Conservation Biology

Campephilus principalis), long assumed to have become extinct in the United States in the 1950s, but reportedly rediscovered in 2004. We analyzed the temporal pattern of the collection dates of 239 geo-referenced museum specimens collected throughout the southeastern United States from 1853 to 1932 and estimated the probability of persistence in 2011 as $<6.4 \times 10^{-5}$, with a probable extinction date no later than 1980. From an analysis of avian census data (counts of individuals) at 4 sites where searches for the woodpecker were conducted since 2004, we estimated that at most 1–3 undetected species may remain in 3 sites (one each in Louisiana, Mississippi, Florida). At a fourth site on the Congaree River (South Carolina), no singletons (species represented by one observation) remained after 15,500 counts of individual birds, indicating that the number of species already recorded (56) is unlikely to increase with additional survey effort. Collectively, these results suggest there is virtually no chance the Ivory-billed Woodpecker is currently extant within its historical range in the southeastern United States. The results also suggest conservation resources devoted to its rediscovery and recovery could be better allocated to other species. The methods we describe for estimating species extinction dates and the probability of persistence are generally applicable to other species for which

on se basan en datos de muestreo para conteos de especies co-ocurrentes que se encuentran en la búsqueda de una especie objetivo. Ilustramos ambos

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métodos con un estudio de caso de Campephilus principalis*, considerada extinta en los Estados Unidos desde la década de 1950, pero supuestamente redescubierta en 2004. Analizamos el patrón temporal de fechas de colecta de 239 especímenes de museo georeferenciados colectados en el sureste de Estados Unidos de 1853 a 1932 y estimamos que la probabilidad de persistencia en 2011 es* $< 6.4 \times 10^{-5}$*, con una probable extinción no posterior a 1980. De un an´*

Poisson models that assume, instead, that a population declines before reaching extinction. However, these methods have proven difficult to implement (Solow 2005).

On the basis of binary time series data for 27 possibly extinct bird populations, Vogel et al. (2009) endeavored to assess the fit of such records to a series of underlying sampling distributions and were unable to reject the uniform distribution for presence–absence data over time. However, statistical power to discriminate among distributions was low, and both the uniform distribution and 2 declining distributions (truncated negative exponential and Pareto) offered a reasonable fit to the binary occurrence data. With this result in mind, Elphick et al. (2010; see also Roberts et al. 2010) applied Solow's (1993*a*) stationary Poisson method and Solow and Roberts' (2003) nonparametric method to estimate extinction dates for 38 rare bird taxa on the basis of physical evidence and expert opinion.

In this paper, we propose a new statistical method for estimating extinction dates that does not assume population sizes are constant in the time periods before extinction and does not treat occurrence records as a binary presence–absence sequence. Instead, our method takes full advantage of counts of specimens (or other reliable occurrence records) recorded during specific time intervals (McCarthy 1998; Burgman et al. 2000).

Dated, georeferenced specimens, deposited in museums and natural history collections around the world, represent a rich source of data for conservation biologists (Burgman et al. 1995; McCarthy 1998; Pyke & Erhlich 2010) and are often the only source of information available on past abundances and geographic distribution. Museum specimen records correspond to distinct occurrence records of different individuals, which is often not the case for visual sightings, photographic records, or other indirect signs of a species' presence. Our method relates specimen records, in a simple way, to population sizes and provides estimates of the probability of occurrence in past or future time intervals.

Programs aimed at rediscovering possibly extinct species (Roberts 2006) sometimes offer a second, and relatively untapped, source of information for the statistical assessment of extinction that is independent of specimen records. Rediscovery programs often use standardized sampling methods developed for species richness inventories (e.g., Hamer et al. 2010) that record individuals of all species encountered or sampled. Although such data do not provide direct information on the probability of the persistence of the target species, they can be used to estimate the minimum number of undetected species in an area, one of which might include the target species. Chao et al. (2009) estimated the probability that additional sampling would reveal an additional species that had been undetected by previous inventories. These analyses yield simple stopping rules for deciding whether the search for a species should be abandoned in a particular area once the probability of detecting a new species becomes very small.

