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Specimen-Based Modeling, Stopping Rules, and the Extinction of the Ivory-Billed Woodpecker

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Abstract: *Assessing species survival status is an essential component of conservation programs. We devised a new statistical method for estimating the probability of species persistence from the temporal sequence of collection dates of museum specimens. To complement this approach, we developed quantitative stopping rules for terminating the search for missing or allegedly extinct species. These stopping rules are based on survey data for counts of co-occurring species that are encountered in the search for a target species. We illustrate both these methods with a case study of the Ivory-billed Woodpecker (*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 sufficient museum collections and field census results are available.*

Keywords: avian censuses, *Campephilus principalis*, extinction estimation, extinction probability, Ivory-billed Woodpecker, museum specimens, species richness estimators, stopping rules

Modelado Basado en Especímenes, Reglas de Decisión y la Extinción de *Campephilus principalis*

Resumen: *La evaluación del estatus de supervivencia de las especies es un componente esencial de los programas de conservación. Diseñamos un nuevo método estadístico para estimar la probabilidad de la persistencia de especies a partir de la secuencia temporal de datos de colecta de especímenes de museo. Para complementar este método, desarrollamos reglas de decisión cuantitativas para terminar la búsqueda de especies ausentes o presuntamente extintas. Estas reglas de decisión 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 análisis de datos de censos aviares (conteos de individuos) en 4 sitios en los que realizaron búsquedas de* C. principalis *desde 2004, estimamos que cuando hay 1-3 especies no detectadas en 3 sitios (uno en Louisiana, Mississippi y Florida). En un cuarto sitio en el Río Congaree (Carolina del Sur), no hubo unidades simples (especies representadas por una observación) después de 15,500 conteos de individuos de aves, lo cual indica que es poco probable que incremente el número de especies ya registradas (56) con mayor esfuerzo de muestreo. Colectivamente, estos resultados sugieren que virtualmente no hay oportunidad para que* C. principalis *exista actualmente en su rango de distribución histórica en el sureste de Estados Unidos. Los resultados también sugieren que los recursos de conservación destinados a su redescubrimiento y recuperación deberían ser asignados a otras especies. Los métodos que describimos para la estimación de las fechas de extinción y la probabilidad de persistencia de especies generalmente son aplicables a otras especies de las que se disponga de suficientes colecciones de museo y censos de campo.*

Palabras Clave: *Campephilus principalis*, censos aviares, especímenes de museo, estimación de la probabilidad de extinción, estimadores de la riqueza de especies, reglas de decisión

Introduction

Increasing effort in conservation biology is being devoted to the analysis of extinction risk (Sodhi et al. 2008) and the search for rare, long unseen, or potentially extinct species (Eames et al. 2005). For many species, statistical methods offer a means to guide and assess these efforts. This paper introduces new statistical tools for this purpose that substantially extend the ability of existing methods (reviewed by Rivadeneira et al. 2009 and Vogel et al. 2009) to maximize the use of available data sources.

In practice, declaring a species extinct is rarely analogous to a coroner's certification of death. Instead, the assessment of extinction requires a probabilistic statement (Elphick et al. 2010) because extinction is very difficult to definitively establish (Diamond 1987). The search for a putatively missing species routinely begins with a retrospective analysis of the temporal sequence of occurrence records, including both dated museum specimens and field sightings. Imagine an idealized string of such temporal records, perhaps derived from annual surveys for a species. If there were no failures to detect an extant species, the data would consist of an uninterrupted string of ones (presences) until the date of extinction and thereafter a continued string of zeroes (absences) after the extinction event.

In reality, there are failures to detect an extant species, including historically rare species endemic to inaccessible places and formerly common, widespread species in decline. Thus, empirical data of this form often consist of irregular sequences of ones and zeroes. The statistical challenge is to distinguish between a terminal string of zeroes, ending in the present, that represents a probable extinction and one that more likely suggests nondetection. In the related context of the intentional eradication of invasive species, Regan et al. (2006) and Rout et al. (2009*a*, 2009*b*) used estimates of the probability of presence after a number of consecutive absences as the basis for decision making in light of trade-offs between the financial cost of continued searching and the ecological benefit of confirmed eradication.

Results of any method that assesses the probability of extinction hinge heavily on the quality of the data, which can range from reliable physical evidence (such as actual specimens or dated biological materials) to unconfirmed visual sightings (McKelvey et al. 2008). Analyses that incorporate more liberal criteria for detection inevitably lead to estimates of more recent (or future) extinction dates. If the confidence interval about these estimates extends to include the present, the statistical analysis implies that the species may be extant, even in the absence of recent occurrence records.

Rivadeneira et al. (2009) recently reviewed 7 existing statistical methods used to estimate extinction dates and associated confidence intervals. All 7 methods treat occurrence records as a binary sequence of presences and absences and assume a stable population size followed by sudden extinction. All but 2 methods poorly predicted known dates of extinction in simulations that modeled declining total detection probability (probability of occurrence $\times$ probability of sampling). Moreover, both these possible exceptions (Roberts & Solow 2003; Solow & Roberts 2003) tended toward excessive type I error (i.e., an extant species is declared extinct) (Rivadeneira et al. 2009).

Collen et al. (2010) showed that, for declining populations, the Roberts and Solow (2003) method (further discussed by Solow [2005]) is prone to both type I and type II errors (i.e., an extinct species is declared extant). In some simulation scenarios, the Roberts and Solow (2003) method tends to yield conservative confidence intervals that are too wide. Solow (1993*b*) proposes nonstationary

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 (Audubon 1832). The rate of specimen accumulation in museums and private collections did not accelerate until after 1850. Some specimens were collected by ornithologists, but the majority of specimens were obtained

