>Exponential</b>	<b>Piecewise Linear</b>	<b>Piecewise Exponential</b>	<b>Lag</b>
Cattle Egret	0%	0%	<b>100%</b>	0%	<b>14</b>
Chestnut Mannikin	23%	<b>71%</b>	7%	0.01%	<b>Exponential</b>
Common Waxbill	3%	0%	<b>97%</b>	0%	<b>23</b>
House Sparrow	44%	33%	19%	4%	<b>None</b>
Japanese Bush-Warbler	25%	0%	<b>75%</b>	0%	<b>19</b>
Java Sparrow	0.03%	0%	<b>99%</b>	0%	<b>19</b>
Lavender Waxbill	0.01%	0%	<b>99%</b>	0%	<b>22</b>
Hwamei	0.55%	0%	<b>99%</b>	0%	<b>13</b>
Northern Cardinal	38%	15%	47%	0%	<b>None</b>
Nutmeg Mannikin	0.83%	35%	64%	0.53%	<b>None</b>
Red Avadavat	0.16%	0%	<b>99%</b>	0%	<b>22</b>
Red-vented Bulbul	<b>95%</b>	0.60%	5%	0%	<b>Linear</b>

Red-whiskered Bulbul	19%	0%	<b>81%</b>	0%	<b>13</b>
Rose-ringed Parakeet	43%	0%	57%	0%	<b>None</b>
Saffron Finch	11%	0%	<b>89%</b>	0%	<b>22</b>
White-rumped Shama	49%	0%	51%	0%	<b>None</b>
Yellow-fronted Canary	0.32%	0%	<b>99%</b>	0%	<b>28</b>

**(B)**

Species	Upper bound maximum abundance			
	Linear	Exponential	Piecewise Linear	Lag
Cattle Egret	2%	<b>96%</b>	2%	<b>Exponential</b>
Chestnut Mannikin	16%	<b>83%</b>	1%	<b>Exponential</b>
Common Waxbill	0%	0%	<b>100%</b>	<b>38</b>
House Sparrow	7%	31%	62%	<b>None</b>
Japanese Bush-Warbler	0.11%	0%	<b>99%</b>	<b>19</b>
Java Sparrow	0.38%	0.40%	<b>99%</b>	<b>19</b>
Lavender Waxbill	0%	0%	<b>100%</b>	<b>24</b>
Hwamei	0.03%	0%	<b>99%</b>	<b>13</b>
Northern Cardinal	46%	47%	7%	<b>None</b>
Nutmeg Mannikin	0.37%	47%	53%	<b>None</b>
Red Avadavat	6%	0%	<b>94%</b>	<b>22</b>
Red-vented Bulbul	3%	0.02%	<b>97%</b>	<b>12</b>
Red-whiskered Bulbul	0.14%	0%	<b>99%</b>	<b>13</b>

Rose-ringed Parakeet	0%	0%	<b>100%</b>	<b>34</b>
Saffron Finch	0%	0%	<b>100%</b>	<b>22</b>
White-rumped Shama	3%	0%	<b>97%</b>	<b>13</b>
Yellow-fronted Canary	0%	0%	<b>100%</b>	<b>28</b>
Species	Observed maximum abundance			
	Piecewise			Lag
	Linear	Exponential	Linear	
Cattle Egret	21%	39%	41%	<b>None</b>
Chestnut Mannikin	20%	<b>78%</b>	2%	<b>Exponential</b>
Common Waxbill	0.27%	0%	<b>99%</b>	<b>37</b>
House Sparrow	10%	35%	55%	<b>None</b>
Japanese Bush-Warbler	0.04%	0%	<b>99%</b>	<b>18</b>
Java Sparrow	0.17%	0.01%	<b>99%</b>	<b>19</b>
Lavender Waxbill	0%	0%	100%	<b>24</b>
Hwamei	0.01%	0%	<b>99%</b>	<b>13</b>
Northern Cardinal	46%	47%	7%	<b>None</b>
Nutmeg Mannikin	0.29%	30%	<b>70%</b>	<b>10</b>
Red Avadavat	14%	0%	<b>86%</b>	<b>22</b>
Red-vented Bulbul	3%	0.02%	<b>97%</b>	<b>12</b>
Red-whiskered Bulbul	0.01%	0%	<b>99%</b>	<b>13</b>
Rose-ringed Parakeet	19%	0%	<b>81%</b>	<b>34</b>
Saffron Finch	0%	0%	<b>100%</b>	<b>22</b>
White-rumped Shama	3%	0%	<b>97%</b>	<b>13</b>

Yellow-fronted Canary	0%	0%	<b>100%</b>	<b>28</b>
Species	Lower bound maximum abundance			
	Linear	Exponential	Piecewise Linear	Lag
Cattle Egret	0%	0%	<b>100%</b>	<b>14</b>
Chestnut Mannikin	23%	<b>71%</b>	7%	<b>Exp</b>
Common Waxbill	3%	0%	<b>97%</b>	<b>23</b>
House Sparrow	46%	35%	19%	<b>None</b>
Japanese Bush-Warbler	25%	0%	<b>75%</b>	<b>19</b>
Java Sparrow	0.03%	0%	<b>99%</b>	<b>19</b>
Lavender Waxbill	0.01%	0%	<b>99%</b>	<b>22</b>
Hwamei	0.55%	0%	<b>99%</b>	<b>13</b>
Northern Cardinal	38%	15%	47%	<b>None</b>
Nutmeg Mannikin	0.83%	35%	64%	<b>None</b>
Red Avadavat	0.16%	0%	<b>99%</b>	<b>22</b>
Red-vented Bulbul	<b>95%</b>	0.60%	5%	<b>Linear</b>
Red-whiskered Bulbul	19%	0%	<b>81%</b>	<b>13</b>
Rose-ringed Parakeet	43%	0%	57%	<b>None</b>
Saffron Finch	11%	0%	<b>89%</b>	<b>22</b>
White-rumped Shama	49%	0%	51%	<b>None</b>
Yellow-fronted Canary	0.32%	0%	<b>99%</b>	<b>28</b>

Table S3. We list the year of the first report in the CBC (first record). We also report the body mass (grams), niche breadth, and propagule pressure associated with each species (see text for more details regarding the units and strategies used to calculate niche breadth and propagule pressure).

Common Name	First record	Body mass	Niche breadth	Propagule pressure
<i>Scientific Name</i>				
Cattle Egret	1966	392	3	121
<i>Bubulcis ibis</i>				
Chestnut Mannikin	1978	13	8	23
<i>Lonchura atricapilla</i>				
Common Waxbill	1966	9	8	24
<i>Estrilda astrild</i>				
House Sparrow	1940	28	9	9
<i>Passer domesticus</i>				
Japanese Bush-Warbler	1960	63	10	177
<i>Cettia diphone</i>				
Java Sparrow	1972	19	4	138
<i>Padda oryzivora</i>				
Lavender Waxbill†	1970	25	8	13
<i>Estrilda caerulescens</i>				
Hwamei	1966	9	7	NA
<i>Garrulax canorus</i>				
Northern Cardinal	1960	45	8	352

<i>Cardinalis cardinalis</i>				
Nutmeg Mannikin <sup>†</sup>	1960	13	8	NA
<i>Lonchura punctulata</i>				
Red Avadavat <sup>†</sup>	1967	10	6	NA
<i>Amandava amandava</i>				
Red-vented Bulbul	1969	33	7	6
<i>Pycnonotus cafer</i>				
Red-whiskered Bulbul	1968	33	7	2
<i>Pycnonotus jocosus</i>				
Rose-ringed Parakeet <sup>†</sup>	1973	118	8	NA
<i>Psittacula krameri</i>				
Saffron Finch <sup>†</sup>	1968	20	7	NA
<i>Sicalis flaveola</i>				
White-rumped Shama <sup>†</sup>	1960	28	2	NA
<i>Copsychus malabaricus</i>				
Yellow-fronted Canary	1961	11	8	48
<i>Serinus mozambicus</i>				

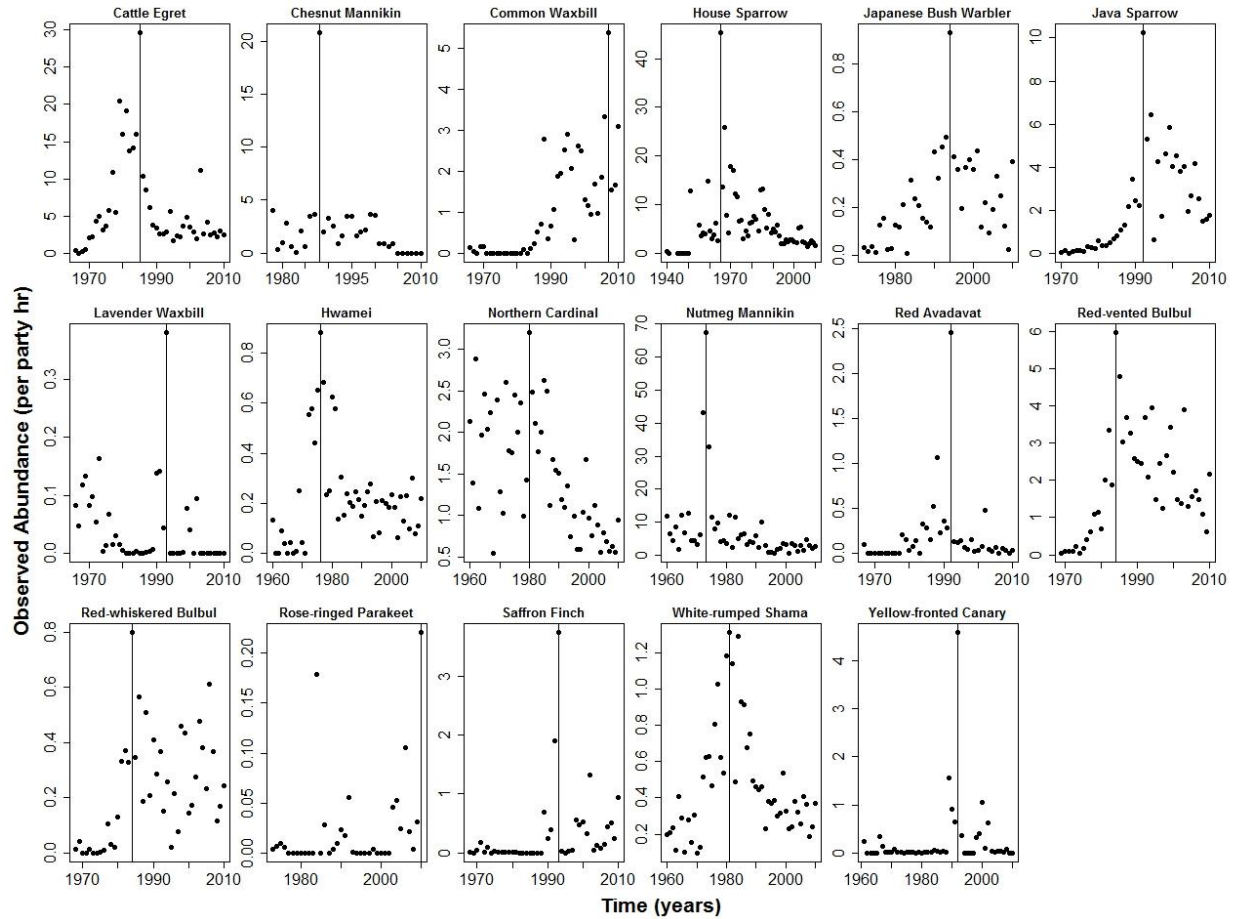


Figure S1. Time series for all 17 exotic bird populations analyzed here. These data were obtained from the Audubon Christmas Bird Counts (CBC) for the Hawaiian Islands. Each time series constitutes data from the date of first record in the CBC to the date of maximum reported abundance, thus the x-axes are not all the same. Similarly, the y-axes have been scaled to each species' maximum abundance, and cannot be compared directly without this consideration. The vertical line in each plot corresponds to the year in which the maximum abundance estimate was observed; we have applied the methods reported in the body of the paper to all data points up to and including that point for each species.



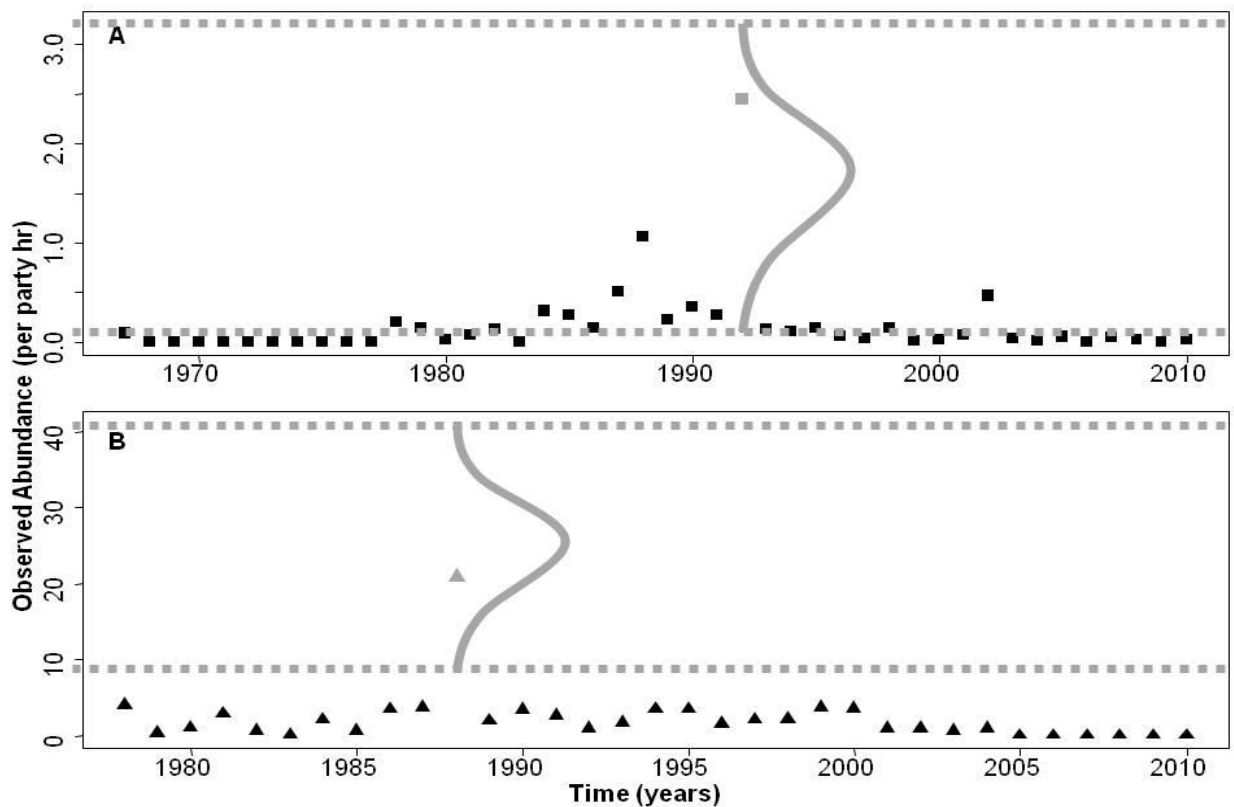


Figure S2. Here we show the process for assimilating the uncertainty about the maximum abundance estimate. The observed maximum abundance is initially treated as the mean of a normal distribution with a uniform variance. Through a Bayesian process, we allow the variance from the entire time series to inform this prior, resulting in a posterior normal distribution with a variance range dictated by the ‘noise’ in the observed count data. Time series with much variation, including having outliers as shown here, have correspondingly wide posterior variances (representing the 95% confidence interval, CI) in which the ‘true’ maximum abundance estimate may lie. Panel **A** shows an example of a time series in which the 95% CI about the maximum abundance estimate overlaps many of the other data points, reducing confidence that the estimate is in fact a demographically dictated maximum instead of a result of noise in the data. In panel **B**, however, the time series has a 95% CI about the maximum abundance estimate that is

always above all other data points, conferring a high degree of confidence that that the observed maximum reflects a true shift in demographic rates, albeit short-lived. Also of note, the scale on the y-axis is far smaller than on the x-axis, making the maximum in panel **A** even easier to explain as ‘noise’ than the maximum in panel **B**, which is an order of magnitude above any other estimate.

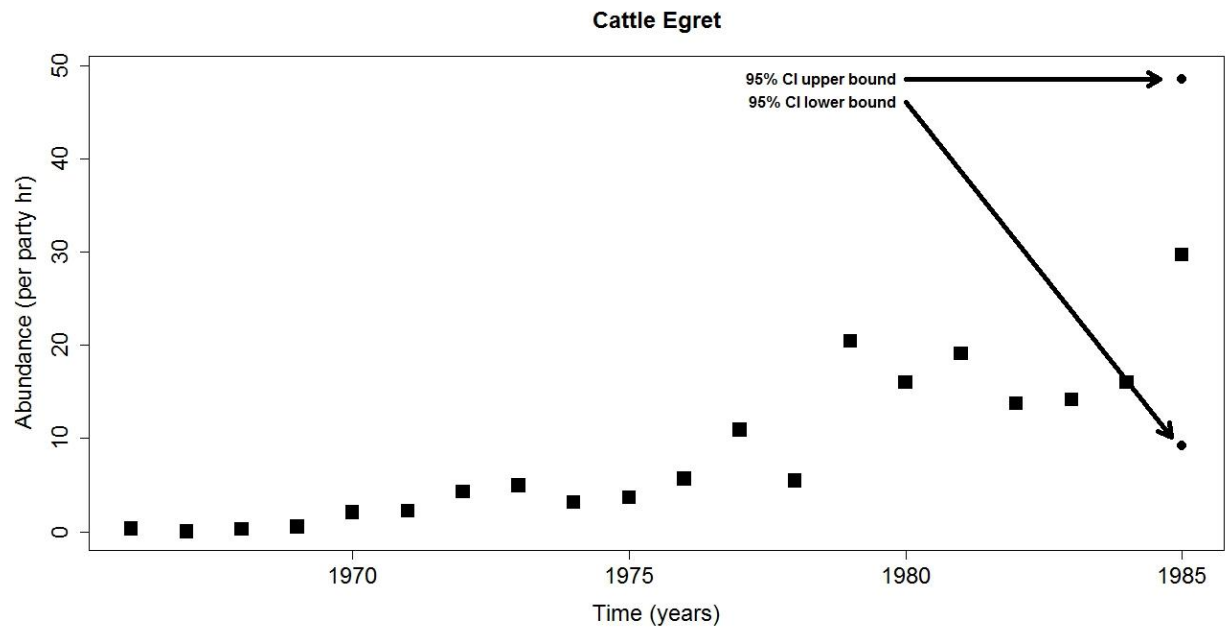


Figure S3–S19. Observed time series for each of the 17 species we evaluated. The most parsimonious of the candidate models is plotted (solid line) alongside the observed time series data (squares), truncated at the maximum observed abundance (see text for details). For those time series in which none of the models provided a robust fit, there is no model line included. We also plot the upper confidence interval maximum value (95% CI upper bound), and the lower confidence interval maximum value (95% CI lower bound) as triangles. These values were substituted for the observed maximum abundance in alternative model fitting exercises to judge the robustness of our proclamation of lags and their lengths (see text for details). For most populations, the best fitting model was the two-piece model, which was allowed to be disconnected.

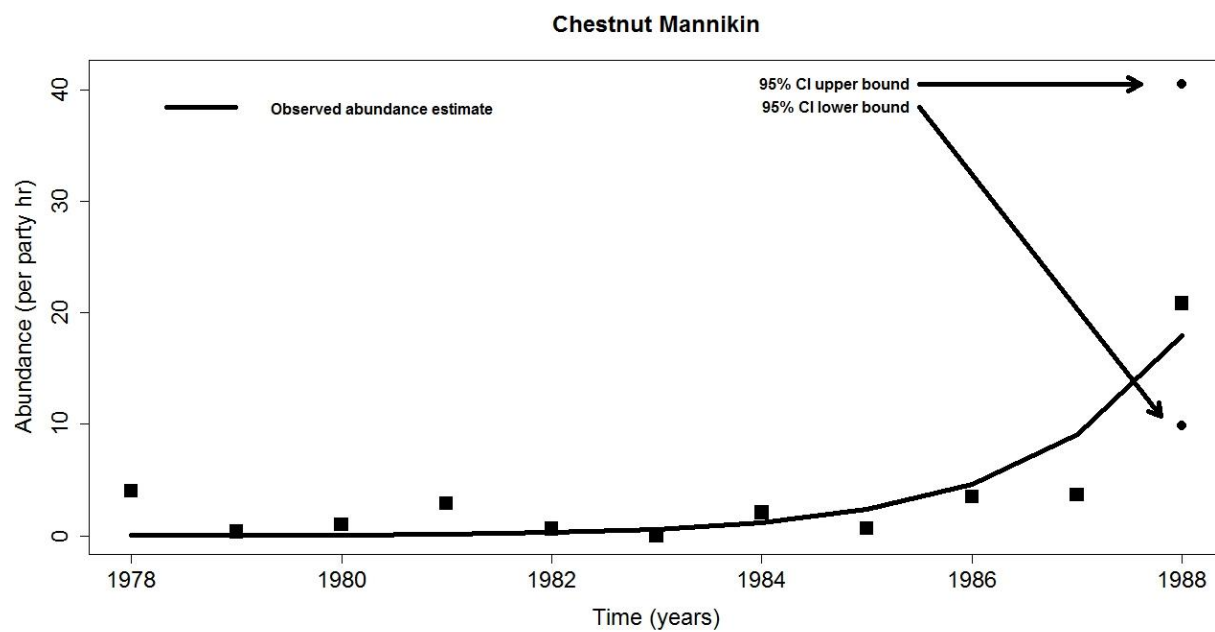


Figure S4.

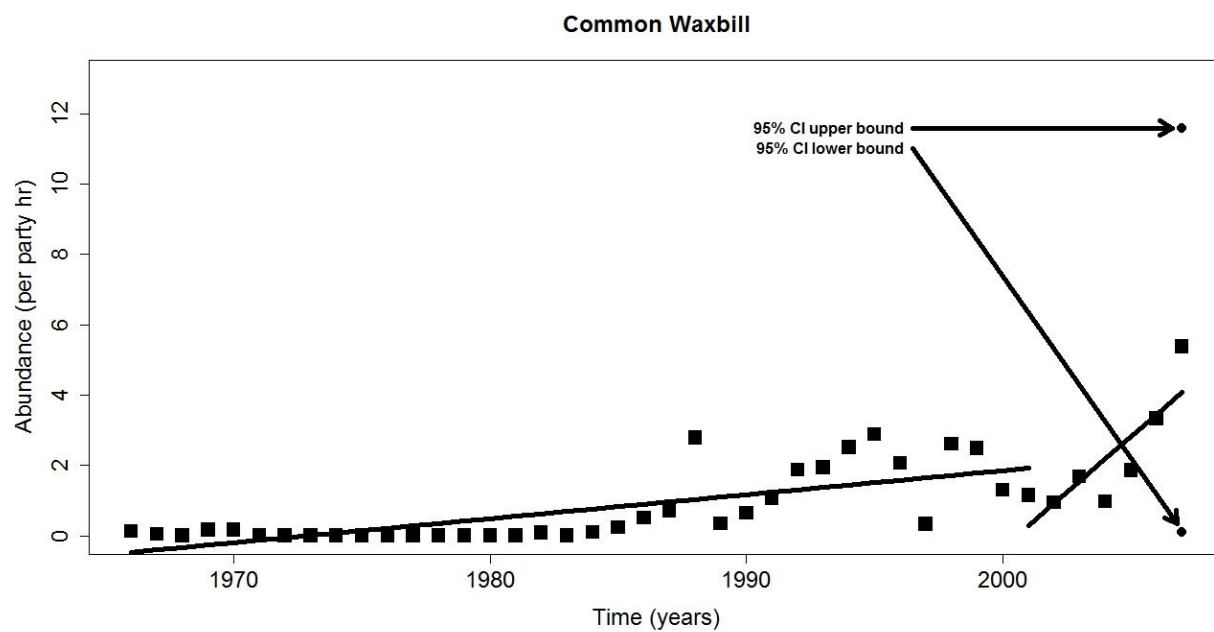


Figure S5.

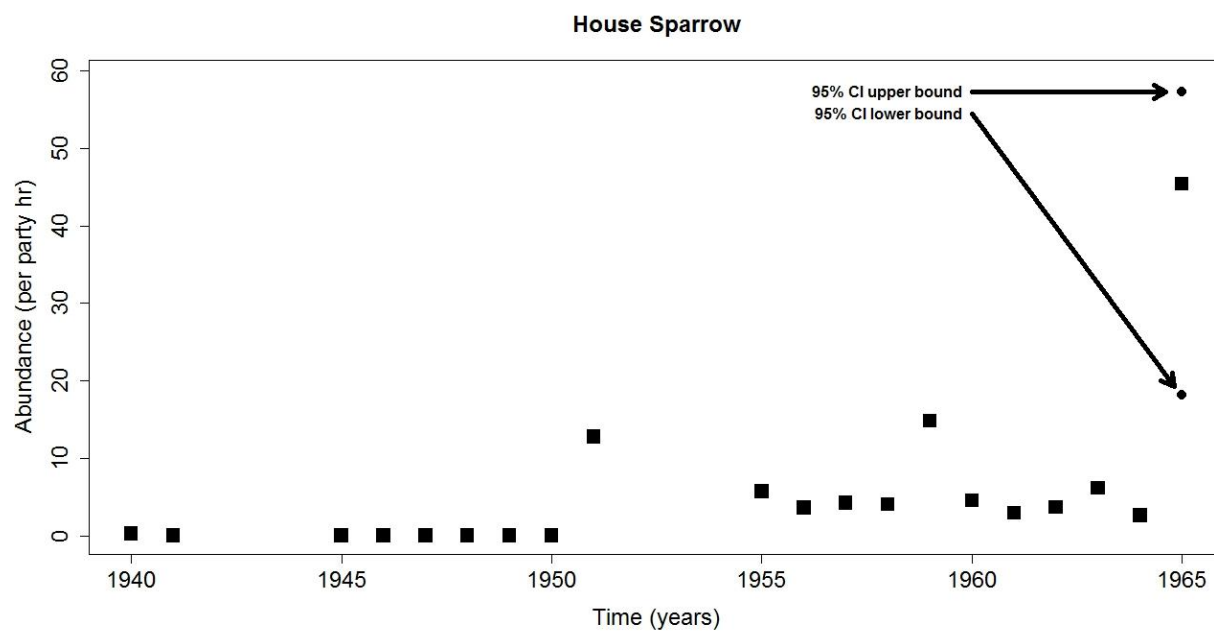


Figure S6.