We analyzed museum specimen records and bird counts from contemporary censuses to illustrate the application of these methods to the case of the Ivory-billed Woodpecker (*Campephilus principalis*), which is generally assumed to have become extinct in southeastern North America in the 1950s (Jackson 2004; Snyder et al. 2009), but was reportedly rediscovered in 2004 (Fitzpatrick et al. 2005, Sibley et al. 2006). The last well-documented population of this large, strikingly-patterned woodpecker disappeared from northeastern Louisiana in the mid-1940s (Jackson 2004; Snyder et al. 2009). Sightings in subsequent decades were sporadic and unconfirmed, and the Ivory-billed Woodpecker was generally presumed extinct until the recent reports from Arkansas. The video image recorded in the Cache River National Wildlife Refuge in 2004 (Fitzpatrick et al. 2005) and a subsequent flurry of uncorroborated sightings captured the public's imagination, precipitated major, fully documented search efforts, and triggered recovery plans under the U.S. Endangered Species Act (U.S. Fish & Wildlife Service 2009). However, the video evidence was soon disputed by independent researchers (Sibley et al. 2006; Collinson 2007), who argue the images are of the similarly sized Pileated Woodpecker (*Dryocopus pileatus*).

Because of the symbolic importance of the Ivory-billed Woodpecker and the potential economic impact of actions mandated under the Endangered Species Act, we think it is essential to quantify the probability that it persists and the probability of discovering it through additional searches. We applied a statistical approach to answer 2 questions. First, on the basis of the temporal distribution of museum specimens collected during the 19th and 20th centuries (Hahn 1963), what is the probability that the woodpecker survives in the 21st century? Second, given the investment in search efforts, since 2004, that have not resulted in an undisputed occurrence record, what is the probability that any additional species will be found at the survey sites with further effort?

Methods

Specimen-Based Analyses

Dated museum specimens from georeferenced localities provide an undisputed record of Ivory-billed Woodpecker occurrences in the United States ($n = 239$; Fig. 1 & Supporting Information). The oldest dated museum specimen was collected in 1806, when the woodpecker was described as "common" within its historic range