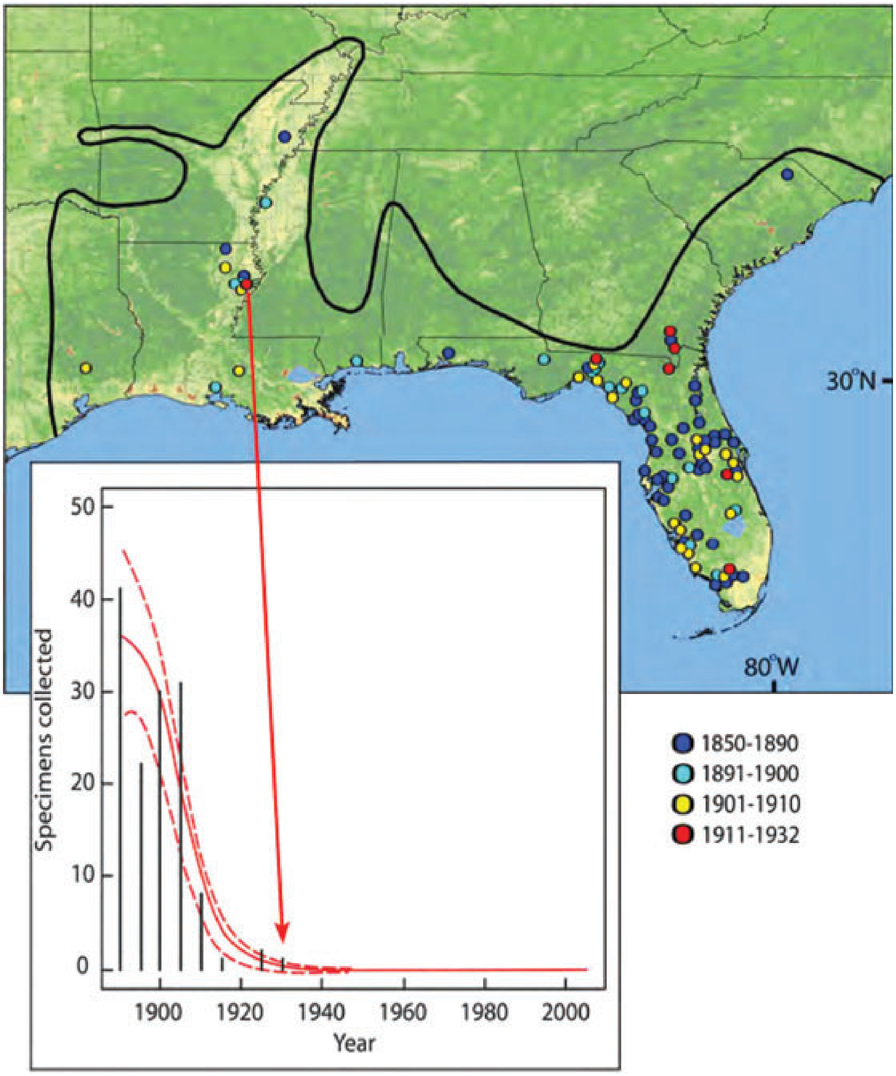

Figure 1. Spatial and temporal distribution of Ivory-billed Woodpecker specimens (black line, approximate historical range boundary of the Ivory-billed Woodpecker [Tanner 1942]; points, 1–6 museum specimens with precise locality data [239 total specimens; Supporting Information]; dark blue points, collections 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 occurred well before commercial hunting activities were effectively regulated by wildlife protection laws. Scientific collecting permits for Ivory-billed Woodpeckers continued to be issued until the early 1930s. After 1932, collecting was prohibited as concern for the species' survival increased. However, individuals continued to be sighted periodically for another decade. The last undisputed sightings of the species occurred in 1944, in the same remnant population in northeastern Louisiana from which the last museum specimen was collected legally in 1932 (Jackson 2004).

In short, the evidence indicates that the decrease in the number of Ivory-billed Woodpecker specimens collected between 1894 and 1932 reflects a true decline in abundance, rather than a decline in collection efforts, which were driven by free-market supply and demand, as evidenced by the high maximum prices for Ivory-billed Woodpeckers at a time when the supply of specimens dried up (Snyder 2007; Snyder et al. 2009). The long history of habitat loss from logging, and of sport and subsistence hunting, strongly suggests that the modest number of scientific specimens collected, in itself, contributed relatively little to the woodpecker's range-wide decline. The diminishing curve of museum specimens collected can be considered a proxy of total population size (Supporting Information).

To model the scientific specimen record as a proxy of population size, we treated the years between 1893 (the starting year of the peak 4-year interval for specimen collection) and 2008 (the final year of the most recent complete 4-year interval) as a series of 29 consecutive 4-year intervals (Supporting Information). We fitted a Poisson generalized additive model to this series (Wood 2006; Supporting Information), estimated the expected number of records (μ_t) in each 4-year interval after 1932, and calculated a corresponding 95% CI (Fig. 1 & Supporting Information).

The last museum specimen was collected in 1932. If the total population size of the Ivory-billed Woodpecker between 1929 and 1932 was N, then the proportion of the population represented by this single specimen is $p \approx 1/N$. One can interpret p as the per capita probability that a woodpecker would be collected as a specimen (or unequivocally documented) within a single, 4-year time interval. If one assumes this per-individual, conditional probability of detection is roughly constant after the 1929–1932 interval, the expected number of specimens μ_t depends on the probability of detection p and the population size n_t in the tth 4-year interval:

$$\mu_t = pn_t.$$

From this relation, n_t can be estimated for any subsequent time interval from the fitted $\hat{\mu}$ as

$$n_t \approx \hat{\mu}_t/p \approx \hat{\mu}_t N.$$

We treated the population size of Ivory-billed Woodpeckers in any specific 4-year interval as a Poisson random variable. Thus, we estimated the probability of population persistence in the tth interval as $1 - \exp(-n_t)$, the total probability of the nonzero classes of the Poisson distribution with mean n_t (Supporting Information). We assumed a Poisson distribution for 2 reasons. First, because the sample size was relatively small, it was statistically preferable for us to use a single-parameter model that could be estimated directly from the data (McCullagh & Nelder 1989). A 2-parameter negative binomial distribution is a generalized form of the Poisson, but it did not provide stable parameter estimates for these data. Second, mechanistic population-growth models of birth and death processes can lead to a Poisson distribution of population sizes (Iofescu & Táutu 1973).

The assumption that the probability of detection per individual (p) (but not the population's size [n_t]) was constant over all the time intervals was conservative for the purpose of estimating the probability of population persistence. If this assumption were in error, and p actually increased after 1932 because increased detection effort was focused on a declining population, then our estimates represent a conservative upper bound for the probability of population persistence.

Because the last undisputed sighting was in 1944, we were able to conduct an important benchmark test of our specimen-based model by estimating persistence probability in the 1941–1944 interval. With the specimen-based generalized additive model, the expected number of records for this interval (Fig. 1 & Supporting Information) was 0.0532. Suppose that, in 1929–1932, the total population size (N) was 100, so that $p \approx 1/100 = 0.01$. The expected population size in 1941–1944 would then be $n_t = 0.0532/p = 5.32$ birds. From the Poisson distribution with a mean of 5.32, the probability of persistence would exceed 0.995. Therefore, if the 1929–1932 population was at least as large as 100 individuals, the species was almost certainly present in 1941–1944. If the hypothetical 1929–1932 total population size was only 20, then $p = 0.05$. In this case, n_t in 1941–1944 would be only 1.064, and the Poisson probability of presence would decrease to 0.655, which is still greater than the probability of absence (0.345). Thus, the generalized additive model that we based on specimen data alone correctly implied the persistence of the Ivory-billed Woodpecker in the 1941–1944 interval, during which individuals were repeatedly sighted in a single dwindling population in Louisiana. However, in the following period, 1945–1948, the expected number of records became 0.524, and in this period the Poisson probability of absence (0.592) exceeded the probability of presence (0.408).

