Conservation Biology

Contributed Paper

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

NICHOLAS J. GOTELLI,* ANNE CHAO,† ROBERT K. COLWELL,‡ WEN-HAN HWANG,§ AND GARY R. GRAVES#

*Department of Biology, University of Vermont, Burlington, VT 05405, U.S.A., email ngotelli@uvm.edu
†Institute of Statistics, National Tsing Hua University, Hsin-Chu 30043, Taiwan
‡Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043, U.S.A.
§Department of Applied Mathematics, National Chung Hsing University, Tai-Chung 402, Taiwan
#Department of Vertebrate Zoology, MRC-116, National Museum of Natural History, Smithsonian Institution, PO Box 37012, Washington, D.C. 20013-7012, U.S.A., and Center for Macroecology, Evolution, and Climate, University of Copenhagen, Denmark

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*

Paper submitted December 21, 2010; revised manuscript accepted April 19, 2011.

Conservation Biology, Volume 26, No. 1, 47–56

DOI: 10.1111/j.1523-1739.2011.01715.x

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 × 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

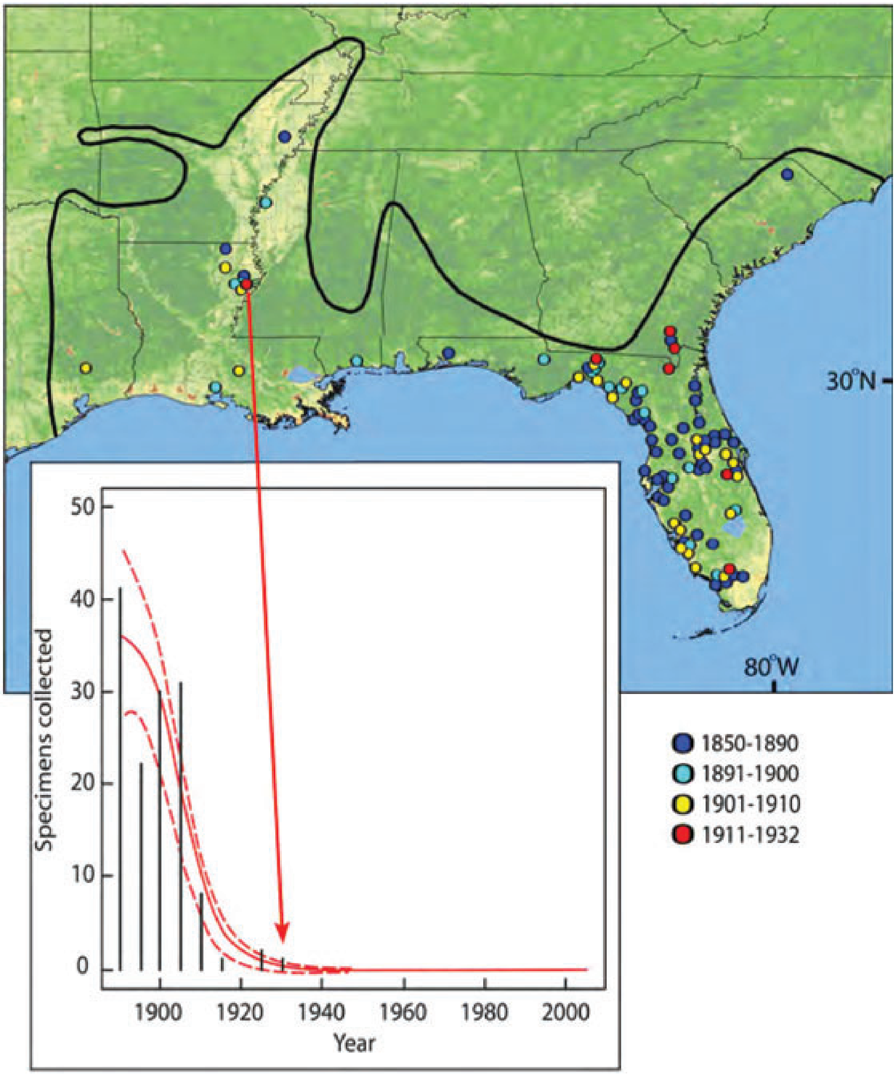

Figure 1. Spatial and temporal distribution of Ivory-billed Woodpecker specimens (black line, approximate historical range boundary of the Ivory-billed Woodpecker [Tanner 1942]; points, 1–6 museum specimens with precise locality data [239 total specimens; Supporting Information]; dark blue points, collections 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