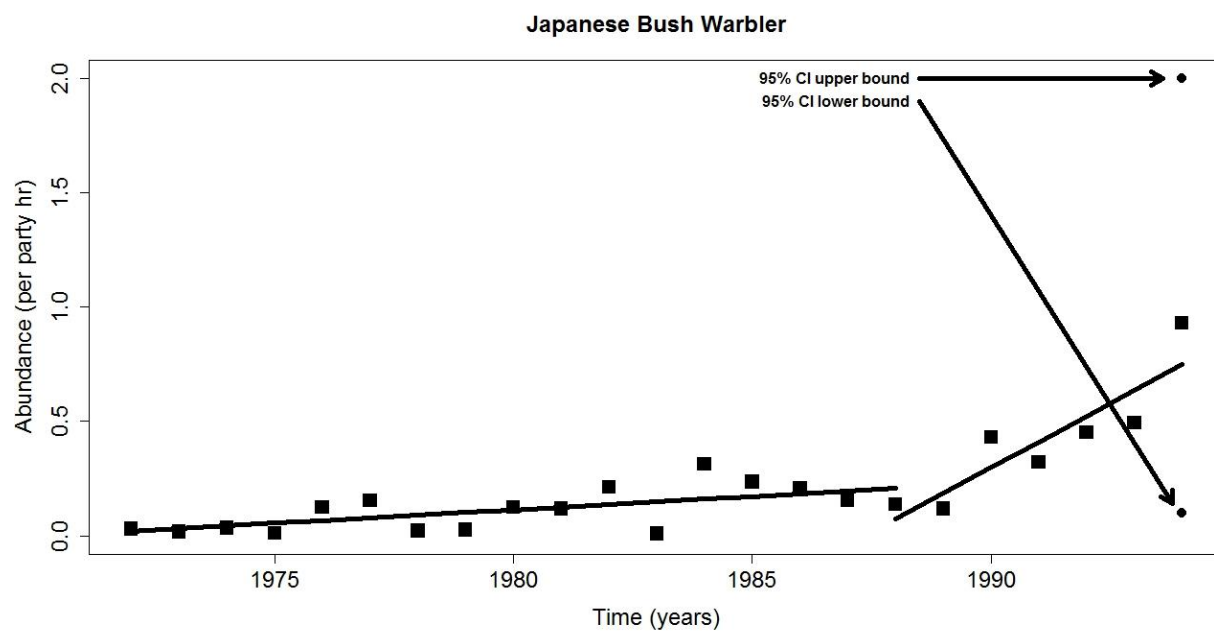


Figure S7.

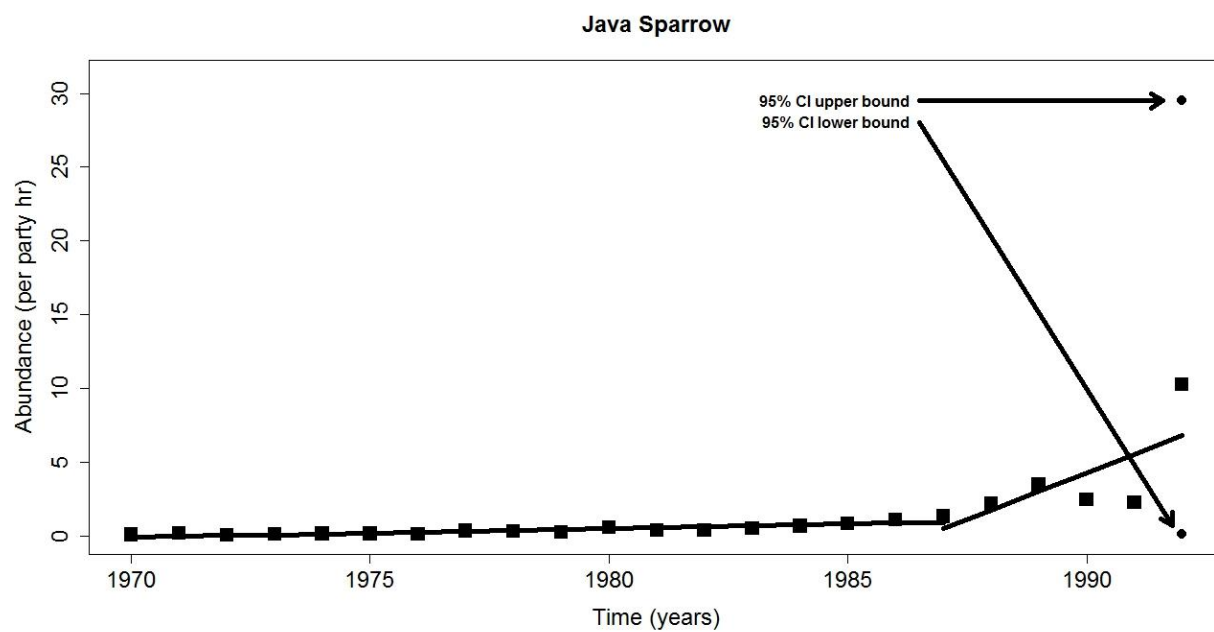


Figure S8.



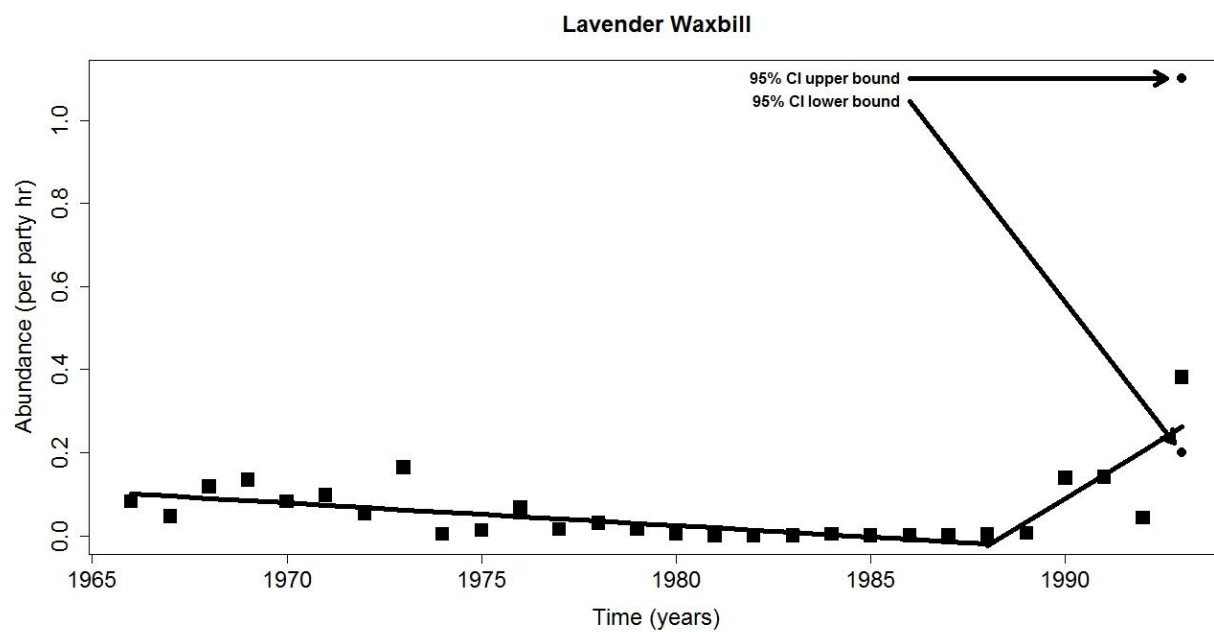


Figure S9.

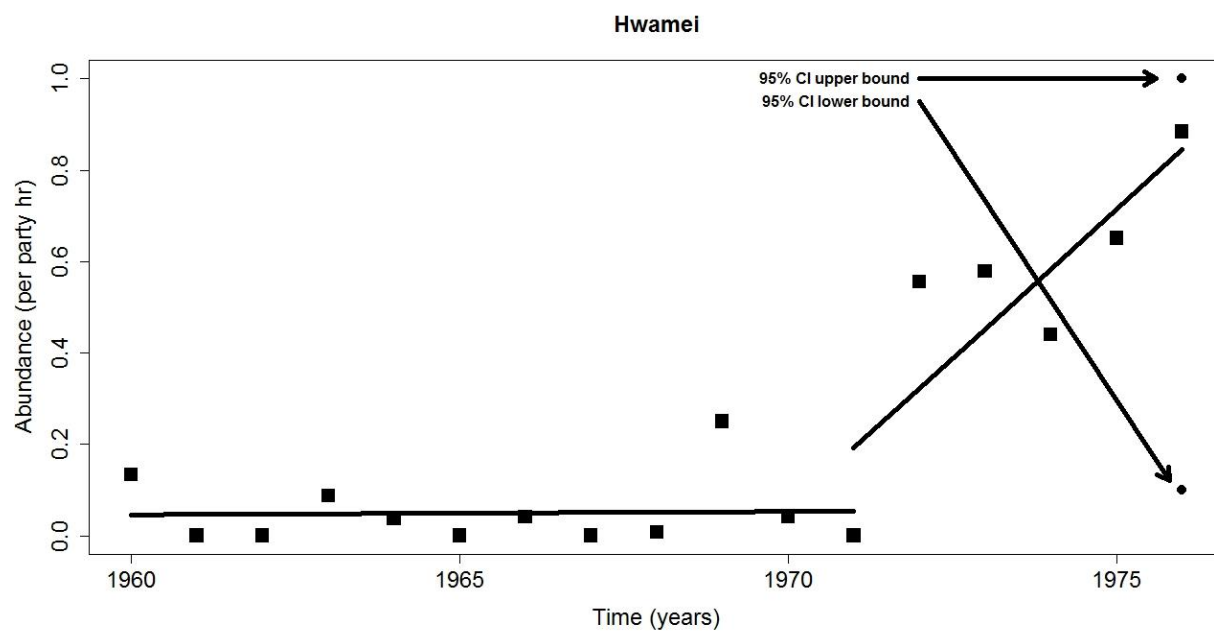


Figure S10.

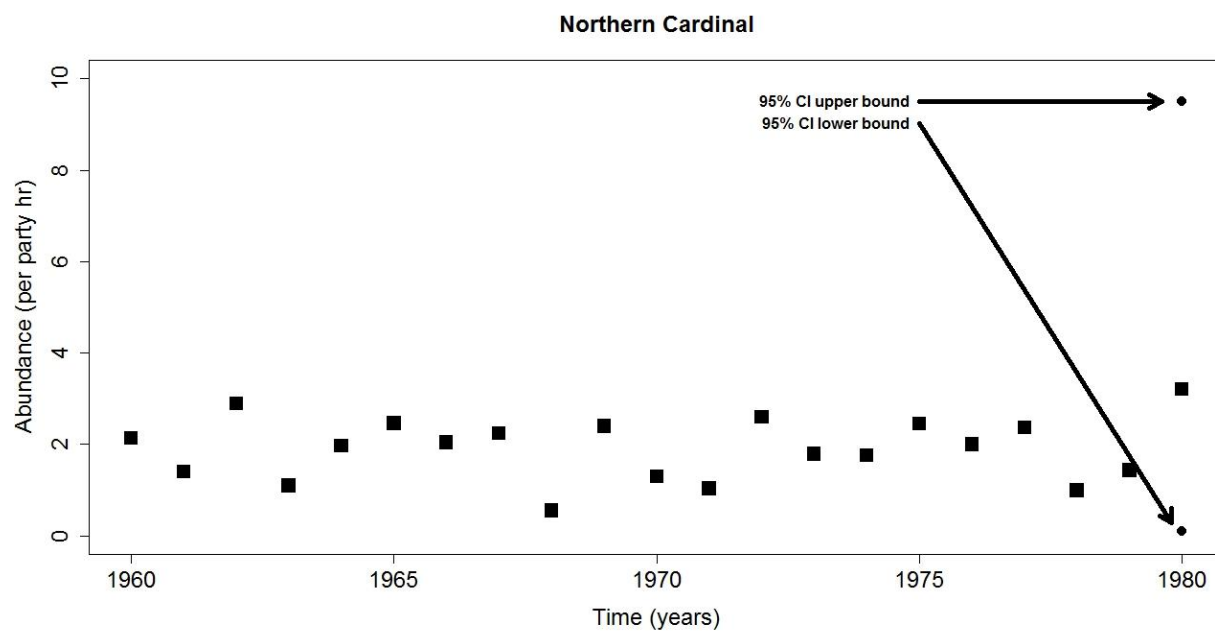


Figure S11.

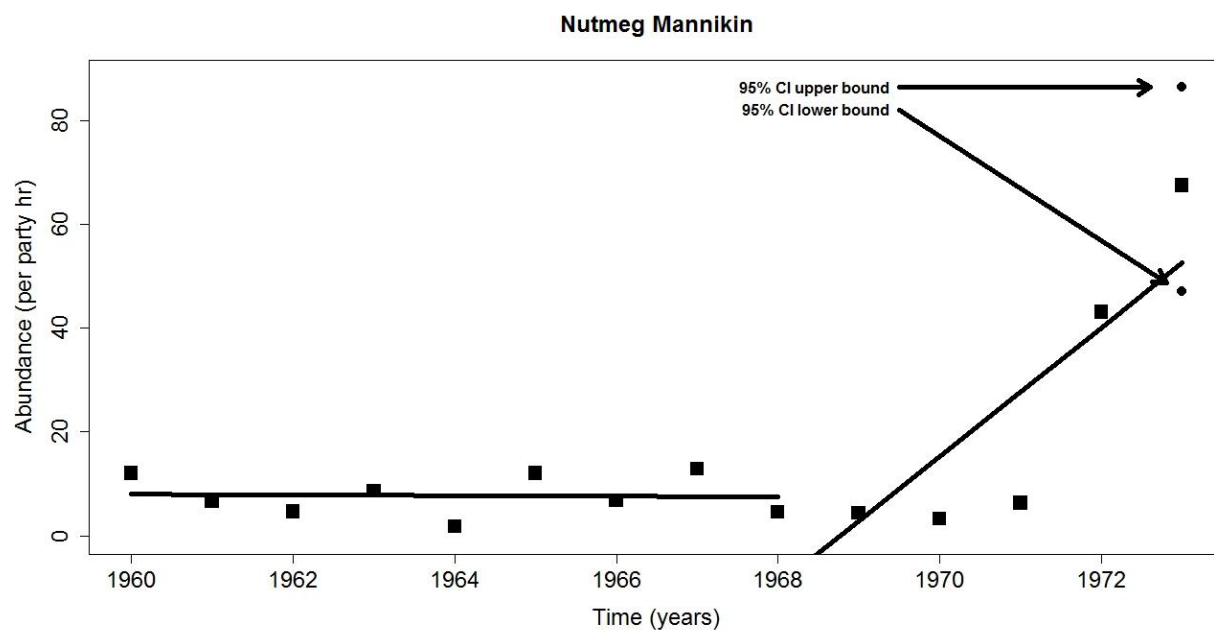


Figure S 12.

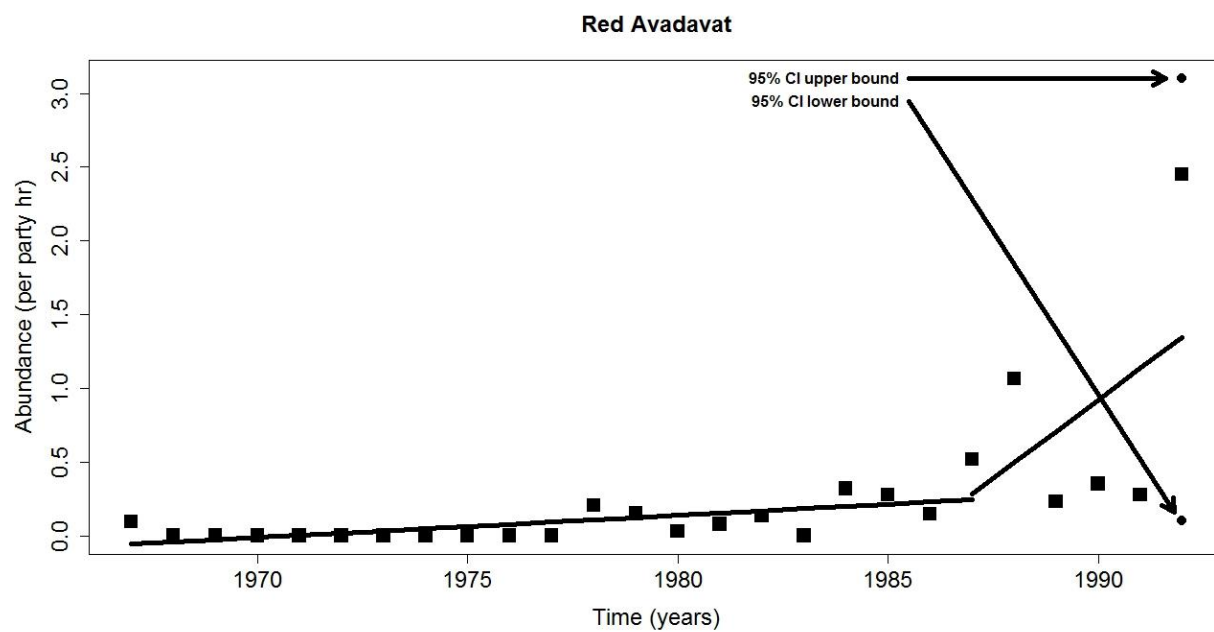


Figure S13.

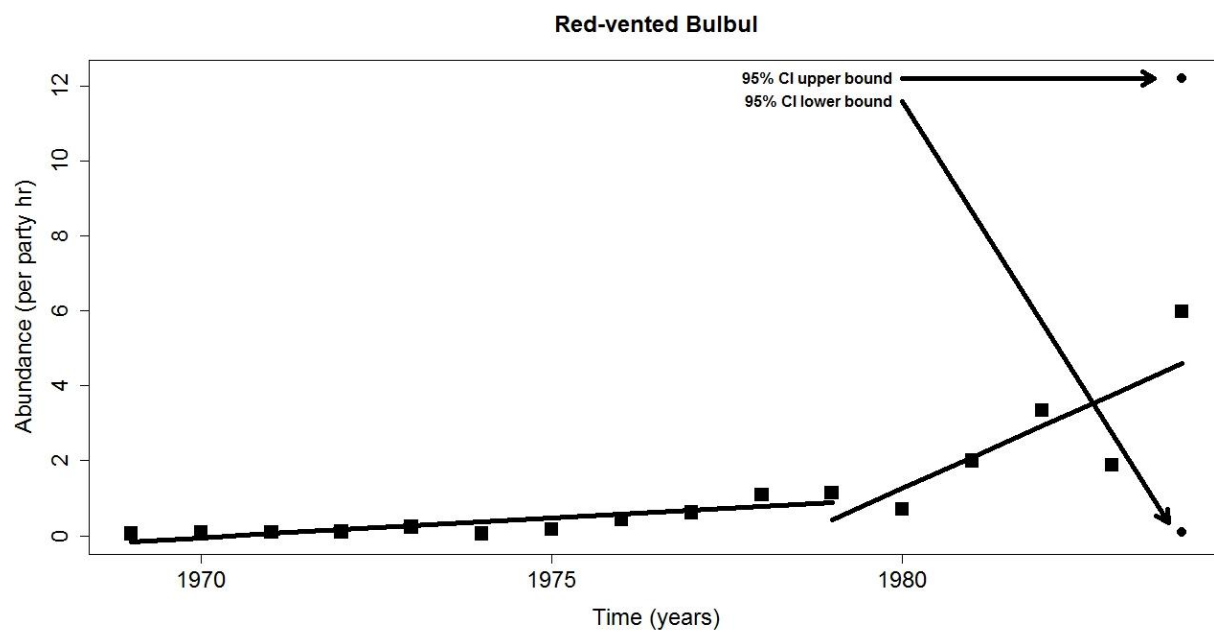


Figure S14.

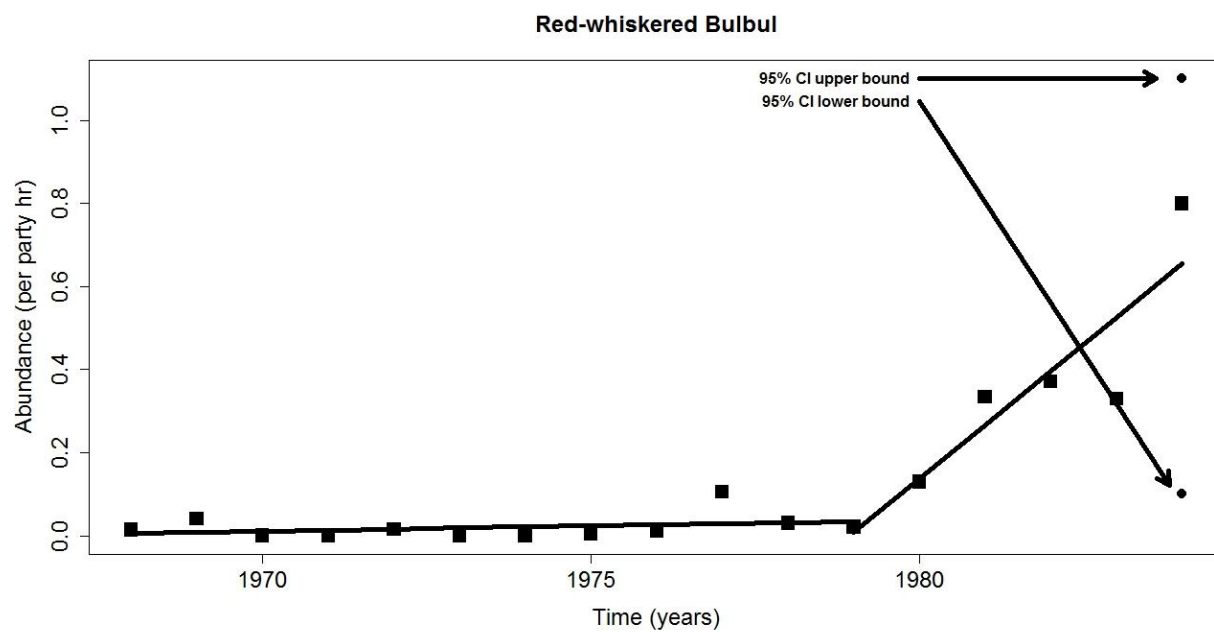


Figure S15.

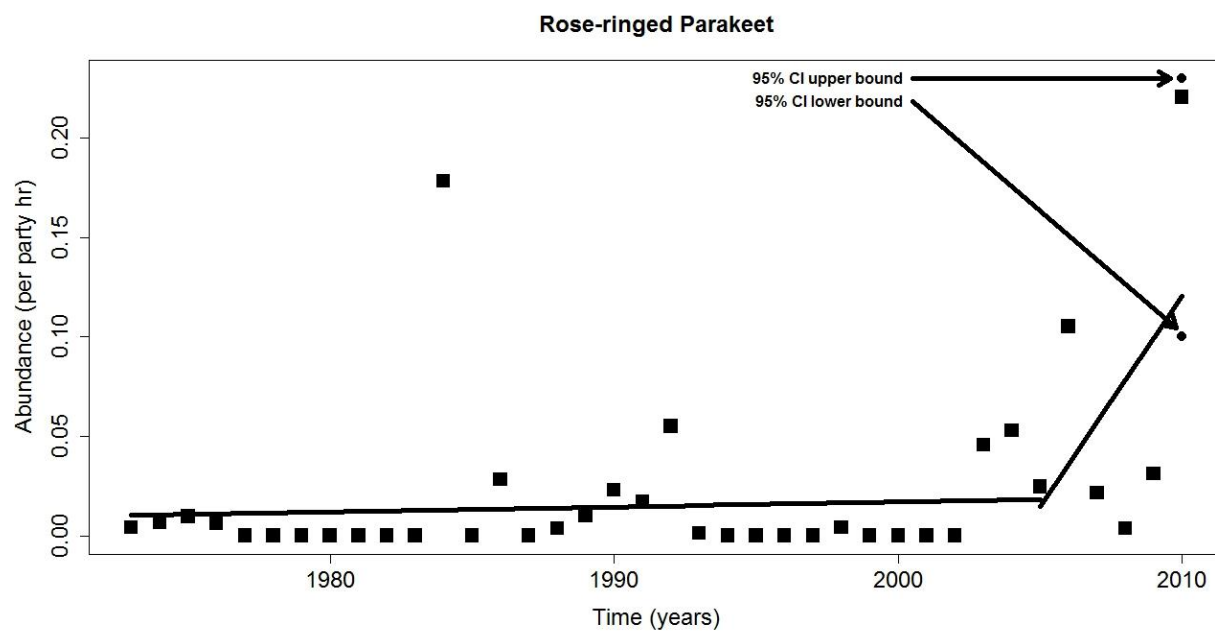


Figure S16.



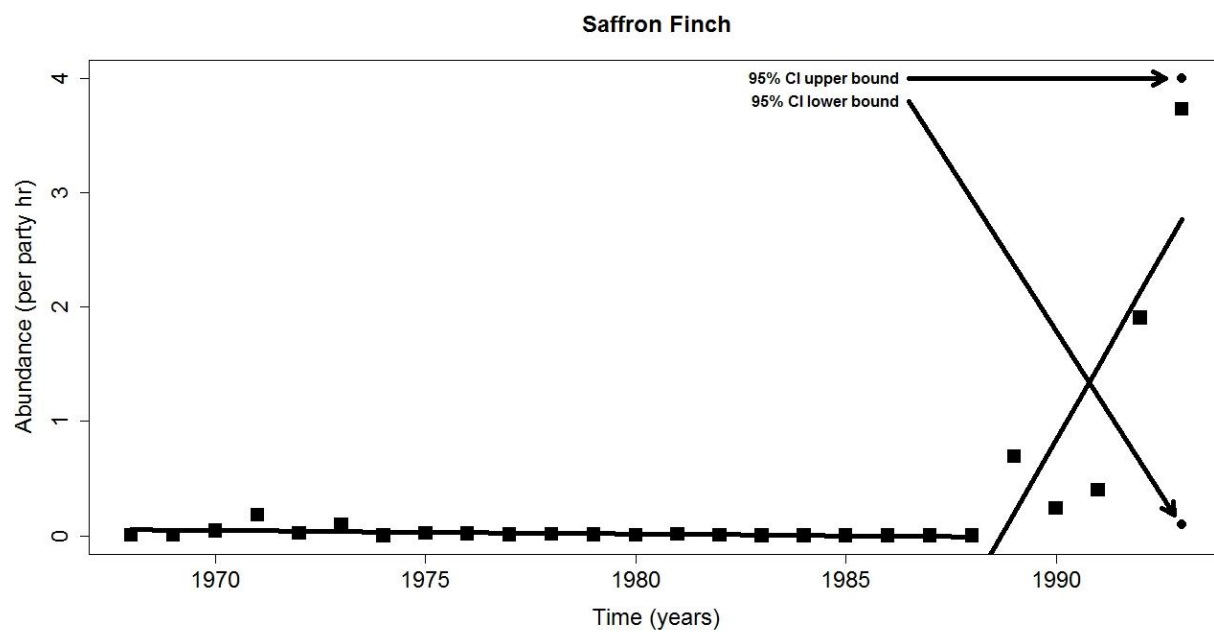


Figure S17.

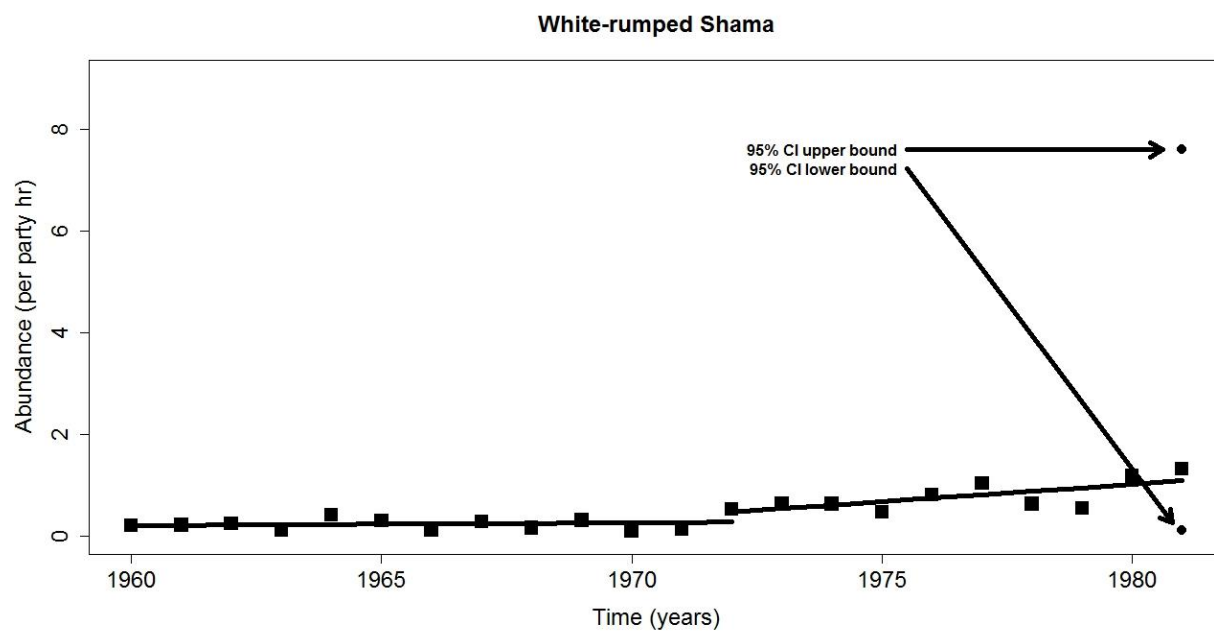


Figure S18.