Analyses of Contemporary Census Data

We analyzed contemporary avian census data collected in the southeastern United States during the search for the Ivory-billed Woodpecker to estimate the probability of observing a species previously undetected by the census. A 4-person team surveyed winter bird populations (December–February) at 4 sites deemed to be among the most promising for relictual populations of the Ivory-billed Woodpecker (Rohrbaugh et al. 2007). Censuses were conducted from sunrise to sunset on foot and from canoes, and similar field methods were used at all census sites. (Raw census data [MST06-07] are available from eBird [2009].)

Although no Ivory-billed Woodpeckers were found, searchers generated standardized census data for other species observed in potential Ivory-billed Woodpecker habitat (Rohrbaugh et al. 2007). We based our analyses on data from the 2006 to 2007 avian censuses from the 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), and Pascagoula River, Mississippi (6,701 individuals, 54 species; Supporting Information).

We evaluated whether the census efforts at these localities were sufficient to discover an Ivory-billed Woodpecker if it had been present and derived a practical stopping rule for deciding when to abandon the search in a particular site. An efficient stopping rule that incorporates rewards of discovery and costs of additional sampling should be triggered at the smallest sample size q satisfying $f_1/q < c/R$, where f_1 is the number of singletons (species observed exactly once during a census),

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

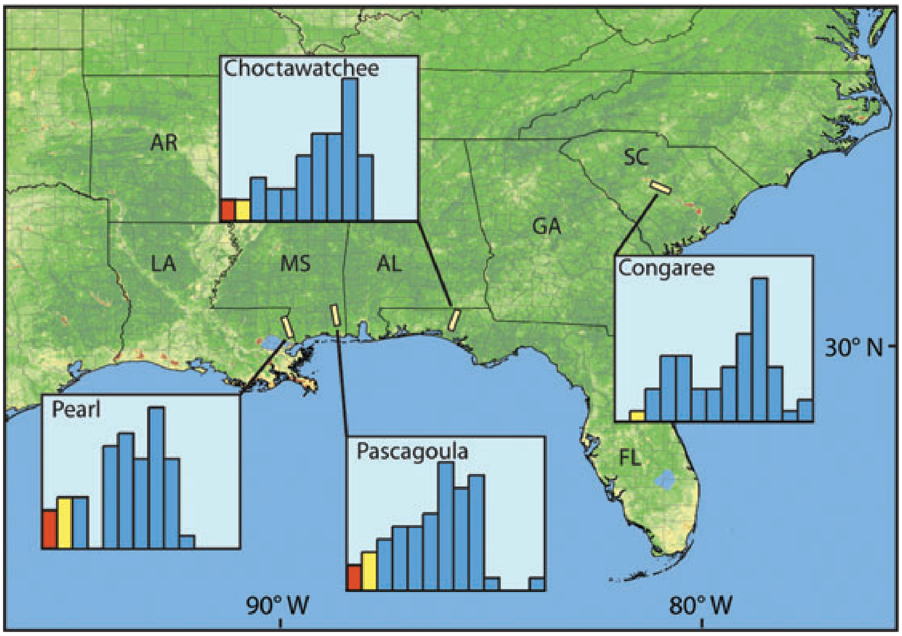

Figure 2. Avian data from 4 bottomland sites in the southeastern United States, where searches for Ivory-billed Woodpeckers were conducted in 2006 and 2007: Congaree River, South Carolina (15,500 individuals, 56 species), Choctawhatchee River, Florida (6,282 individuals, 55 species), Pearl River, Louisiana 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 censused would represent a new species was very low: Choctawhatchee River, $p^* = 3.18 \times 10^{-4}$; Pearl River, $p^* = 8.97 \times 10^{-4}$; Pascagaoula River, $p^* = 2.98 \times 10^{-4}$; and Congaree River, $p^* = 8.32 \times 10^{-9}$.

Discussion

Our results suggest that the probability of persistence in 2011 of the Ivory-billed Woodpecker was $<10^{-5}$ and that the species' probable extinction date was between 1960 (if the population size in 1929–1932 was 20) and 1980 (if the 1929–1932 population was 1000; Table 1 & Supporting Information). These estimates, which

Table 2. Species richness estimates (SE) and estimated number of undetected species on the basis of 3 methods.[a]

	Species richness estimate			*Estimated number of undetected species*		
Census location	*Chao1*	*ACE[b]*	*jackknife*	*Chao1*	*ACE[b]*	*jackknife*
Congaree River (South Carolina)	56 (≈0)	56 (≈0)	56 (≈0)	0	0	0
Choctawhatchee River (Florida)	56 (1.9)	56 (1.3)	57 (2.0)	1	1	2
Pearl River (Louisiana and Mississippi)	55 (1.8)	56 (1.7)	57 (2.4)	1	2	3
Pascagoula River (Mississippi)	55 (1.3)	55 (1.3)	56 (2.0)	1	1	2

[a]See Supporting Information for computational details.
[b]Abundance-based coverage estimator.

assume a constant search effort, are on the optimistic side because the collective search effort for the Ivory-billed Woodpecker has increased tremendously since 1932.

The exhaustive avian censuses carried out to date in the search for the Ivory-billed Woodpecker (Fig. 2 & Supporting Information) also make it unlikely that additional species will be detected at these 4 sites (Table 2) without expending almost as much additional effort as has already been invested. Of course, even if extensive further censuses were to yield additional species, there is no guarantee that the Ivory-billed Woodpecker would be among them. At the Pearl River site, for example, more plausible candidates for new species observations are American Woodcock (*Scolopax minor*) and Red-headed Woodpecker (*Melanerpes erythrocephalus*).

Inevitably, considerable uncertainty must be associated with the statistical estimation of extinction times from historical specimen records. For example, use of the Poisson generalized additive model to project specimen numbers (Fig. 1) cannot be rigorously justified for application to sparse data, and parameter estimates, such as the size of the Ivory-billed Woodpecker population in 1929–1932 (Table 1), can be difficult to establish.

In view of these uncertainties, an effective strategy is to analyze extinction times from a completely different statistical perspective and determine whether the results are consistent. Elphick et al. (2010) and Roberts et al. (2010) applied Solow's (1993*a*, 2005) method, which is derived from extreme value theory, to estimate the extinction year of the Ivory-billed Woodpecker. They based their analyses on physical evidence of museum specimens, photographs, and sound recordings as well as on reports of visual sightings confirmed by independent experts. These data were represented as a binary sequence of annual presences (at least one individual detected in year t) and absences (no individual detected in year t). Elphick et al. (2010) and Roberts et al. (2010, their Table 2) based their analysis on 39 presences between 1897 and 1944, which correspond to the quantitative data used in our analyses (Supplemental Information) reduced to simple yearly presence data plus additional records after 1932.

