Estimated dates of recent extinctions for North American and Hawaiian birds

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ABSTRACT

Series of sighting records – the years in which a species has been recorded – can be used to infer whether species have gone extinct, and when extinctions occurred. We compiled sighting records for 52 rare bird species, subspecies, and distinct island populations from North America and Hawaii, 38 of which proved adequate for such analyses. Using a data set that combines non-controversial sight records with those for which physical evidence exists, no populations were judged likely to be extant, including those that have not been declared extinct. The 'alalā was the only species with a 95% confidence interval around the extinction date that extended beyond 2009, suggesting that this population is the least unlikely to be extinct. Although all are probably extinct, populations were ranked according to their likelihood of persistence, so that any future searches can be prioritized to minimize the risk that resources are spent on extinct species. Estimated extinction dates spanned the period from the 1840s–2000s, with evidence for a peak in the early 1900s. On average, only about 4 years passed between a species' last sighting and its estimated extinction date, and the 95% confidence intervals around extinction dates extended 9–26 years after the last sighting. Long gaps between sightings were very rare. Mean and median gap sizes between consecutive sightings within sighting records were 2.5 and 0 years, respectively. Gaps between the last and penultimate sightings were smaller than average gap sizes earlier in sighting records. Finally, a non-parametric method that can be calculated with more limited data proved a weak substitute for using more complete sighting records.

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1. Introduction

Demonstrating beyond all doubt that a species is extinct is essentially impossible because there is always some chance, however small, that searches have been inadequate (Solow, 1993a; Reed, 1996). The rediscovery of species after decades in which they were not reported (Keith and Burgman, 2004; Butchart et al., 2006) and the continued discovery of species new to science, even in well studied groups such as birds (Peterson, 1998), illustrate the ease with which species can go undetected. Any judgment of extinction, therefore, is inherently probabilistic (McInerny et al., 2006).

Determining the point at which one should cease efforts to re-find species that are putatively extinct ("extaille", *sensu* Banks, 1976) is a problem that has been long recognized (e.g., Hodge, 1911). Premature declarations of extinction are of great concern to conservation biologists, who do not want to mistakenly end protection efforts (Collar, 1998). On the other hand, continuing

protection efforts after a species' demise would divert important resources away from those species that continue to be in need of protection (Chadès et al., 2008). Identifying extinction dates also can provide insights into the extinction process (Caughley, 1994; Ferraz 2003; Roberts and Solow, 2003). Consequently, decisions about whether a species has gone extinct have many repercussions (Diamond, 1987; Butchart et al., 2006), including how limited conservation funds are used; how decisions for taxa with different needs are balanced; how conservation assessments are made; and how research is prioritized.

Given the large number of putatively extinct species, and the difficulty and expense of conducting sufficiently thorough searches to ensure a high degree of confidence that a species truly is extinct (e.g., Scott et al., 1986, 2008; Reynolds and Snetsinger, 2001), Butchart et al. (2006) developed a framework for categorizing the level of confidence that a species no longer persists. This method considers evidence for and against extinction and the time since the species was last reliably reported, and uses information such as how well a decline has been documented, severity of known threats, search effort, and ease of detection. Quantifying components of this model would increase the ease with which species can be directly compared, which might facilitate difficult choices about resource allocation.

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For example, quantitative methods for estimating extinction likelihood and predicted year of extinction from series of sighting data are available (e.g., Solow, 2005; Rivadeneira et al., 2009). These methods do not address all components of the Butchart et al. (2006) model, and should not be used in isolation when making conservation decisions. They do, however, provide a basis for quantifying one axis of investigation, while making explicit assumptions about some of the others (Roberts et al., in press). With these methods, the probability of detection and amount of search effort, for instance, are not assumed to be constant over the period of investigation (i.e., they can differ from year to year; Solow, 2005). Most of the methods assume only that there is no long-term trend in these variables (one exception is that of Solow, 1993b, which assumes a systematic decline in detectability as extinction is approached). The use of these methods, thus, provides one step towards a more quantitative assessment of whether and when species have gone extinct.