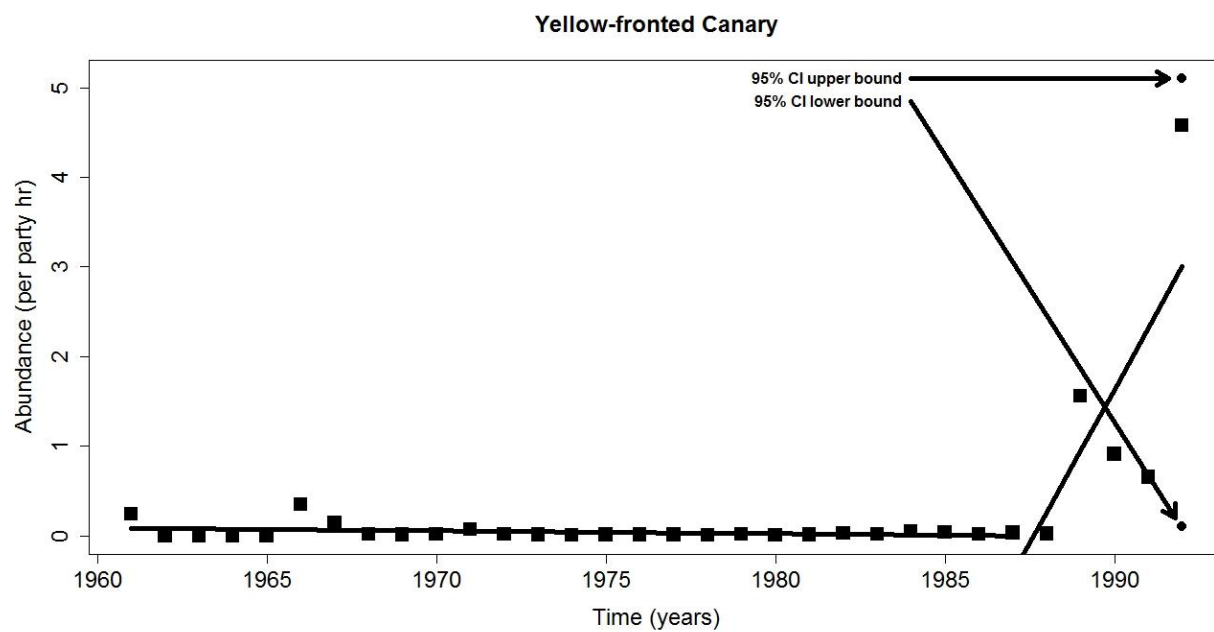


Figure S19.

## **Chapter 2: A novel approach for detecting population collapses**

Article Type: Original Article

Kevin Aagaard\* & Julie L. Lockwood

Graduate Program in Ecology & Evolution, and Department of Ecology, Evolution, &  
Natural Resources, Rutgers University, New Brunswick, NJ 08901 USA

\*Corresponding author: [aagaard@scarletmail.rutgers.edu](mailto:aagaard@scarletmail.rutgers.edu), (telephone) 848-932-3213,  
(fax) 732-932-8746

JLL email: [lockwood@aesop.rutgers.edu](mailto:lockwood@aesop.rutgers.edu)

## ABSTRACT

- (1) Detecting population collapses (crashes, failures, rapid declines) is of considerable importance within a variety of applied biological fields including conservation and fisheries. Collapses are broadly defined as substantial drops in abundance over relatively short time periods. Here, we develop a flexible, rigorous method to account for uncertainty in the two components of this definition: proportional loss and the time frame over which this loss occurs. We then employ this approach to evaluate the prevalence of collapses among native Hawaiian birds.
- (2) We develop a Bayesian approach to account for uncertainty an observed maximum abundance, which is a necessary step when defining collapses as a percentage drop from this value. This uncertainty is then translated into confidence limits around the magnitude of decline that should be considered a collapse. Finally, we employ three different statistical functions—linear, exponential, and a LOESS curve— to assess the period of collapses.
- (3) Using these methods, we show that six of 12 declining native bird populations on Hawaii have declined by >90% over the span of 10 years, with the uncertainty estimates for the remaining six being too large to render collapse classifications. It took on average 3.3 ( $\pm 2.9$ ) years for populations to collapse from their maximum abundance.
- (4) The dearth of standardized methodology to quantify population collapses is in part due to the lack of systematic tools for assessing uncertainty within time series for populations across taxonomic groups, of different sizes, and from multiple locations.

The method we present here helps fill these gaps and can be readily applied to any system with sufficient time series of abundance data.

**KEY WORDS:** Audubon Christmas Bird Counts, birds, collapses, conservation, Hawaiian Islands, population

## INTRODUCTION

Rapid and substantial declines in population abundance result from changes in climate, over-harvesting, infectious diseases, and habitat destruction (e.g., Houlahan *et al.*, 2000; Coulson *et al.*, 2001; Green, 2003; Eterovick *et al.*, 2005; Mullan *et al.*, 2005; Conrad *et al.*, 2006; LaDeau *et al.*, 2007; Pinsky *et al.*, 2011). Such declines have been given many names in the literature (e.g., crashes, rapid declines); for consistency, here we adhere to the most often used term, ‘collapse’ (e.g., Simberloff & Gibbons, 2004; Hutchings & Reynolds, 2004; Mullan *et al.*, 2005; Pinsky *et al.*, 2011, Cooling *et al.*, 2012). No matter their cause, identifying a population collapse is critical for policy-makers and managers if they are to swiftly institute response measures that can stop, or perhaps reverse, the decline. We suggest that existing methods used to classify and quantify collapses fail to adequately incorporate uncertainty about their magnitude and time frame. Without consideration of uncertainty, policy-makers and managers risk either failing to detect a collapse when it is occurring or expending limited capital to address a population that is not in a steep decline. Here we provide a novel method to account for uncertainty in defining a collapse while continuing to allow for its context-specific uses—a crucial aspect of this topic given the breadth of its relevance.

Biologists have developed several ways to describe population increases, however there are comparatively few tools for consistently classifying and quantifying population declines. For this reason, there is a tendency in the literature to identify and define collapses on a case-by-case basis. In some studies, collapses were quantified as reductions in population size that left abundance at or below 10% of the maximum for three or more years (Mullan *et al.*, 2005; Pinsky *et al.* 2011). In other studies, collapses

were quantified as rates of decline of over 90% within a 10-year period (Conrad *et al.*, 2006), or by calculating the standard error of changes in abundance from year to year and recording drops in this value through time (Caruso & Lips, 2013). This variety speaks to the need to settle on a flexible but rigorous definition of collapse that can be used across taxa and regardless of the underlying causes. A common denominator among most definitions of collapse is that they are the product of two inter-related measures: a proportional reduction in abundance from a recorded maximum value, and the time frame over which this reduction occurred. We suggest that in attempting to quantify a collapse it is vital to account for uncertainty in each of these quantities.

All declines (including collapses) represent a drop from an observed maximum to a lower abundance value within a time series. Any empirical time series will show year-to-year variation in abundance, even when the population is large and near its maximum and has been corrected for observational or process error (Kéry & Schaub, 2012). Thus it is not straightforward to determine what abundance value to use as the benchmark from which to calculate a percent decline. However, this decision is critical since declines are measured from this value, so any uncertainty in its designation represents uncertainty in the magnitude of observed decline. Once we have identified the maximum value and calculated uncertainty around it, we still require a consistent process to determine how much time it took for the population to decline by a given magnitude from this value. Uncertainty in choosing what sampling event represents the benchmark maximum translates into uncertainty in how long it takes for a population to decline by a specified proportion. Furthermore, the same year-to-year variation in abundance estimates present near the maximum value will remain (or be magnified) when considering low abundance



values. This variation makes it very difficult to determine in what year abundance dropped below any specified threshold value.

Below we describe a method for explicitly accounting for these two inter-related sources of uncertainty, and then we apply our solution to the native birds in Hawaii as a test case for its use. Islands typically support high levels of biodiversity and endemism, and Hawaii in particular is home to several rare endemic birds (Pyle & Pyle, 2009). We use >50 years of abundance data from Audubon Christmas Bird Counts (CBC; National Audubon Society, 2010) to evaluate 12 species that have consistently appeared in surveys and have experienced at least one population decline over their period of record. Using our method, we determined which of these populations showed a collapse. For our purposes, we define a collapse as a reduction of at least 90% within the longer of 10 years or three generations (World Conservation Union, 2001); however our method applies to any magnitude and duration of decline that may be of conservation concern.

## MATERIALS AND METHODS

### *Case study background*

Hawaii was home to over 100 endemic bird species before human colonization, with 48 of these becoming extinct prior to the arrival of Europeans in 1778, and another 23 since (Leonard, 2008). Of the 42 currently extant endemic bird species, 29 species and two sub-species are currently listed as endangered; several of these have not been observed in over 40 years and are likely extinct (Pyle & Pyle, 2009). Hawaii's birds have suffered from over-exploitation, massive habitat loss and fragmentation, invasive species, and emerging infectious disease (Pyle & Pyle, 2009). For these reasons, the Hawaiian

avifauna has been the subject of intense scrutiny in terms of the conservation status of its endemic birds, and there is a continuing need to assess when their populations (threatened or not) suffer unexpected declines in abundance (Leonard, 2008). Our results inform these efforts, while also serving to demonstrate the advancements and limitations of our method.

Residents of Hawaii have participated in the CBC since 1938, yielding an uncommonly long record of annual abundance information for many of native bird species (National Audubon Society, 2010). CBC counts involve searches for all species seen within a fixed location of known size (15 mile diameter circle) during one day, with the number of individuals observed per species recorded. These counts are standardized (by time of year and location) and are reported in terms of effort per party hour (e.g., one person counting for 10 hours equates to five people counting for two). There are between seven and nine CBC count circles visited by observers across the archipelago each year, depending on participation and expert availability. Of these, we utilize six in our analysis because they intersect substantial native habitat (where nearly all remaining endemic Hawaiian birds reside) and have been surveyed consistently enough that we could extract at least 10 consecutive years of data.

Because we are using the CBC, which is an exclusively land-based survey, we included only endemic year-round resident bird species of Hawaii. We excluded what Pyle & Pyle (2009) term ‘breeding visitors’ that breed on the islands but spend a substantial part of their lives elsewhere ( $n = 14$ ). Of the remaining 34 species, all but two are endemic to a single island. Thus, these 32 species’ annual abundance records are captured by a single count circle (though not the same single count circle for all 32

species). All results for these species are therefore based on counts within the single circle that overlaps their geographical range.

Two species that we consider occur across the archipelago, the ‘apapane (*Himatione sanguinea*) and the ‘i‘iwi (*Vestiaria coccinea*). Both species have been noted to move between islands (Pyle & Pyle, 2009). The ‘i‘iwi, however, only occurred in two count circle records, one on Kauai and one on the Big Island, which are located >250 miles apart. We consider each of these as two independent population of ‘i‘iwi, and analyze abundance records within each of their count circles separately. In contrast, the ‘apapane occurred in three count circles on three different islands that are located close enough to each other that there is a reasonable chance that individuals of these species could move between them (Kauai, Oahu, and the Big Island). We treat the record for ‘apapane as a single archipelago-wide population, pooling the data from the three count circles. To account for inter-count circle differences when pooling data for the ‘apapane, we followed the approach of Link *et al.* (2006). This method requires scaling the abundance estimates within each circle based on effort variation across count circles, so that they can be compared to one another. These corrections remove the influence of the varying use of count circles from year to year.

### *Method requirements*

We apply four criteria for selecting abundance records to analyze. First, a population must display a decline at some point in their period of record, because a collapse presupposes at least one episode of decline (i.e. a continuously growing population cannot simultaneously be classified as collapsed). Second, the data must have been

collected from a sampling area that reasonably approximates either the geographic range of the targeted species, or a discrete subpopulation. This requirement can be relaxed without reducing the performance of our model if there is a clear reason that a non-discrete subset of a species is of particular economic or ecological importance (see Mullon et al. 2005). Third, there must be at least as many consecutive sampling events in the record as the length of time needed to define a collapse. For our purposes, we define a collapse as a <90% decline within 10 years or three generations. All of the species we consider have generation times of 1-3 years, leaving the 10-year cut-off as our default collapse time frame. Therefore, we did not include any species that did not have at least a 10-year span of abundance records. This limit can (and should) be specific to the species being considered and the time frame chosen for the collapse definition. There is, however, a lower limit to the number of years of data included (or sampling events, if censuses occur more frequently than once a year), since fewer data complicate model fitting (see below).

Finally, we only consider species that were likely present over their period of record, while accounting for low probabilities of detecting individuals in censuses—often very low for rare species (Delaney & Leung, 2010). Ideally a time series will include information on detection probability, which can then be used to directly evaluate the likelihood that a recorded zero abundance value in any given year was a true absence versus a non-detection (Kéry & Schaub, 2012). In such cases, the following step may not be needed. This ideal is rarely met however, especially with time series that are collected over a long time period or over large spatial scales as is the case with the CBC (and other large-scale citizen science programs). Thus, to determine whether a species was present

(but uncounted) or truly absent in our data, we use a detection threshold assessment in OpenBUGS v. 3.2.1 (Lunn *et al.*, 2009), assuming a wide range of detection probabilities.

We use a Bayesian approach to formulate expected probabilities of the population being present for the duration of their time series ( $P$ ) based on their recorded abundances. We set detection probability values ( $p_d$ , the probability of an observer detecting an individual given that the individual is actually present) to be between (but excluding) zero and one ( $0.1 \leq p_d \leq 0.9$ ). We increment  $p_d$  by 0.1 within this range for each run of the persistence model. We assume that the theoretical presence or absence of individuals ( $T_p$ ) follows a Bernoulli distribution, with the probability of presence ( $r$ ) and absence ( $q$ ) equal to 0.5. We also assume the actual detections (present or absent,  $Z$ ) follow a Bernoulli distribution, with a probability equal to the probability of detection. Our model has this form, following McCarthy (2007):

$$T_p \sim \text{Bern}(r)$$

$$P = p_d * T_p$$

$$p_d = (0.1 \text{ to } 0.9)$$

$$Z[i] \sim \text{Bern}(P)$$

$Z$  is informed by the actual across-years data for each population; years ( $i$ ) with positive abundance values reported are taken as years in which the species was present, while years with abundance reports of 0 are taken as years in which the species was absent. This model produces  $P$  for each population across a variety of detection probabilities, given the observed data. If we calculate a species as likely ‘present’ for at least 10 years of their period of record and across all possible detection probabilities, then we determine that it meets our criteria for persistence.

With these requirements met, we can apply the components of our method that seek to quantify the level of uncertainty about the maximum estimated abundance and the length of time of a population's decline.

### *Uncertainty about collapse magnitude*

The first step of our method involves calculating the uncertainty about the observed maximum abundance ( $\mu$ ). Our goal is to obtain the estimated variance about  $\mu$  as a way to set the likely upper and lower limits for a collapse, given the variance in counts across all years of observation. To account for this uncertainty we perform a separate Bayesian analysis, also in OpenBUGS v. 3.2.1 (Lunn *et al.*, 2009), to estimate the error of the observed maximum abundance for all species (Aagaard & Lockwood, 2014). Essentially, we are accounting for the fact that the observed value of interest (in this case, maximum abundance) represents an estimate of some 'true' unobservable value (whatever the maximum actually is), and therefore has associated error. Unfortunately, we have no way to know what this error is since the 'true' value is unobservable. However, we can estimate this error using the variance in abundance calculated across the entire period of record. If this variance is large, then we should be cautious about placing too much statistical belief in the observed maximum value, and we should be correspondingly cautious about classifying a decline from this value as a 'collapse'. Alternatively, small variance suggests that the observed maximum is a better estimate of the true maximum and we can more confidently declare a population as collapsed if it declined by 90% or more from this value.

To estimate the error of the observed maximum abundance estimate, we first determine the variance present in each population's entire time series, using the following model, adapted from Aagaard & Lockwood (2014):

$$Y[i] \sim N(\mu[i], \sigma^2),$$

$$\mu[i+1] = \mu[i] * \lambda[i],$$

$$\lambda[i] \sim N(\lambda, \tau),$$

$$\tau \sim \text{Unif}(0, 10),$$

$$\sigma^2 \sim \text{Unif}(0, 100),$$

where  $Y$  is the time series for each target population, with  $i$  representing each year's count within the time series,  $\mu$  is the estimated maximum abundance for each population (assuming year to year exponential growth, with the mean growth rate =  $\lambda$  and variance  $\tau$ ), and  $\sigma^2$  is the variance about the annual estimates, at first unknown and therefore given an uninformative prior. We allow this model to run for 10,000 iterations, with a burn-in of 1,000 to allow for convergence. It is relevant to note that the data we use in our case study are derived from count data, but have been standardized using information on the number of observers and length of time spent observing. Therefore these data are continuous and not discrete, making the use of a normal rather than Poisson prior distribution appropriate. We caution that this may not hold for other count data and such data should be parameterized appropriately within our model framework (i.e. using a Poisson).

With the estimated variance in hand, we then determine the 95% credible interval (CI) for the variance around the observed maximum abundance. The upper bound of the 95% CI represents the highest estimate of the true maximum abundance for the

population, while the lower bound represents the lowest estimate. Therefore, the 95% CI itself represents the range in which we have the most belief that the true maximum abundance resides (in fact, we are 95% confident of this). In accordance with our definition of a collapse (i.e. having declined by 90%), we reduce these upper and lower CI values by 90% to establish upper and lower thresholds of collapse. We call the area within these upper and lower thresholds as the *zone of probable collapse* (Figure 1). Thus, if a population declines into the zone of probable collapse we are 95% confident that it has declined by  $\geq 90\%$  of the highest estimate (the upper bound of the 95% CI) of its maximum abundance. If abundance records decline through this zone (below the lower bound of the 95% CI) we are then 95% confident that this species has collapsed below the most conservative estimate of its maximum abundance. We term such declines as *true collapses*. Thus, populations that have a large variance (wide CI) around the observed maximum abundance value have a correspondingly wide zone of probable collapse, and vice versa. This action allows us to fully incorporate our statistical belief about the true value of the maximum abundance into our classification of populations as ‘collapsed’.

#### *Uncertainty about collapse duration*

The second step of our method involves definitively determining the year in which a population has passed into the zone of probable collapse. To reduce ambiguity, we apply a model-fitting approach to identify the intersection of the predicted population trend with the zone of probable collapse (Figure 1). We apply three functions to each time series from the year of the maximum observed abundance to the final year on record: a



negative exponential, a linear, or a LOESS model. We fit the models directly to the count data, without transformation, using least squares linear regression for the negative exponential and linear functions, and the LOESS curve using the built-in LOESS function in R v. 3.0.2 (R Development Core Team, 2012). We used an exponential decline of the form  $N_t = N_0 * e^{-(r * t)}$ , and a linear model of the form  $N_t = r * t + N_0$ ; where  $N_t$  is the population size at a given time (with  $N_0$  being the initial population),  $e$  is the natural logarithm,  $r$  is the rate of population growth, and  $t$  is time. The LOESS curve fits the best polynomial to the function using local fitting. We selected from among these models using Akaike's an information criterion, corrected for small sample size (AICc), which penalizes for extra parameters (Burnham & Anderson, 2002), and report the coefficient of determination ( $R^2$ ) as a goodness-of-fit metric. We use this modeling approach to establish a consistent, repeatable procedure for determining in what year a population passes into the zone of probably collapse.

## RESULTS

After omitting any native species that did not exhibit a population decline at any point within their time series ( $n = 16$ ), and those that had fewer than 10 years worth of annual abundance data ( $n = 6$ ), we were left 12 populations to which to apply our method (Table 1). Each of these 12 populations passed our persistence test; whether we assumed a detection probability of 0.1 or 0.9 they were all deemed likely present for the duration of their time series ( $P \geq 0.99$ ).

Our method estimated uncertainty about the observed maximum abundance for each population to range between CI widths of two to over 30 (see Supporting Information,

Figures S1-S12). This range resulted from different scales of abundance for each population, in addition to the difference in variation within each population's time series—the primary metric our method is aimed at inferring. One population, the Oahu 'elepaio (*Chasiempis ibidis*), had a large estimated variance leading to a wide zone of probable collapse (Figure S9). The data for this species also does not exhibit a clear trend, thus the function fit to the data is correspondingly uninformative ( $R^2 = 0.35$ ). Similarly, some species, like the Hawaii creeper (*Oreomystis mana*), Hawaii 'elepaio (*Chasiempis sandwichensis*), and Hawaiian hawk (*Buteo solitaries*; Figures S3-S5), exhibited seemingly anomalous single-year spikes in abundance. The upper bounds on the zones of probable collapse for these three species, however represented 12%, 13%, and 13% of their maximum abundance estimate, respectively. That is, despite the potentially aberrant maxima for these species, estimates of uncertainty about their observed values were low enough to produce quite narrow ranges for their zones of probable collapse.

We found evidence for probable and true collapses in one and three populations respectively (Figure 2). It took an average of 5.0 ( $\pm 2.2$ ) years for populations to collapse from their maximum abundance into the zone of probable collapse. The longest collapse we found was for the Hawaii hawk, which took eight years, while the shortest—the Hawaii 'elepaio—took three years. The LOESS curve function was selected as the best model for 11 of 12 populations, with the Oahu 'elepaio best fit by a negative exponential function. Populations exhibiting a collapse declined by an average of 97% from their observed maximum abundances. The average decline from the lower bounds of the maximum abundance CI was 95%, and the average decline from the upper bounds was

98%. While eight populations were not found to have collapsed by our definition, they did still experience pronounced population declines relative to their observed maximum abundance. Overall, the average decline for all 12 populations was 87%, with average declines from the lower and upper bounds of their maximum abundance CI of 82% and 91%, respectively. In fact, all of the 12 species ultimately declined by at least 60% from their observed maximum abundance.

## DISCUSSION

Population collapses are of critical concern in conservation management settings, with implications extending to emerging infectious diseases, excessive exploitation of populations, variable global climate trends, and rampant habitat loss (World Conservation Union, 2001). In these and other more enigmatic situations, ecologists have been ill prepared to identify and describe patterns of collapse in standardized ways. To optimize management strategies and allocate resources, we require methods that can be readily and systematically applied to a wide range of taxa without sacrificing the necessary flexibility of a definition. We provide a rigorous and robust way to calculate uncertainty about the magnitude and duration of a population decline, while also allowing the precise value of these two metrics to be set according to whatever definition of collapse that is deemed appropriate by a governing group.

For our case study, we defined a collapse as a  $\geq 90\%$  reduction in abundance occurring within the shorter of 10 years or three generations in keeping with the IUCN designation of a critically endangered species (World Conservation Union, 2001). We found all 12 populations of Hawaiian birds we evaluated showed 66% or larger

proportional declines in abundance from an observed maximum, thus indicating that each could be considered worthy of rapid conservation action. However, because of the uncertainty around the true value of the observed maximum, the width of the zone of collapse varied by an order of magnitude across populations. This variation translated into uncertainty as to how long it took for a population to decline into this zone as well. When these two sources of variation are made explicit, eight of the 12 populations could not be clearly designated as collapsed. Importantly, given the need to identify collapses of conservation concern, we demonstrated that our method is easily applied to rare as well as more common species. We detected collapses in species with maximum abundance estimates ranging from less than 0.4 to more than 45 individuals per party hour. Whether the six populations that we show did collapse (according to our definition and methods) are worthy of rapid conservation actions is not for us to decide; however, our results certainly can inform such decisions.

Our method highlights two additional uncertainties about declaring population collapses, and our results for Hawaiian birds illustrate these issues well. First, existing definitions of collapses measure only a proportional and not the absolute value of a decline in abundance. Thus, it does not matter whether the drop begins with a population at high or low abundance, or ends with high or low abundance, merely that it goes from *higher* to *lower* abundance. Our method will calculate the uncertainty associated with identifying when and how fast any given proportional drop occurs, but it is agnostic about how large or fast this drop must be to warrant conservation action. We chose to evaluate a stringent definition of collapse, however if we had chosen to be less restrictive in either the time frame or the proportional drop more of the populations we considered

would have qualified as ‘collapsed’. The decision about where to draw the defining lines is not straight forward and should be made by those seeking to identify and act on collapses. We suggest this decision should be informed by the target species’ biology, suspected mechanism of collapse, and perhaps the monetary or political costs and benefits associated with declaring collapses.

Second, our method takes a simplistic but standard approach to identifying the maximum observed abundance within a time series. Whatever the value of the observed maximum is, that is the value used as the benchmark for calculating proportional drops. This aspect of our method mirrors many other definitions of, and methods for identifying, collapses (e.g., Mullan *et al.*, 2005; Conrad *et al.*, 2006; Pinsky *et al.*, 2011; Caruso & Lips, 2013). However, it is clear from the Hawaiian bird populations that some of these maximum values represent temporary jumps in abundance, and thus the return to more ‘normal’ abundance values will be classified as a collapse. Our approach helps to identify those jumps that are within the variation seen across all survey years, and appropriately places less emphasis on those that are clearly within the ballpark of this variance. But if those jumps are well outside of expectations based on the entire period of record, they will be given relatively high weight (low variance) in our approach. This level of statistical certainty in the observed maximum is well warranted; the value is high enough that we would not consider it a sampling anomaly for example. However, it is not clear how much conservation weight this maximum abundance should receive. We see this within three of the six populations that we consider to have collapsed (Hawaii creeper, Hawaii ‘elepaio, and Hawaiian hawk; see Supporting Information). Here again the degree to which conservation action should be based on these drops is up to those seeking to

identify and act on collapses. This decision can be guided by the absolute value of abundance that is realized after these drops, the regularity with which similarly sized drops occur across the period of record, and the suspected drivers of such drops.

When populations suddenly decline in abundance, they warrant attention no matter their cause. Perhaps the more relevant question is one of deciding what response these declines merit, especially given that some responses carry substantial economic and political costs (e.g., harvest moratoriums, trade restrictions, and land use restrictions). Our methods seek to inform these response decisions by making two inter-related sources of uncertainty in quantifying severe declines transparent to decision-makers. We also highlight two other issues associated with evaluating population declines that are worthy of continued investigation, and there may be many more. Such investigations seem central to furthering the goal of biodiversity and managing biological resources in a sustainable manner.

#### ACKNOWLEDGEMENTS

We thank E. Green, D. Simberloff, N. Fefferman, J. Burkhalter, O. Robinson, D. Fonseca, O. Jensen, and the P. Morin Lab for their methodological advice and feedback on various drafts of this manuscript. The authors report no conflicts of interest.

#### DATA ACCESSIBILITY

CBC data: <http://netapp.audubon.org/cbcoobservation/>

R scripts: uploaded as supporting information.