In spite of the differing assumptions and treatment of the data (discussed fully in Supporting Information), the conclusions of Elphick et al. (2010) and Roberts et al. (2010) are qualitatively consistent with our findings. Their analysis of physical evidence yielded a probable extinction date for the Ivory-billed Woodpecker of 1941, with an upper 95% confidence interval of 1945 (Table 1 in Elphick et al. 2010; Fig. 1 in Roberts et al. 2010). Although their estimated extinction dates differ from ours (1941 vs. 1980), our analyses of museum specimens (Fig. 1) and records from contemporary avian censuses (Fig. 2) and the alternative analyses of Roberts et al. (2010) and Elphick et al. (2010) all point to the inescapable conclusion that the Ivory-billed Woodpecker is now extinct.

The reported rediscovery of the Ivory-billed Woodpecker has been one of the most controversial findings in conservation biology, and the survey program designed to confirm that report among the most intensive and costly. Certainly, such rigorous, quantitative rediscovery programs will not be implemented for most possibly extinct species; thus, the methods we used to analyze census data for the woodpecker cannot be applied often. Similarly, for many species, museum specimen series are either too meagre or too idiosyncratically obtained (Pyke & Ehrlich 2010) to justify the application of our Poisson generalized additive model.

Nevertheless, when the data justify it, the analytical methods we developed can be applied to other retrospective analyses of museum-collection records and to records from standardized field surveys, 2 important sources of data that are based on evidentiary standards (McKelvey et al. 2008). Moreover, our method can be adapted for use with Rout et al.'s (2009*a*, 2009*b*) analyses of eradication programs for invasive species. These tools can help guide expectations of search-efforts and optimize the allocation of limited conservation resources in the search for other rare species (Chadès et al. 2008) or for invasive species that have putatively been eradicated (Rout et al. 2009*a*, 2009*b*).

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Supporting Information

The following information is available online: general statistical methods for analysis of museum specimen data (Appendix S1); compilation of Ivory-billed Woodpecker museum specimen data (Appendix S2); statistical analyses of Ivory-billed Woodpecker museum specimen data (Appendix S3); statistical analyses of Ivory-billed

Woodpecker contemporary census data (Appendix S4); comparisons with other published analyses of Ivory-billed Woodpecker extinctions (Appendix S5); frequency distribution of museum specimen data (Appendix S6); frequency counts of museum specimen data (Appendix S7); frequency distribution of binned specimen data (Appendix S8); fitted Poisson general additive model (Appendix S9); persistence probabilities as a function of population size (Appendix S10); frequency counts for contemporary avian census data (Appendix S11); and species counts at each of 4 census sites (Appendix S12). The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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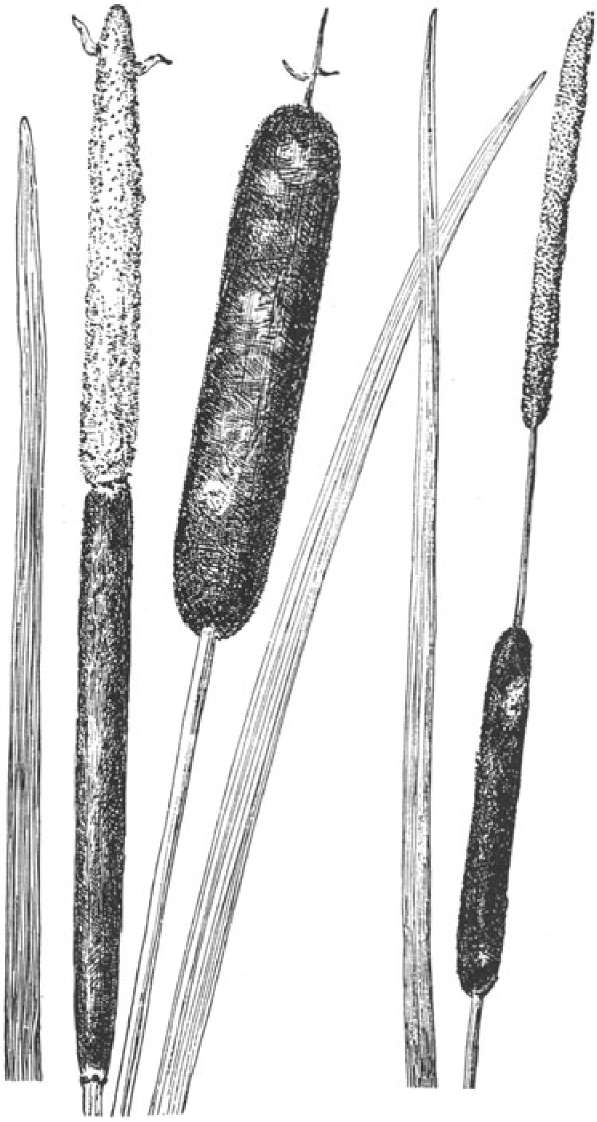

Appendix S1. A general statistical method for estimating the probability of persistence from museum specimen records

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 greatly from one year to the next, it is difficult to model the temporal trend as a smooth curve. Therefore, it will usually be necessary to first group (bin) the data into multi-year intervals to reveal prominent temporal trends. The results of the statistical anlaysis are potentially sensitive to the size of the binned interval. Typically, large intervals (i.e. more data points per bin) lead to a smaller variance but a larger bias, whereas narrow intervals (fewer data points per bin) lead to a smaller bias but a larger variance. Appendix S3 demonstrates how to determine an optimal bin size using the Ivory-billed Woodpecker data as an example.

Step 2. After binning, there are T time-interval bins. Let Y_t , t = 1, 2, .., T be the the number of records for the t-th period, where t =1 is the first binned interval. We first fit a smoothed curve to the specimen data. If we can assume that the fitted curve of specimen numbers generally reflects population size pattern, then the fitted series can be used to estimate population abundance. There are many statistical models can be used to model a time series (and any covariate predictor variables). We use a generalized additive model (GAM), which combines the properties of generalized linear models with additive models. The GAM model specifies a distribution function for Y_t (Poisson, normal, binomial etc.) and a link function g, which relates $\mu_t = E(Y_t)$ to the time-varying covariates $\{x_{1t}, x_{2t}, ..., x_{mt}; t = 1, 2, ..., T\}$ as:

$$g(\mu_t) = \alpha + f_1(x_{1t}) + f_2(x_{2t}) + ... + f_m(x_{mt}) \,. \qquad \text{(S1)}$$

Here “additive” refers to the sum of the functions of f_1, f_2,…, f_m. Each function of f_1, f_2,…, f_m can be parametric (including linear or quadratic or generalized linear models) or non-parametric (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. 2006) 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 $\{\hat{\mu}_t; t = 1, 2, ..., T\}$. 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 p in the k-th period can be estimated by the sample proportion Y_k/N. We assume this probability p is a constant in all intervals after time k. Next we estimate the expected population size in any time interval $t > k$ as $n_t \approx \hat{\mu}_t / p \approx \hat{\mu}_t N / Y_k$. The probability of persistence (of at least one individual) in the t-th interval can be estimated as $P(n_t > 0)$.