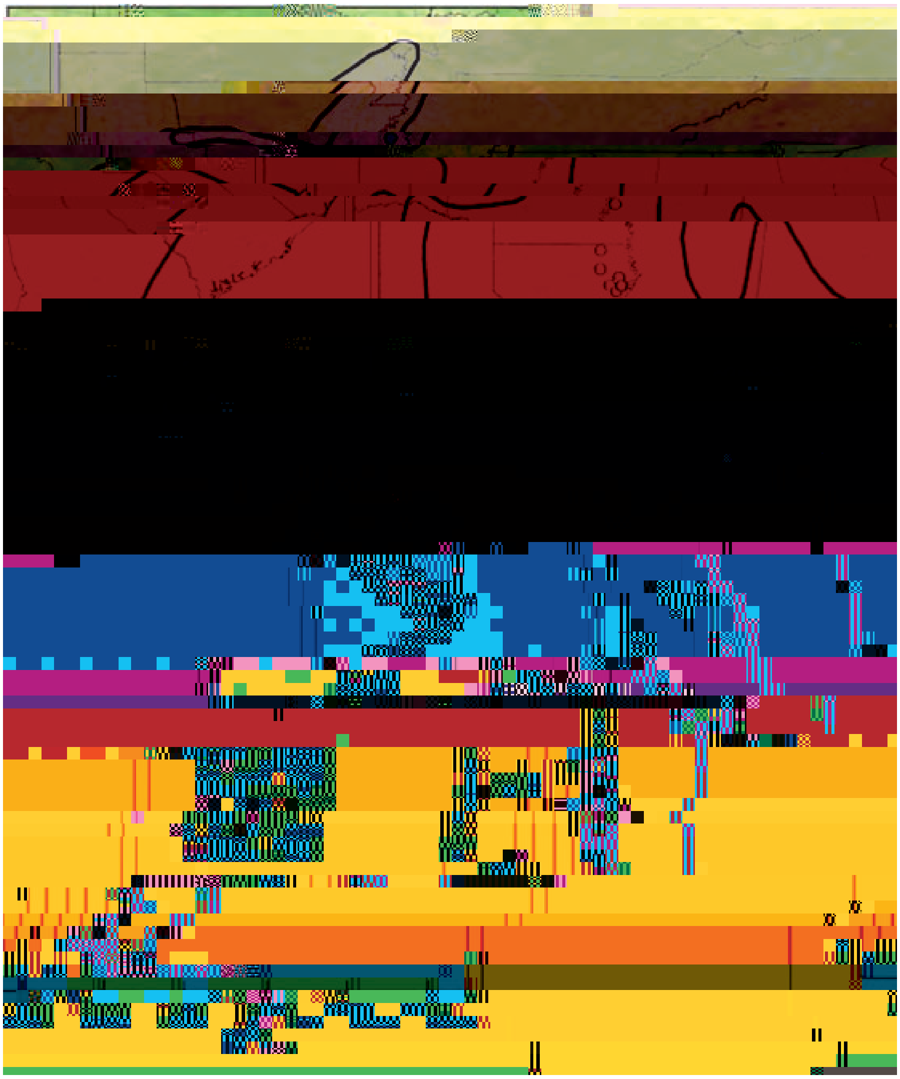

Figure 1. Spatial and temporal distribution of Ivory-billed Woodpecker specimens (black line, approximate historical range boundary of the Ivory-billed Woodpecker [Tanner 1942]; points, 1–6 museum specimens with precise locality data [239 total specimens; Supporting Information]; dark blue points, collections made 1850–1890, when specimen numbers in museum collections were increasing [Supporting Information]; yellow, light blue, and red points, collections made 1891–1932, when specimen numbers were declining [see inset]; solid red curve, data in 4-year interval bins fitted with Poisson generalized additive model; dashed red lines, 95% CI; red arrow, originates in northeastern Louisiana, where the last specimen was collected in 1932).

through a network of professional collectors in the southern states, particularly Florida. As the species became progressively rarer during the 1870s and 1880s (Hasbrouck 1891), the demand for specimens increased, resulting in high retail prices and intensive unregulated hunting by professional collectors (Hasbrouck 1891; Snyder 2007; Snyder et al. 2009). The number of specimens collected peaked between 1885 and 1894 and then declined rapidly as local populations were extirpated by changes in land use, subsistence and trophy hunting, and collecting for museums (Fig. 1 & Supporting Information). The decline in abundance and specimen accumulation rates oc-

c is the cost of making a single observation, and R is the reward for detecting each previously undetected species (Rasmussen & Starr 1979). Because R for an Ivory-billed Woodpecker is extremely large relative to c, c/R is close to zero. Thus, a simple, empirical stopping rule is to stop searching when each observed species is represented by at least 2 individuals in the sample ($f_1 = 0$). The same stopping rule can be derived independently from theorems originally developed by Turing and Good for cryptographic analyses (Good 1953, 2000). Both derivations imply that when $f_1 = 0$, the probability of detecting a new species approaches zero. We applied this stopping rule to the census data for the set of species that regularly winter in bottomland forest, such as the Ivory-billed Woodpecker, which was sedentary and occupied year-round territories.

To estimate the number of undetected species at the 4 sites, we used 3 species richness estimators that rely on information contained in the frequency distribution of rare species: Chao1, abundance-based coverage estimator (ACE), and the first-order jackknife (Colwell & Coddington 1994; Chao 2005; Supporting Information). To estimate the additional sampling effort needed to find these undetected species, we used equations recently derived by Chao et al. (2009).

What is the probability p^* that sampling one additional individual in a site will yield a previously undetected species? Turing and Good obtained the first-order approximation $p^* \approx \frac{f_1}{n}$, which is the proportion of singletons in the sample of n individuals (Good 1953, 2000). We extended Turing's formula to apply to samples in which the rarest species abundance class is not necessarily the singleton class (Supporting Information). When doubletons (f_2) form the rarest abundance class, the probability of obtaining a previously undetected species is $p^* \approx \frac{2f_2}{n^2}$.

Results

Specimen-Based Analyses

Our specimen-based model predicted the probability of persistence of the Ivory-billed Woodpecker in 2005–2008, the most recent complete 4-year interval. The estimated number of specimen records between 2005 and 2008 was $\hat{\mu}_t = 6.4 \times 10^{-7}$ (SE $= 5.9 \times 10^{-6}$; Supporting Information). The predicted probability of population persistence depends on the assumed population size (N) in 1929–1932. The estimated persistence probability ranged from 1.3×10^{-5} for $N = 20$, to 0.0006 for $N = 1000$, and to 0.0313 for $N = 50{,}000$ (Table 1).

