Roberts, David L., Jari?, Ivan and Solow, Andrew R. (2017) *On the functional extinction of the Passenger Pigeon.* Conservation Biology, 31 (5). pp. 1192-1195. ISSN 0888-8892.

On the functional extinction of the Passenger Pigeon (*Ectopistes migratorius*)

David L. Roberts[1], Ivan Jarić[2,3*] and Andrew R. Solow[4]

[1] Durrell Institute of Conservation and Ecology, School of Anthropology & Conservation, Marlowe Building, University of Kent, Canterbury, Kent, CT2 7NR, United Kingdom

[2] Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany

[3] Institute for Multidisciplinary Research, University of Belgrade, KnezaViseslava 1, 11000 Belgrade, Serbia

[4] Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

[*] Corresponding author: Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany; phone: +49 (0)30 64181 766, fax: +49 (0)30 64181 626; E-mail: jaric@igb-berlin.de

Running head: Passenger Pigeon functional extinction

Keywords: *Ectopistes migratorius*; functional extinction; museum specimens; North America; passenger pigeon; reproductive failure.

Word count: **2248**

Acknowledgements

The authors thank the handling editor and the three anonymous reviewers for providing helpful comments and suggestions. The authors acknowledge the sponsorship provided by the Alexander von Humboldt Foundation and the Federal German Ministry for Education and Research, as well as the support by the Project No. 173045, funded by the Ministry of Education, Science and Technological Development of the Republic of Serbia.

On the functional extinction of the Passenger Pigeon (*Ectopistes migratorius*)

Abstract

The Passenger Pigeon (*Ectopistes migratorius*) was a social breeder and it has been suggested that the species experienced functional extinction, defined as a total reproductive failure, prior to its actual extinction in the early years of the 20th century. Here, we apply a novel statistical method to a record of egg specimens and so-called skin specimens to test for functional extinction. The results indicate that the species did not become functionally extinct, suggesting that proposals to reverse its rapid decline in the late 19th century could have been successful.

Introduction

At the time of the European settlement of North America, the Passenger Pigeon (*Ectopistes migratorius*) was arguably the most abundant bird species on Earth. By the turn of the 19th century, however, populations were declining as a result of hunting, nest disturbance, and habitat loss (Halliday 1980; Blockstein & Tordoff 1985; Bucher 1992; Jackson & Jackson 2007). The species became extinct on 1 September 1914 with the death of a solitary 29-year old female called Martha in the Cincinnati Zoo (Herman 1948), with extinction in the wild around a decade earlier (Elphick et al. 2010). The decline of the Passenger Pigeon did not go unnoticed. As early as 1857, the Ohio legislature considered, but ultimately rejected, legislation to limit hunting (Greenberg 2014). Other failed efforts at the state and local level followed (Herman 1948; Brewster 1889; Greenberg 2014; Schulz et al. 2014).

Lack of social facilitation, reproductive failure, increased natural predation and Allee effects were also suggested as secondary causes of decline, once their population dropped below a certain threshold (Herman 1948; Halliday 1980; Blockstein & Tordoff 1985; Bucher 1992). The Passenger Pigeon was highly social, nesting in enormous colonies, with breeding success highly dependent on social facilitation (Hung et al. 2014; Stanton 2014). As a result, it may have experienced functional extinction – defined as permanent reproductive failure prior to true extinction (Ricciardi et al. 1998; Bull et al. 2009; Waters et al. 2013) – as its numbers collapsed near the end of the 19th century (Halliday 1980). The failure of several breeding attempts, conducted for different purposes with small captive populations (Herman 1948; Mallinson 1995; Fuller 2014; Yeoman 2014), could be also taken as an evidence of the importance of social facilitation in breeding (Mallinson 1995), although there are other plausible causes such as inbreeding or inadequate rearing conditions. The possibility of functional extinction raises the question whether the efforts to protect the species in the wild had any prospect of forestalling extinction.

While a number of methods are available to detect true extinction based on sightings of individuals (Solow 2005), functional extinction is more difficult to detect because reproductive events are typically not observed. Here, we test for functional extinction in the Passenger Pigeon using museum specimens of physical remains and eggs. The results of the analysis suggest that functional extinction was not the ultimate extinction mechanism in this species.