Most applications of these methods have focused either on illustrating new theoretical developments or have examined individual, high profile species (e.g., Roberts and Solow, 2003; Solow et al., 2006). Applying these methods systematically to quantify extinction patterns across suites of species is less common, probably because the necessary data sets are difficult to create (though see Burgman et al., 1995; McInerny et al., 2006; Patten et al., in press), but might have more practical value than isolated case studies. We have compiled temporal sequences of sighting records for all bird taxa (species, subspecies, or distinct island populations) from the United States and Canada that are presumed or suspected to have gone extinct during the past 200 years. We selected this set of populations because birds are generally well known, and because there has been considerable professional and amateur interest in finding rare species in this region for a long time. In addition, several species from this region have gone unseen for decades (North American Bird Conservation Initiative, 2009), but have not been declared extinct. Previously, we used a version of this data set to evaluate the underlying distributional assumptions of different methods for inferring the extinction parameters (Vogel et al., 2009). We concluded that, for our suite of species, a simple model that assumes a stationary Poisson process (Solow, 1993a) is more appropriate than the alternatives (e.g., Solow, 1993b; 2005; Roberts and Solow, 2003).

Here, we use the stationary Poisson method to estimate persistence probabilities and extinction dates for each population in order to determine which, if any, are likely to be extant and worthy of additional searches. Using the resulting information, we then examined the temporal patterns of North American and Hawaiian bird extinctions over the past two centuries, and tested whether there is evidence that the extinction rate has changed. Next, we determined the typical lag between the last sighting date and the estimated extinction date for a population, and between sequential sightings in extant populations, both of which provide insights into how long one should wait before inferring extinction. We also tested the hypothesis that as a species approaches extinction its inter-sighting interval changes. Finally, we examined whether a non-parametric alternative to the extinction model that we used, which can be calculated with only the two most recent sightings (Solow and Roberts, 2003), provides a good approximation of the results we obtained from our entire data sets.

2. Methods

2.1. Species selection and data compilation

We collated sighting information for 52 rare bird species, subspecies, and distinct island populations (see Supplementary material). We limited our evaluation to presumptive extinctions during the last two centuries because those prior to this time are unlikely to have a time series of good sighting records. We included a species/population if it has been designated as extinct by the US Fish and Wildlife Service (US Fish and Wildlife Service, 2006), is thought by many to be extinct, or has not been seen without controversy for over a decade. For our analyses we excluded several species for which there were too few records to use the sighting record methods (<5, after Solow, 2005; Table 1), and the Santa Barbara Island song sparrow (*Melospiza melodia graminea*), which recent work suggests is not a valid subspecies (Patten, 2001; Patten and Pruett, 2009).

Sighting dates were defined as the years in which a species was recorded along with adequate documentation to satisfy experts on the species. This final criterion is somewhat unsatisfactory as expert opinion can differ (McKelvey et al., 2008). Consequently, we classified sightings according to three different data standards (Roberts et al., in press). First, we limited each analysis to those cases for which there was unambiguous physical evidence. In most cases, this involved a specimen, but we also accepted uncontroversial photographs, video, and sound recordings for which we could ascertain the year in which they were obtained. Second, we expanded each data set to also include additional records for which sufficient documentation exists to satisfy experts (termed "independent expert opinion"). Our calculations were based on these two data sets. Third, we also compiled information on controversial sightings that we judged to lack firm evidence. This group included any records for which there is published controversy caused by experts disagreeing on whether the records should be accepted. We did not conduct additional analyses based on this most liberal data set, but some of these records may be valid and we report them to allow others to reanalyze the data as they see fit. All sighting record data are provided as Supplementary material, and are available with any updates from the authors. When a date range was reported for a single sighting, such as "1890s" or "1900–1901", we used the mid-date in our analyses, erring towards the later, more conservative, date when necessary (i.e., 1895 and 1901 in the examples given).

Sighting dates were compiled by first searching monographs containing compilations of occurrence data for each species. These included the Birds of North America Series (http://bna.birds.cornell.edu/bna/); Hahn's (1963) monograph on museum specimens; Scott et al. (1986), Pyle and Pyle (2009), Gorreson et al. (2009), and Banko's series of monographs, for Hawaiian birds; and various individual books on focal species (see Supplementary material for a full list of sources used to compile sighting records). These monographs were supplemented by searches of the primary literature (e.g., using Web of Science, Google Scholar) and government documents. Finally, we searched the Global Biodiversity Information Facility's (GBIF) Data Portal (www.gbif.net), the Ornithological Information System (ORNIS; http://olla.berkeley.edu/ornisnet/), the Maculay Library's archive of animal sound and video recordings (http://macaulaylibrary.org/index.do), and the Visual Resources for Ornithology (VIREO) photo library (http://vireo.acnatsci.org/) to look for archived physical evidence not described in our other sources. When it was ambiguous how to assign sightings to one of our three data standards, we followed the judgments made by authors of the most recent thorough external review, such as a major monograph.