On the basis of these probabilities, if we set a persistence probability of <0.05 as the criterion of probable extinction, the estimated extinction interval for the Ivory-billed Woodpecker ranged from 1961–1964 for $N = 20$, to 1969–1972 for $N = 100$, and to 1981–1984 for $N = 1000$ (Table 1 & Supporting Information). Persistence later than 2008 was unlikely unless the hypothetical population size was $>50{,}000$ individuals in 1929–1932. With a persistence probability of <0.01 as the criterion for probable extinction (last column in Table 1), extinction was projected to have occurred in 1969–1972 for $N = 20$, in 1977–1980 for $N = 100$, in 1993–1996 for $N = 1000$, and after 2008 for $N = 50{,}000$. Tanner (1942) estimated that approximately 22 woodpeckers were alive in the southeastern United States during the late 1930s. The likelihood that the total population size at this time was 10,000–50,000 individuals is low. Thus, for a more realistic population size in 1929–1932 of <100, the estimated probability of persistence was 6.4×10^{-5} and the probable extinction date was no later than 1980 (Table 1).

Table 1. Hypothetical total population sizes of Ivory-billed Woodpeckers from 1929 to 1932, the corresponding predicted probability of persistence in the time interval 2005 to 2008, and the estimated extinction interval (the earliest period for which the probability of persistence is <0.05 or <0.01).

Hypothetical 1929–1932 population size	*Probability of persistence 2005–2008*	*Estimated extinction interval (<0.05)*	*Estimated extinction interval (<0.01)*
20	1.3×10^{-5}	1961–1964	1969–1972
100	6.4×10^{-5}	1969–1972	1977–1980
500	0.0003	1977–1980	1989–1992
1,000	0.0006	1981–1984	1993–1996
5,000	0.0032	1993–1996	2001–2004
10,000	0.0063	1997–2000	2005–2008
50,000	0.0313	2005–2008	>2008

Analyses of Contemporary Census Data

According to results of the stopping-rule analysis, the search for Ivory-billed Woodpeckers should be halted at the Congaree River site. After 15,500 observations, there were no singletons and therefore almost zero probability of detecting the woodpecker or any other species not already observed that winters regularly in bottomland hardwood forests at this locality. Surveys at each of the other 3 sites have accumulated fewer than half this number of observations, and each of these surveys included one or more winter-resident species represented by only a single individual (Fig. 2). Because of the large sample sizes used in these surveys, the 3 estimators converged to very similar predictions of between 1 and 3 undetected species at each of the 3 sites (Table 2 & Supporting Information). Estimates of the additional number of observations needed to find these undetected species for the Choctawhatchee River and Pearl River sites were 6613 and 3061 individuals, respectively, about the same as the number of individuals already sampled. For the