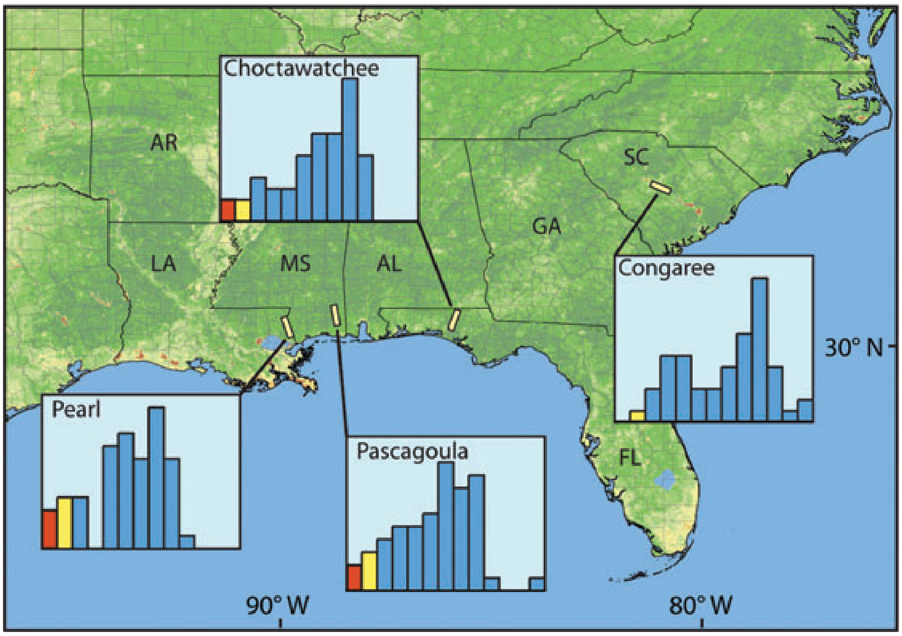

Figure 2. Avian data from 4 bottomland sites in the southeastern United States, where searches for Ivory-billed Woodpeckers were conducted in 2006 and 2007: Congaree River, South Carolina (15,500 individuals, 56 species), Choctawhatchee River, Florida (6,282 individuals, 55 species), Pearl River, Louisiana 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*).

Acknowledgments

We thank S. Haber and P. Sweet for providing information on Ivory-billed Woodpecker specimens in the American Museum of Natural History, C. Elphick for extensive comments on the manuscript, and M. Rivadeneira and K. Roy for help in understanding their related work. N.J.G. and R.K.C. were supported by the U.S. National Science Foundation. A.C. and W.H. were funded by the Taiwan National Science Council. G.R.G. was supported by the Alexander Wetmore Fund, Smithsonian Institution, and the Center for Macroecology, Evolution, and Climate, University of Copenhagen. This study is a contribution of the Synthetic Macroecological Models of Species Diversity Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by the National Science Foundation, the University of California, Santa Barbara, and the State of California.

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.

Literature Cited

Audubon, J. J. 1832. Ornithological biography. E. L. Carey and A. Hart, editors. Philadelphia, Pennsylvania.

Burgman, M. A., R. C. Grimson, and S. Ferson. 1995. Inferring threat from scientific collections. Conservation Biology **9:**923–928.

Burgman, M., B. Maslin, D. Andrewartha, M. Keatley, C. Boek, and M. McCarthy. 2000. Inferring threat from scientific collections: power tests and an application to Western Australian Acacia species. Pages 7–26 in S. Ferson and M. Burgman, editors. Quantitative methods for conservation biology. Springer-Verlag, New York.

Chadès, I., E. McDonald-Madden, M. A. McCarthy, B. Wintle, M. Linkie, and H. P. Possingham. 2008. When to stop managing or surveying cryptic threatened species. Proceedings of the National Academy of Sciences of the United States of America **105:**13936–13940.

Chao, A. 2005. Species estimation and applications. Pages 7907–7916 in N. Balakrishnan, C. B. Read, and B. Vidakovic, editors. Encyclopedia of statistical sciences **12**. 2nd edition. Wiley, New York.

Chao, A., R. K. Colwell, C.-W. Lin, and N. J. Gotelli. 2009. Sufficient sampling for asymptotic minimum species richness estimators. Ecology **90:**1125–1133.

Collen, B., A. Purvis, and G. M. Mace. 2010. When is a species really extinct? Testing extinction inference from a sighting record to inform conservation assessment. Diversity and Distributions **16:**755–764.

Collinson, J. M. 2007. Video analysis of the escape flight of Pileated Woodpecker *Dryocopus pileatus*: does the Ivory-billed Woodpecker *Campephilus principalis* persist in continental North America? BMC Biology **5:**8.

Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences **345:**101–118.

Diamond, J. M. 1987. Extant unless proven extinct? Or, extinct unless proven extant? Conservation Biology **1:**77–79.

Eames, J. C., H. Hla, P. Leimgruber, D. S. Kelly, S. M. Aung, S. Moses, and S. N. Tin. 2005. Priority contribution. The rediscovery of Gurney's Pitta *Pitta gurneyi* in Myanmar and an estimate of its population size based on remaining forest cover. Bird Conservation International **15:**3–26.

eBird. 2009. An online database of bird distribution and abundance. Avian Knowledge Network and Cornell Laboratory of Ornithology, Ithaca, New York, and National Audubon Society, Washington, D.C. Available from http://www.avianknowledge.net (accessed December 2010).

Elphick, C. S., D. L Roberts, and J. M. Reed. 2010. Estimated dates of recent extinctions for North American and Hawaiian birds. Biological Conservation **143**:617–624.

Fitzpatrick, J. W., et al. 2005. Ivory-billed Woodpecker (*Campephilus principalis*) persists in continental North America. Science **308:**1460–1462.