2.2. Inferring extinction

For each population, we calculated the likely extinction date and the probability of a valid observation in 2009 given the prior sighting record, using models that assume a uniform (stationary Poisson) distribution (Solow, 1993a; Vogel et al., 2009). Sightings were organized as $t_1 < t_2 < \cdots < t_n$, where years are numbered

Table 1

Bird taxa evaluated, IUCN risk category (BirdLife International, 2009; CR = critically endangered, EW = extinct in the wild, EX = extinct), year of last confirmed sighting, number of years with confirmed records (n). Using equations from the text, we calculated the probability of a sighting record in 2009 (p), estimated year of extinction, and the upper 95% bound on that estimate. Estimates are given using just physical evidence (PE), and for independent expert opinion (IEO), which includes physical evidence; "Both" indicates that these sighting records are identical. Dashes indicate cases where calculations could not be done because there are fewer than five records.

Common name	IUCN	Data type	Last record	n^a	p	Estimated extinction year	Upper 95% bound
Labrador duck *Camptorhynchus labradorius*	EX	Both	1875	11	1E−7	1878	1887
Heath hen *Tympanuchus cupido cupido*	EX	PE	1931	18	2E−8	1933	1939
		IEO	1932	39	1E−17	1933	1936
Laysan rail *Porzana palmeri*	EX	PE	1940	17	8E−7	1943	1950
		IEO	1944	28	4E−10	1946	1950
Hawaiian rail *P. sandwichensis*	EX	PE	1864	6	0.007	1878	1934
		IEO	1884	7	0.009	1899	1952
Eskimo curlew *Numenius borealis*	CR	PE	1963	16	3E−4	1967	1977
		IEO	1963	29	2E−7	1965	1970
Great auk *Pinguinus impennis*	EX	Both	1844	17	2E−13	1846	1851
Passenger pigeon *Ectopistes migratorius*	EX	Both	1901	22	3E−17	1902	1904
Carolina parakeet *Conuropsis carolinensis*	EX	PE	1914	26	2E−15	1915	1918
		IEO	1914	28	2E−16	1915	1918
Ivory-billed woodpecker *Campephilus principalis*	CR	PE	1939	22	1E−9	1941	1945
		IEO	1944	39	5E−15	1945	1948
'Alalā (Hawaiian crow) *Corvus hawaiiensis*	EW	PE	2002	17	0.610	2015	2048
		IEO	2003	68	0.170	2006	2013
Kaua'i 'ō'ō *Moho braccatus*	EX	PE	1976	16	0.042	1985	2007
		IEO	1987	36	0.009	1991	2000
O'ahu 'ō'ō *M. apicalis*	EX	Both	1837	3	–	–	–
Bishop's 'ō'ō (Moloka'i) *M. bishopi*	EX	PE	1902	4	–	–	–
		IEO	1904	5	1E−4	1906	1917
Bishop's 'ō'ō (Maui) *M. bishopi*	EX	PE	None	–	–	–	–
		IEO	1901	1	–	–	–
Hawai'i 'ō'ō *M. nobilis*	EX	PE	1902	13	1E−6	1906	1916
		IEO	1902	14	4E−7	1906	1915
Kioea *Chaetoptila angustipluma*	EX	Both	1859	3	–	–	–
San Clemente [Bewick's] wren *Thryomanes bewickii leucophrys*	–	Both	1941	20	2E−7	1944	1950
Laysan millerbird *Acrocephalus familiaris familiaris*	EX	PE	1913	9	7E−6	1916	1926
		IEO	1916	12	2E−7	1919	1926
Kāma'o *Myadestes myadestinus*	EX	PE	1987	13	0.194	1999	2030
		IEO	1987	41	0.004	1991	1999
'Amaui *M. woahensis*	EX	Both	1825	1	–	–	–
Oloma'o (Moloka'i) *M. lanaiensis rutha*	CR	PE	1907	6	1E−4	1910	1923
		IEO	1980	12	0.049	1988	2009
Oloma'o (Lāna'i) *M. lanaiensis lanaiensis*	CR	PE	1933	4	–	–	–
		IEO	1934	9	4E−4	1939	1955
Bachman's warbler *Vermivora bachmanii*	CR	PE	1959	31	1E−7	1961	1967
		IEO	1962	49	7E−11	1964	1967
Dusky seaside sparrow *Ammodramus maritimus nigrescens*	–	PE	1980	35	3E−4	1983	1990
		IEO	1980	48	1E−5	1982	1987
'Ō'ū (Kaua'i) *Psittirostra psittacea*	CR	PE	1976	11	0.041	1984	2007
		IEO	1989	25	0.013	1993	2002
'Ō'ū (Hawai'i)	CR	PE	1977	15	0.022	1984	2001
		IEO	1987	33	0.003	1990	1998
'Ō'ū (O'ahu)	EX	PE	1846	2	–	–	–
		IEO	1899	4	–	–	–
'Ō'ū (Moloka'i)	EX	PE	1907	4	–	–	–
		IEO	1907	5	6E−4	1911	1928
'Ō'ū (Lāna'i)	EX	PE	1927	6	0.003	1934	1959
		IEO	1927	8	4E−4	1932	1948
'Ō'ū (Maui)	EX	PE	1901	2	–	–	–
		IEO	1901	6	1E−4	1905	1919
Lāna'i hookbill *Dysmorodrepanis munroi*	EX	Both	1913	1	–	–	–
Lesser koa-finch *Rhodacanthis flaviceps*	EX	Both	1891	1	–	–	–
Greater koa-finch *R. palmeri*	EX	PE	1896	3	–	–	–
		IEO	1896	6	1E−7	1897	1900