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## TABLES AND FIGURES

Table 1. Characteristics and results of variation analysis for each species (common and Latin names). ‘Collapse’ indicates whether the species exhibited a true, probable, or no collapse. ‘L’ lists the length of time each species occurred in the Christmas Bird Count record. ‘Max’ is the year in each species record in which the maximum abundance was observed—shown in the ‘Observed Max’ column. The highest and lowest estimated values for the true abundance are reported in the ‘Upper’ and ‘Lower’ columns, respectively.

Species	Collapse	L	Max	Upper	Observed Max	Lower
<b>Oahu ‘elepaio</b>	None	39	1	0.48	0.3387	0.2
<i>Chasiempis ibidis</i>						
<b>Oahu ‘amakihi</b>	None	37	19	2.02	1.5128	1
<i>Hemignathus flavus</i>						
<b>Hawaii ‘elepaio</b>	Probable	38	25	15.54	11.6923	7.84
<i>Chasiempis</i>						
<i>sandwichensis</i>						
<b>Hawaii ‘akepa</b>	None	38	5	1.95	1.5625	1.18
<i>Loxops coccineus</i>						
<b>Hawaii creeper</b>	True	38	25	1.81	1.5385	1.26
<i>Oreomystis mana</i>						
<b>Hawaiian hawk</b>	True	38	25	1.18	0.9231	0.67
<i>Buteo solitaries</i>						



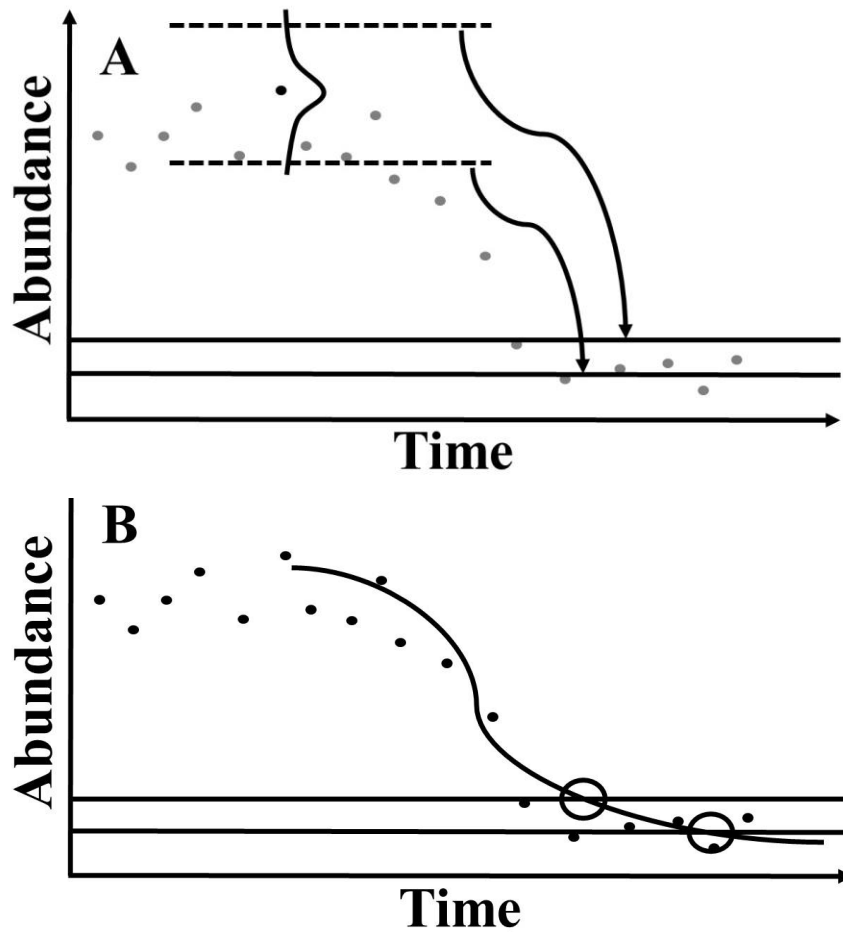


Figure 1. Here we show the process for incorporating uncertainty into determinations of collapses. (A) We fit an uninformative, normal prior distribution to the maximum abundance estimate and calculated the 95% credible interval (CI) of the resulting posterior distribution (informed by the variance in the whole time series; dashed lines). We calculated 10% of the 95% CI limits, with bounds defining the zone of probable collapse (solid lines). (B) We next fit the best model (chosen by AICc) to the declining portion of the data (black curve). We can see that the example population declined into and through the zone of probable collapse (circles mark the intersections), thus exhibiting a pattern of a true collapse.

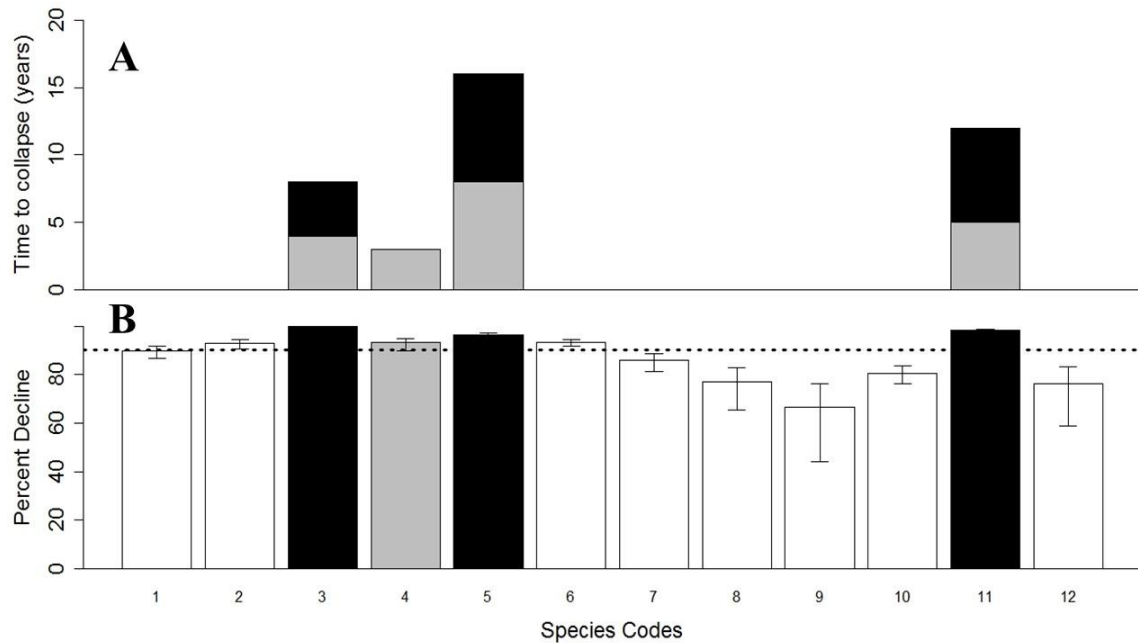


Figure 2. (A) Length of collapse (from maximum to  $> 10\%$ ). Only populations that decline into the zone of probable collapse or lower are included. Gray bars represent the time between maximum observed abundance and decline below the 90% threshold. Gray and black bars represent the time to 90% reduction and then to true collapse. For example, the Hawaii creeper took four years to decline into the zone of probable collapse (gray bar), and four more years to decline below this zone (black bar).

(B) Results in terms of the percent decline from maximum observed abundance. Bar colors correspond to the collapse classification (white = no collapse, gray = probable collapse, black = true collapse). The dashed line marks the 90% threshold marking a collapsed population. Whiskers represent the upper bounds for the maximum abundances estimated from our methods to approximate uncertainty in the observed value. Species codes: 1—‘apapane; 2—Hawaii ‘akepa; 3—Hawaii creeper; 4—Hawaii ‘elepaio; 5—Hawaiian hawk; 6—‘i‘iwi on Hawaii; 7—‘i‘iwi on Kauai; 8—Kauai ‘amakihi; 9—Kauai ‘elepaio; 10—Oahu ‘amakihi; 11—oahu elepaio; 12—‘ōma‘o.

## SUPPORTING INFORMATION

Table S1. Corrected Akaike's an information criterion (AICc) for each model as applied to each species. The lowest scoring AICc is in bold.

Species	Model AICc		
	Linear	Exponential	LOESS
<b>Oahu Elepaio</b>	-79.571	<b>-81.433</b>	-3.71632
<b>Oahu Amakihi</b>	19.3307	22.0766	<b>-0.05097</b>
<b>Hawaii Elepaio</b>	75.6794	68.934	<b>5.334665</b>
<b>Hawaii Akepa</b>	28.4295	25.2595	<b>-0.80557</b>
<b>Hawaii Creeper</b>	19.9316	6.0508	<b>0.826338</b>
<b>Hawaiian Hawk</b>	3.65509	<b>-8.3019</b>	0.479696
<b>Iwi on Hawaii</b>	98.5807	86.0925	<b>6.899577</b>
<b>Omao</b>	88.4989	68.2285	<b>5.995836</b>
<b>Iwi on Kauai</b>	21.8895	9.7546	<b>2.639876</b>
<b>Kauai Amakihi</b>	46.7302	47.5136	<b>5.636754</b>
<b>Kauai Elepaio</b>	46.1588	37.4741	<b>3.745369</b>
<b>Apapane</b>	241.288	259.607	<b>4.828842</b>

Figure S1. Time series of apapane with its fitted LOESS curve declining into the zone of probable collapse. The ‘10% Upper’ reported refers to the value on the y-axis corresponding to 10% of the upper bound of the 95% confidence interval (CI) about estimate of the maximum observed abundance (top solid line; see Figure 2 in paper). The ‘10% Lower’ is similarly the y-axis value corresponding to 10% of the lower bound of the 95% CI about the estimate of the maximum observed abundance (bottom solid line). The ‘Minimum value’ is the lowest value estimated from the applied function. The ‘ $R^2$ ’ is the coefficient of determination of the function applied to the time series, to serve as a goodness of fit measure (greater values represent better fit).

