

## The two extinctions of the Carolina parakeet

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1 **ABSTRACT**

2 Due to climate change and habitat conversion, estimates of the number of species extinctions  
3 over the next century are alarming. Coming up with solutions for conservation will require many  
4 different approaches, including exploring the extinction processes of recently extinct species.  
5 Given that parrots are the most threatened group of birds, information regarding parrot extinction  
6 is especially pressing. While most recent parrot extinctions have been island endemics, the  
7 Carolina parakeet (*Conuropsis carolinensis*) had an 18th-century range covering nearly half of  
8 the present-day United States, despite which, they went extinct in the 20th century. The major  
9 cause of their extinction remains unknown. As a first step to determining what caused their  
10 extinction, we used a newly published, extensive dataset of Carolina parakeet observations  
11 combined with a Bayesian extinction estimating model to determine the most likely date of their  
12 extinction. By considering each of the two subspecies independently, we found that they went  
13 extinct ~30 years apart: the western subspecies (*C. c. ludovicianus*) around 1914 and the eastern  
14 subspecies (*C. c. carolinensis*) either in the late 1930s or mid-1940s. Had we only considered all  
15 observations together, this pattern would have been obscured, missing a major clue to the  
16 Carolina parakeet's extinction. Since the Carolina parakeet was a wide-ranging species that went  
17 extinct during a period of rapid agricultural and industrial expansion, conditions that mirror those  
18 presently occurring in many parts of the world where parrot diversity is highest, any lessons we  
19 can glean from their disappearance may be vital to modern parrot conservation efforts.

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## 24 INTRODUCTION

25 We are entering the early stages of the “Sixth Mass Extinction” (Ceballos et al. 2015), where  
26 estimates of the proportion of species to go extinct over the next century are dire (e.g., Urban  
27 2015, Carlson et al. 2017) and species may not be able to adapt quickly enough to respond to  
28 climate change (Keogan et al. 2018, Radchuk et al. 2019). This amount of loss will destabilize  
29 already compromised ecosystems, while conservation agencies are finding it difficult to plan for  
30 the challenges and uncertainty ahead (Armsworth et al. 2015). While our best guesses about how  
31 and when species will go extinct in the future are largely based on model predictions, much can  
32 be gained by studying the spatial, temporal, and mechanistic processes that led to recent  
33 extinctions (e.g., Stanton 2014, Bond et al. 2019). Investigating the past may not only allow us to  
34 recover some of the natural history lost with the extinction of these species but may also yield  
35 important insights that can inform conservation actions now and in the future.

36 Parrots are one of the most threatened orders of birds, with ~ 43% of all species listed as  
37 near-threatened or worse by the IUCN (Marsden & Royle 2015), and they face many different  
38 pressures, including habitat loss and trapping (Snyder et al. 2000). Parrots are “keystone  
39 mutualists,” providing many important ecosystem functions (Tella et al. 2015, Blanco et al.  
40 2016). The loss of parrots would affect plant species especially, contributing to ecosystem  
41 instability. While a handful of parrot species have gone extinct over the past few centuries, most  
42 were endemic to islands (Olah et al. 2016). There is, however, one notable exception – the  
43 Carolina parakeet (*Conuropsis carolinensis*), which had a geographic range an order of  
44 magnitude larger than the average for all other recently extinct parrot species (Olah et al. 2016).  
45 Even though Carolina parakeets were charismatic and were of considerable interest to

46 ornithologists during the 1800s, we know little about their biology or how and when they went  
47 extinct.

48         The Carolina parakeet is one of the four forest-dependent bird species to go extinct within  
49 the continental United States since the arrival of Europeans (Pimm & Askins 1995). Before its  
50 decline, the Carolina parakeet was widely distributed, with a range stretching from the mid-  
51 Atlantic coast to Nebraska, and south to Florida (Burgio et al. 2017). The Carolina parakeet has  
52 two subspecies (*C. c. ludovicianus* and *C. c. carolinensis*) but was not studied in detail while  
53 extant. Thus, much of the information regarding their natural history is speculative. Accounts of  
54 the species show a gradual population decline starting with European colonization (Snyder and  
55 Russell 2002). By the early 1800s, Audubon (1831) noted a marked decline in their population  
56 numbers and range, although he still considered them relatively common. During their decline,  
57 the species' range receded from east to west toward the Mississippi River (except in Florida),  
58 and from north to south, along the Ohio River, seemingly in concert with the expansion of  
59 European expansion, destruction of bottomland forests, and the rise of intensive agriculture  
60 (Askins 2000).