The fitting results in Step 3 can be used to determine an optimal bin size for a particular data set. For each size interval that is tested, we obtain the fitted series and calculate the adjusted R-square as a measure of the closeness of the fitted values and the data. The bin size that yields the largest adjusted R^2 from the fitted models is then selected (e.g., a 4-year interval for the Ivory-billed Woodpecker data).

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Appendix S2. Compilation of museum specimen data for the Ivory-billed Woodpecker and historical trends in collecting activity.

Specimen data were compiled from Hahn (1963) with additional data from Jackson (2004) and Ornis (2004). More than 400 Ivory-billed Woodpecker specimens are deposited in North American and European museums. Many specimens prepared as taxidermy mounts during the first half of the 19th century lack museum labels with date and locality data. However, the quality of data accompanying specimens collected after 1880 was relatively good because the species was already considered rare by ornithologists and specimens were highly coveted by museums and private collectors, both of which placed a premium on well-prepared skins and accurate locality data.

A substantial proportion of specimens obtained by professional collectors after 1890 were sold directly to museums and private collectors (Jackson 2004; Snyder *et al.* 2009). Professional collectors often employed networks of local hunters to obtain specimens. In the early 1890s, Arthur T. Wayne, one of the more prolific collectors of Ivory-billed Woodpeckers in Florida, paid local hunters and trappers up to US$5 ($123 in today's currency) for specimens in good condition (Snyder *et al.* 2009). For comparison, unskilled laborers in rural regions of the southeastern United States were paid < $1 per day during the 1890s (U.S. Bureau of Labor 1904). Cash bounties offered by professional collectors and specimen dealers were potent incentives for local woodsmen to seek out relictual populations. During 1894, specimens were offered for retail sale at $15 per specimen ($369 in today's currency; Jackson 2004). Retail valuations of specimens more than tripled after 1900 as demand greatly outstripped supply (Jackson 2004). None of the states (Texas, Louisiana, Mississippi, Georgia, Florida, South Carolina) known to support Ivory-billed Woodpecker populations after 1900 (Tanner 1942; Jackson 2004) had laws protecting the species from commercial collecting in 1903 (Ducher 1903).

Despite the enormous economic incentive, specimen production decreased markedly after 1906 as most of the well-known populations were extirpated. Legal prohibition of commercial collecting did not occur until the passage of the Migratory Bird Treaty Act of 1918, but effective regulation of hunting activity of any kind was rare or nonexistent in remote regions of the rural southeastern United States through the 1930s. State-sanctioned collecting permits for Ivory-billed Woodpeckers were issued as late as 1932 (Jackson 2004). Populations were also subjected to intense subsistence hunting and curiosity shooting (Snyder *et al.* 2009). These sources of mortality are thought to have greatly outweighed the impact of specimen collecting on relict populations in the 20th century (Snyder *et al.* 2009).

It is likely that the decline of Ivory-billed Woodpecker populations began more than a millennium ago when American Indian populations expanded greatly in eastern North America after the introduction of maize cultivation from Mexico. Prized for their bills and plumage, this species figures frequently in Mississippian culture (800-1500 CE) burial goods, including carved pipe bowls, shell gorgets, and ceramics (Brain & Phillips 1996; Jackson 2004). Ivory-billed Woodpecker plumage and bills were traded as curios and ceremonial objects by American Indians as late as the 19th century, whereas intensive subsistence hunting, trophy hunting, and scientific collecting by European Americans continued through the early 20th century (Jackson 2004; Snyder *et al.* 2009).

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 they harbored), including the Singer Tract and another large parcel near Rosedale, Mississippi (Jackson 2004; Snyder *et al.* 2009).

In short, the museum specimens on which our analysis is based represent the tail of a long decline in populations. Our models are based on the premise that the dwindling rate of specimen accumulation in museum collections mirrors steep population declines throughout the historic range of the species, particularly given the premium prices paid for specimens by museums and private collectors after 1880.

Analyses were limited to dated specimens with locality data (at least state). Date refers to the date of collection rather than the accession date in museums. A few specimens of doubtful provenance or lacking verifiable dates on museum labels were omitted from the analysis. Although we only used specimens with reliable locality data, it should be noted that our analyses are not spatially structured, and instead model the temporal decline of the Ivory-billed Woodpecker after 1880 throughout its geographic range.

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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 collected specimens in the binned intervals (vertical black lines in Fig. 1) includes not only the counts of specimens collected from 1893 to 1932, but also the uninterrupted string of zeroes from 1933 to 2008, during which no additional specimens were collected. To our knowledge, scientific collecting permits for Ivory-billed Woodpeckers were not issued after 1932 and no additional specimens were collected after this date. For this reason, projection of the curve in Fig. 1, detailed below, must be interpreted as the expected number of IBW specimens that could have been collected, had hunting continued, in each four-year interval after 1932, on the assumption that the decline illustrated in Appendix S6 continued on the same trajectory after 1932.

We fitted a smoothed curve to the museum specimen data (solid and dashed red lines in text Fig. 1) and used the fitted series to estimate Ivory-billed Woodpecker abundance in each 4-year interval. We then converted the projected abundance into an estimate of the probability of persistence of the woodpeckers in each 4-year interval, including the most recent complete interval of 2005-2008.

As discussed in the main text, we assume that the decrease in specimens after 1894 reflects a true decline in Ivory-billed Woodpecker abundance. To model this decline, we assume that Y_t is a Poisson random variable with mean $E(Y_t) = \mu_t$ where Y_t is the number of records for the *t*-th four-year period, where t =1 stands for the time period 1893-1896 (the interval with the greatest number of specimens). We fitted a Poisson GAM to the data after the specimen peak of 1893. In the model, $\{Y_t; t = 1, 2, \ldots\}$ have different means due to decreasing population size, and the means are dependent on time. We considered a log link function and the following simple form of a GAM in Eq. (S1) with time as the sole predictor variable:

$$\log \mu_t = \alpha + f(t), \qquad \text{(S2)}$$

where α denotes an unknown baseline constant and $f(t)$ denotes an unknown smooth function of time. Both α and $f(t)$ are estimated from the data.