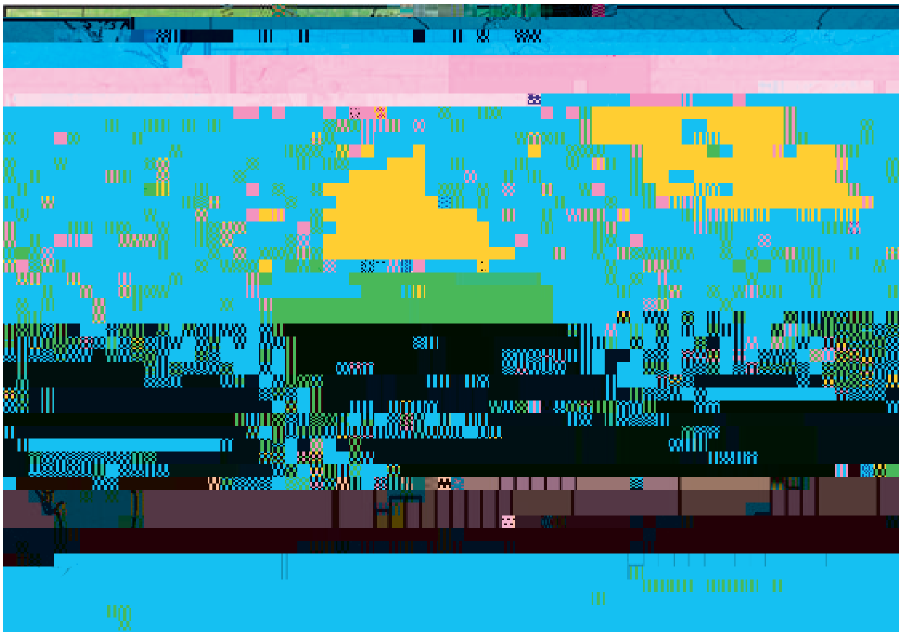

Figure 2. Avian data from 4 bottomland sites in the southeastern United States, where searches for Ivory-billed Woodpeckers were conducted in 2006 and 2007: Congaree River, South Carolina (15,500 individuals, 56 species), Choctawhatchee River, Florida (6,282 individuals, 55 species), Pearl River, Louisiana and Mississippi (3,343 individuals, 54 species), Pascagoula River, Mississippi (6,701 individuals, 54 species). Histograms depict the number of species represented by a particular number of individuals on an octave scale (1, 2, 3–4, 5–8, 9–16, . . . , 2049–4096), which is commonly used to represent species abundance data (Magurran 2004) (red, singletons [species for which exactly 1 individual has been recorded in a census]; yellow, doubletons [species for which exactly 2 individuals have been recorded in a census]; y-axis range, 0–15 species). No singletons were detected at Congaree River.

Pascagoula River site, the required additional number of observations was estimated at 4179, approximately two-thirds of the number sampled to date.

At all 4 sites, the probability p^* that the next individual

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Vogel, R. M., J. R. M. Hosking, C. S. Elphick, D. L. Roberts, and J. M. Reed. 2009. Goodness of fit of probability distributions for sightings as species approach extinction. Bulletin of Mathematical Biology ,701–719.

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Appendix S1. A general statistical method for estimating the probability of persistence from museum specimen records

Step 1. The analysis uses museum specimen frequency data in the form of yearly records as in Appendix S6. Because the raw (yearly) counts typically vary (including nonparametric regression). Thus the GAM is flexible and can be fit to many different kinds of temporal trends. To estimate each f(t), we fit the widely used penalized regression spline model (Wahba 1990, Ruppert et al. 2003) and selected cubic regression splines as the basis for constructing each f(t). The penalized regression spline model controls the degree of smoothness by adding a penalty to the likelihood function. This model usually provides a better fit than parametric linear or quadratic models. The implementation of the penalized regression spline can be found in many software applications, including the Proc Glimmix in SAS. A widely used and free software is the mgcv package in R (Wood, 2006) which can be downloaded from http://www.r-project.org/. We used Ivory-billed Woodpecker data as an example in Appendix S3 to illustrate the model fitting procedures.

Step 3. After the model fitting, we obtain a fitted time series $\{\hat{\mu}_t, t = 1, 2, \ldots, T\}$. Let k be the latest time period with non-zero specimen records. That is, after time period k, there are no specimen records ($Y_t = 0$ for $t > k$). For a hypothetical population size N in the time interval k, define p as the probability that any individual would be collected as a specimen within a single time interval. This probability billed Woodpecker data).

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Range contraction undoubtedly began in earnest with clearing of forests along the lower Atlantic coastal plain in the Colonial period. The final period of extinction started after the Civil War, when northern timber companies purchased huge tracts of cheap "government owned" land in the southern states. Most virgin timber was cut between 1870 and 1930 (Williams 1989). Remnant stands lasted until the early 1940s, but the demand for lumber during WW II for gun stocks, cargo pallets, and plywood for PT boats finished those tracts off (and the woodpeckers

Brain, J. P., and P. Phillips. 1996. Shell gorgets. Styles of the late prehistoric and protohistoric Southeast. Peabody Museum Press, Peabody Museum of Archaeology and Ethnology,

Appendix S3. Application to Ivory- billed Woodpecker museum specimen frequency data

In this Appendix, we apply the general estimation procedures in Appendix S1 to the Ivory-billed Woodpecker specimen data and present details that are specific to this data set. Because the yearly specimen totals for Ivory-billed Woodpecker in museums (Appendix S7; panel A of Appendix S6) varied considerably, we binned these data in 4-year intervals to smooth the series (Appendix S8; panel B of Appendix S6). The interval size of 4-year was selected because it generated the largest adjusted R^2 compared with other bin intervals from 1-year to 5-years (adjusted R^2 values were 50%, 69%, 82%, 86%, and 84% respectively). The time series for

ashed red lines in text Fig.