61         It is unclear exactly why the Carolina parakeet went extinct. People shot Carolina  
62 parakeets for sport, food, feathers, scientific collections, and to protect crops (Snyder and Russell  
63 2002). However, it seems unlikely that overexploitation was a major contributor to their  
64 extinction (McKinley 1980, Snyder 2004). Others have suggested other potential causes, such as  
65 competition for food with other avian species, habitat loss, competition with introduced  
66 European honey bees (*Apis mellifera*) over nesting/roosting sites, disease, and pressure from  
67 trapping for the pet trade (McKinley 1980, Brunswig et al. 1983, Pimm and Askins 1995, Snyder  
68 & Russell 2002).

69           Additionally, it is also unclear *when* the Carolina parakeet went extinct. At the turn of the  
70 twentieth century, the Carolina parakeet could be found only in Florida, South Carolina, and a  
71 few isolated regions west of the Mississippi River (Hasbrouck 1891, Snyder 2004). The last  
72 captive Carolina parakeet died in a zoo about 100 years ago in 1918. The last “accepted” sighting  
73 of the parakeet occurred in Florida in 1920 (Snyder 2004), but there were reports of the Carolina  
74 parakeet into the 1930s and 1940s in both Florida and the Carolinas (Snyder 2004) which were  
75 likely legitimate (Wright 2005). Determining exactly when the Carolina parakeet went extinct is  
76 the first step in unraveling the mystery of how they went extinct, a question that may help  
77 provide valuable information for parrot conservation and for any future “de-extinction” efforts,  
78 for which they are considered a good candidate (Seddon et al. 2014). Here, we use a newly  
79 published, extensive dataset of Carolina parakeet occurrence (Burgio et al. 2018), paired with  
80 recent advances in extinction date estimation (Solow and Beet 2014, Kodikara et al. 2018), to  
81 determine when these iconic parakeets went extinct.

## 82   **METHODS**

### 83   **Data collection**

84   We collected and georeferenced locality data from Carolina parakeet specimens found in natural  
85 history collections around the world and observations of Carolina parakeets published in the  
86 literature from 1564 to 1944 (see Burgio et al. [2018] for the description of the data collection  
87 methods and a link to the freely available dataset). We then split our dataset by subspecies. We  
88 considered all occurrence points west of the Appalachian crest and west of Alabama to be *C. c.*  
89 *ludovicianus* and points east of the Appalachian crest and east of the state of Mississippi to be *C.*  
90 *c. carolinensis*. These broad geographic delineations are generally accepted as the range limits of

91 the two subspecies (Ridgway 1916, Swenk 1934), and are consistent with the subspecies  
92 identifications listed on all 261 labeled museum specimens represented in the dataset for which  
93 subspecies was recorded or inferred.

94 We determined the level of certainty of each observation based on expert opinion from  
95 the literature, from Snyder (2004) and 18 articles by McKinley (1960, 1964, 1965, 1976, 1977a,  
96 1977b, 1978a, 1978b, 1978c, 1978d, 1979a, 1979b, 1979c, 1979d, 1981, 1985, McKinley &  
97 James 1984, McKinley & Hardy 1985). We truncated our analysis at 1800, as observations  
98 before 1800 were sporadic due, primarily, to a lack of consistent occurrence records and also  
99 because this was the point at which Audubon (1831) noted decreasing numbers of Carolina  
100 parakeets. Within this framework, we used the entire dataset and designated physical evidence,  
101 such as a specimen, as “1”, while observations considered legitimate by expert opinion, but not  
102 interrogable in the present as “2”, and controversial as “3.” When individual years had multiple  
103 records, we always used the evidence with the highest certainty (Figure 1a, 1b). While the last  
104 "official" sighting of the Carolina Parakeet was in 1920 (Snyder 2004), contemporary experts  
105 consider the sightings in the Santee swamp area in South Carolina the 1930s to be legitimate  
106 (Snyder 2004, Wright 2005), therefore we treated all reported sightings after 1920 as  
107 unconfirmed, aside from those sightings in South Carolina.