In related work, Jarić et al. (2016) tested for functional extinction of the ship sturgeon (*Acipenser nudiventris*) in the Danube River. This earlier work differed from the present one in two important ways. First, the timing of reproductive events was determined from the ages of captured specimens. Second, the species was known not to be truly extinct. In contrast to the present study, the results suggested that the ship sturgeon is functionally extinct. As the species is not truly extinct, this result pointed to the need for a breeding program in addition to other protective measures, if it is to be saved.

Materials

The Ornis2 database (http://ornis2.ornisnet.org/ accessed 20th July 2015) contains records from a total of 798 Passenger Pigeon specimens. Of these, 94 are eggs and 597 are bodily remains referred to here as (but not restricted to) skins. Our basic assumption is that the former represent direct evidence of reproductive events while the latter represent traditional species sightings. We excluded duplicate specimens (e.g., eggs collected from the same nest), specimens lacking a date or location of collection (the latter potentially being indicative of captive origin), and specimens clearly of captive origin (e.g., the specimen listed as 'Marta'). Finally, two skin specimens from 1906 were excluded as their reliability has been questioned (Reed pers. comm.; Schorger 1955). This resulted in a total of 44 eggs and 213 skins. We assume that all the specimens are correctly identified (but see Roberts et al. 2010 regarding the reliability of museum specimens). Histograms of the collection dates are shown in Figure 1.

Method

The basic statistical model is that the sighting times of eggs $X_1, X_2, \ldots, X_m$ are independent and follow a discrete uniform distribution over the interval $(0, \tau_f)$ where 0 corresponds to the beginning of the observation period and τ_f is the unknown functional extinction time. Similarly, the sighting times of skins $Y_1, Y_2, \ldots, Y_n$ are independent and follow a discrete uniform distribution over the interval $(0, \tau_e)$ where τ_e is the unknown true extinction time with $\tau_e \geq \tau_f$. Interest centers on testing the null hypothesis $H_o : \tau_f = \tau_e$ that functional extinction did not occur prior to true extinction against the one-sided alternative hypothesis $H_1 : \tau_f < \tau_e$ that it did.

Let $X_{(m)}$ be the time of the most recent egg sighting and $Y_{(n)}$ be the time of the most recent skin sighting. The likelihood under this model is:

$$L(\tau_f, \tau_e) = \tau_f^{-m} \tau_e^{-n} \qquad (1)$$

for $\tau_f \geq X_{(m)}$, $\tau_e \geq Y_{(n)}$ and 0 otherwise. It is necessary to distinguish between two cases. Suppose that $X_{(m)} \leq Y_{(n)}$. In this case, under H_1, the maximum likelihood (ML) estimates of τ_f and τ_e are $X_{(m)}$ and $Y_{(n)}$, respectively, while under H_o both are equal to $Y_{(n)}$. In the case that $X_{(m)} > Y_{(n)}$, the ML estimates of τ_f and τ_e are both equal to $X_{(m)}$ under both H_1 and H_o. It follows that the likelihood ratio statistic for testing H_o against H_1 is an increasing function of:

$$T = \begin{cases} \dfrac{Y_{(n)}}{X_{(m)}} & X_{(m)} \leq Y_{(n)} \\ 1 & X_{(m)} > Y_{(n)} \end{cases} \qquad (2)$$

so that a test based on *T* will give exactly the same p-value as a test based on the likelihood ratio statistic, with H_o rejected for large values of *T*.

The significance of the observed value T_{obs} of *T* can be assessed through the so-called mid-*p* value:

$$p = pr(T > T_{obs}) + \frac{1}{2} pr(T = T_{obs}) \qquad (3)$$

where the probabilities are calculated under H_o. The mid-*p* value is appropriate when, as here, the test statistic has a discrete component (Berry & Armitage 1995).