We used the *mgcv* package (Wood 2006) in the *R* software environment (R Development Core Team 2008) to carry out the fitting and computation of the penalized regression spline model (Wahba 1990; Ruppert *et al.* 2006), We used cubic regression splines (Wahba 1990; Ruppert *et al.* 2006) to construct a smooth function $f(t)$. For these data, the goodness of fit test yielded a chi-squared statistic $\chi^2 = 21.95$ with 25.7 effective degrees of freedom. From the chi-square distribution, the *P*-value = 0.68, implying that the fit of the model to the data was adequate. The fitted model projects the decline in specimen abundance after 1893 (Fig. 1, Appendix S9) into more recent time intervals. We focus on inference after 1932 because the last specimen was collected in that year.

To relate the estimated number of Ivory-billed Woodpecker records in each four-year interval to the 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 during the 1929-32 interval, and collecting was illegal after 1932, this interval represents the latest opportunity to infer *p* from specimen data. Assume the total living population size from 1929-32 is *N*, then *p* is approximately 1/*N* because there was only one specimen collected in this interval. Thus, we have $p \approx 1/N$ in the interval 1929-32. For purposes of the model, we assume that probability of detection *p* is roughly a constant after 1932. In fact, the intensity of searches for Ivory-billed Woodpecker increased substantially after the last known population in Louisiana disappeared in 1944. If *p* increased with time, then our analyses over-estimate persistence probabilities.

Given a hypothetical value of the 1929-32 population size *N*, we can then estimate the expected population size of Ivory-billed Woodpeckers in time interval *t* after 1932 as $n_t \approx \hat{\mu}_t / p \approx \hat{\mu}_t N$. Assuming the population size in any time interval is a Poisson random variable, the probability of persistence (of at least one individual) in the *t*-th interval can be estimated as $1 - \exp(-n_t)$, which is the probability that a Poisson random variable with mean n_t takes a non-zero value (Table S4).

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Appendix S4. Statistical analysis of field survey data

Our statistical method for analyzing census data is based principally on the concept of the Good-Turing frequency formulas (Good 1953, 2000), which helped the British decode German military ciphers for the Wehrmacht Enigma cryptographic machine during World War II. Alan Turing is considered to be the founder of modern computer science. His non-intuitive idea (an empirical Bayesian approach), as applied to the Ivory-billed Woodpecker search problem, is that inference regarding the probable number of undetected species depends on frequencies of rare species in the same census area. To apply this concept to our multinomial model for the Ivory-billed Woodpecker search problem, the species pool considered must be sufficiently large, frequency data for rare (detected) species must be available, and the sample size should be large.

Ivory-billed Woodpeckers are (or were) conspicuous, diurnal, and sedentary, occupying year-round territories (Tanner 1942; Jackson 2004). For the purpose of analysis, the pool of species could be limited appropriately to species that are known to be sedentary, year-round residents of bottomland forests at the four census sites. We expanded the analyses, however, to include both resident and migratory species that normally winter in floodplain forest habitats, including early successional regeneration in canopy gaps. Expanding the sampling pool in this way increases information about rare species, and therefore potentially increases the estimated number of undetected species that might be present. We included some species found along roadsides in bottomland forested habitats (e.g., Mourning Dove) that typically occur in agricultural areas and old-fields. However, species strongly associated with agriculture and pastures (*e.g.*, Killdeer, Eastern Meadowlark) were excluded from the analyses. Herons, cormorant, anhinga, ducks, and coot were excluded, but we included a few species generally associated with rivers and oxbow lakes in bottomland forest (e.g., Bald Eagle, Osprey, Belted Kingfisher, Tree Swallow). Strictly nocturnal species (e.g., Eastern Screech-Owl) were excluded.

The four sites, searching periods, observed species richness and sample sizes are as follows.

(1) Congaree River, South Carolina: 26 searching days (7 December 2006 to 5 January 2007); 15,500 individuals and 56 species were observed.

(2) Choctawhatchee River, Florida: 14 searching days (23 January 2007 to 7 February 2007); 6282 individuals and 55 species were observed.

(3) Pearl River, Louisiana: 9 searching days (10 February 2007 to 18 February 2007); 3343 individuals and 54 species were observed.

(4) Pascagoula River, Mississippi: 9 searching days (20 February 2007 to 28 February 2007); 6701 individuals and 54 species were observed.

We used a non-parametric approach to estimating species richness based on frequency counts (f_1, f_2, …, f_{10}), where f_r denotes the number of species represented by exactly r individuals in sample. The first ten frequency counts for each site appear in Appendix S11. The detailed data, including species name and the abundance of each observed species, are provided in Appendix S12.

In the Congaree River site, for example, the ten least common species had observed frequencies $f_1 = 0$, $f_2 =1$, $f_3 = 0$, $f_4 =3$, $f_5 =2$, …, $f_{10} = 1$. That is, there were no singletons, one doubleton, no species observed three times, three species observed four times, two species observed five times,…, and one species observed ten times. In the Congaree River census, 13 of 56 species were relatively rare, observed 10 or fewer times. From a statistical point of view, census data from common species carry almost no information about undetected species; most species richness estimators are based on inferences derived from the frequency of relatively rare species.

Three estimators of species richness are used in the analysis. All of these estimators converge to the true species richness, including undetected species, when sample size is sufficiently large.

(1) The Chao1 estimator (Chao 1984)

This estimator is referred to as the Chao1 estimator in the ecological literature (Colwell & Coddington 1994). This estimator uses only the numbers of singletons and doubletons to obtain a lower bound of species richness: D is the observed species richness, f_1 is the number of singletons, and f_2 is the number of doubletons.

$$\hat{S}_{chao1} = \begin{cases} D + f_1^2/(2f_2), & \text{if } f_2 > 0 \\ D + f_1(f_1-1)/2, & \text{if } f_2 = 0 \end{cases}.$$

(2) ACE (Abundance Coverage-based Estimator; Chao 2005) is based on the first ten frequencies (f_1, f_2, …, f_{10}):

$$\hat{S}_{ACE} = D_{abun} + \frac{D_{rare}}{\hat{C}_{rare}} + \frac{f_1}{\hat{C}_{rare}}\hat{\gamma}_{rare}^2,$$

where D_{abun} denotes the number of species in the abundant species group (*i.e.*, species with frequency greater than 10), D_{rare} denotes the number of species in the rare species group (*i.e.*, species with frequency less than or equal to 10), $\hat{C}_{rare} = 1 - f_1/\sum_{i=1}^{10} i f_i$ is the estimated sample coverage in the rare species group, and $\hat{\gamma}_{rare}^2$ is the estimated square of CV (coefficient of variation, a measure that characterizes the variation of species abundances) in the rare group:

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

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

$$\hat{S}_{Jackknife} = D + [(n-1)/n]\, f_1$$

That is, only the number of singletons is used to estimate the number of undetected species. Chao1, ACE, and the Jackknife estimator are easily calculated with the software applications EstimateS (Colwell 2006) and SPADE (Chao & Shen 2003). The results are shown in Table 2 of the main text.

