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

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29

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

2

3 **Abstract**

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

10

11

12 **Introduction**

13 At the time of the European settlement of North America, the Passenger Pigeon
14 (*Ectopistes migratorius*) was arguably the most abundant bird species on Earth. By the turn of
15 the 19th century, however, populations were declining as a result of hunting, nest disturbance,
16 and habitat loss (Halliday 1980; Blockstein & Tordoff 1985; Bucher 1992; Jackson & Jackson
17 2007). The species became extinct on 1 September 1914 with the death of a solitary 29-year old
18 female called Martha in the Cincinnati Zoo (Herman 1948), with extinction in the wild around a
19 decade earlier (Elphick et al. 2010). The decline of the Passenger Pigeon did not go unnoticed.
20 As early as 1857, the Ohio legislature considered, but ultimately rejected, legislation to limit
21 hunting (Greenberg 2014). Other failed efforts at the state and local level followed (Herman
22 1948; Brewster 1889; Greenberg 2014; Schulz et al. 2014).

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

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

42 In related work, Jarić et al. (2016) tested for functional extinction of the ship sturgeon
43 (*Acipenser nudiiventris*) in the Danube River. This earlier work differed from the present one in
44 two important ways. First, the timing of reproductive events was determined from the ages of

45 captured specimens. Second, the species was known not to be truly extinct. In contrast to the
46 present study, the results suggested that the ship sturgeon is functionally extinct. As the species
47 is not truly extinct, this result pointed to the need for a breeding program in addition to other
48 protective measures, if it is to be saved.

49

50 **Materials**

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

62

63 **Method**

64 The basic statistical model is that the sighting times of eggs X_1, X_2, \dots, X_m are
65 independent and follow a discrete uniform distribution over the interval $(0, \tau_f)$ where 0
66 corresponds to the beginning of the observation period and τ_f is the unknown functional

67 extinction time. Similarly, the sighting times of skins Y_1, Y_2, \dots, Y_n are independent and follow a
 68 discrete uniform distribution over the interval $(0, \tau_e)$ where τ_e is the unknown true extinction
 69 time with $\tau_e \geq \tau_f$. Interest centers on testing the null hypothesis $H_o : \tau_f = \tau_e$ that functional
 70 extinction did not occur prior to true extinction against the one-sided alternative hypothesis
 71 $H_1 : \tau_f < \tau_e$ that it did.

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

74
 75
$$L(\tau_f, \tau_e) = \tau_f^{-m} \tau_e^{-n} \quad (1)$$

76
 77 for $\tau_f \geq X_{(m)}$, $\tau_e \geq Y_{(n)}$ and 0 otherwise. It is necessary to distinguish between two cases. Suppose
 78 that $X_{(m)} \leq Y_{(n)}$. In this case, under H_1 , the maximum likelihood (ML) estimates of τ_f and τ_e
 79 are $X_{(m)}$ and $Y_{(n)}$, respectively, while under H_o both are equal to $Y_{(n)}$. In the case that
 80 $X_{(m)} > Y_{(n)}$, the ML estimates of τ_f and τ_e are both equal to $X_{(m)}$ under both H_1 and H_o . It
 81 follows that the likelihood ratio statistic for testing H_o against H_1 is an increasing function of:

82
 83
$$T = \begin{cases} \frac{Y_{(n)}}{X_{(m)}} & X_{(m)} \leq Y_{(n)} \\ 1 & X_{(m)} > Y_{(n)} \end{cases} \quad (2)$$

84

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

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

89

$$90 \quad p = pr(T > T_{obs}) + \frac{1}{2} pr(T = T_{obs}) \quad (3)$$

91

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

94 Let the ordered values of the pooled sighting times be $Z_{(1)} < Z_{(2)} < \dots < Z_{(m+n)}$ and let j be
 95 the rank of $X_{(m)}$ among these. Conditional on the pooled sighting times, the event $T > T_{obs}$ is
 96 equivalent to the event that $Z_j, Z_{j+1}, \dots, Z_{m+n}$ are all skins. Under H_o , the probability of this