Table 1 (*continued*)

Common name	IUCN	Data type	Last record	n^a	p	Estimated extinction year	Upper 95% bound
Kona grosbeak *Chloridops kona*	EX	Both	1892	3	–	–	–
Greater ʻamakihi *Hemignathus sagittirostris*	EX	Both	1901	5	4E−5	1903	1911
Lesser ʻakialoa *H. obscurus*	EX	Both	1903	18	5E−8	1907	1915
Greater ʻakialoa (Oʻahu) *H. ellisianus ellisianus*	EX	PE	1838	2	–	–	–
		IEO	1892	3	–	–	–
Greater ʻakialoa (Lānaʻi) *H. e. lanaiensis*	EX	PE	1892	1	–	–	–
		IEO	1894	2	–	–	–
Greater ʻakialoa (Kauaʻi) *H. e. stejnegeri*	EX	PE	1960	11	0.006	1967	1985
		IEO	1969	19	8E−4	1973	1984
Nukupuʻu (Oʻahu) *H. lucidus lucidus*	EX	Both	1838	2	–	–	–
Nukupuʻu (Kauaʻi) *H. l. hanapepe*	"likely EX"	Both	1899	7	6E−7	1901	1906
Nukupuʻu (Maui) *H. l. affinis*	CR	Both	1896	3	–	–	–
Oʻahu ʻalauahio *Paroreomyza maculate*	CR	PE	1968	10	0.086	1981	2020
		IEO	1968	21	0.004	1974	1989
Maui ʻalauahio (Lānaʻi) *P. montana*	EX	PE	1928	7	0.001	1934	1954
		IEO	1937	10	3E−4	1942	1956
Kākāwahie *P. flammea*	EX	PE	1907	11	2E−6	1910	1920
		IEO	1963	15	0.004	1969	1985
Maui ʻākepa *Loxops coccineus ochraceus*	EX	PE	1901	6	1E−4	1905	1919
		IEO	1980	15	0.030	1987	2004
Oʻahu ʻākepa *L. c. rufus*	EX	PE	1893	4	–	–	–
		IEO	1901	5	0.029	1916	1986
ʻUla-ʻai-hāwane *Ciridops anna*	EX	Both	1892	2	–	–	–
Hawaiʻi mamo *Drepanis pacifica*	EX	PE	1892	6	0.029	1911	1985
		IEO	1898	7	0.019	1915	1975
Black mamo *D. funerea*	EX	Both	1907	4	–	–	–
Laysan honeycreeper [ʻapapane] *Himatione sanguinea freethii*	–	PE	1913	9	1E−6	1915	1923
		IEO	1923	14	2E−4	1930	1948
Poʻo-uli *Melamprosops phaeosoma*	CR	PE	2004	7	0.408	2008	2024
		IEO	2004	27	0.020	2005	2008