Let the ordered values of the pooled sighting times be $Z_{(1)} < Z_{(2)} < \ldots < Z_{(m+n)}$ and let *j* be the rank of $X_{(m)}$ among these. Conditional on the pooled sighting times, the event $T > T_{obs}$ is equivalent to the event that $Z_{\mathrm{j}}, Z_{j+1}, \ldots, Z_{m+n}$ are all skins. Under H_o, the probability of this event is given by the hypergeometric distribution as $\dfrac{\binom{n}{m+n-j+1}}{\binom{m+n}{m+n-j+1}}$. The event $T = T_{obs}$ is equivalent to the event that Z_{j} is an egg and $Z_{\mathrm{j+1}}, Z_{j+2}, \ldots, Z_{m+n}$ are all skins. Under H_o, the probability of this event is given by $\dfrac{m}{m+n}\dfrac{\binom{n}{m+n-j}}{\binom{m+n-1}{m+n-j}}$. Combining these results gives:

$$p=\frac{\binom{n}{m+n-j+1}}{\binom{m+n}{m+n-j+1}}+\frac{1}{2}\frac{m}{m+n}\frac{\binom{n}{m+n-j}}{\binom{m+n-1}{m+n-j}} \qquad (4)$$

The result in (4) is valid provided no sighting of either type has the same rank *j* as $X_{(m)}$. It is possible to modify the result based on the hypergeometric distribution to account for such ties. A convenient alternative, however, is to approximate the mid-*p* value by simulation. This would involve repeatedly distributing *m* egg sightings and *n* skin sightings randomly over the observation period, calculating the value $T^{\bullet}$ of *T*, and approximating the mid-*p* value by the proportion of times that $T^{\bullet}$ exceeds T_{obs} plus one-half the proportion of times $T^{\bullet}$ equals T_{obs}.

Results

We took the observation period to begin in 1890 (Table 1). The uniformity assumption was tested using the chi squared goodness-of-fit statistic (Snedecor & Cochran 1989) with significance assessed via simulation. The null hypothesis of uniformity can not be rejected for either egg or skin sightings. The corresponding record contained a total of 6 eggs and 27 skins. For this data set, $m = 6$, $n = 27$, and $j = 29$. In this case, the mid-*p* value given in Equation 4 is 0.38 and the null hypothesis of no functional extinction can not be rejected by conventional standards of statistical significance.

Particularly given the small number of egg sightings, the question arises as to the power of this test. To address this, we conducted the following simulation experiment. Keeping the observation period and the sighting record for skins fixed, we distributed 6 egg sightings according to the discrete uniform distribution over the interval (0, τ_f) for selected values of τ_f and applied the test to the simulated data. For each value of τ_f, we repeated the procedure 1000 times and approximated the power of the test by the proportion of times that H_o was correctly rejected. The results are summarized in Table 2. Although the test has low power for functional extinction occurring after 1894, power jumps to 1 for functional extinction occurring in 1894 (or earlier). We conclude that, while the null hypothesis that functional extinction did not occur cannot be rejected at conventional significance levels, it would be difficult to detect it had it occurred a few years before true extinction.

Discussion

This paper has described a novel test for functional extinction based on sighting records of individuals and of reproductive events (in this case, eggs). As with other statistical tests, conditional on functional extinction having occurred, as the numbers of sightings in the two records increases, the null hypothesis is certain to be rejected for arbitrarily small - and therefore biologically uninteresting - values of this difference. We note that, because of the discreteness of time, functional extinction occurring prior to, but in the same year as, true extinction comports with H_o. Particularly if the null hypothesis is rejected, it therefore may be of interest to construct a confidence interval for the interval $\tau_e - \tau_f$ between functional extinction and actual extinction. While this issue does not arise with the Passenger Pigeon, we are currently working on the construction of such a confidence interval.

It is worth noting that the maximum potential time lag observed in data following the last confirmed reproduction can not exceed the maximum longevity of a species. While there are no data on the lifespan of Passenger Pigeon in the wild, in captivity it ranged from 15 years on average up to the maximum reported age of 29 years (Martha; Herman 1948). Although the inference of functional extinction can be more challenging in short-living species, the method presented here should provide reasonable power if the dataset contains sufficient number of records after the last egg collection.

Statistical method presented here indicated that the Passenger Pigeon did not become functionally extinct prior to its actual extinction in the wild. It is important to emphasize, however, that the results do not negate the possibility that Allee effects contributed to its decline.

Although it is, of course, too late, the results presented here suggest that hunting control efforts might have been successful and that captive breeding efforts were not necessary. On a more positive note, the demise of the Passenger Pigeon was a major impetus for Federal legislation – including the Lacey Act of 1900, the Weeks-McLean Act of 1913, and the Migratory Bird Treaty Act of 1918 – to protect wild birds from the same fate.