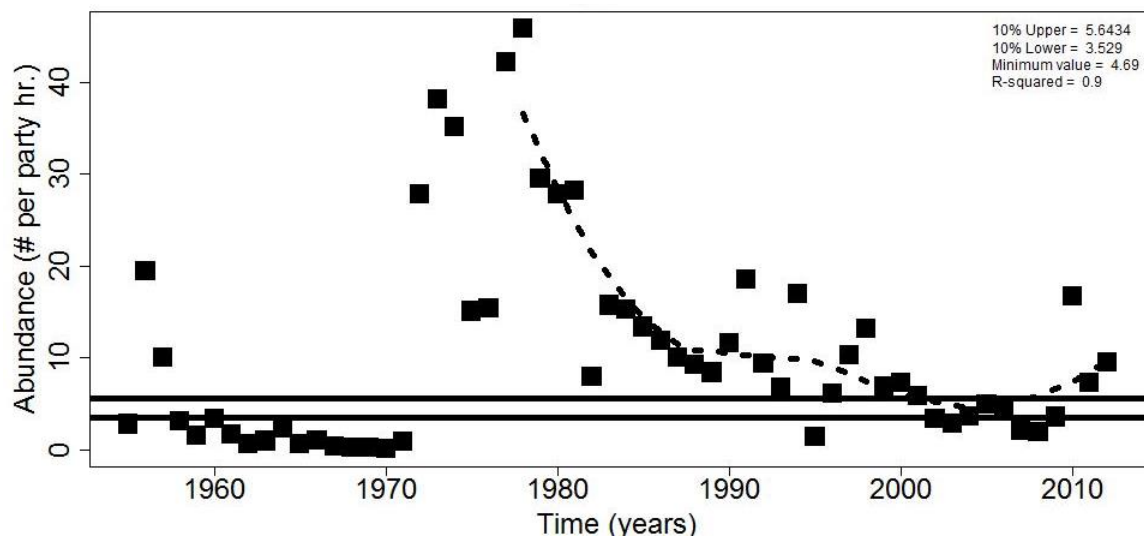


Figure S2. Hawaii akepa

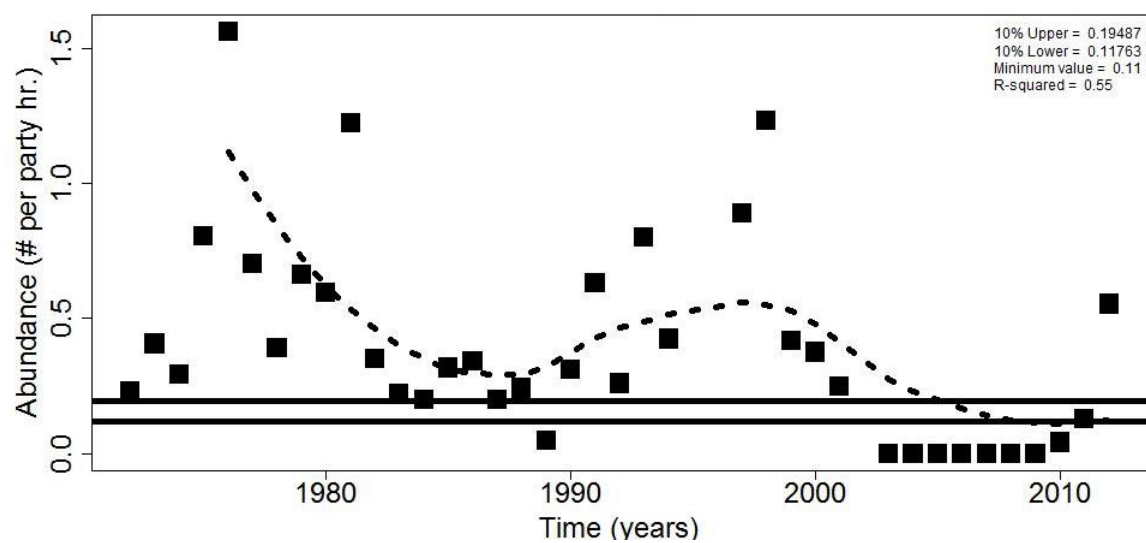


Figure S3. Hawaii creeper

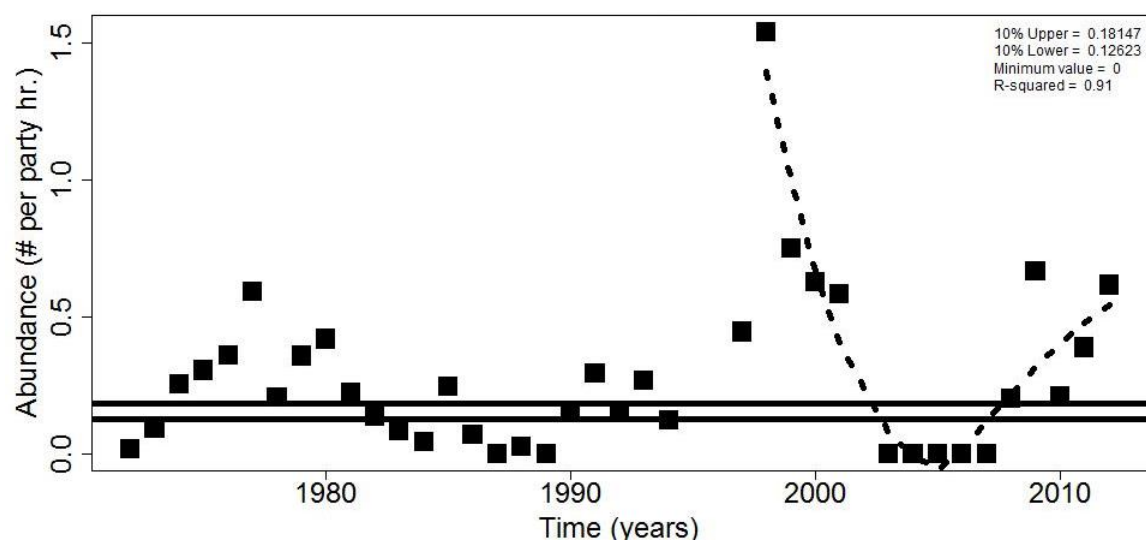




Figure S4. Hawaii elepaio

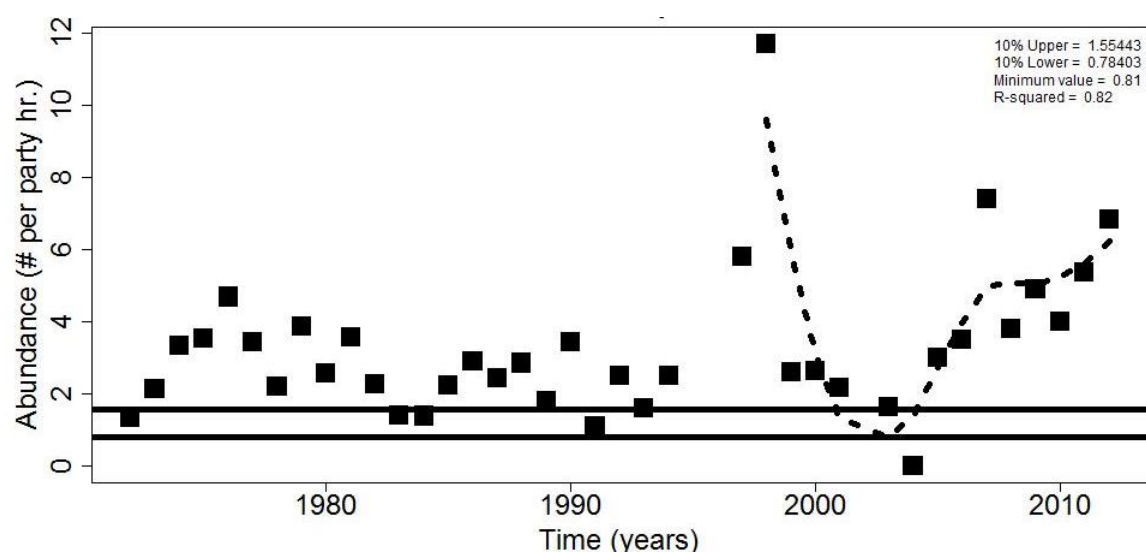


Figure S5. Hawaiian hawk

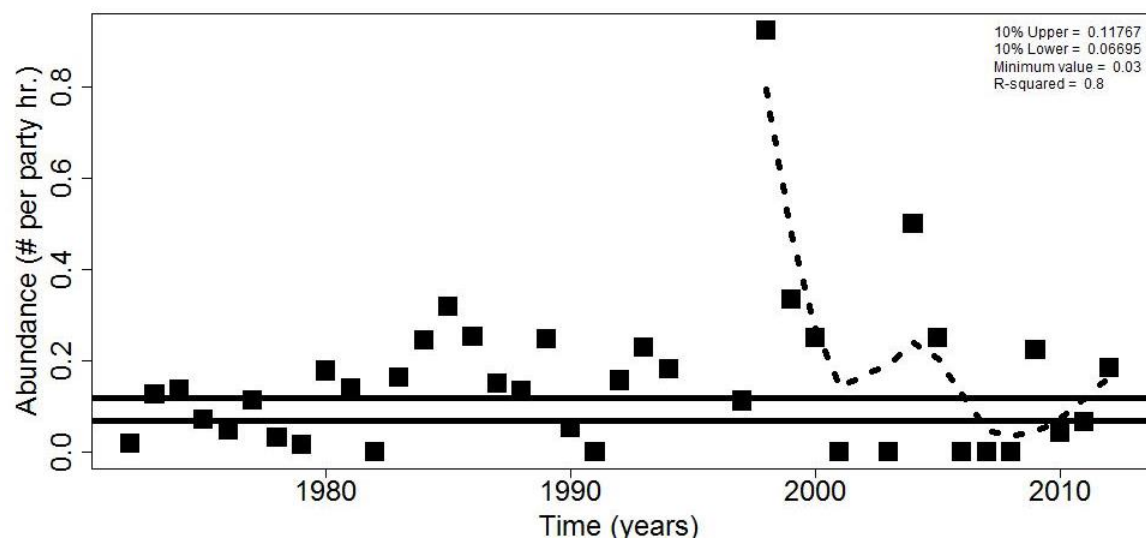


Figure S6. Kauai amakihi

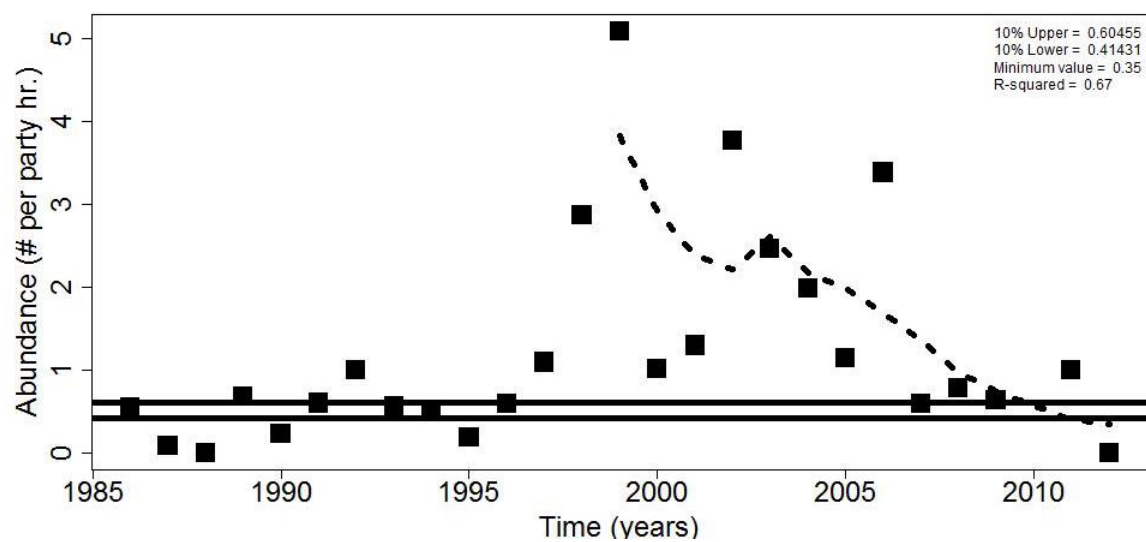


Figure S7. Kauai elepaio

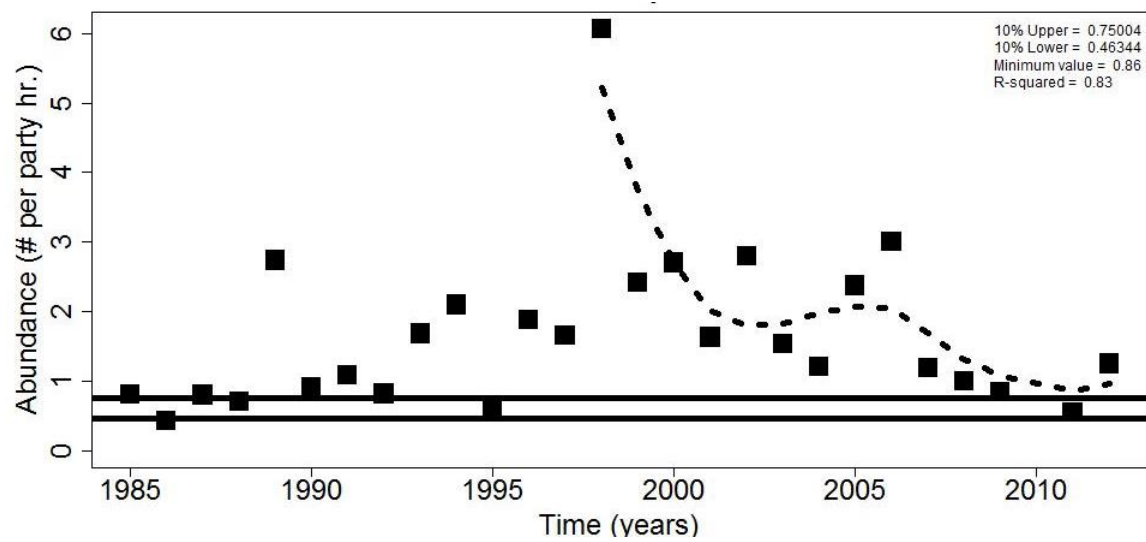


Figure S8. Oahu amakihi

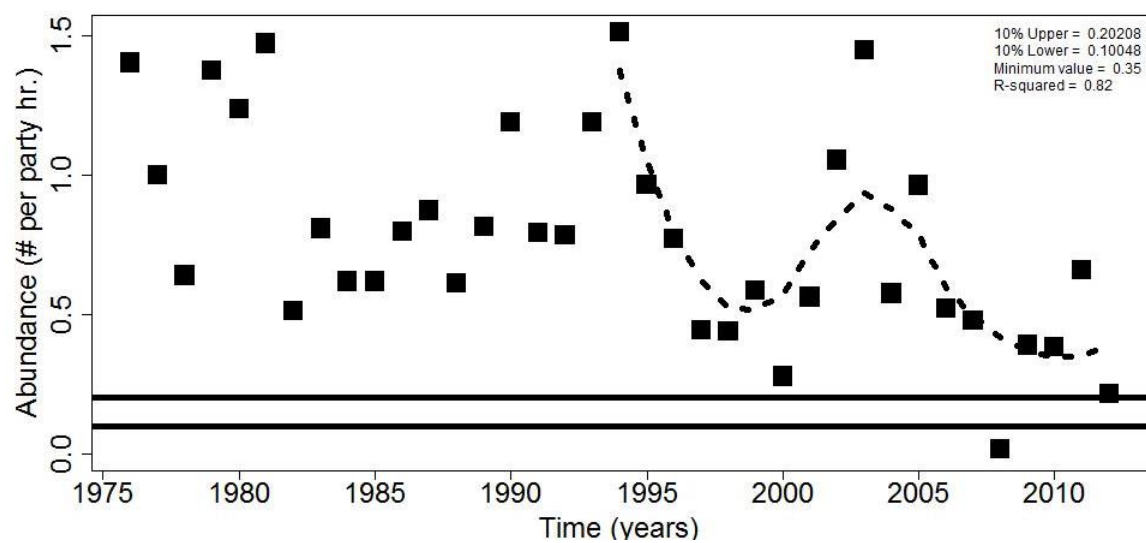


Figure S9. Oahu elepaio

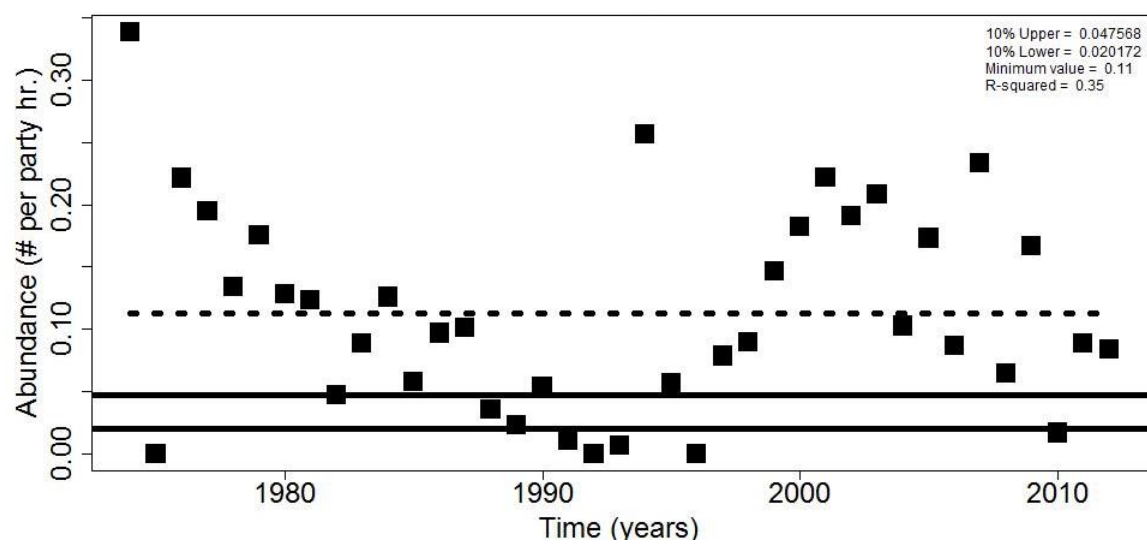


Figure S10. Omao

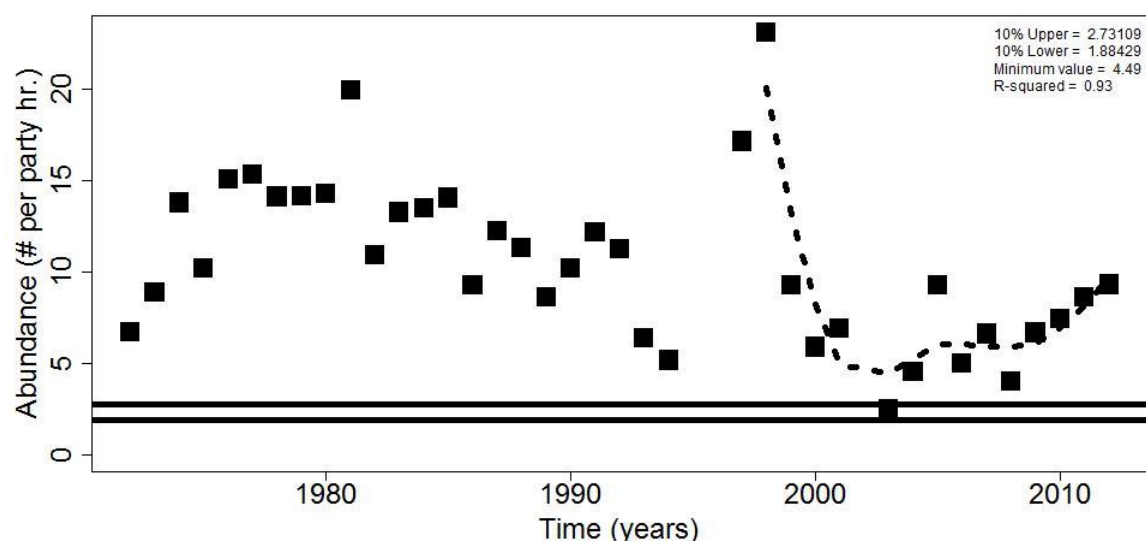


Figure S11. Volcano (Hawaii) iiwi

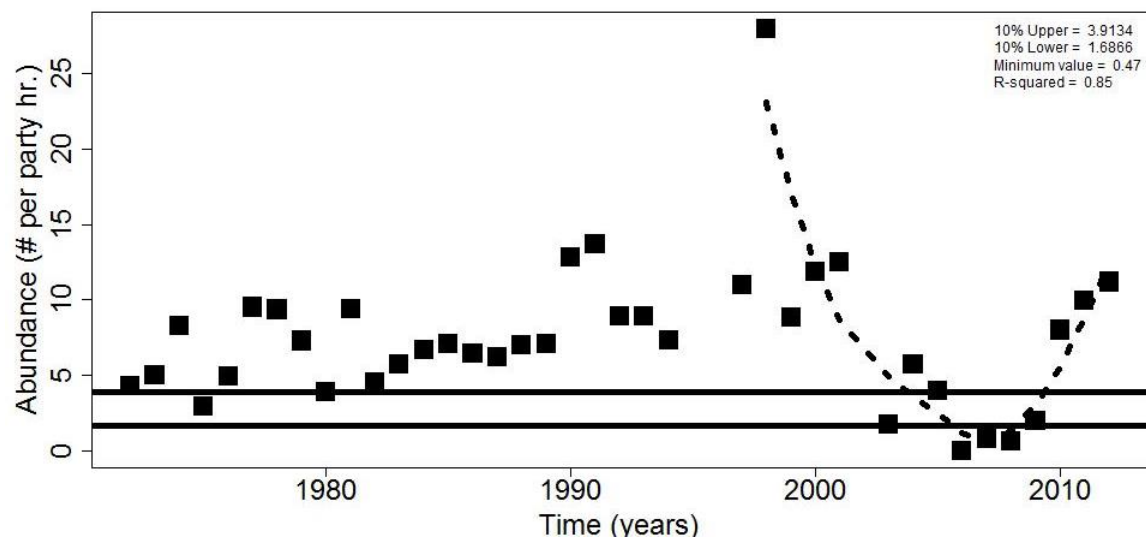
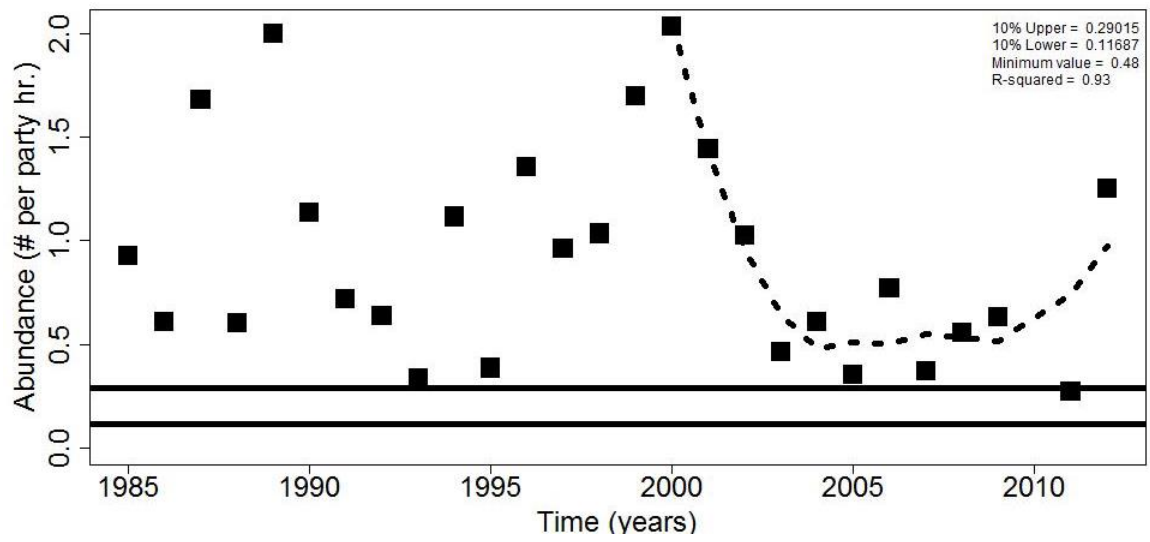




Figure S12. Waimea (Kauai) iiwi



**Chapter 3: The occurrence of population collapses in exotic species**

Article Type: Original Article

Kevin Aagaard\* and Julie L. Lockwood

Graduate Program in Ecology and Evolution, and Department of Ecology, Evolution, and  
Natural Resources, Rutgers University, New Brunswick, NJ 08901 USA

\*Corresponding author: [aagaard@scarletmail.rutgers.edu](mailto:aagaard@scarletmail.rutgers.edu), (telephone) 848-932-3213,  
(fax) 732-932-8746

JLL email: [lockwood@aesop.rutgers.edu](mailto:lockwood@aesop.rutgers.edu)

## ABSTRACT

Exotic species have had undeniably profound effects both ecologically and economically, yet we lack fundamental knowledge about their population dynamics. A particularly vexing phenomenon is spontaneous collapses among populations of established exotic species. Based on criteria used by the IUCN to classify species as threatened with extinction, we consider a population to have collapsed if it has experienced a  $\geq 90\%$  reduction in abundance within 10 years or three generations, whichever metric is greater. We use a recently developed method to identify population collapses and apply it to the exotic birds of Hawaii. We show that 14 of 54 established exotic bird species on Hawaii experienced probable collapses, three leading to near extinction. Declines from maximum abundances (ranging from 135.47 to 0.11 individuals per party hour) into a zone of probable collapse took on average 4.6 ( $\pm 1.9$ ) years, with minima between 9.87 and 0. Collapse of exotic populations has been under-studied empirically and theoretically, yet its implications for invasion ecology are profound. We show that collapses may be more common among exotic species than previously expected. Applying these methods to other taxa and locations is crucial for improving our understanding of exotic species population dynamics and management of invasive species.

KEY WORDS: Audubon Christmas Bird Counts, biological invasions, collapses, exotic species, Hawaiian Islands, population, birds

## INTRODUCTION

Unexpected population declines of exotic populations, commonly referred to as collapses, have been a persistently discussed but understudied topic within biological invasions (McDonald and Wells 2010, Burnaford et al. 2011, Cooling et al. 2012, Moore et al. 2012). Population collapses within exotic species occur for no obvious reason, that is, not through hunting, fishing, or management (Simberloff and Gibbons 2004). Such collapses have profound implications for how we view the process of species invasion, and subsequently manage those exotic species that cause ecological or economic harm (Simberloff and Gibbons 2004, Cooling et al. 2012). However, because there is no accepted quantitative definition for population collapses, there is no way to assess their prevalence within or across taxa, much less predict when and where they will occur (Simberloff and Gibbons 2004). Building on several definitions of population collapse (also termed ‘crashes’) within the conservation biology literature, we derive a quantitative definition of exotic species collapse. We then survey for collapses within a taxonomic group that has many exotic species (birds), illustrating their prevalence and providing a protocol for surveying for collapses in other taxa and ecosystems.

Classic population growth models (e.g., exponential, logistic) are often employed to approximate the population dynamics of exotic species (Sakai et al. 2001, Forsyth et al. 2013). For example, most models of geographic range expansion assume logistic or exponential growth (Lockwood et al. 2013). Also, management recommendations tend to place a high premium on enacting eradication efforts quickly after a species has been introduced in part because there is the assumption that the population will experience exponential (or logistic) growth (Ricciardi et al. 2013). While it is appealing to use long-

accepted population growth models in this context, it is becoming clear that exotic species' population trajectories are often more complex than these models allow, regularly including long lag phases or boom-and-bust events (Crooks and Soulé 1999, Strayer et al. 2006, Williamson 1996, Crooks and Soulé 1999, Aikio et al. 2010, Aagaard and Lockwood 2014a). Collapses provide further evidence of the complexity of population growth of exotic species. If collapses are common, and we can predict which populations will exhibit collapses, perhaps managers will have the opportunity to successfully eliminate harmful exotic species at their lowest abundance, when they are at their most easily eradicated, long after initial establishment has occurred (McDonald and Wells 2010, Cooling et al. 2012). Collapses also suggest that currently abundant exotic species may not remain abundant into the future, which can greatly modify perceptions of their long-term potential for imposing ecological or economic harm (Strayer et al. 2003).

As with native species (Aagaard and Lockwood 2014b), an inherent issue in detecting population collapses is determining the timing and magnitude required to classify a species as 'collapsed'. Conservation biologists (including those in fisheries) have derived several ways to identify populations that have declined by such a magnitude and rate that they warrant special concern (e.g., Mullon et al. 2005, World Conservation Union 2001, Green 2003). Although nearly all these definitions consider large drops that occur over short time periods as being of concern, no standard quantitative definition has emerged from this literature. We adopt the IUCN criterion for classifying a (native) species as threatened with extinction as our definition here. This definition requires that a population experience a  $\geq 90\%$  reduction in abundance within 10 years or three generations, whichever metric is greater. We choose this definition in part because

Simberloff and Gibbons (2004) used a similar definition in their seminal survey for exotic species collapses. However, this definition also requires a population to experience a very sharp rate of decline, which means that exotic species that exhibit moderate drops in abundance will not qualify as ‘collapsed’. Having a conservative definition in this regard seems prudent, at least initially, since we do not want to over interpret population fluctuations.

Even with a robust definition, there is one remaining issue that crops up when applying it to exotic species. We must determine whether or not an exotic species has successfully established a persistent population. Exotic populations, by definition, are founded from only a few individuals (Lockwood et al. 2013). It is possible that these founders do not represent a viable population, and thus they will eventually all die (i.e., they have consistently low survival and/or virtually no reproduction leading to no population growth). This scenario will lead to a (likely rapid) decline in number of individuals counted over time, eventually to extinction, but it is not a collapse. Thus, we assert that only after an exotic population has become established can it experience a collapse, requiring that we must first develop and apply a consistent criterion for determining exotic population establishment and evaluate collapses only within this group.

Using a quantitative definition of collapse and establishment, we evaluate the prevalence of collapses within the exotic birds of Hawaii. Islands are hotspots for exotic bird invasions, and Hawaii in particular ranks as one of the top 10 most invaded locations worldwide in terms of number of exotic birds established (Blackburn et al. 2009, Moulton et al. 2001). We take advantage of an uncommonly complete database

containing >70 years of abundance data to evaluate which exotic birds have established self-sustaining populations on one or more of the Hawaiian Islands, and then whether or not any of these show evidence of a population collapse.

## METHODS

Since the 1800s over 100 exotic bird species have been released onto Hawaii for various reasons, including for aesthetic appeal, as biocontrol agents, or as cage-escapees (Moulton et al. 2001, Pyle and Pyle 2009). Residents of Hawaii have participated in Christmas Bird Counts (CBC) since 1938, yielding an exceptionally long record of annual abundance data for 54 of these exotic bird species (National Audubon Society 2010). Many of these species were initially introduced to Hawaii after the CBC began, thus providing us with a nearly complete account of these species' population trajectories (Table 1; Pyle and Pyle 2009). We use the full CBC record of these 54 species to evaluate whether each species successfully established a self-sustaining population on the islands, and of these, which experienced population collapses (Table 1). Note that all species evaluated here have short enough generation times that our collapse definition functionally becomes an evaluation of a <90% decline over 10 years.

There are seven to nine CBC circles visited by observers across the archipelago each year, depending on participation and expert availability. Counts involve searches for all species seen within a fixed location of known size (15 mile diameter circle) during one day, with the number of individuals observed per species recorded. These counts are standardized (by time of year and location) and are reported in terms of effort per party hour (e.g., one person counting for 10 hours equates to five people counting for two),

although there is associated error that must be accounted for. Many fundamental sampling biases are accounted for within CBC records by temporally and spatially standardized methodology and by scaling count estimates by survey effort (party hours). Despite this, it was crucial for us to account for variation among count circles when estimating the threshold for declaring a ‘collapse’. For inter-count circle differences, we followed the approach of Link et al. (2006), which requires scaling the abundance estimates based on effort variation of all of the count circles, such that they can be compared to one another. These corrections remove the influence of the varying use of count circles from year to year, and allow for archipelago-wide abundance inferences.

We follow the methods detailed by Aagaard and Lockwood (2014a) to statistically evaluate population persistence and identify collapsed populations. We initially applied two filters to the CBC data to derive a set of species that were clearly established, but that also showed a decline during their period of record. In the first filter, we removed any species that never showed evidence of a decline in abundance over any 10-year period in its record ( $n = 21$ ). Second, of the remaining 33 species, we removed any species that was not likely present for the duration of its record. Many species will show zero-counts in a CBC abundance record, with such counts being more likely if the species is rare. Superficially, zero-counts indicate that a species was truly absent from the count area. However, a species with a zero-count (even several zero-counts) may have simply been missed by observers even though it was actually present (i.e. it has a low detection probability). Thus, our task was to determine which species persisted within Hawaii for at least 10 years, recognizing that some sampling events would show zeroes because of low probabilities of detection.



Because the CBC, like many long-term population data sources, does not provide a mechanism to calculate detection probability directly, we used a Bayesian approach to assess species presence during their record ( $P$ ) while varying detection probabilities within a range of values. We varied the detection probability ( $p_d$ , the probability of an observer detecting an individual given that the individual is actually present) such that  $0.1 \leq p_d \leq 0.9$ . We incremented  $p_d$  by 0.1 within this range for each of our model iterations (see below for more details on these). We assumed that both the theoretical presence or absence of individuals ( $T_p$ ), and the actual detections (present/absent,  $Z$ ) followed a Bernoulli distribution, where the probability of presence ( $r$ ) and absence ( $q$ ) equal to 0.5, and with  $Z = P$ :

$$T_p \sim \text{Bern}(r)$$

$$P = p_d * T_p$$

$$p_d = (0.1 \text{ to } 0.9)$$

$$Z[i] \sim \text{Bern}(P)$$

$Z$  was informed by the actual across-years CBC data for each species; years ( $i$ ) with positive abundance values reported were taken as years in which the species was present while years with abundance reports of 0 were taken as years in which the species was absent. This model produced  $P$  for each population across a variety of detection probabilities, given the observed data. If we calculated a species as likely ‘present’ for at least 10 years of their period of record and across all possible detection probabilities, we included it in our survey for collapses. Species that were present for at most nine or fewer years of their CBC record under any probability of detection are considered not established, and excluded from further consideration.

After applying these filters, we next accounted for uncertainty in the maximum abundance estimate for each species we evaluated. Our definition of a collapse, as well as all others so far published, require the calculation of the percentage decline from a maximum abundance. In our definition, a population collapsed when it declines by 90% or more away from this maximum. However, the observed maximum abundance is one point estimate within a long string of annual abundance estimates. By setting a strict definition of a collapse as a decline from this single value, we are ignoring any uncertainty about that point (e.g., perhaps this maximum was a result of observer bias, or an unusual year).

To estimate the error of the observed maximum abundance estimate, we first determine the variance present in each population's entire time series, using the following model, adapted from Aagaard & Lockwood (2014):

$$\begin{aligned}
 Y[i] &\sim N(\mu[i], \sigma^2), \\
 \mu[i+1] &= \mu[i] * \lambda[i], \\
 \lambda[i] &\sim N(\lambda, \tau), \\
 \tau &\sim \text{Unif}(0, 10), \\
 \sigma^2 &\sim \text{Unif}(0, 100),
 \end{aligned}$$

where  $Y$  is the time series for each target population, with  $i$  representing each year's count within the time series,  $\mu$  is the estimated maximum abundance for each population (assuming year to year exponential growth, with the mean growth rate =  $\lambda$  and variance  $\tau$ ), and  $\sigma^2$  is the variance about the annual estimates, at first unknown and therefore given an uninformative prior. Because our data are derived from count data, having been standardized using information on the number of observers and length of time spent

observing, they are continuous and not discrete, making the use of a normal rather than Poisson prior distribution appropriate. For each population we are applying an uninformative prior to the variance estimate about the maximum abundance, not assuming anything about the cross-species distribution of maximum abundance estimates. We ran this model for 10,000 iterations, with a burn-in of 1,000 to allow for convergence.

Using these estimated variance distributions, we derive the 95% Credible Intervals (CI) around each species' observed maximum abundance and employ this to establish a 'zone of probable collapse'. We set this zone by reducing the upper and lower CI by 90%, following our definition of collapse (i.e. a reduction in abundance of >90%, see above). For example, an observed maximum abundance of 100 with a lower CI of 50 and an upper CI of 150 would have a zone of probable collapse defined by the values 5 and 15. To determine whether a species' abundance had declined into this zone within the defined time frame (i.e. within 10 years, see above), we fit the best of three models (linear, exponential, and polynomial) to the series of abundance estimates starting with the maximum and ending with the most recent surveys (2010). We selected the best-fit model of this set using a corrected form of Akaike's information criterion' (AICc) to account for small sample sizes (Burnham and Anderson 2002). Using the generated best-fit line, we calculated the number of years between when the maximum abundance was attained to when estimated abundance dropped into the zone of probable collapse. Although one could identify when a population declined into the zone of collapse visually, fitting a statistical model to the series of abundance estimates helped greatly in identifying when a species' entered into the collapse zone by 'smoothing' the abundance

trend. All Bayesian analyses were performed in OpenBUGS v. 3.2.3 (Lunn et al. 2009), and all model fitting was done in R v. 3.1.0 (R Development Core Team 2014).

## RESULTS

We found that all 33 populations were present for a sufficient length of time to be considered established, regardless of the theoretical detection probability ( $p_d$ ) used. That is, the probability of presence,  $P$ ,  $\geq 0.99$  for every population whether  $p_d = 0.1$  or  $0.9$ . Even populations with a considerable number of years of abundances reported as ‘0’ (e.g., the lavender waxbill; Supporting Information, Figure S15) were estimated to be present for the duration for their time series and are thus considered established (although clearly uncommon).

We show that populations varied substantially in the uncertainty about their observed maximum abundance, which we expected for two reasons. First, the scale for abundance estimates varied by several orders of magnitude across populations, from hundreds of counted individuals per party hour for some, to fractions of individuals for others (Table 1). Second, the variation within each time series differed greatly. Some populations had aberrant observed maximum abundances (chestnut mannikin; Figure S3), while others had maximum abundances that were far more consistent with abundance estimates across their record (house finch; Figure S7). Similarly, some populations had very similar credible interval (CI) widths but widely divergent maximum abundance estimates. For example, the cattle egret and common myna each yielded CI widths of about four, but the reported maximum abundance estimates differed by an order of magnitude (29.7 and 135.5, respectively; Figures S2 and S4).

Of the 33 established exotic birds on Hawaii, 19 showed reductions of  $\geq 90\%$  at some point in their period of record. Because we constrained the definition of a collapse to occur within the span of 10 years, some of the populations that declined by  $>90\%$  did not constitute collapses ( $n = 5$ ). Thus, 14 of these 19 populations fit our definition of collapse (Figure 1, Supporting Information). Of those 14 collapses, 10 were rapid enough and of sufficient magnitude that the populations were found to have declined below the lower bounds of the zone of probable collapse. For these species, observed declines exceeded even the most conservative estimate of what magnitude and rate of a decline would constitute a collapse. The average number of years between maximum abundance and the upper threshold of the collapse zone was  $4.6 \pm 1.9$  SD (Figure 1).

For species exhibiting a collapse, maximum abundance ranged from low (ring-necked pheasant, 0.4 individuals/party hour, or i/ph) to high (cattle egret, 30 i/ph). Similarly, among those populations not exhibiting collapses, maximum abundance estimates ranged from low (kalij pheasant, 0.34 i/ph) to high (zebra dove, 57 i/ph). While the sample size is small, this suggests that factors influencing collapses go beyond populations simply existing at low or high abundances for extended periods.

## DISCUSSION

Researchers have recognized the possibility of population collapses in exotic species for decades (Williamson 1996), but there have been only a few examples and case studies provided in the recent literature (McDonald and Wells 2010, Burnaford et al. 2011, Cooling et al. 2012, Moore et al. 2012). The issues associated with quantitatively defining a collapse certainly have stymied more systematic searches. Our collective

ignorance about the prevalence of collapses has led to their exclusion from general models of exotic species population dynamics, and policy formation and management efforts directed at invasive exotic species (Simberloff and Gibbons 2004). Our results indicate that collapses likely occurred in a quarter (14) of the 54 exotic birds established in Hawaii, suggesting such complex population dynamics may be more common than previously suspected.

The common occurrence of collapses in exotic species' affects our broader ecological understanding of biological invasions in three main ways; by (1) refining our expectations for 'typical' population growth and thus improving our approach to management, (2) informing mechanisms that influence population growth patterns, and (3) modifying how we may view the longevity of exotic species' impacts. What follows is an exploration of each of these three points.

First, population collapses present vexing complications for the formation of eradication or control decisions related to invasive exotic species. The existence of collapses seems to advocate for 'do-nothing' management schemes for such species. The argument for this approach is that currently abundant exotic populations may not remain at high population levels indefinitely (Cooling et al. 2012). If such species are targeted for control or eradication, both of which require investments of capital that scales with abundance, it may be more cost-effective to delay action until the population has collapsed. Why waste resources driving population size down when 'nature' will do some of this work for you if given enough time? It is certainly far more efficient to invest in eradicating or controlling only the exotic populations that are likely *not* to collapse than to invest in managing all problematic exotic species. If our results are indicative of the

prevalence of population collapses across many other exotic taxa, then there is large premium on finding ways to predict whether or not invasive exotic species will collapse. Our methodology is central to progress on that front since it is impossible to test for predictors without a consistent and easily applied way of classifying a species as collapsed.

Second, the biological mechanisms behind exotic species' population collapses are not well explored in part because there has been no accepted quantitative definition of collapse. We suggest that our method can fill this gap, and furthermore can be applied across a wide variety of taxa, across species with widely divergent population sizes, and across multiple exotic populations of the same species. This flexibility allows robust assessments of the various mechanisms proposed for exotic species collapses including, among many others, the acquisition of novel enemies in the introduced range (e.g., parasite spillback; Kelly et al. 2009), density-dependent population growth (Sakai et al. 2001), or changes in abiotic conditions (Strayer et al. 2006, McDonald and Wells 2010). Particular mechanisms behind population collapses may be more likely to occur within species with specific life history traits, populations that exceed certain threshold abundance levels, or within certain ecosystems. In this regard, our finding of collapses being common among exotic birds on Hawaii could be a product of the traits of birds, the ecological conditions on oceanic islands, or the range of maximum abundances they attain. Without a broader survey for collapses across more species and locations, however, we cannot assess the uniqueness of our results.

Third, and finally, the occurrence of collapses has important implications for assessing exotic species' impacts. There is good evidence that the degree of ecological or

economic impact an exotic species imposes increases with its abundance (Ricciardi et al. 2013). Thus, when an exotic species' population collapses, we should expect to see a marked reduction in that species' impact (Strayer et al. 2003). This rule of thumb, however, is tempered by the dearth of knowledge surrounding *how* exotic species' abundance scales to ecological and economic impacts (Yokomizo et al. 2009, Thiele et al. 2010). For example, our definition of collapse need not result in a population decreasing to low abundance, but rather to drastically *lower* abundance. Thus, even after a collapse has occurred, some species will remain at high enough abundance that they will still impart substantial ecological or economic impacts if their per capita effects on valuable assets are sufficiently large. Presently, ecologists do not have a sufficient mechanistic understanding of how impacts relate to abundance to make this distinction between species without investigation (Lockwood et al. 2013). We therefore advocate for future research focused on improving our understanding of this relationship, as well as our understanding of atypical population dynamics of exotic species and methods to predict them.

#### ACKNOWLEDGEMENTS

We thank E. Green, N. Fefferman, D. Simberloff, J. Burkhalter, O. Robinson, and the Morin Lab for their methodological advice and feedback on various drafts of this manuscript. The authors report no conflicts of interest.



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## TABLES AND FIGURES

Table 1. We report the year of introduction (I), the length of the Christmas Bird Count record (L), and the results of the collapse analysis.  $A_{\max}$ , maximum abundance;  $\text{Max}_{10\%}$ , 10% of the upper bound of the estimated observed abundance;  $\text{Min}_{10\%}$ , 10% of lower bound of the estimated observed abundance;  $A_{\min}$ , the minimum abundance as estimated from the most parsimonious function;  $\Delta T_{10\%}$ , the time (in years) between the maximum abundance and  $\text{Max}_{10\%}$  (populations with true collapses have both the time to decline below  $\text{Max}_{10\%}$  and  $\text{Min}_{10\%}$ , with the latter in parentheses). Only 90% reductions in < 10 years are considered collapses (i.e., the common myna, for example did not collapse).