As discussed in the main text, we assume that the decrease in specimens after 1894 reflects a true decline in Ivorythe corresponding estimated population size, we define p as the probability that any individual, living woodpeckers would be collected as a specimen or otherwise reliably detected and recorded within a single, 4-year time interval. Because the last specimen was collected

Wahba, G. 1990. Smoothing models for observational data. SIAM, Philadelphia.

Wood, S. N. 2006. Generalized additive models: An introduction with R. Chapman and Hall/CRC Press, Boca Raton.

Appendix S4. Statistical analysis of field survey data

Our statistical method for analyzing census lakes in bottomland

(coefficient of variation, a measure that characterizes the variation of species abundances) in the rare group:

$$\hat{\gamma}^2_{rare} = \max\left\{ \frac{D_{rare}}{C_{rare}} \frac{\sum_{i=1}^{10} i(i-1) f_i}{(\sum_{i=1}^{10} i f_i)(\sum_{i=1}^{10} i f_i - 1)} - 1,\ 0 \right\}$$

(3) The first-order Jackknife estimator (Burnham & Overton 1978) has the following form

$$\hat{S}_{jack1} = S_{obs} + [(n-1)/n] f_1$$

$$P^* = \frac{r!\, f_r}{n^r}.$$

Turing's formula represents the special case of r = 1. For the four census sites, the probabilities of detecting a new species with the next individual censused are discussed in the main text.

Supplementary references

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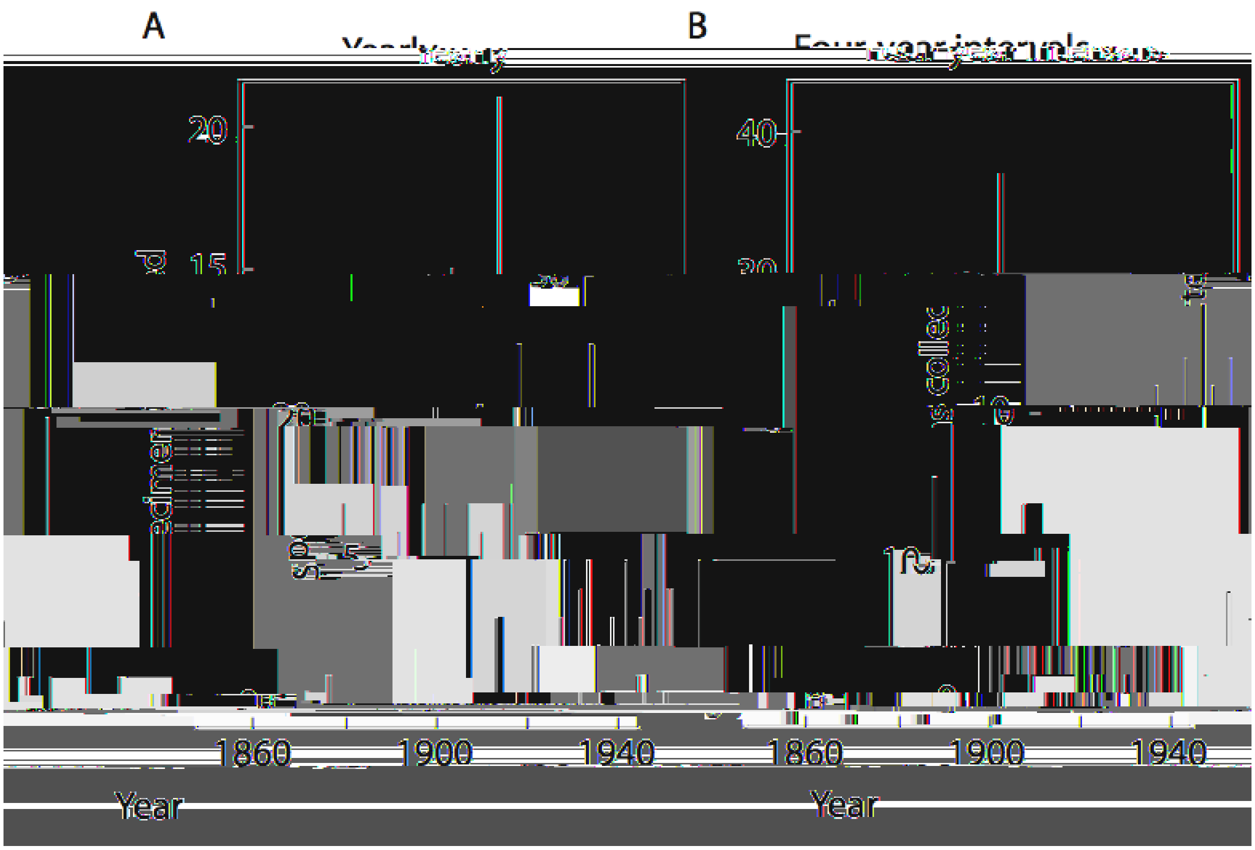
Appendix S5. Comparisons with other published analyses of Ivory-billed Woodpecker extinctions.