Literature cited

Berry G, Armitage P. 1995. Mid-*P* confidence intervals: a brief review. Statistician **44**:417-423.

Blockstein DE, Tordoff HB. 1985. A contemporary look at the extinction of the passenger pigeon. American Birds **39**:845-851.

Brewster W. 1889. The present status of the wild pigeon (*Ectopistes migratorius*) as a bird of the United States, with some notes on its habits. The Auk **6**(4):285-291.

Bucher EH. 1992. The causes of extinction of the passenger pigeon. In Current Ornithology **9**: 1-36. Power DM (Ed). New York: Plenum Press.

Bull J, Nilsen EB, Mysterud A, Milner-Gulland EJ. 2009. Survival on the border: a population model to evaluate management options for Norway’s wolves *Canis lupus*. Wildlife Biology **15**:412-424.

Elphick CS, Roberts DL, Reed JM. 2010. Estimated dates of recent extinctions for North American and Hawaiian birds. Biological Conservation **143**:617-624.

Fuller E. 2014. The passenger pigeon. Princeton University Press.

Greenberg J. 2014. A feathered river across the sky: the passenger pigeon's flight to extinction. New York: Bloomsbury Publishing USA.

Halliday TR. 1980. The extinction of the passenger pigeon *Ectopistes migratorius* and its relevance to contemporary conservation. Biological Conservation **17**:157-162.

Herman WC. 1948. The last passenger pigeon. The Auk **65**(1):77-80.

Hung CM, Shaner PJL, Zink RM, Liu WC, Chu TC, Huang WS, Li SH 2014. Drastic population fluctuations explain the rapid extinction of the passenger pigeon. Proceedings of the National Academy of Sciences **111**:10636-10641.

Jackson JA, Jackson BJS. 2007. Extinction: the passenger pigeon, last hopes, letting go. The Wilson Journal of Ornithology **119**(4):767-772.

Jarić I, Gessner J, Solow AR. 2016. Inferring functional extinction based on sighting records. Biological Conservation **199**:84-87.

Mallinson JJC. 1995. Conservation breeding programmes: an important ingredient for species survival. Biodiversity and Conservation **4**:617-635.

Roberts DL, Elphick CS, Reed JM. 2010. Identifying anomalous reports of putatively extinct species and why it matters. Conservation Biology **24**(1):189-196.

Ricciardi A, Neves RJ, Rasmussen JB. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. Journal of Animal Ecology **67**:613-619.

Snedecor GW, Cochran WG. 1989. Statistical Methods, Eighth Edition. Iowa State University Press.

Schorger AW. 1955. The Passenger Pigeon: its natural history and extinction. University of Wisconsin Press, Madison.

Schulz JH, Otis DL, Temple SA. 2014. 100th anniversary of the passenger pigeon extinction: Lessons for a complex and uncertain future. Wildlife Society Bulletin **38**(3):445-450.

Solow AR. 2005. Inferring extinction from a sighting record. Mathematical Biosciences **195**(1):47-55.

Stanton JC. 2014. Present-day risk assessment would have predicted the extinction of the passenger pigeon (*Ectopistes migratorius*). Biological Conservation **180**:11-20.

Waters CG, Story R, Costello MJ. 2013. A methodology for recruiting a giant clam, *Tridacna maxima*, directly to natural substrata: a first step in reversing functional extinctions? Biological Conservation **160**:19-24.

Yeoman B. 2014. Why the passenger pigeon went extinct. Audubon Magazine **116**(3):28-33.

Table 1. Sightings of Passenger Pigeon (*Ectopistes migratorius*) since 1890. Number of sightings in a given year indicated in parentheses.