Common Name	I	$A_{\max}$	$\Delta T_{10\%}$
California Quail ( <i>Callipepla californica</i> )	1818	0.20	4
Cattle Egret ( <i>Bubulcus ibis</i> )	1959	29.68	6 (7)
Chestnut Mannikin ( <i>Lonchura atricapilla</i> )	1959	20.84	5 (6)
Common Myna ( <i>Acridotheres tristis</i> )	1866	135.47	N/A
Gray Francolin ( <i>Francolinus pondiceranus</i> )	1958	0.48	N/A
Greater Necklaced Laughingthrush ( <i>Garrulax pectoralis</i> )	1919	0.13	4
House Finch ( <i>Haemorhous mexicanus</i> )	1859	6.54	N/A
House Sparrow ( <i>Passer domesticus</i> )	1871	38.30	N/A
Hwamei (Melodious Laughingthrush) ( <i>Garrulax canorus</i> )	1900	0.89	N/A
Indian Silverbill ( <i>Lonchura malabarica</i> )	1965	1.88	4 (4)

Japanese Bush Warbler ( <i>Cettia diphone</i> )	1929	1.41	N/A
Japanese White-eye ( <i>Zosterops japonicas</i> )	1929	12.19	N/A
Java Sparrow ( <i>Padda oryzivora</i> )	1865	10.44	N/A
Kalij Pheasant ( <i>Lophura leucomelanos</i> )	1962	0.34	N/A
Lavender Waxbill ( <i>Estrilda caerulescens</i> )	1965	0.77	3 (3)
Northern Cardinal ( <i>Cardinalis cardinalis</i> )	1929	3.20	N/A
Northern Mockingbird ( <i>Mimus polyglottos</i> )	1928	0.46	N/A
Nutmeg Mannikin ( <i>Lonchura punctulata</i> )	1866	67.4	8 (9)
Orange-cheeked Waxbill ( <i>Estrilda melpoda</i> )	1965	0.61	3 (4)
Red-billed Leiothrix ( <i>Leiothrix lutea</i> )	1917	7.76	N/A
Red-crested Cardinal ( <i>Paroaria coronata</i> )	1928	5.72	N/A
Red-vented Bulbul ( <i>Pycnonotus cafer</i> )	1965	5.98	N/A
Red-whiskered Bulbul ( <i>Pycnonotus jocosus</i> )	1965	0.87	N/A
Red Avadavat ( <i>Amandava amandava</i> )	1900	2.75	3 (3)
Ring-necked Pheasant ( <i>Phasianus colchicus</i> )	1866	0.78	5
Saffron Finch ( <i>Sicalis flaveola</i> )	1965	3.81	3 (4)
Skylark ( <i>Alauda arvensis</i> )	1865	1.07	9 (10)
Spotted Dove ( <i>Spilopelia chinensis</i> )	1855	11.09	N/A
Western Meadowlark ( <i>Sturnella neglecta</i> )	1928	1.06	21

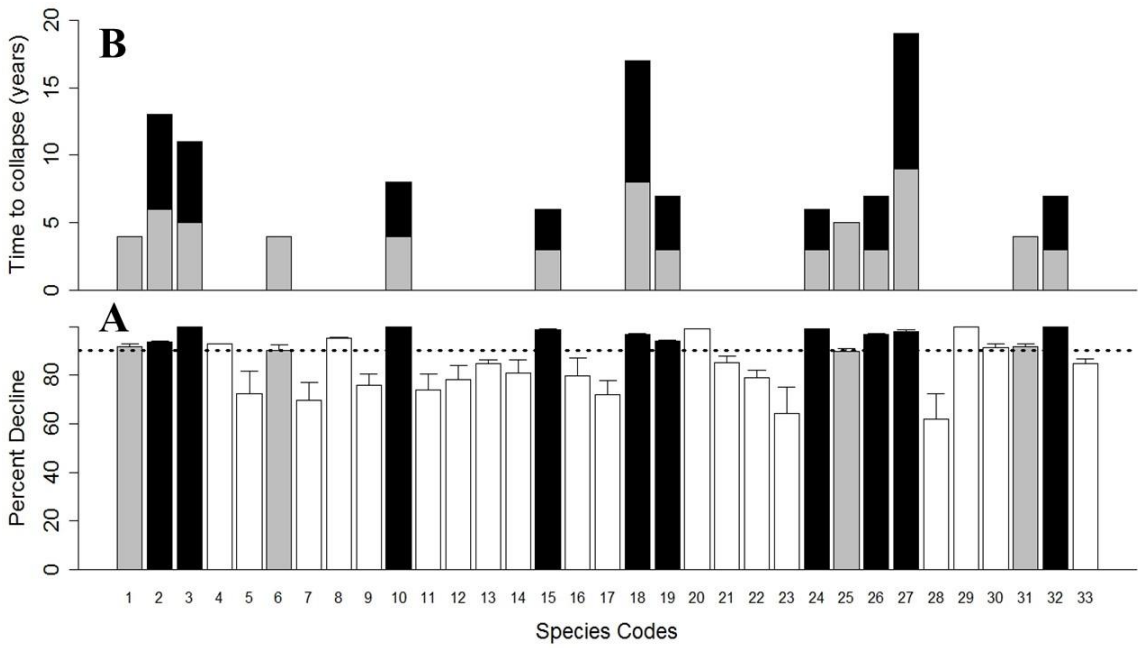
White-rumped Shama ( <i>Copsychus malabaricus</i> )	1931	1.32	N/A
Yellow-faced Grassquit ( <i>Tiaris olivaceus</i> )	1974	0.11	4
Yellow-fronted Canary ( <i>Serinus mozambicus</i> )	1964	4.68	3 (4)
Zebra Dove ( <i>Geopelia striata</i> )	1922	57.13	N/A

## FIGURE LEGENDS

Figure 1. (A) Results in terms of the percent decline from maximum observed abundance. Bar colors correspond to the collapse classification (white = no collapse, gray = probable collapse, black = true collapse). The dashed line marks the 90% threshold marking a collapsed population. Whiskers represent the upper bounds for the maximum abundances estimated from our methods to approximate uncertainty in the observed value (see Aagaard and Lockwood, in prep Figure 1). (B) Length of collapse (from maximum to > 10%). Only populations that decline into the zone of probable collapse or lower are included. Gray bars represent the time between maximum observed abundance and decline below the 90% threshold. Gray *and* black bars represent the time to 90% reduction and then to true collapse. For example, the chestnut mannikin took 4 years to decline into the zone of probable collapse (gray bar), and 12 more years to decline below this zone (black bar).

Species codes: 1—California quail; 2—cattle egret; 3—chestnut mannikin; 4—common myna; 5—gray francolin; 6—greater-necklaced laughingthrush; 7—house finch; 8—house sparrow; 9—hwamei; 10—Indian silverbill; 11—Japanese bush warbler; 12—Japanese white-eye; 13—Java sparrow; 14—kalij pheasant; 15—lavender waxbill; 16—northern cardinal; 17—northern mockingbird; 18—nutmeg mannikin; 19—orange-checked waxbill; 20—red-billed leiothrix; 21—red-crested cardinal; 22—red-vented bulbul; 23—red-whiskered bulbul; 24—red avadavat; 25—ring-necked pheasant; 26—saffron finch; 27—skylark; 28—spotted dove; 29—western meadowlark; 30—white-rumped shama; 31—yellow-faced grassquit; 32—yellow-fronted canary; 33—zebra dove.

Figure 1.



## APPENDICES

Table S1. Corrected Akaike's an information criterion (AICc) for each model as applied to each species. The lowest scoring AICc is in bold.

Species	Model AICc		
	Linear	Exponential	LOESS Curve
California Quail	-193.6368365	<b>-216.2893032</b>	-5.423001901
Cattle Egret	163.2277081	113.6757628	<b>4.441602486</b>
Chestnut Mannikin	129.246556	97.72198377	<b>4.436342462</b>
Common Myna	384.3751016	318.0456379	<b>6.523524567</b>
Gray Francolin	-6.098093166	<b>-8.970088998</b>	16.53458522
Greater Necklaced Laughingthrush	-138.4995886	<b>-146.0520022</b>	-5.177673517
House Finch	102.0210239	97.69417497	<b>2.034891655</b>
House Sparrow	300.5359209	276.2493188	<b>4.661385582</b>
Hwamei	-29.37056378	<b>-43.47250514</b>	-2.549582339
Indian Silverbill	33.98982657	28.13728021	<b>1.22675829</b>
Japanese Bush-Warbler	-6.811249207	<b>-17.68020951</b>	-0.764117483
Japanese White-eye	212.2802495	210.0505314	<b>2.944624081</b>
Java Sparrow	82.00683137	75.12540274	<b>3.502912788</b>
Kalij Pheasant	-7.286244612	<b>-12.03379604</b>	10.45876064
Lavender Waxbill	-32.67894625	<b>-54.23155889</b>	-2.499554779
Northern Cardinal	37.34833956	56.60492911	<b>-0.323252334</b>
Northern Mockingbird	-80.54365415	<b>-82.98277113</b>	-3.300099234
Nutmeg Mannikin	288.0326671	193.9778925	<b>5.604039219</b>



Orange-cheeked Waxbill	-72.94490217	<b>-96.79232058</b>	-3.695617153
Red-billed Leiothrix	172.3628712	141.5401123	<b>0.200197877</b>
Red-crested Cardinal	117.3515164	82.48558419	<b>0.832036597</b>
Red-vented Bulbul	76.29861966	78.16142324	<b>1.673354406</b>
Red-whiskered Bulbul	-12.58861723	<b>-20.58243895</b>	-1.720823219
Red Avadavat	33.32195181	<b>0.606438517</b>	0.713155724
Ring-necked Pheasant	-30.38691509	<b>-62.54538276</b>	-2.568570435
Saffron Finch	50.92717815	33.51066923	<b>2.152694333</b>
Sky Lark	<b>-3.580435913</b>	-0.071327405	2.878619672
Spotted Dove	174.4421598	172.1305088	<b>2.39834412</b>
Western Meadowlark	<b>-8.666648502</b>	-1.381150248	-2.375709449
White-rumped Shama	<b>-5.30422339</b>	6.189977302	-1.859019788
Yellow-faced Grassquit	-134.7911759	<b>-148.6859477</b>	-5.905582001
Yellow-fronted Canary	57.63965253	28.99604567	<b>1.97210287</b>
Zebra Dove	325.673958	309.2567708	<b>5.353991729</b>

Figure S1. Time series of California quail with its fitted negative exponential declining into the zone of probable collapse. The ‘10% Upper’ reported refers to the value on the y-axis corresponding to 10% of the upper bound of the 95% confidence interval (CI) about estimate of the maximum observed abundance (top solid line; see Figure 2 in paper). The ‘10% Lower’ is similarly the y-axis value corresponding to 10% of the lower bound of the 95% CI about the estimate of the maximum observed abundance (bottom solid line). The ‘Minimum value’ is the lowest value estimated from the applied function. The ‘ $R^2$ ’ is the coefficient of determination of the function applied to the time series, to serve as a goodness of fit measure (greater values represent better fit).

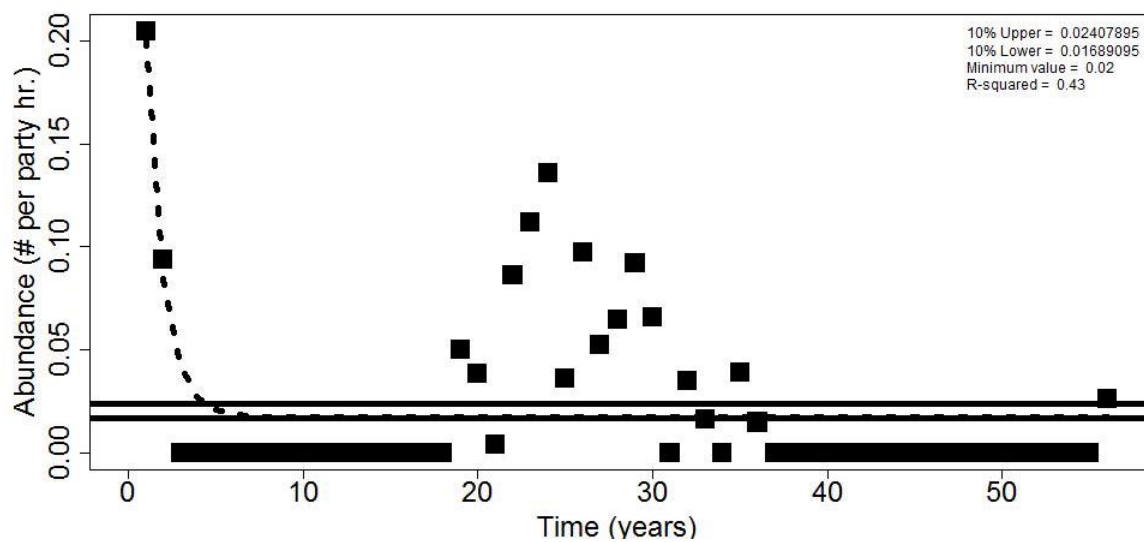


Figure S2.

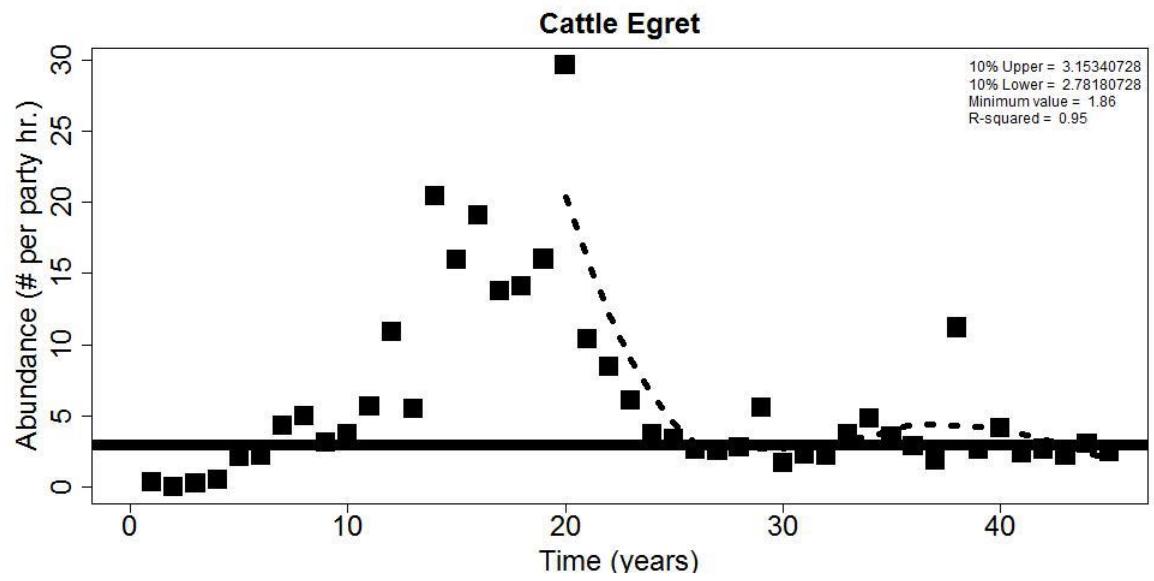


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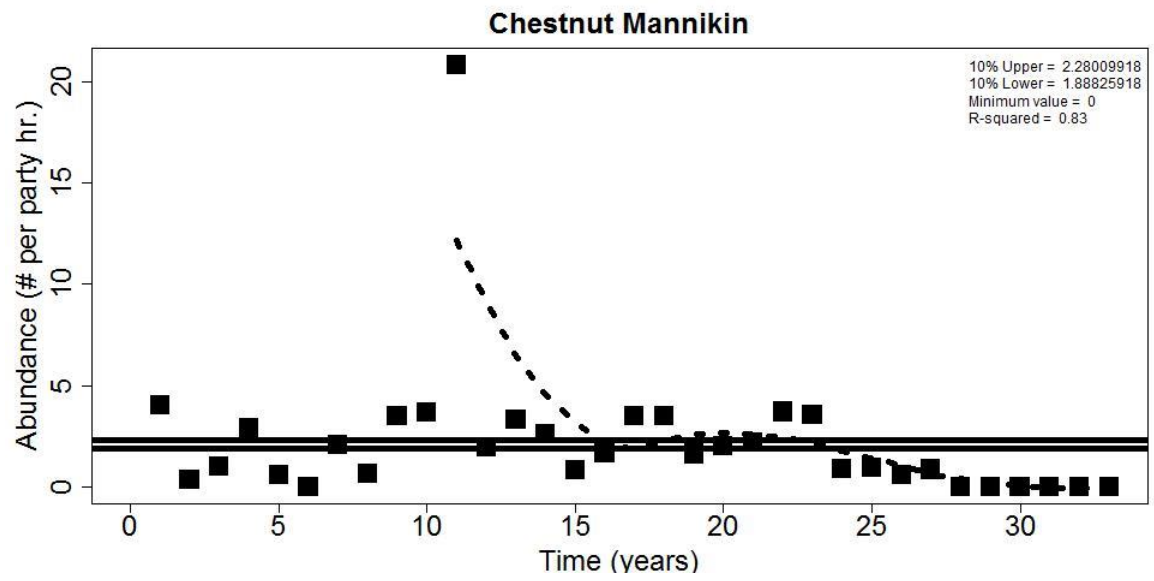


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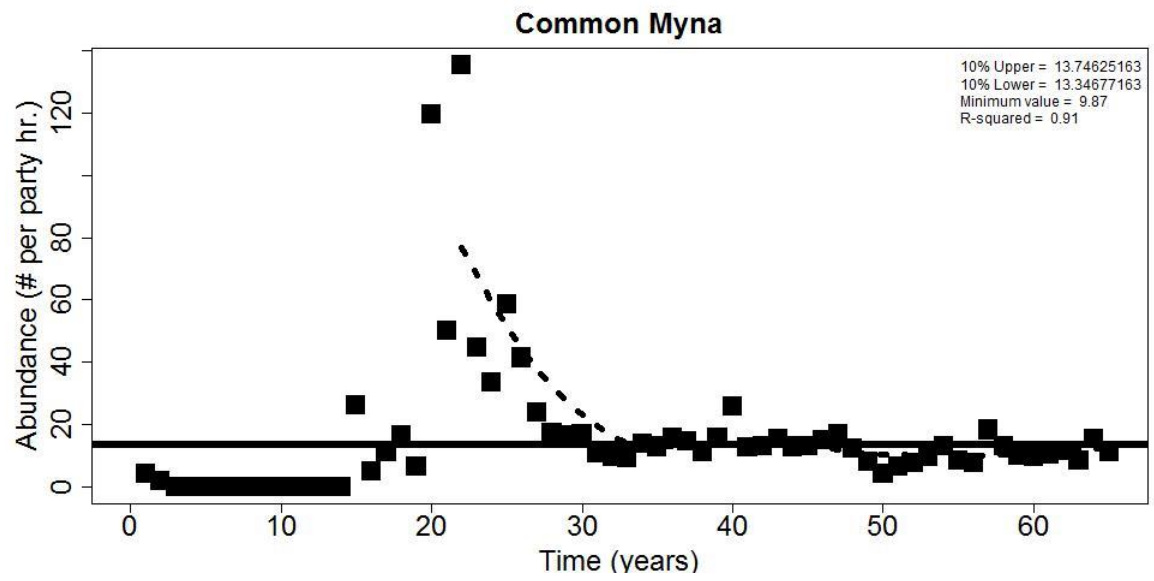


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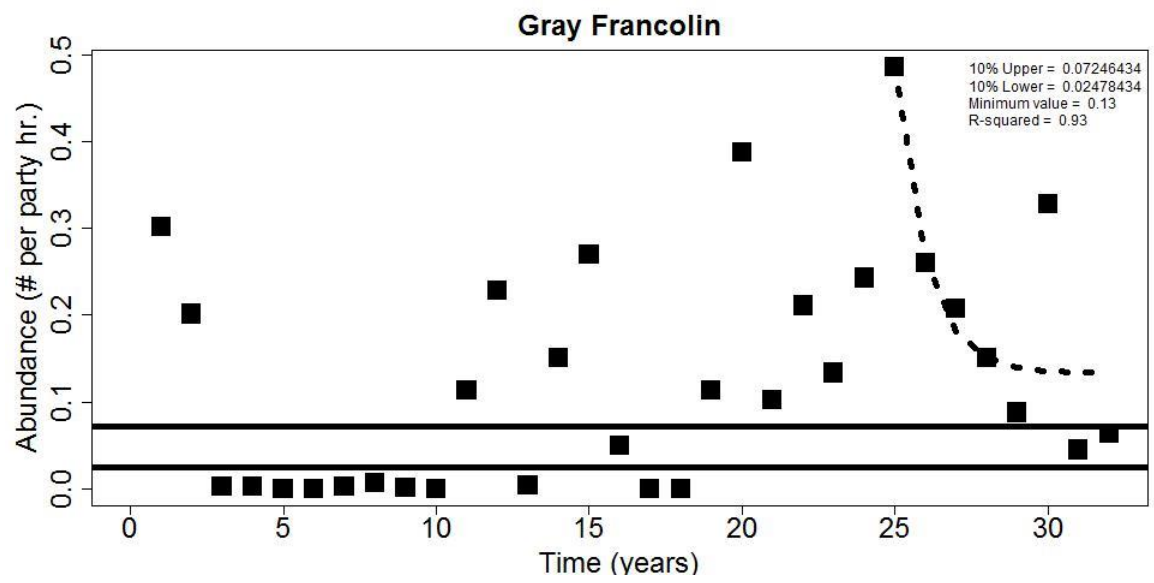


Figure S6.

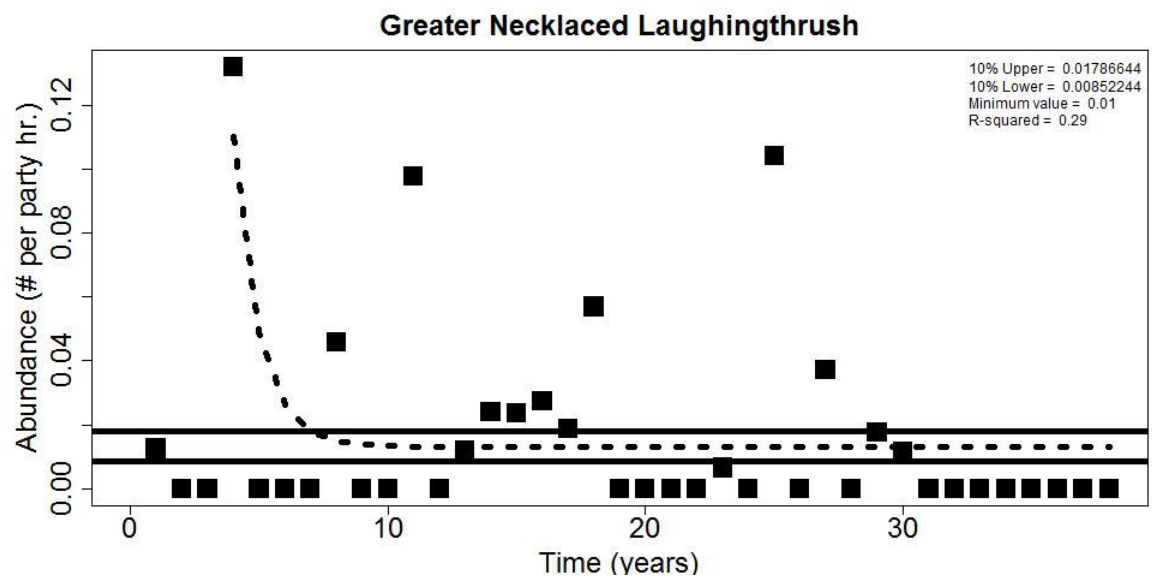


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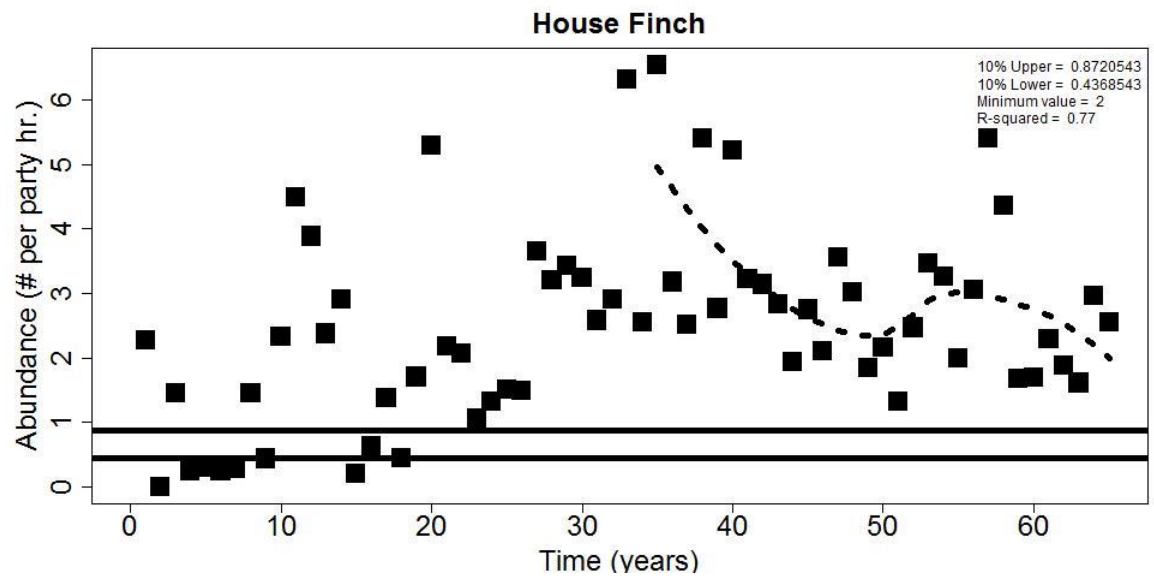




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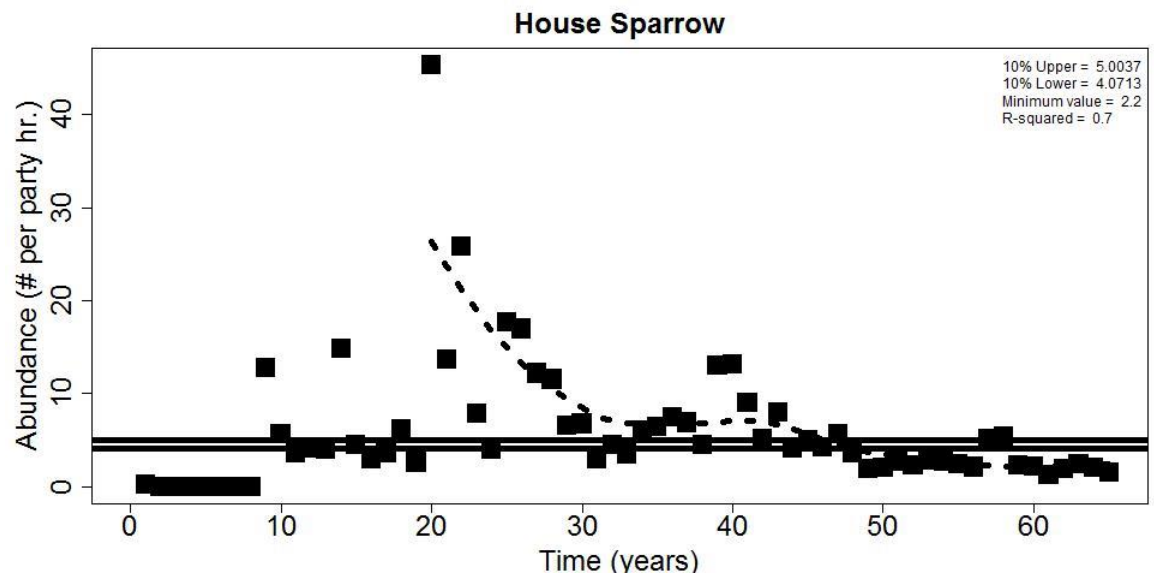