[a] Any differences between values for n in this table and those found for species treated in Vogel et al. (2009) reflect revisions from updated information or an expanded sighting series.

starting with $t_1 = 0$. The expected number of years from the start of the sighting record to the year of extinction can be estimated as $\hat{T}_E = \frac{n+1}{n} t_n$ and the expected year of extinction is T_E plus the year of t_1. We also calculated the number of years to the upper 95% confidence bound for T_E using $T_E^u = t_n / \alpha^{1/(n-1)}$, where $\alpha = 0.05$ (after Solow, 2005). Note that we use $n − 1$, not n, in this equation because the first sighting date is used as the start of T (see McInerny et al., 2006), making our confidence bounds wider than they would have been under the original formulation. From this calculation we determined the upper confidence bound for the extinction year. To determine whether a species is likely to have gone extinct, we used the equation $p = (t_n/T)^{n-1}$ (after Solow, 1993a) to give the probability of a valid observation in 2009, where T is the time interval between the year of the first sighting and the target year (2009 for our analyses). For each population, we first conducted these calculations for a sighting record including just dates with physical evidence, and then after adding in all dates supported by independent expert opinion (see also Roberts et al., in press).

2.3. Patterns in extinction records

To determine whether extinction rates changed over the time spanned by our data we tested whether the lengths of the periods between the estimated extinction dates for different populations had changed over time. We used general linear models to fit both linear and quadratic functions and determined which model was best supported using AIC$_c$ (Burnham and Anderson, 2002). Average

and maximum lags between last sightings and estimated extinction dates, and gap sizes between sightings within sighting records, were determined to infer how long populations were likely to persist without observations. Finally, we calculated p using Solow and Roberts's (2003) non-parametric approximation, which uses only the last two observations in a sighting record: $p = \frac{(T_n - T_{n-1})}{(T - T_{n-1})}$, where T is defined as described above, T_n is the time interval from the first observation to the last observation, and T_{n-1} is the time interval from the first observation to the penultimate observation. The results of this method were compared to those using the entire sighting series using simple and Spearman rank correlation.

3. Results

Of the 52 populations for which we collated data, we had sufficient information to conduct analyses for 32 using the physical evidence sighting records, and 38 when independent expert opinion records were added. Here, we present results for the larger set of 38 populations, noting results based on just physical evidence sightings only when they differed qualitatively. Estimated extinction dates for the 38 populations ranged from 1846 to 2006, with the upper 95% bounds on these estimates ranging from 1851 to 2013. Based on these analyses, only for the ʻalalā (*Corvus hawaiiensis*) is there any indication that persistence is likely. Other species for which the 95% confidence interval around the predicted extinction date includes dates after 2000 were (in decreasing likelihood
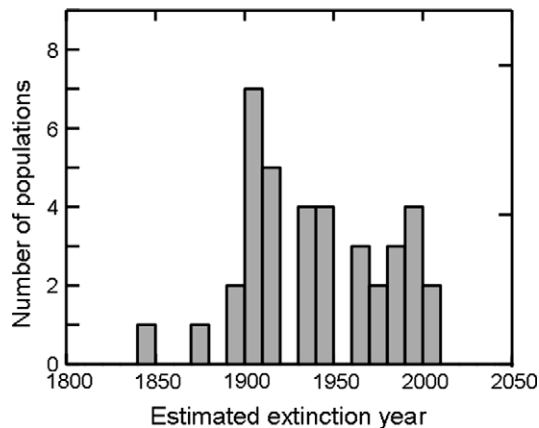
Fig. 1. Frequency distribution showing the number of populations estimated to have gone extinct within each decade. Estimated extinction dates are based on sighting records that include all observations supported by physical evidence or independent expert opinion.

Fig. 2. Frequency distribution showing the sizes of gaps between consecutive sightings, from all sighting records combined.

of persistence), the olomaʻo population on Molokaʻi (*Myadestes lanaiensis rutha*), Maui ʻākepa (*Loxops coccineus ochraceus*), poʻo-uli (*Melamprosoma phaeosoma*), ʻōʻū (*Psittirostra psittacea*) on Kauaʻi, and Kauaʻi ʻōʻō (*Moho braccatus*) (Table 1). Analyses based on sighting records that include only reports with physical evidence, estimate extinction dates before 2000 for all populations except ʻalalā and poʻo-uli. Wider confidence intervals around the estimated extinction dates characterized the physical evidence sighting records for several species (Table 1), as expected given their sparser nature.