Turing and Good (Good 1953, 2000) obtained the first-order approximation of the probability P^* that sampling one additional individual will yield a previously undetected species as $P^* \approx f_1 / n$, which is the proportion of singletons in the sample. With sufficient effort, as additional individuals are found of species initially represented as singletons, this probability approaches zero. We have extended Turing's formula to apply to samples in which the rarest species abundance class is not necessarily the singleton class. If f_r is the expected occurrence frequency for the rarest abundance class in a sample of n individuals (i.e., $f_j = 0$ for all $j < r$), then the approximate probability that the next individual observed will represent a species new to the survey is

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

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.

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

Solow's (1993) method is usually interpreted to assume that the total population size remains constant through time followed by a sudden stochastic extinction (a stationary Poisson process) (e.g., Solow 2005). In contrast, our quantitative specimen-based analysis assumes that the diminishing curve of specimen records (Fig. 1 inset) after 1890 reflects a gradual population decline of the Ivory-billed Woodpecker throughout its geographic range, which would seem to make the Solow (1993) method inappropriate.

However, an increasing census effort applied to a decreasing population ('sampling type 4' with gradual extinction, in the simulations of Rivadeneira et al. 2009) could, in principle, also yield an approximately uniform 'total probability' of detection up until extinction. Roberts et al. (2010) justified their application of Solow's (1993) method on the finding by Vogel et al. (2009, their Table 2) that data for the populations they considered best fit a uniform distribution of temporal occurrences, including a data series of 13 'undisputed records' for the Ivory-billed Woodpecker (an earlier version of the Elphick et al. [2010] dataset, spanning 1897-1939).

However, a potential complication with these analyses is that the crucial terminal sequence of presence-absence records for the Ivory-billed Woodpecker from 1933 to 1944, analyzed by Elphick et al. (2010) and Roberts et al. (2010), were all made in a single remnant population that declined to extinction in northern Louisiana (see Fig. 1; Tanner 1942; Jackson 2004). Moreover, because the lifespan of an Ivory-billed Woodpecker was probably 10 years or more (U.S. Fish & Wildlife Service 2009), many of these observations were likely of the same individuals. In contrast, our specimen-based analysis (Fig. 1) is based on the cumulative database of dated specimens, each of which can be counted only once, removing at least one key source of non-independence.

Scott et al. (2008) carried out the only other quantitative analysis of the post-2004 rediscovery program for Ivory-billed Woodpecker of which we are aware, although they did not use data for the other species recorded, as we did. Instead, these authors estimated the probability that a population of n Ivory-billed Woodpeckers could have been present, given the area of woodpecker habitat covered by the searchers, assuming a spatially uniform probability of encounter. Unless the population was smaller than 1 or 2 individuals, the search effort was sufficient to conclude (with $P > 0.95$) that the Ivory-billed Woodpecker was not present in the searched area.

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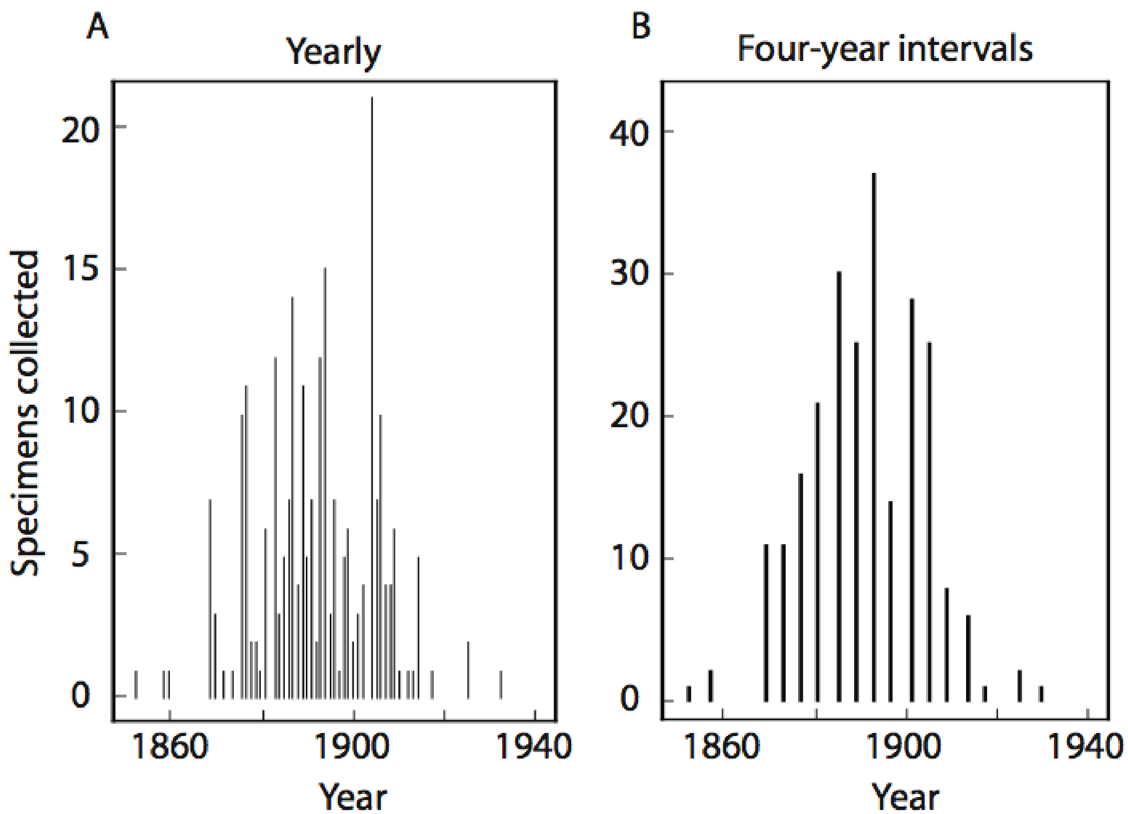
Appendix S6. Dated museum specimens of Ivory-billed Woodpeckers from known georeferenced localities.



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
1858	0	1879	2	1900	2	1921	0
1859	1	1880	1	1901	3	1922	0
1860	1	1881	6	1902	4	1923	0
1861	0	1882	0	1903	0	1924	0
1862	0	1883	12	1904	21	1925	2
1863	0	1884	3	1905	7	1926	0
1864	0	1885	5	1906	10	1927	0
1865	0	1886	7	1907	4	1928	0
1866	0	1887	14	1908	4	1929	0
1867	0	1888	4	1909	6	1930	0
1868	0	1889	11	1910	1	1931	0
1869	7	1890	5	1911	0	1932	1
1870	3	1891	7	1912	1	>1932	0

Tabled numbers are yearly frequency data (zero means that no museum specimens were collected that year).

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

Period	Frequency	Period	Frequency	Period	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 $\hat{\mu}_t$ and the standard error se($\hat{\mu}_t$) in each four-year interval.