Good, I. J. 1953. The population frequencies of species and the estimation of population parameters. Biometrika **40:**237–264.

Good, I. J. 2000. Turing's anticipation of empirical Bayes in connection with the cryptanalysis of the naval Enigma. Journal of Statistical Computation and Simulation **66:**101–111.

Hahn, P. 1963. Where is that vanished bird? An index to the known specimens of the extinct and near extinct North American species. Royal Ontario Museum, University of Toronto, Toronto.

Hamer, A. J., S. J. Lane, and M. J. Mahony. 2010. Using probabilistic models to investigate the disappearance of a widespread frog-species complex in high-altitude regions of south-eastern Australia. Animal Conservation **13:**275–285.

Hasbrouck, E. M. 1891. The present status of the Ivory-billed Woodpecker (*Campephilus principalis*). Auk **8:**174–186.

Iofescu, M., and P. Táutu. 1973. Stochastic processes and applications in biology and medicine. Volume II. Models. Springer-Verlag, Berlin.

Jackson, J. A. 2004. In search of the Ivory-billed Woodpecker. Smithsonian Institution Press, Washington, D.C.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Science, Oxford, United Kingdom.

McCarthy, M. A. 1998. Identifying declining and threatened species with museum data. Biological Conservation **83:**9–17.

McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. 2nd edition. Chapman and Hall/CRC, Boca Raton, Florida.

McKelvey, K. S., K. B. Aubry, and M. K. Schwartz. 2008. Using anecdotal occurrence data for rare or elusive species: the illusion of reality and a call for evidentiary standards. BioScience **58:**549–555.

Pyke, G. H., and P. R. Ehrlich. 2010. Biological collections and ecological/environmental research: a review, some observations and a look to the future. Biological Reviews **85:**247–266.

Rasmussen, S., and N. Starr. 1979. Optimal and adaptive search for a new species. Journal of American Statistical Association **74:**661–667.

Regan, T. J., M. A. McCarthy, P. W. J. Baxter, F. Dane Panetta, and H. P. Possingham. 2006. Optimal eradication: when to stop looking for an invasive plant. Ecology Letters **9:**759–766.

Rivadeneira, M. M., G. Hunt, and K. Roy. 2009. The use of sighting records to infer species extinctions: an evaluation of different methods. Ecology **90:**1291–1300.

Roberts, D. L. 2006. Extinct or possibly extinct? Science **312:**997.

Roberts, D. L., C. S. Elphick, and J. M. Reed. 2010. Identifying anomalous reports of putatively extinct species and why it matters. Biological Conservation **24:**189–196.

Roberts, D. L., and A. R. Solow. 2003. When did the dodo become extinct? Nature **426:**245.

Rohrbaugh, R., M. Lammertink, K. Rosenberg, M. Piorkowski, S. Barker, and K. Levenstein. 2007. 2006–07 Ivory-billed Woodpecker surveys and equipment loan program. Report. Cornell Laboratory of Ornithology, Ithaca, New York. Available from http://www.birds.cornell.edu/ivory/pdf/FinalReportIBWO_071121_TEXT.pdf (accessed December 2010).

Rout, T. M., Y. Salomon, and M. A. McCarthy. 2009*a*. Using sighting records to declare eradication of an invasive species. Journal of Applied Ecology 46:110–117.

Rout, T. M., C. J. Thompson, and M. A. McCarthy. 2009*b*. Robust decisions for declaring eradication of invasive species. Journal of Applied Ecology 46:782–786.

Sibley, D. A., L. R. Bevier, M. A Patten, and C. S. Elphick. 2006. Comment on 'Ivory-billed Woodpecker (*Campephilus principalis*) persists in continental North America. Science Online **311:**DOI: 10.1126/science.1114103.

Snyder, N. F. R. 2007. An alternative hypothesis for the cause of the Ivory-billed Woodpecker's decline. Monograph of the Western Foundation of Vertebrate Zoology **2:**1–58.

Snyder, N. F. R., D. E. Brown, and K. B. Clark. 2009. The travails of two woodpeckers: Ivory-bills and Imperials. University of New Mexico Press, Albuquerque.

Sodhi, N. S., et al. 2008. Correlates of extinction proneness in tropical angiosperms. Diversity and Distributions **14:**1–10.

Solow, A. R. 1993*a*. Inferring extinction from sighting data. Ecology **74:**962–964.

Solow, A. R. 1993*b*. Inferring extinction in a declining population. Journal of Mathematical Biology **32:**79–82.

Solow, A. R. 2005. Inferring extinction from a sighting record. Mathematical Biosciences **195:**47–55.

Solow, A. R., and D. L. Roberts. 2003. A nonparametric test for extinction based on a sighting record. Ecology **84:**1329–1332.

Tanner, J. T. 1942. The Ivory-billed woodpecker. Research report 1. National Audubon Society, New York.

U.S. Fish and Wildlife Service. 2009. Recovery plan for the Ivory-billed Woodpecker (*Campephilus principalis*). U.S. Fish and Wildlife Service, Atlanta.

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 **71:**701–719.

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