Estimated extinction dates were spread across the entire time from the 1840s until the 2000s, with some evidence for a peak just after 1900 (Fig. 1). A regression of the periods between consecutive extinctions versus time was better fit by a quadratic function (inter-extinction interval = $0.0023(\text{year})^2 - 8.88(\text{year}) + 8652$) than by a linear function (adjusted $r^2 = 0.40$ vs. 0.08, respectively; $\Delta AIC_c = 14.0$), suggesting that extinction rates increased during the early part of the evaluation period and subsequently slowed. Repeating this analysis using only physical evidence, resulted in slightly weaker evidence that extinction rates were higher during the early 1900s (adjusted $r^2 = 0.29$ vs. 0.02; $\Delta AIC_c = 8.7$), but no qualitative difference.

The average lag between the last sighting and the estimated extinction date was only 4.3 years (95% CI = 3.1–5.6 years; max = 17 years), and the last sighting year was a highly effective predictor of the estimated year of extinction ($y = 0.986x + 32.13$; $r^2 = 0.99$, $P < 0.001$). This equation is equivalent to an average lag of 6.2 years in 1850, decreasing to a lag of 4.0 years by 2010. The slope of this equation, however, was not significantly different from 1.0 (95% CI: 0.95–1.02) suggesting that the lag has not changed over time. As expected, given the properties of the model, the main outlier species was that with the longest gaps between sightings: Hawaiʻi mamo (*Drepanis pacifica*). Similarly, the time lag between the last sighting and the upper 95% confidence limit for the extinction date were closely related ($y = 0.892x + 225.9$; $r^2 = 0.790$, $P < 0.001$; slope not significantly different from 1.0, 95% CI = 0.74–1.05), with an average lag ranging from ∼26 years in 1850 to ∼9 years in 2010.

The lag between a population's last sighting and its estimated extinction date is determined by both the number of sightings in the extinction record and the lengths of the gaps between sightings. Comparing the relationships between the number of sightings, average gap size, and maximum gap sizes, and the lags that were calculated from our empirical data sets, we found that the lag was most closely correlated with mean gap size ($r = 0.99$;
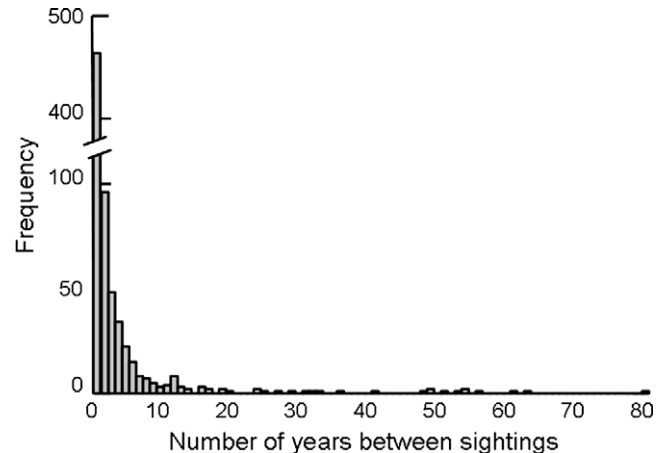
compared to $r = 0.74$ for the maximum gap size and $r = -0.38$ for the sample size). Similarly, the mean gap size was most closely related to the difference between the estimated extinction date and the upper 95% confidence limit for this date, which provides a measure of the uncertainty in the estimated extinction date ($r = 0.98$; compared to $r = 0.60$ for the maximum gap size and $r = -0.42$ for the sample size).

Next, we examined the sizes of gaps between consecutive observations within sighting records. Although the maximum gap size between consecutive sightings was 79 years (for Hawaiian rail *Porzana sandwichensis*), long gaps were exceedingly rare (Fig. 2). Combining information from all sighting records, the median gap size was 0 years and the mean was 2.5 years (95% CI = 1.9–3.0 years). Of 742 gaps, less than 1% were longer than 50 years and 81% were of two years of less. Because the equation we used to estimate extinction dates is reportedly sensitive to especially large gaps at the end of the sighting record (Burgman et al. 1995), we also tested whether the last gap in a given sighting record was, on average, larger than the mean size of prior gaps from the same record. We found no evidence of this problem; in fact the last gaps were generally smaller than the average of prior gaps (means = 2.1 vs. 4.1 years, respectively; paired t-test, $t_{37} = 2.90$, $P = 0.006$).