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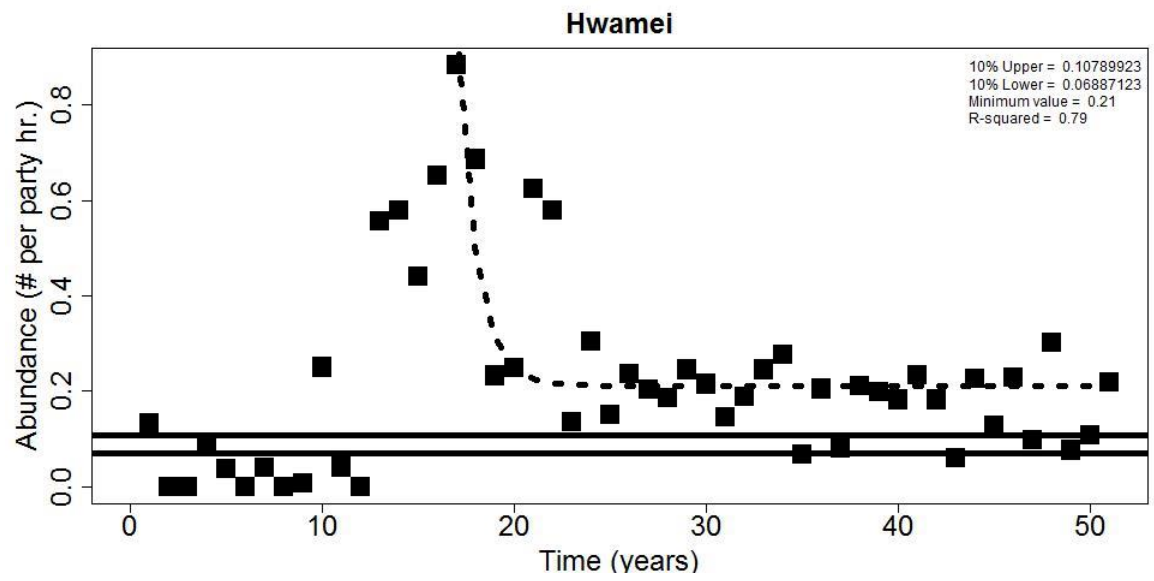


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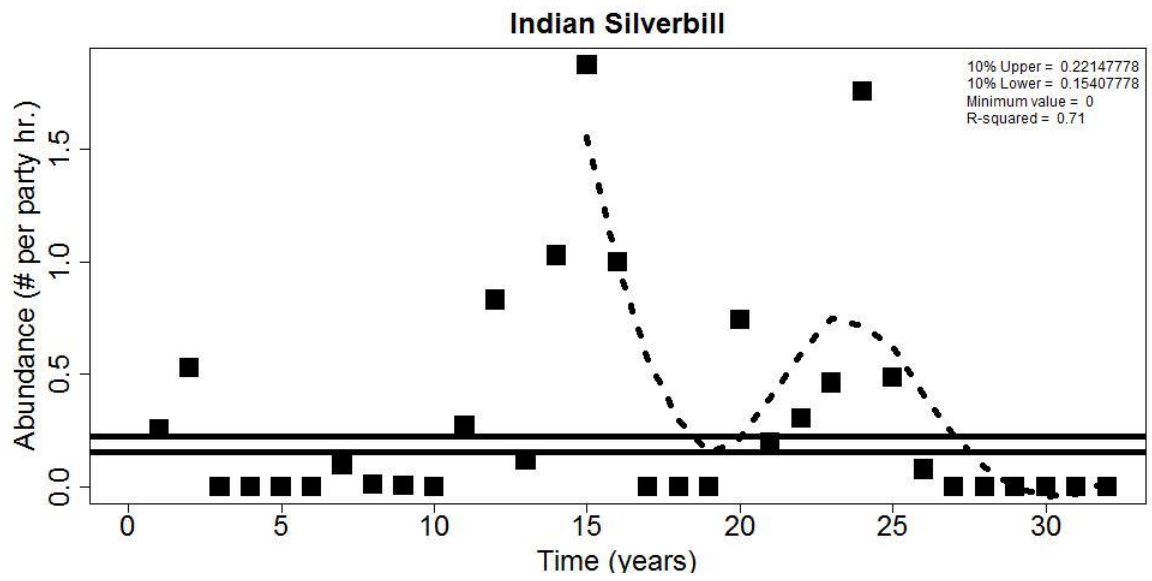


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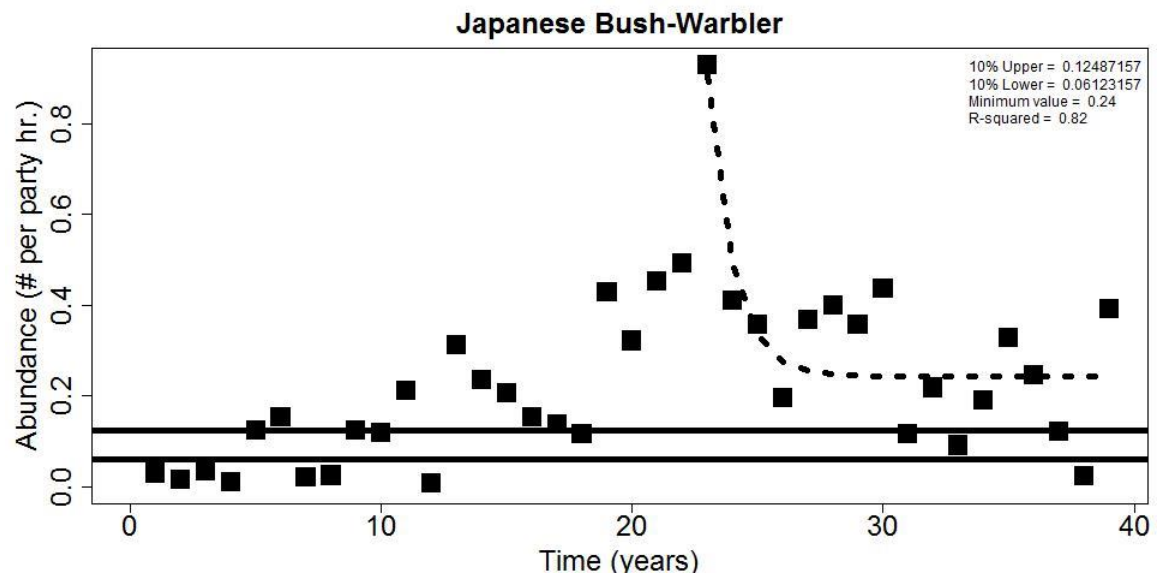


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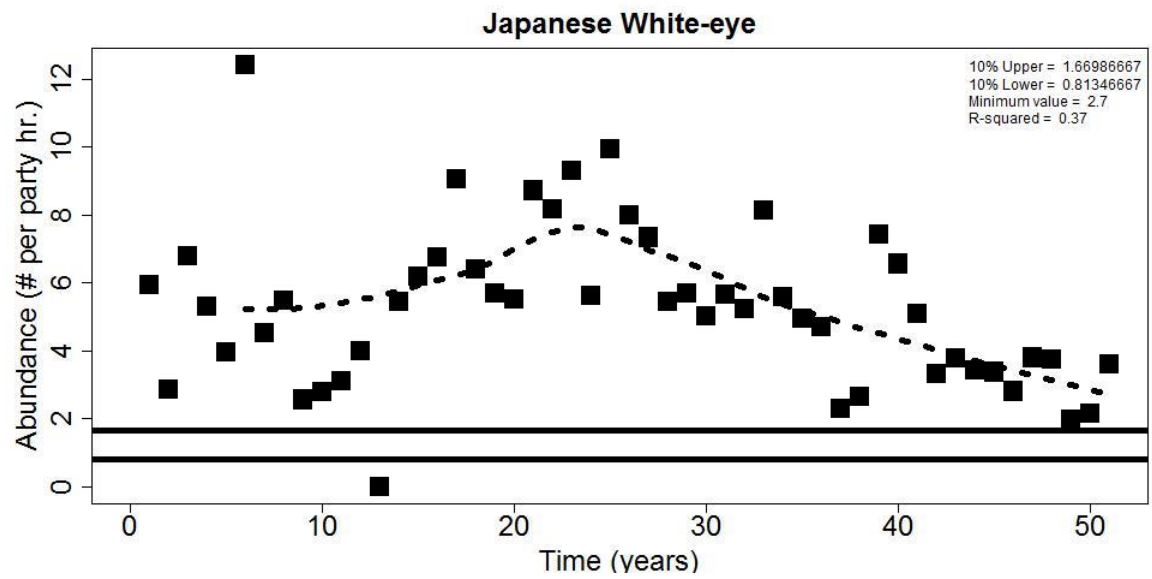


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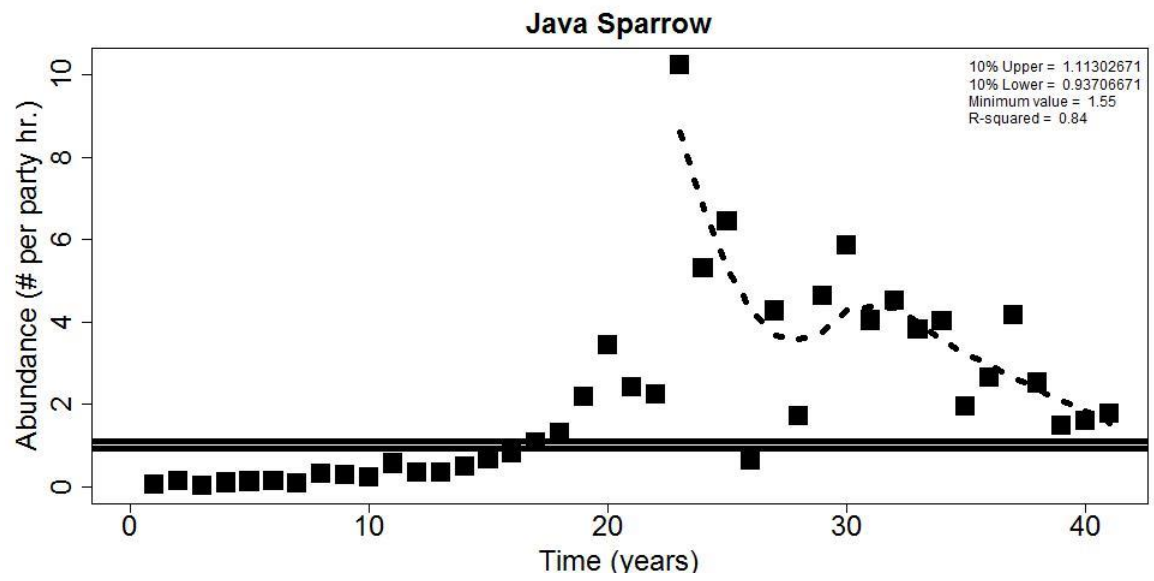


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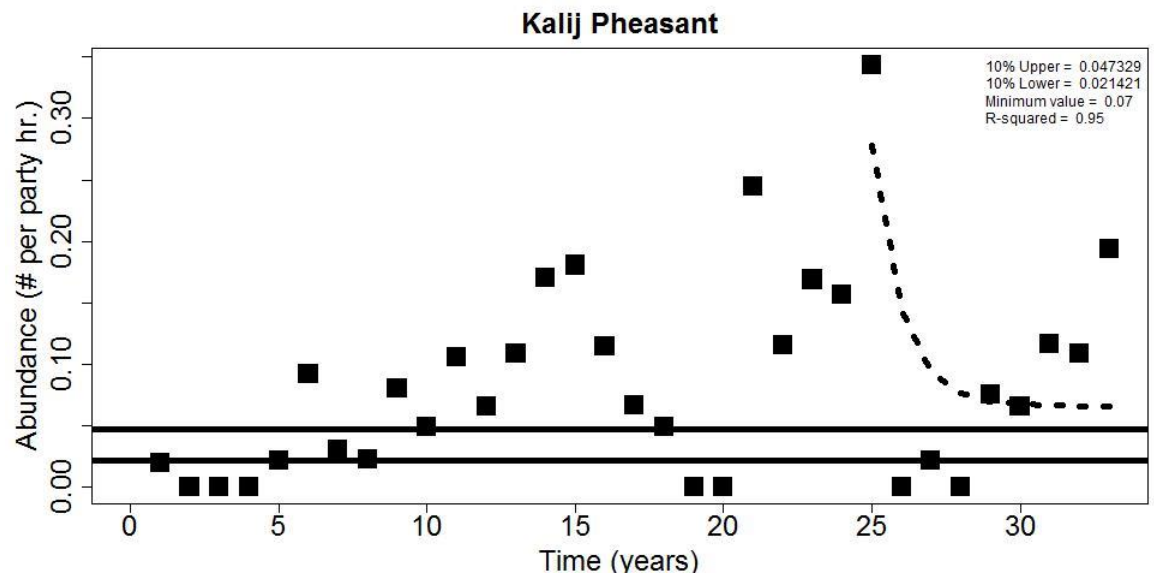


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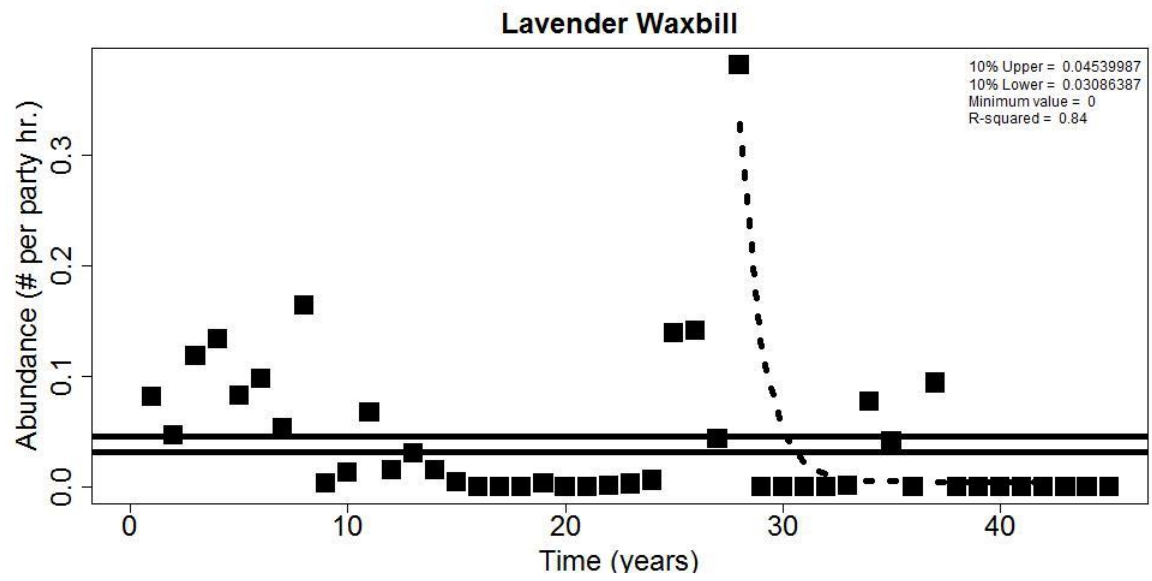




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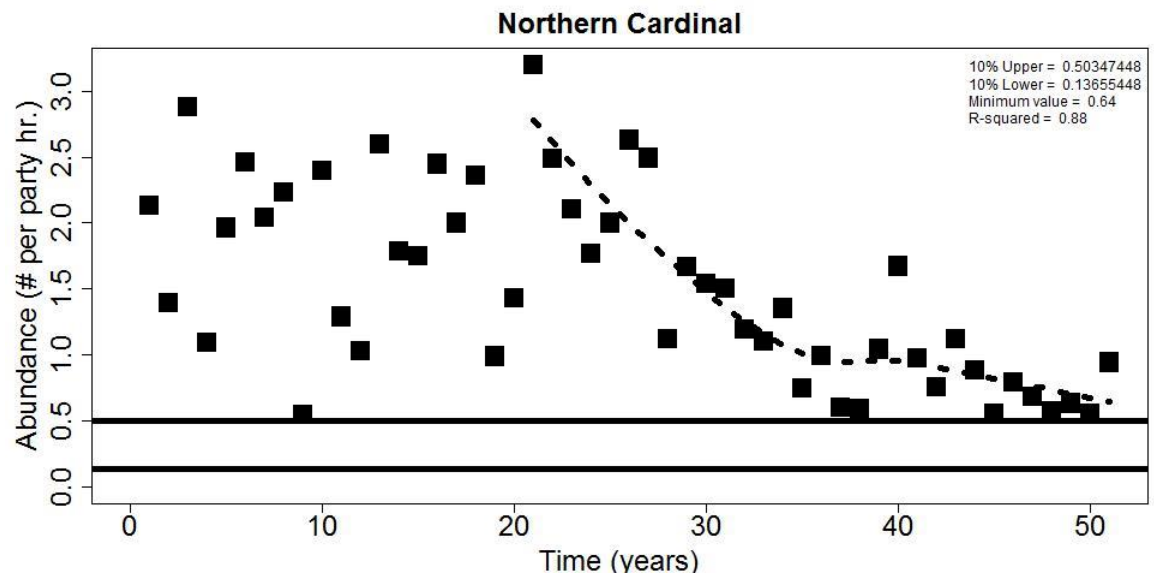


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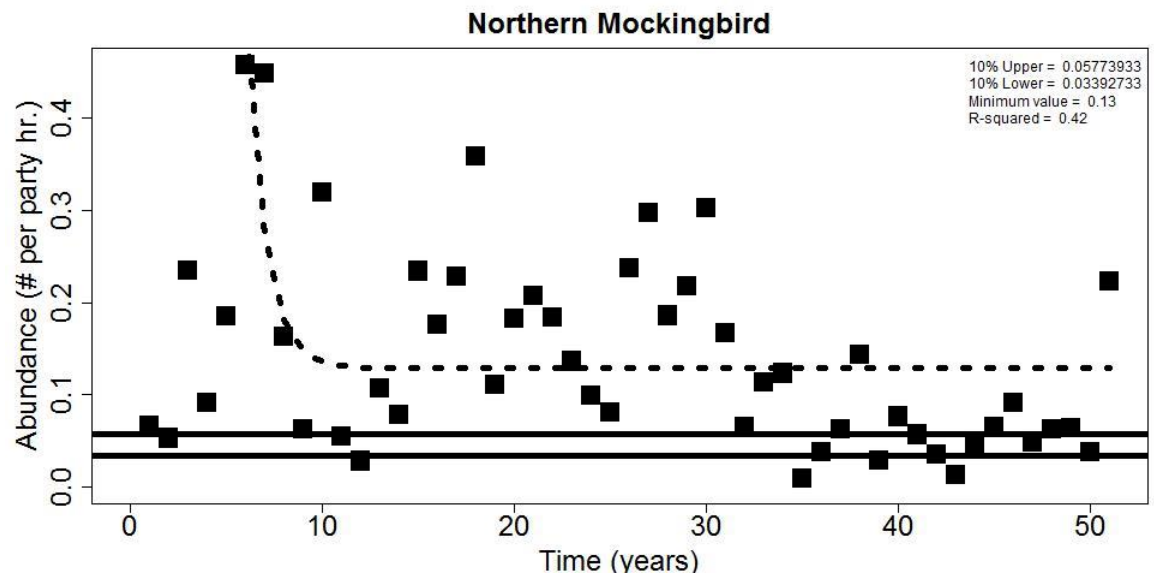


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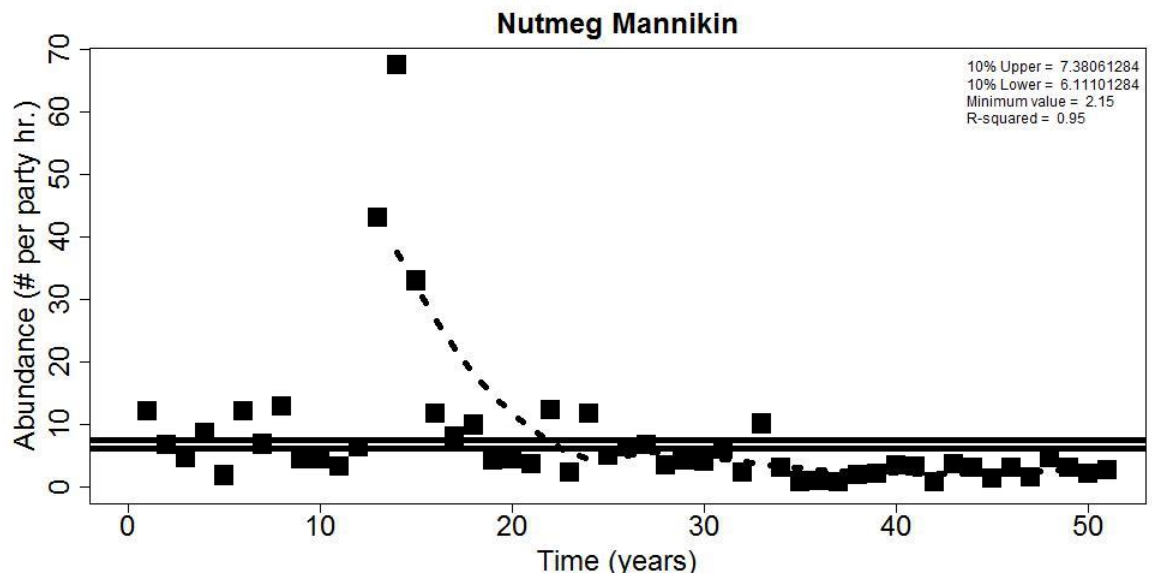


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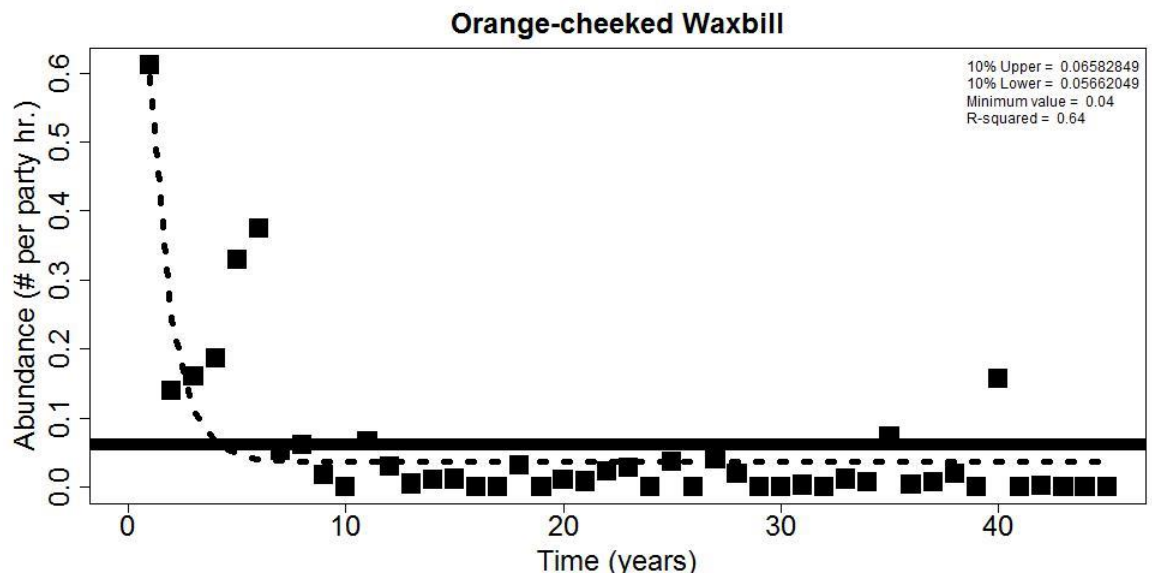


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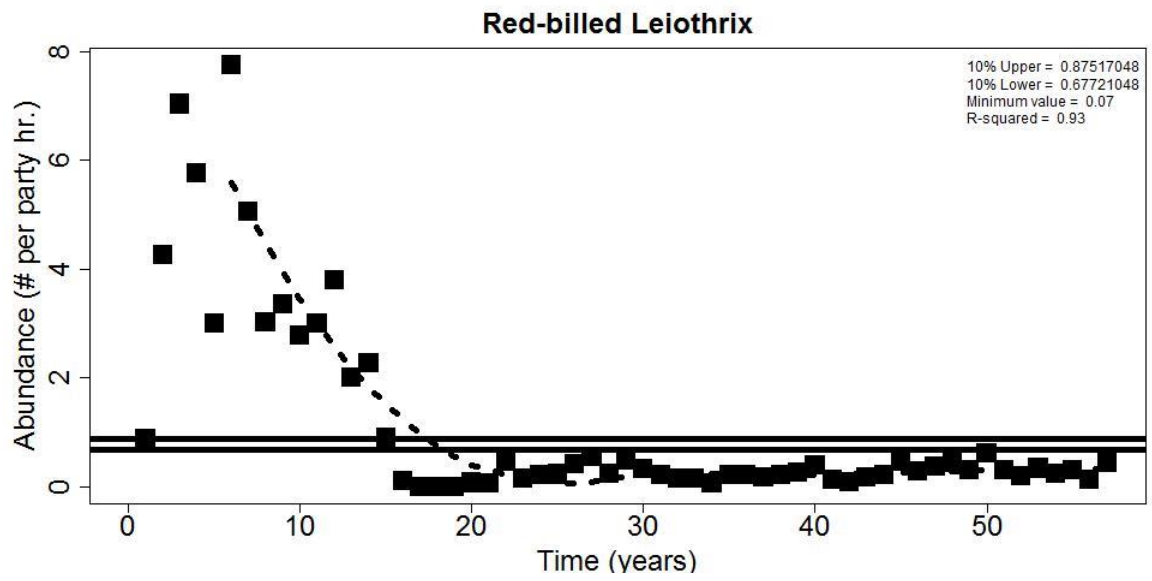


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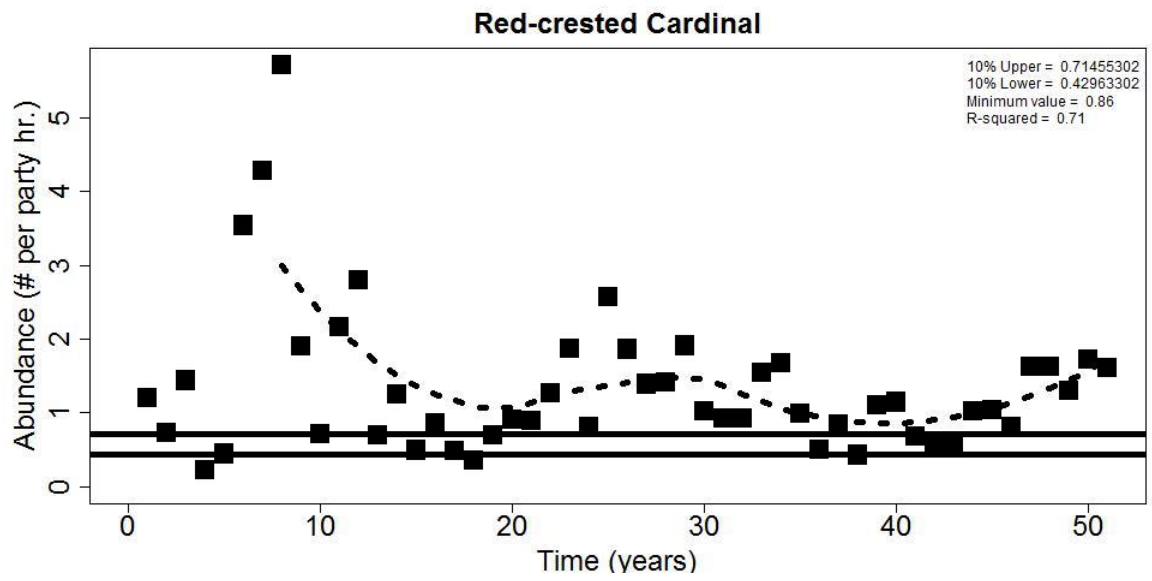