Period	$\hat{\mu}_t$	se($\hat{\mu}_t$)	Period	$\hat{\mu}_t$	se($\hat{\mu}_t$)
1929-32	0.4225	0.2468	1969-72	0.000375	0.001495
1933-36	0.2157	0.1634	1973-76	0.000184	0.000829
1937-40	0.1078	0.1048	1977-80	9.08×10^{-5}	0.000457
1941-44	0.0532	0.0657	1981-84	4.47×10^{-5}	0.00025
1945-48	0.0262	0.0401	1985-88	2.20×10^{-5}	0.000136
1949-52	0.0129	0.024	1989-92	1.08×10^{-5}	7.32×10^{-5}
1953-56	0.0064	0.0142	1993-96	5.33×10^{-6}	3.93×10^{-5}
1957-60	0.0031	0.0082	1997-00	2.62×10^{-6}	2.10×10^{-5}
1961-64	0.0015	0.0047	2000-04	1.29×10^{-6}	1.12×10^{-5}
1965-68	8.00×10^{-4}	0.0027	2005-08	6.36×10^{-7}	5.94×10^{-6}

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
1985-88	0.00044	0.002198	0.010943	0.021766	0.1042	0.1975	0.6672
1989-92	0.000217	0.001083	0.005402	0.010774	0.0527	0.1027	0.4182
1993-96	0.000107	0.000533	0.002663	0.005318	0.0263	0.0519	0.2340
1997-00	5.25×10^{-5}	0.000262	0.001312	0.002622	0.013	0.0259	0.1230
2000-04	2.58×10^{-5}	0.000129	0.000646	0.001291	0.0064	0.0128	0.0626
2005-08	1.27×10^{-5}	6.36×10^{-5}	0.000318	0.000636	0.0032	0.0063	0.0313

N: total population size of Ivory-billed Woodpeckers in 1929-32. Gray shading indicates a probability < 0.05.

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

Census Site	Frequency counts											Species detected	Individuals
	1	2	3	4	5	6	7	8	9	10	>10		
Congaree River	0	1	0	3	2	2	1	1	2	1	43	56	15500
Choctawhatchee River	2	2	2	2	2	1	0	0	1	0	43	55	6282
Pearl River	3	4	2	2	0	0	0	0	0	0	43	54	3343
Pascagoula River	2	3	4	0	1	1	1	2	0	0	40	54	6701

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

Species		Census locality			
		Congaree River	Choctawhatchee River	Pascagoula River	Pearl River
Meleagris gallopavo	Wild Turkey	93	21	14	1
Coragyps atratus	Black Vulture	277	177	31	62
Cathartes aura	Turkey Vulture	324	157	147	68
Pandion haliaetus	Osprey	0	0	3	2
Haliaeetus leucocephalus	Bald Eagle	0	0	1	1
Accipiter striatus	Sharp-shinned Hawk	18	3	1	0
Buteo lineatus	Red-shouldered Hawk	126	82	88	70
Buteo jamaicensis	Red-tailed Hawk	28	9	6	4
Aquila chrysaetos	Golden Eagle	2	0	0	0
Falco sparverius	American Kestrel	0	1	2	3
Scolopax minor	American Woodcock	7	2	5	0
Zenaida macroura	Mourning Dove	0	5	3	0
Strix varia	Barred Owl	184	96	60	34
Megaceryle alcyon	Belted Kingfisher	45	24	43	14
Melanerpes erythrocephalus	Red-headed Woodpecker	9	13	0	0
Melanerpes carolinus	Red-bellied Woodpecker	670	498	339	244
Sphyrapicus varius	Yellow-bellied Sapsucker	511	390	122	98
Picoides pubescens	Downy Woodpecker	344	156	77	75
Picoides villosus	Hairy Woodpecker	110	40	32	21
Colaptes auratus	Northern Flicker	1100	211	213	204
Dryocopus pileatus	Pileated Woodpecker	571	177	216	116
Sayornis phoebe	Eastern Phoebe	386	215	63	79
Vireo griseus	White-eyed Vireo	10	4	8	2
Vireo solitarius	Blue-headed Vireo	101	145	19	11
Cyanocitta cristata	Blue Jay	4	63	37	12
Corvus brachyrhynchos	American Crow	365	45	37	21
Corvus ossifragus	Fish Crow	4	170	92	13
Tachycineta bicolor	Tree Swallow	0	5	7	2
Poecile carolinensis	Carolina Chickadee	323	138	74	76
Baeolophus bicolor	Tufted Titmouse	344	116	46	41
Sitta carolinensis	White-breasted	157	0	0	0

	Nuthatch				
Sitta pusilla	Brown-headed Nuthatch	16	0	0	0
Certhia americana	Brown Creeper	42	21	11	14
Thryothorus ludovicianus	Carolina Wren	309	119	94	57
Troglodytes aedon	House Wren	0	6	3	24
Troglodytes troglodytes	Winter Wren	394	114	15	21
Regulus satrapa	Golden-crowned Kinglet	307	127	27	16
Regulus calendula	Ruby-crowned Kinglet	770	435	98	80
Polioptila caerulea	Blue-gray Gnatcatcher	9	53	42	45
Sialia sialis	Eastern Bluebird	325	29	8	26
Catharus guttatus	Hermit Thrush	254	161	44	126
Turdus migratorius	American Robin	164	247	169	238
Dumetella carolinensis	Gray Catbird	5	1	2	21
Toxostoma rufum	Brown Thrasher	8	4	14	16
Bombycilla cedrorum	Cedar Waxwing	212	281	150	291
Vermivora celata	Orange-crowned Warbler	16	36	22	31
Dendroica coronata	Yellow-rumped Warbler	321	453	250	158
Dendroica dominica	Yellow-throated Warbler	4	3	0	0
Dendroica pinus	Pine Warbler	152	107	12	11
Mniotilta varia	Black-and-White Warbler	41	32	3	1
Geothlypis trichas	Common Yellowthroat	0	22	33	31
Pipilo erythrophthalmus	Eastern Towhee	82	14	19	4
Passerella iliaca	Fox Sparrow	6	0	0	3
Melospiza melodia	Song Sparrow	15	2	35	55
Melospiza Georgiana	Swamp Sparrow	6	57	184	231
Zonotrichia albicollis	White-throated Sparrow	639	63	202	220
Junco hyemalis	Dark-eyed Junco	164	0	0	2
Cardinalis cardinalis	Northern Cardinal	525	235	245	142
Agelaius phoeniceus	Red-winged Blackbird	2217	219	3164	66
Euphagus carolinus	Rusty Blackbird	28	54	0	37
Quiscalus quiscula	Common Grackle	2097	316	2	25
Icterus galbula	Baltimore Oriole	5	0	0	0
Carduelis tristis	American Goldfinch	254	108	67	77