Finally, we found that p values obtained using the simple non-parametric method of Solow and Roberts (2003) were only weakly correlated with those obtained from more complete sighting records ($r = 0.39$), although their ranking of species was better correlated ($r_s = 0.77$).

4. Discussion

Based on our analyses, all of the populations studied are very likely extinct. The confidence interval around the estimated extinction date for the ʻalalā extends beyond the current time, suggesting that this is the population that is most likely to be extant. Even in this case, however, the possibility of persistence is not high, and if confirmed sightings are not forthcoming by 2014 it would be reasonable to conclude with a high level of confidence that the population is extinct. Of the remaining populations, those for which there is the greatest (albeit small) chance of persistence, and thus for which additional search efforts would be least unlikely to fail, are the olomaʻo population on Molokaʻi, Maui ʻākepa, poʻo-uli, ʻōʻū on Kauaʻi, and the Kauai ʻōʻō. Using only physical evidence produces wider confidence intervals around the estimated extinction dates for some species, but this result is simply a by-product of

the sparser sighting records, which necessarily contain longer gaps between sightings. Given the lack of controversy over the intervening observations in these time series, we judge the data set with only physical evidence to be overly conservative. Overall, these findings support the notion that, if money is to be spent searching for possibly extinct species in the United States, then these Hawaiian species should be prioritized over mainland species (cf. Leonard, 2008).

An obvious concern about these conclusions is whether the sighting records on which our analyses are based are accurate. Uncertainty comes in various forms (Regan et al., 2002), and in this case at least three issues arise. First, additional observations may have been made and not included in our sighting records. If the additional dates fall between the extremes in our sighting records they will reduce the mean gap size, which would have the effect of reducing the lag between the last sighting and the estimated extinction date and improving confidence in those estimates. In these cases, our conclusions will be robust to additional data and, if anything, are conservative with respect to assuming prematurely that extinction has occurred.

A second potential problem is the inadvertent exclusion of valid reports from after the last year in a sighting record, which would move estimated extinction dates forward in time. Because potentially extinct species are of great interest, such records are likely to be known, but they may be controversial (e.g., Fitzpatrick et al., 2005, 2006; Sibley et al., 2006, 2007). For our analyses, we required a high burden of proof before including dates in our sighting records and did not include controversial sightings (listed in Supplementary material), but different standards could be set (Roberts et al., in press). Exactly which data standard is used to determine what constitutes an acceptable observation is probably less important than ensuring that a common standard is applied to all species. Such internal consistency is critical when ranking species based on conservation needs (e.g., to allocate funds for searches) and the development of such standards should be an important goal for conservation biologists (Harrison and Stiassny, 1999; McKelvey et al., 2008; Roberts et al., in press).

Third, reports that were included in sighting records may be erroneous. By only including those that are widely accepted, we have aimed to minimize the risk of including such reports. Nonetheless, one cannot rule out errors in specimen labeling, entry into on-line databases, and situations where experts are all in error. For example, we found several errors in the on-line databases for specimen collections, including cases of archived recordings that the original sound recordists told us were attributed to the wrong species following taxonomic changes. The only solution for such problems is to stress the importance of careful record taking, database proofing, and long-term archiving of documentary material.

A related issue for many species is that historical data generally were not collected with a well defined sampling scheme in mind. Consequently, it often is impossible to estimate parameters that are commonly considered in modern ecological surveys (e.g., search effort, detection rates, etc.; Williams et al., 2002). Sighting record methods for estimating extinction do not require that these parameters be fixed, but many assume that there has not been directional change over time, and a significant decline in search effort or detectability could lead one to underestimate the lag between the last sighting and the extinction date (Rivadeneira et al., 2009). For the populations included in this study, such a decline is unlikely because of greatly increased interest in bird-watching over the time period evaluated, large-scale declines of the habitats occupied by rare species (i.e., decreasing areas that require searches), improved accessibility to remote areas, and better equipment for detecting species (Roberts et al., in press). Moreover, our prior work suggests that it is appropriate to assume a stationary Poisson process for our data sets (Vogel et al., 2009). Our findings that gaps between observations were shorter at the end of sighting records also indicates that, if anything, detection rates improved as species approach extinction. Simulations suggest that sighting record methods (including the one used here) are more likely to overestimate than underestimate the width of confidence intervals when sampling is uniform or increases towards extinction time (Rivadeneira et al., 2009), again suggesting that we are unlikely to have concluded that extinction has occurred when it has not.