for Hawaiian forest birds and the Ivory-Billed Woodpecker. Avian Conservation and Ecology 3: http://www.ace-eco.org/vol3/iss2/art3/

Appendix S6. Dated museum specimens of Ivory-billed Woodpeckers from known georeferenced localities.



A. Yearly frequency data for museum specimens of the Ivory-billed Woodpecker. B. Museum specimen data binned in 4-year intervals. Data for the descending portion of collection curve also appear in Fig. 1 (graph inset).

Appendix S7. Temporal distribution of museum specimens of Ivory-billed Woodpecker collected in the United States since 1850.

Year	Frequency	Year	Frequency	Year	Frequency	Year	Frequency
1850	0	1871	0	1892	2	1913	1
1851	0	1872	1	1893	12	1914	5
1852	0	1873	0	1894	15	1915	0
1853	1	1874	1	1895	3	1916	0
1854	0	1875	0	1896	7	1917	1
1855	0	1876	10	1897	1	1918	0
1856	0	1877	11	1898	5	1919	0
1857	0	1878	2	1899	6	1920	0

Appendix S8. Binned yearly frequency distribution of museum specimens of the Ivory-billed Woodpecker

Period	Frequency	Period	Frequency		Frequency
1853-56	1	1881-84	21	1909-12	8
1857-60	2	1885-88	30	1913-16	6
1861-64	0	1889-92	25	1917-20	1
1865-68	0	1893-96	37	1921-24	0
1869-72	11	1897-00	14	1925-28	2
1873-76	11	1901-04	28	1929-32	1
1877-80	16	1905-08	25	> 1932	0

Zero means that there were no museum specimens collected in that four-year period. These data are plotted in Fig. 1 (inset graph) and in Figure S1.

Appendix S9. The Poisson GAM fitted number of Ivory-billed Woodpecker records $\hat{P}_t$ and the standard errors ($\hat{P}_t$) in each four-year interval.

Period

Appendix S10. Probabilities of persistence in different time intervals as a function of hypothetical population size.

Year	N=20	N=100	N=500	N=1000	N= 5000	N=10000	N=50000
1929-32	0.9998	1	1	1	1	1	1
1933-36	0.9866	1	1	1	1	1	1
1937-40	0.8842	1	1	1	1	1	1
1941-44	0.6552	0.9951	1	1	1	1	1
1945-48	0.4081	0.9273	1	1	1	1	1
1949-52	0.2278	0.7254	0.9984	1	1	1	1
1953-56	0.1197	0.4713	0.9587	0.9983	1	1	1
1957-60	0.0609	0.2696	0.7921	0.9568	1	1	1
1961-64	0.0305	0.1433	0.5386	0.7871	0.9996	1	1
1965-68	0.0151	0.0733	0.3166	0.533	0.9778	0.9995	1
1969-72	0.0075	0.0368	0.1709	0.3125	0.8464	0.9764	1
1973-76	0.0037	0.0183	0.0881	0.1684	0.6024	0.8419	0.9999
1977-80	0.001815	0.00904	0.044389	0.086808	0.3649	0.5967	0.9893
1981-84	0.000894	0.004461	0.022104	0.04372	0.2003	0.3605	0.893

Appendix S11. The first ten frequency counts in four sites censused for Ivory-billed Woodpeckers.

Census Site	Frequency counts	S

Appendix S12 Avian species and number of individuals censused at four localities in the southeastern United States.

Species	Census locality	
	Congaree River	Choctawhatchee River

Sitta pusilla	Nuthatch Brown-					