97 event is given by the hypergeometric distribution as $\frac{\binom{n}{m+n-j+1}}{\binom{m+n}{m+n-j+1}}$. The event $T = T_{obs}$ is

98 equivalent to the event that Z_j is an egg and $Z_{j+1}, Z_{j+2}, \dots, Z_{m+n}$ are all skins. Under H_o , the

99 probability of this event is given by $\frac{m}{m+n} \frac{\binom{n}{m+n-j}}{\binom{m+n-1}{m+n-j}}$. Combining these results gives:

100

101
$$p = \frac{\binom{n}{m+n-j+1}}{\binom{m+n}{m+n-j+1}} + \frac{1}{2} \frac{m}{m+n} \frac{\binom{n}{m+n-j}}{\binom{m+n-1}{m+n-j}} \quad (4)$$

102

103 The result in (4) is valid provided no sighting of either type has the same rank j as $X_{(m)}$.

104 It is possible to modify the result based on the hypergeometric distribution to account for such

105 ties. A convenient alternative, however, is to approximate the mid- p value by simulation. This

106 would involve repeatedly distributing m egg sightings and n skin sightings randomly over the

107 observation period, calculating the value T^* of T , and approximating the mid- p value by the

108 proportion of times that T^* exceeds T_{obs} plus one-half the proportion of times T^* equals T_{obs} .

109

110 **Results**

111 We took the observation period to begin in 1890 (Table 1). The uniformity assumption

112 was tested using the chi squared goodness-of-fit statistic (Snedecor & Cochran 1989) with

113 significance assessed via simulation. The null hypothesis of uniformity can not be rejected for

114 either egg or skin sightings. The corresponding record contained a total of 6 eggs and 27 skins.

115 For this data set, $m = 6$, $n = 27$, and $j = 29$. In this case, the mid- p value given in Equation 4 is

116 0.38 and the null hypothesis of no functional extinction can not be rejected by conventional

117 standards of statistical significance.

118 Particularly given the small number of egg sightings, the question arises as to the power

119 of this test. To address this, we conducted the following simulation experiment. Keeping the

120 observation period and the sighting record for skins fixed, we distributed 6 egg sightings

121 according to the discrete uniform distribution over the interval $(0, \tau_f)$ for selected values of τ_f
122 and applied the test to the simulated data. For each value of τ_f , we repeated the procedure 1000
123 times and approximated the power of the test by the proportion of times that H_o was correctly
124 rejected. The results are summarized in Table 2. Although the test has low power for functional
125 extinction occurring after 1894, power jumps to 1 for functional extinction occurring in 1894 (or
126 earlier). We conclude that, while the null hypothesis that functional extinction did not occur
127 cannot be rejected at conventional significance levels, it would be difficult to detect it had it
128 occurred a few years before true extinction.

129

130 **Discussion**

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

141 It is worth noting that the maximum potential time lag observed in data following the last
142 confirmed reproduction can not exceed the maximum longevity of a species. While there are no

143 data on the lifespan of Passenger Pigeon in the wild, in captivity it ranged from 15 years on
144 average up to the maximum reported age of 29 years (Martha; Herman 1948). Although the
145 inference of functional extinction can be more challenging in short-living species, the method
146 presented here should provide reasonable power if the dataset contains sufficient number of
147 records after the last egg collection.

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

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

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230 **Table 1.** Sightings of Passenger Pigeon (*Ectopistes migratorius*) since 1890. Number of
231 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)

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

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τ_f	Approximate power
1894	1.000
1895	0.254
1896	0.089
1897	0.027

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262

263 **Figure legend**

264

265 **Figure 1.** Passenger Pigeon (*Ectopistes migratorius*) sighting record, based on the collection

266 dates of eggs and skins from museum collections.