## 108 **Analyses**

109 We estimated the date of extinction for all Carolina parakeets generally and both subspecies  
110 specifically. Given that our dataset combined physical evidence (i.e., specimens) and  
111 observations with varying degrees of reliability, we used the Bayesian extinction estimating  
112 equations proposed by Solow et al. (2012) and modified by Solow and Beet (2014). We ran the

113 analyses in the R package “spatExtinct” (Carlson et al. 2018a). This modeling approach weighs  
114 various types of evidence based on their reliability (Solow et al. 2012), and considers the validity  
115 of certain and uncertain sightings independently (Boakes et al. 2015, Kodikara et al. 2018),  
116 which is especially useful in inferring extinction dates ( $\tau_E$ ) of recently extinct species with both  
117 specimen and observation data (Carlson et al. 2018b, Bond et al. 2019). Of the two models  
118 presented in Solow and Beet (2014), we used “Model 2” because some of “uncertain”  
119 observations are from reportedly dubious sources (e.g. egg hunters with a vested interest in  
120 selling more expensive Carolina parakeet eggs) and “Model 2” is appropriate when uncertain  
121 sightings are more likely invalid (Kodikara et al. 2018). We ran these analyses independently for  
122 each subspecies (*C. c. carolinensis*:  $n = 76$ ; *C. c. ludovicianus*:  $n = 80$ ), and both subspecies  
123 together ( $n = 116$ ).

## 124 **RESULTS**

125 We estimated that the eastern subspecies, *C. c. carolinensis*, likely went extinct somewhere in  
126 the late 1930s or the mid-1940s, with the two most likely values for  $\tau_E$  in 1938 and 1944 (Fig.  
127 1c) while the western subspecies, *C. c. ludovicianus* went extinct 25-30 years earlier; the most  
128 likely value for  $\tau_E$  was 1913 (Fig. 1c). When considering both subspecies together, the extinction  
129 estimate doesn’t differ much from the estimate for *C. c. carolinensis* since the highest probability  
130 of  $\tau_E$  was 1939 (Fig. 1c); however, failing to consider each subspecies individually obscures  
131 important distinctions between the two, especially for inferring causation.

## 132 **DISCUSSION**

133 The two separate subspecies of the Carolina parakeet appeared to go extinct ~30 years apart, far  
134 later than currently believed, beyond the currently accepted date of 1920 and the most recent

135 analysis that estimated they went extinct around 1915 (Elphick et al. 2010). Elphick et al. (2010),  
136 however, used a less complete dataset and did not take into account uncertain sightings. While  
137 largely dismissed at the time (Snyder 2004), our results lend credibility to the sightings in South  
138 Carolina in the late 1930s. It is even possible that the observation from North Carolina in 1944  
139 reported to Roger Tory Peterson (Snyder 2004) may have been accurate, as well as the mystery  
140 population of Carolina parakeets in Florida reported by ornithologist Oscar Baynard to persist  
141 well into the late 1930s, but for which he refused to disclose the location (Snyder 2004). That the  
142 western subspecies went extinct first despite occupying a larger range (Burgio et al. 2017) is  
143 curious, and suggests a lower initial population, or different or more severe pressures.

144         The Carolina parakeet continues to be one of the most popular proposed targets for de-  
145 extinction projects (Seddon et al. 2014). Aside from the ethical issues surrounding de-extinction  
146 generally (see Blockstein 2017), unless researchers can identify the major driver of their  
147 extinction, de-extinction efforts for the Carolina parakeet may be doomed to fail at great expense  
148 in both time and money. Despite a lack of evidence, many believe that farmers, egg poachers,  
149 and trappers pushed the species to extinction (McKinley 1980, Snyder 2004), buoyed in part by  
150 the lurid anecdote of a farmer shooting the parakeets in his orchard found in Audubon's  
151 foundational book on North American birds (Audubon 1831). While the evidence is indeed  
152 scant, researchers who have focused on this species over the past 60+ years point to a disease  
153 likely transmitted from domestic poultry as the most likely cause but have not settled on which  
154 disease (McKinley 1980, Snyder and Russell 2002). Finally, the landscape across the parakeet's  
155 former range has shifted dramatically since their decline started around 1800, which would make  
156 de-extinction efforts difficult at best, especially when considering the uncertainty associated with  
157 climate change.