Although concerns about the effects of sampling patterns appear to be unwarranted for our data sets, the same may not be true for organisms with different characteristics (cf. Rivadeneira et al., 2009). This conundrum leaves the modern conservation biologist with a choice between discarding historical knowledge in the quest for statistical purity, or basing decisions on imperfect data sets (cf. Elphick, 2008). Although, limitations of existing data must be recognized and accounted for in policy decisions, we consider the latter approach to be generally preferable.

In addition to providing information about the relative likelihood of persistence of the species studied, our analyses provide general insights into the use of sighting records for inferring extinction. First, the patterns of gaps within sighting records, in which the vast majority of gaps are small, and the small average lag between the last sighting of a species and the estimated extinction date, both suggest that even rare species are unlikely to go many years without being detected as long as there is some search effort. There are exceptions to this generalization, but most well documented cases of species being rediscovered after long periods of no sightings, involve species from remote areas (e.g., Bauer et al., 2000; Eames et al., 2005), or species that are highly cryptic (e.g., Zimmer et al., 2001; Köhler et al., 2005). Sighting records for such species would be expected to look very different from those in our study, with many more long gaps between sightings. Analyses of such sighting records would thus suggest a longer lag between the last sighting and the year in which extinction could be safely assumed. In contrast, long gaps between well-documented records were exceedingly rare in our data sets, and gap sizes generally declined over time supporting the notion that long gaps are increasingly unlikely as methods of detection improve and suitable habitat declines. Our data suggest that, for moderately conspicuous species in well studied, accessible regions, even the most extreme lags between the last sighting and extinction will be less than 20 years, and that lags of only a few years are generally to be expected. Clearly, these analyses should be replicated with other suites of sighting records before extending quantitative guidelines to other groups of organisms, but they suggest that rules of thumb that have been proposed (e.g., 20 times the gap between the last two sightings; Solow and Roberts, 2003) may be too conservative for the majority of cases.

A second general result was that the lag between the last sighting and the estimated extinction date was not highly dependent on the sample size. Although additional analyses are desirable, this result implies that as long as sighting records are long enough for the estimated mean gap size to be stable (i.e., little influenced by subsequent records), adding additional records may be superfluous. In fact, lengthening records backwards in time, simply to increase the sample size, might prove counterproductive because it increases the risk that the sighting process will change over the course of the record.

Although sample size was only loosely correlated with extinction lag and uncertainty over the extinction date, comparison of our main results to those obtained using the simple non-parametric method proposed by Solow and Roberts (2003) suggest that one cannot make good estimates using only the last two observations of a species. An earlier comparison, using data from a set of orchid species, superficially suggested a good correlation between methods, but this result is driven by one data point: Using the

p values from that analysis we found that the correlation coefficient (*r*) dropped from 0.95 to 0.04 after removal of this one influential datum. For our data sets, the non-parametric method performed better when only the ranking of populations in terms of extinction likelihood was considered.

5. Conclusions

Sighting record models, coupled with standardized methods for accepting observations as valid, provide a method for systematically evaluating the likelihood that species persist and for prioritizing search efforts for potentially extinct species. Our results suggest that all of the populations that we studied are probably extinct, but we identify those species for which additional searches would most likely be worthwhile. In assessing extinction likelihood, more detailed analyses incorporating quantitative information on search effort and detectability are likely to increase the accuracy of inferences, but the necessary information is generally lacking, especially for large suites of species for which prioritizations must frequently be made. Sighting record methods, therefore, provide an important compromise that allows one to make systematic inferences from historical data when more detailed approaches are impossible. As such, they can help conservation practitioners to make difficult decisions when time and money are too limited to conduct detailed searches for all species, or to collect the detailed information required to make triage decisions about the allocation of funds more rigorous (cf. Chadès et al., 2008).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.11.026.

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