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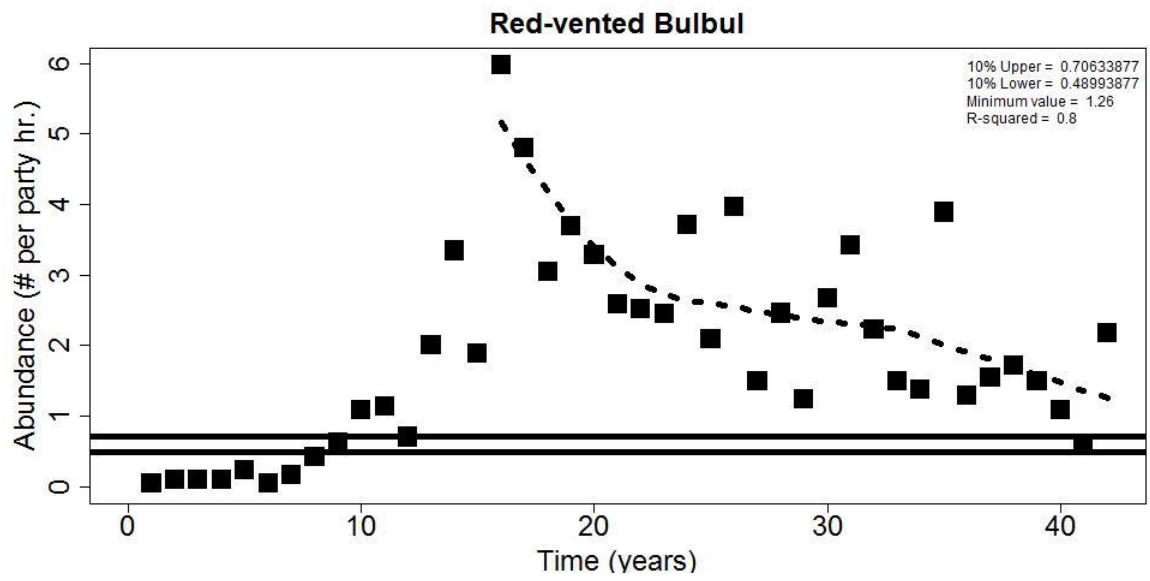


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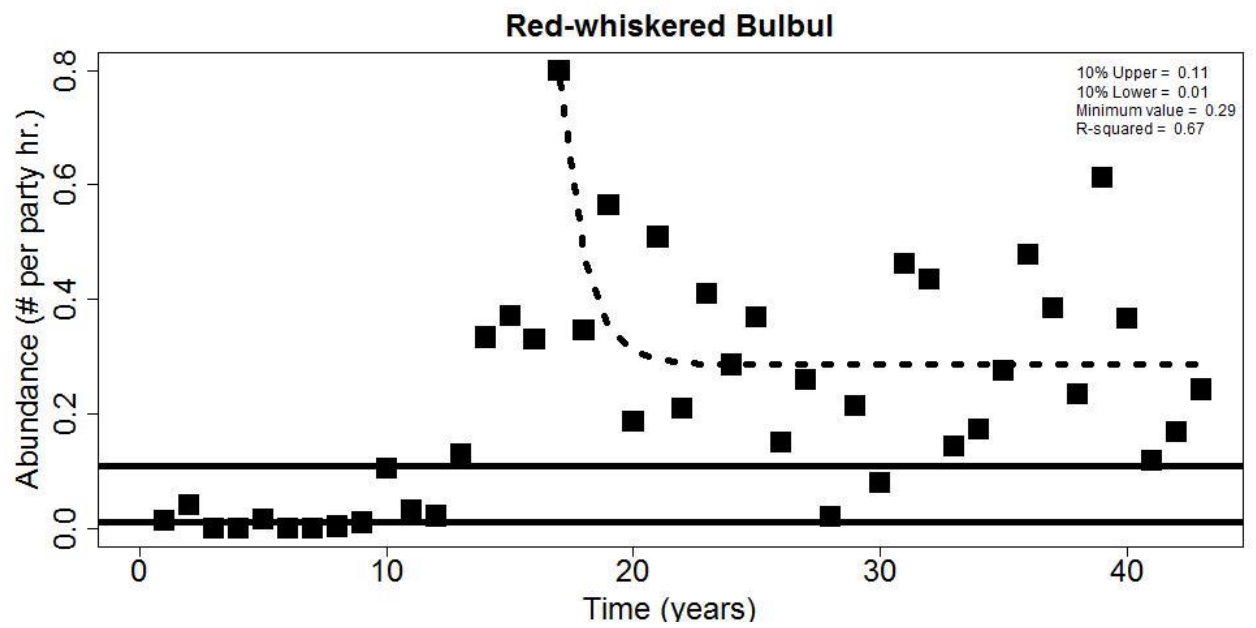




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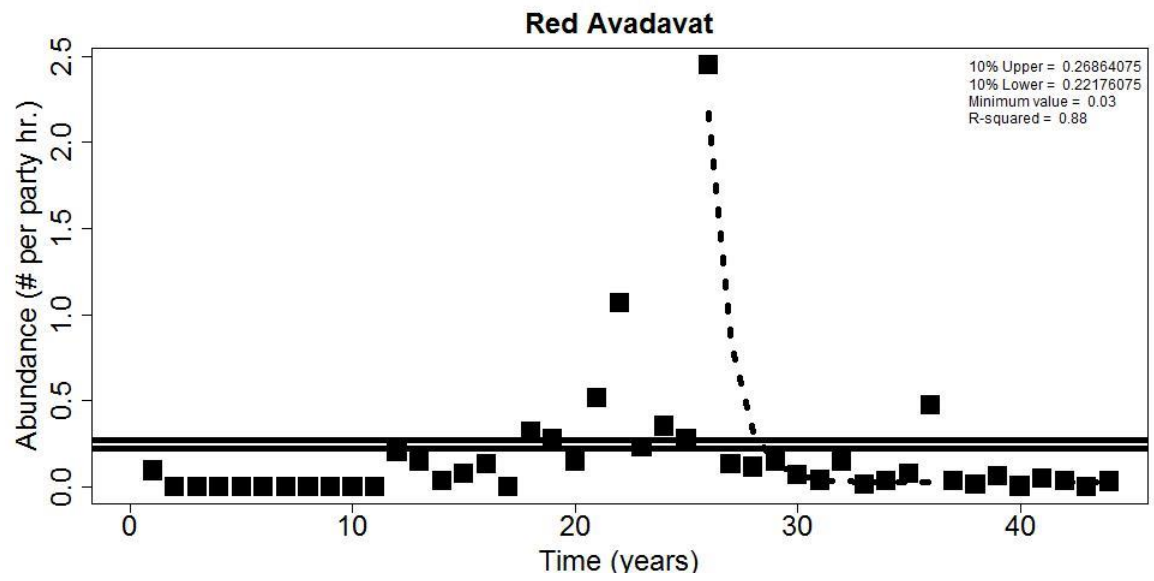


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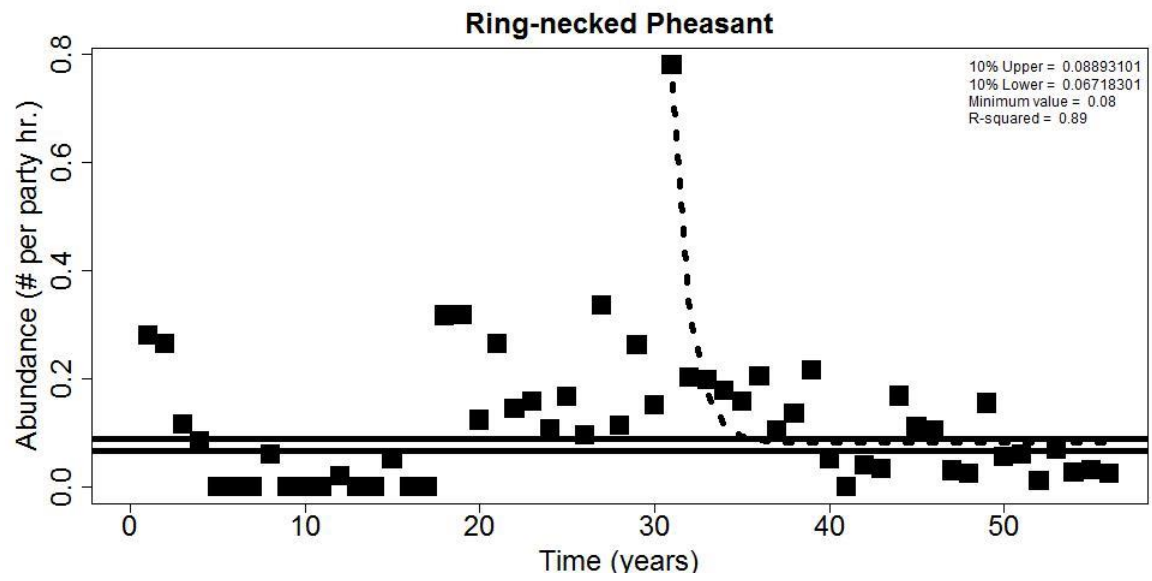


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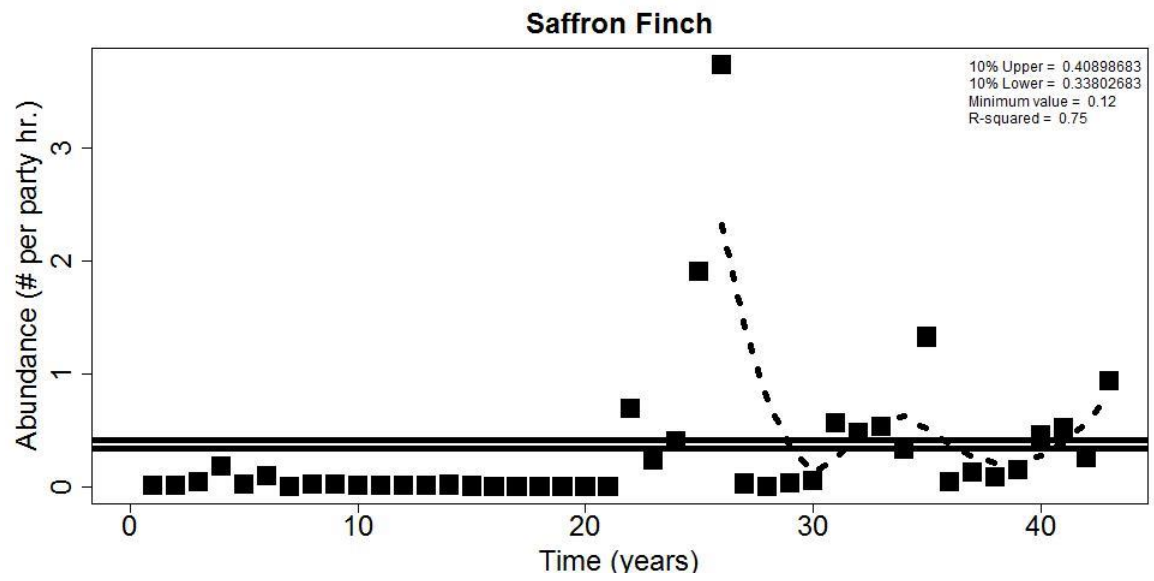


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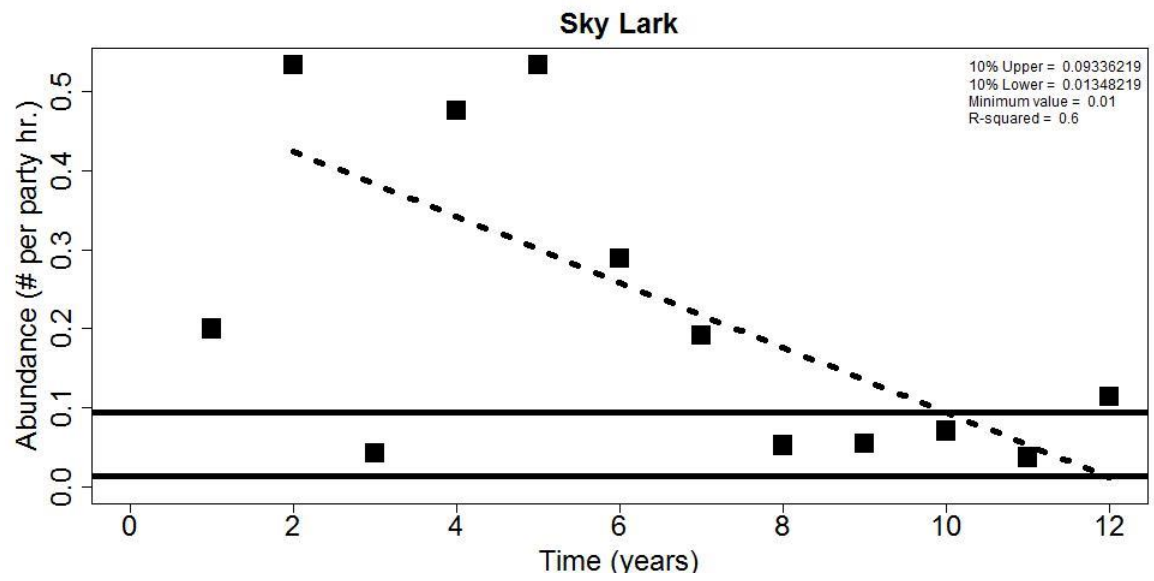


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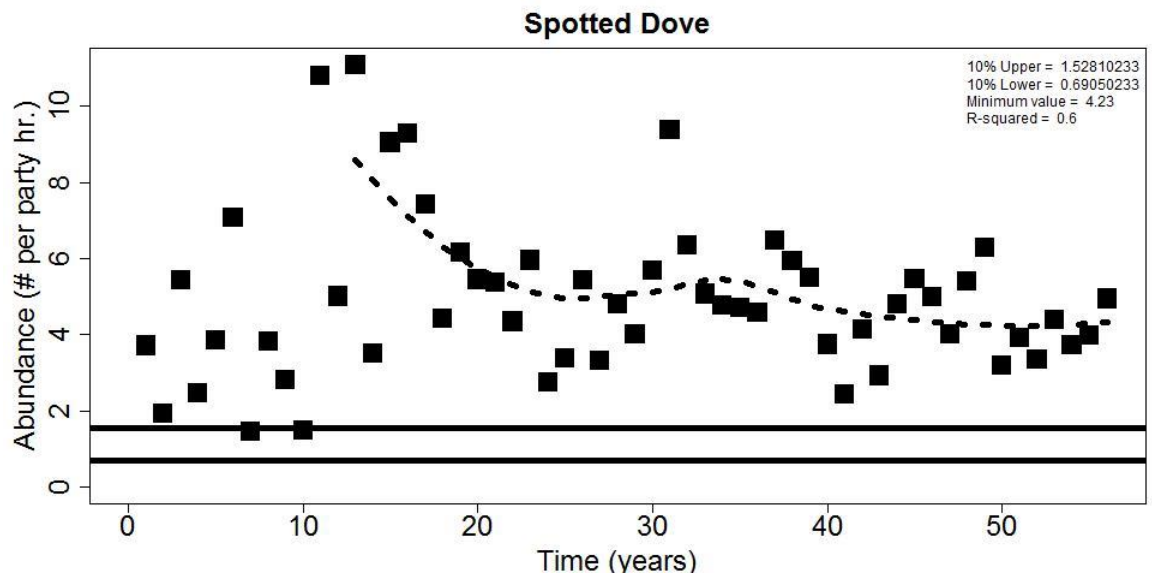


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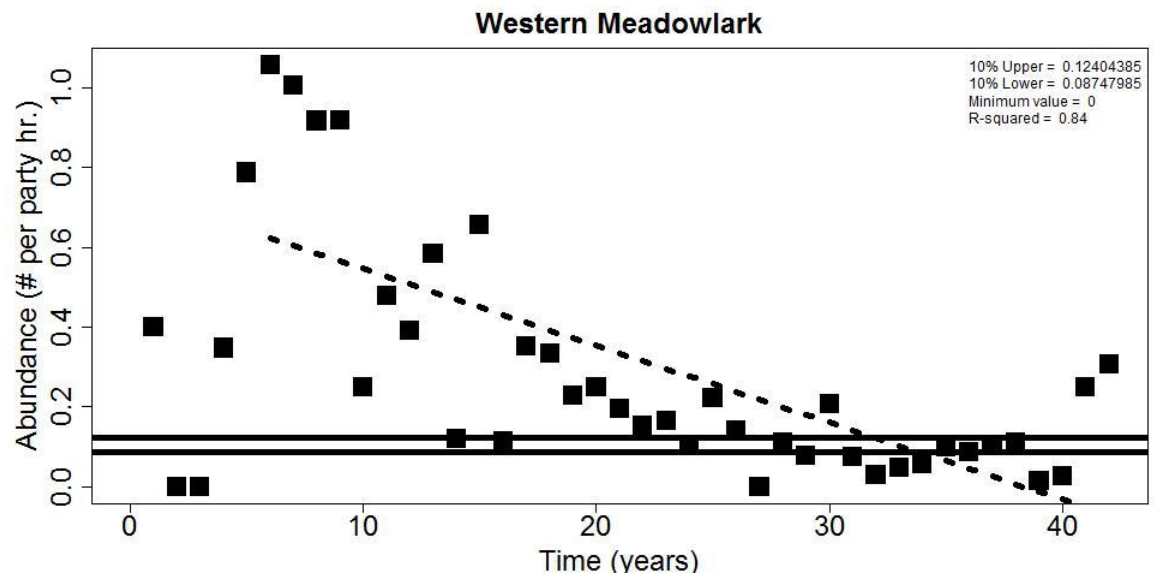


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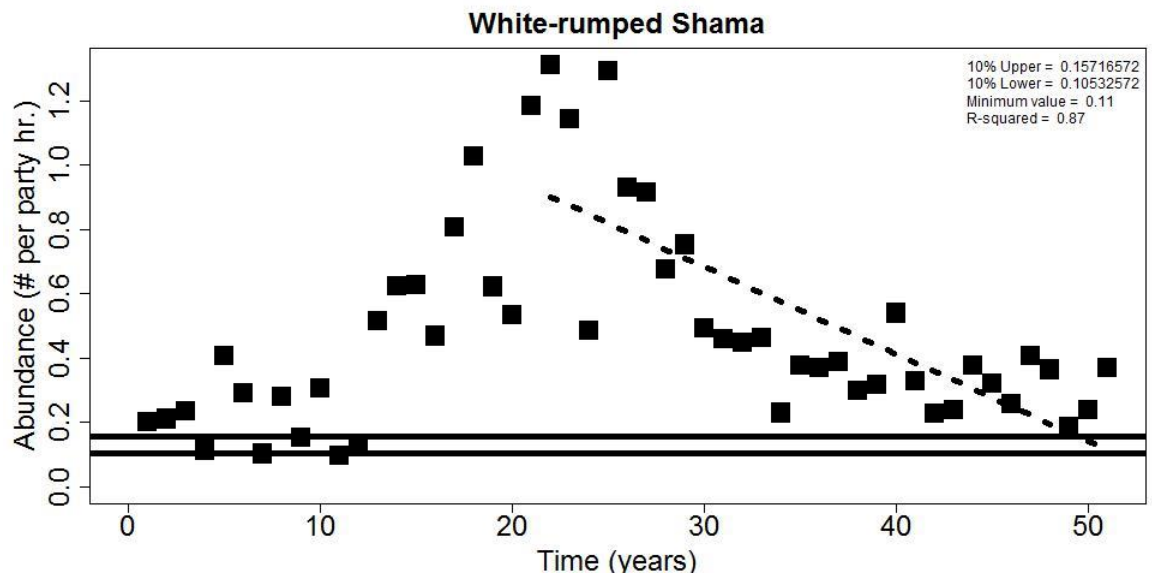


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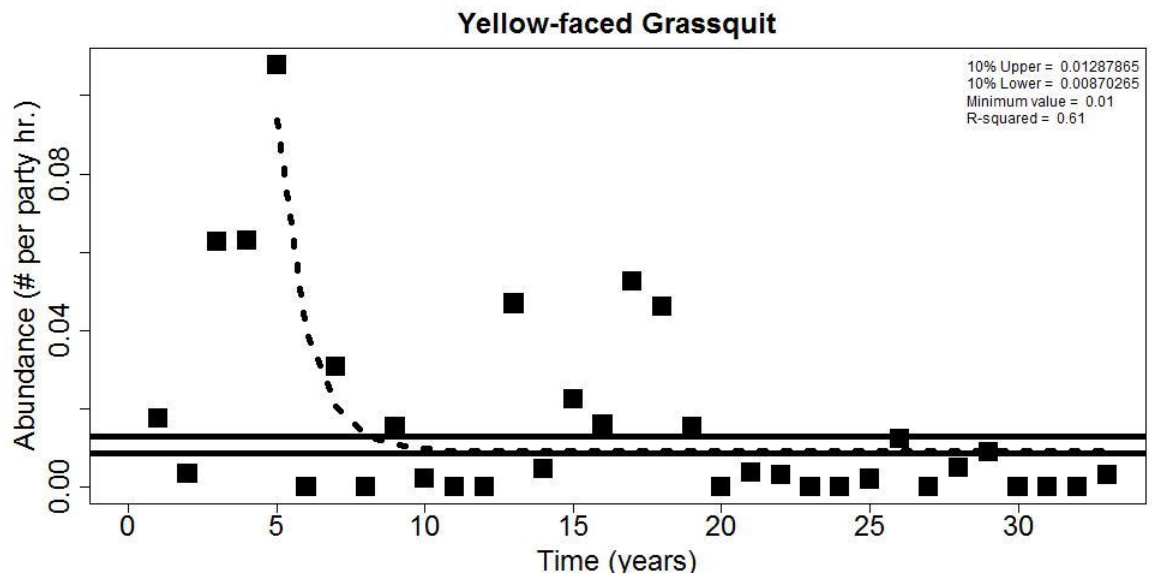




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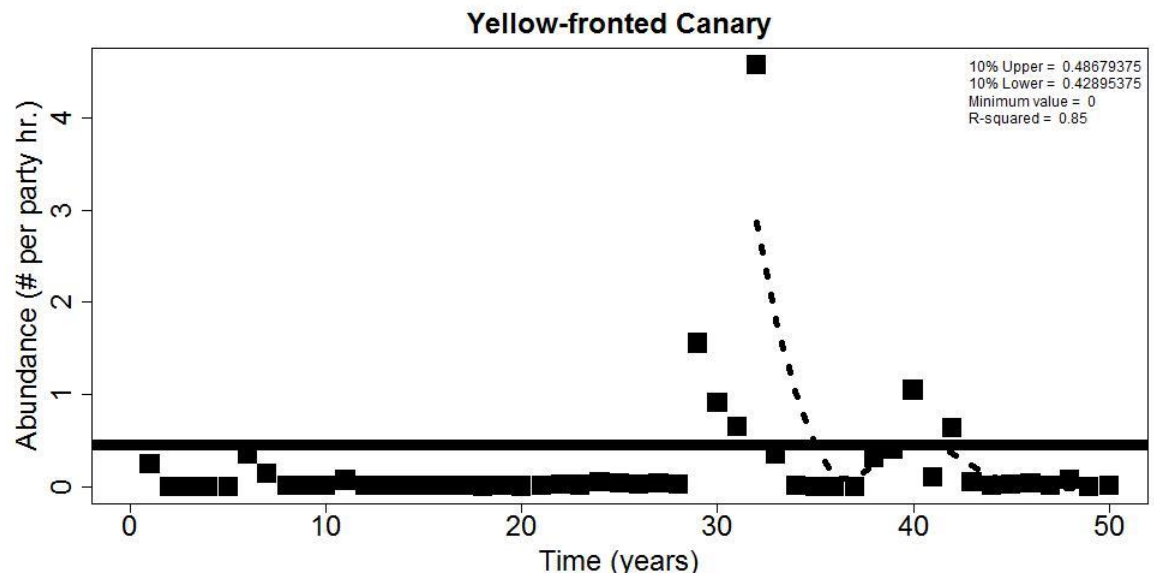
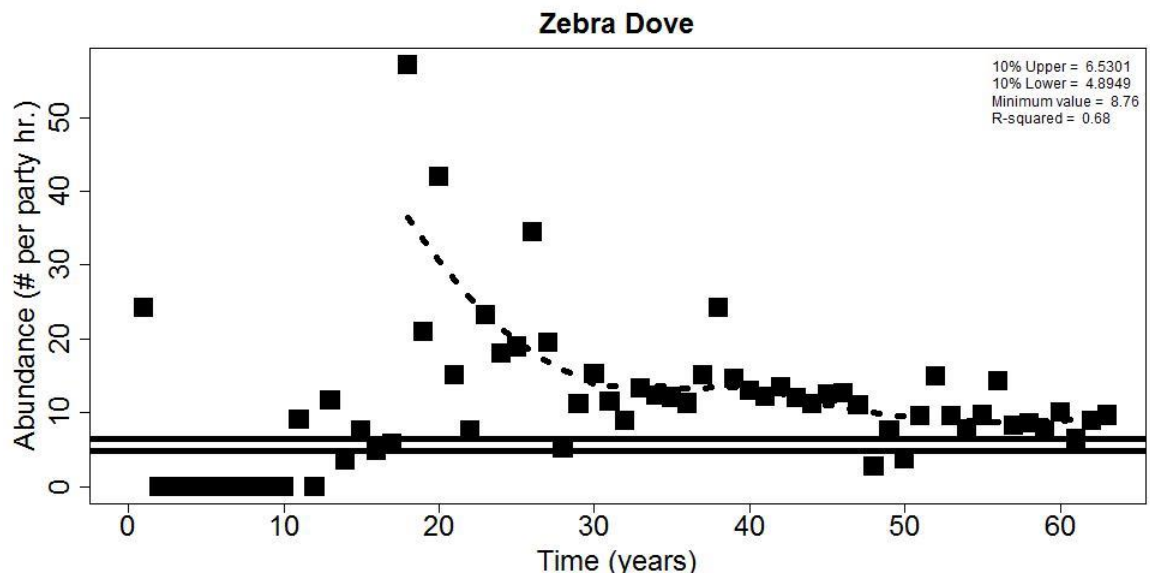


Figure S33.



## Conclusion

Advancing our knowledge regarding the prediction of population dynamics and those exotic populations that may become invasive or those native populations that may collapses is an important goal to improve conservation and management efforts. Greater understanding of species' population biology will better prepare us to deal with very rare populations when they are detectable but before they are so common that management is intractable, and will help manage increasingly rare native species as they collapse. My work advances the fields of conservation and invasion ecology in terms of both theory and application of population biology by exploring complex population dynamics. I rely on time series of abundance data extensively, a proxy for population impacts. The impact in each of these traditional density-impact curves is in terms of economic cost, but can convert to ecological impacts.

My results provide insight regarding the extent and degree of these impacts; e.g., long lag phases will lead to delays in impact. Additionally, population collapses may result in such rapid and dramatic decline that the population has almost no impact. My dissertation has directly addressed the questions and provides important and novel results on these fronts.

Because there is no agreed upon definition for lag phases, it is difficult to assess their prevalence and underlying mechanisms. Based on recent research, I overcome this issue and define a lag as a discrete stage in population growth with a clear end point after which the population transitions into a phase of faster growth. Thus, I set a single stage process against two stage processes for objective quantification of lag phases. I determined that 15 out of 17 exotic avian populations on the Hawaiian Islands considered

experienced lag phases. This suggests that management officials cannot afford to delay management actions for exotic species that have existed in low numbers for a long time, as their rarity may not continue indefinitely.

After assessing lag phases, I investigated their inverse, population collapses. Collapses are similarly poorly defined both empirically and quantitatively. I used IUCN criteria for endangered species as my quantitative definition: a decline in abundance of  $\geq 90\%$  within the longer of 10 years or three generations. I use Bayesian hierarchical models to determine the 90% reduction and to identify the appropriate ‘previous abundance’ with which to establish the lower-bound threshold. I found collapses in six of 12 endemic Hawaiian birds and 16 of 33 established exotic populations with enough data to which to apply our method. I have shown the utility of these methods for the identification and description of collapses, which may be a more common feature of exotic species’ population dynamics than previously thought, and also clearly occurs in native species’ population growth patterns as well.