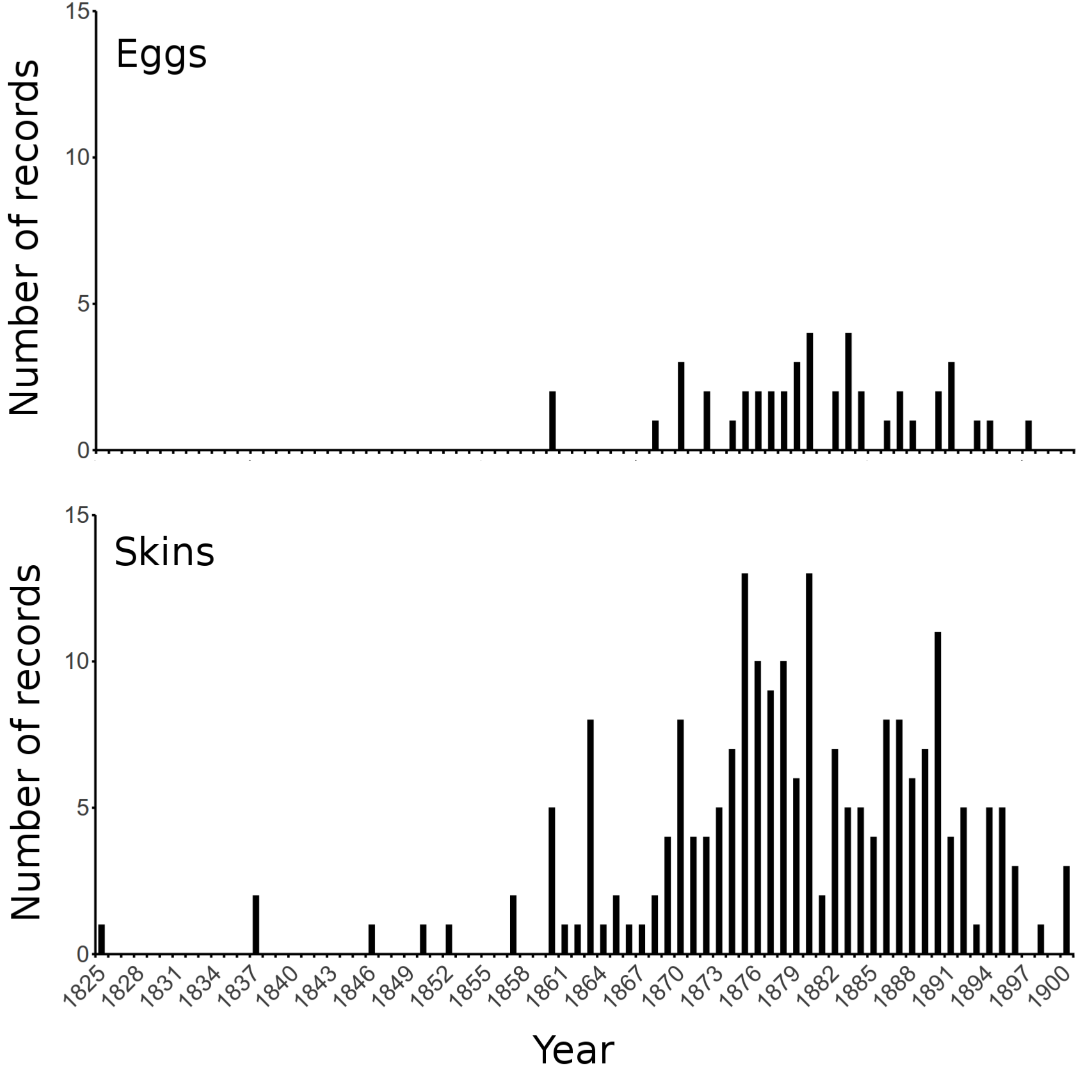
Type of sightings	Sighting years
Eggs	1891 (3), 1893 (1), 1894 (1), 1897 (1)
Skins	1891 (4), 1892 (5), 1893 (1), 1894 (5), 1895 (5), 1896 (3), 1898 (1), 1900 (3)

Table 2. Approximate power of the test for functional extinction for selected values of τ_f .

τ_f	Approximate power
1894	1.000
1895	0.254
1896	0.089
1897	0.027

Figure legend

Figure 1. Passenger Pigeon (*Ectopistes migratorius*) sighting record, based on the collection dates of eggs and skins from museum collections.


Eggs
Skins
Number of records
Number of records
0
5
10
15
0
5
10
15
1825
1828
1831
1834
1837
1840
1843
1846
1849
1852
1855
1858
1861
1864
1867
1870
1873
1876
1879
1882
1885
1888
1891
1894
1897
1900
Year