158            Learning the most likely extinction dates of the two subspecies of the Carolina parakeet  
159 is the first of many steps needed to solve the mystery that has eluded researchers for well over 50  
160 years. That the two subspecies went extinct 30 years apart is an important clue which has  
161 implications for how we interpret the loss of this species and consider the factors that pushed a  
162 species that appeared stable in 1800 to be found only in small populations in remote areas 100  
163 years later. The limitations in both landscape change data and occurrence data may make it  
164 difficult to rule out habitat loss as a major factor (but see Pimm and Askins 1995). Advances in  
165 genetic analyses, as seen recently seen with passenger pigeons (*Ectopistes migratorius*; Hung et  
166 al. 2015), or examining the few preserved specimens in natural history museums for signs of  
167 disease (e.g., Rothschild & Panza 2005) may help shed light on what ultimately drove the  
168 Carolina parakeet to extinction. The Carolina parakeet was a wide-ranging species and faced  
169 challenges of the rapid agricultural expansion and industrialization of the United States during  
170 the 20th century, a process being repeated today in many areas where parrots are found. Given  
171 that parrots are so threatened, determining the cause of the Carolina parakeet extinction is  
172 especially pressing.

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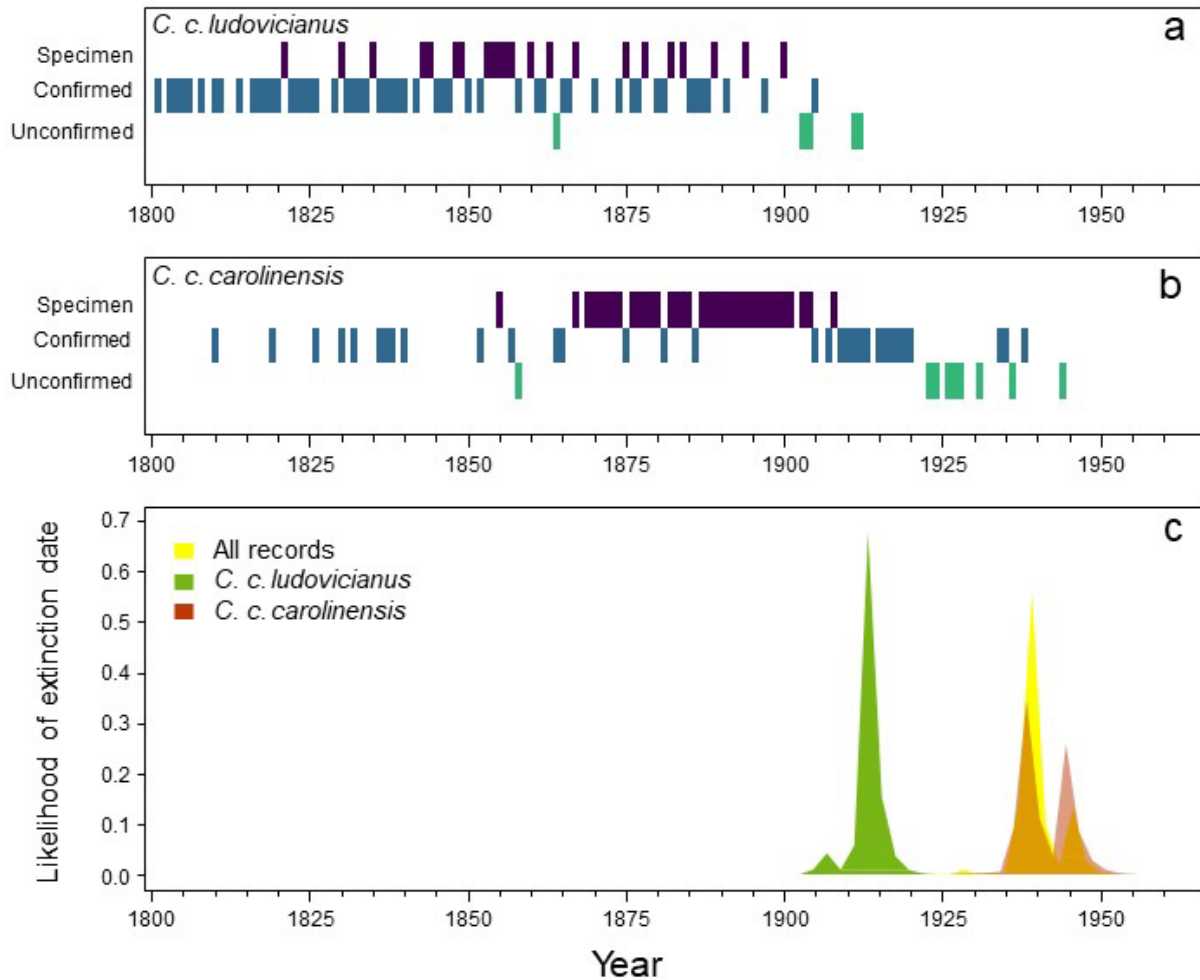
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293 **Figure 1. a.** The sighting record for *C. c. carolinensis*. **b.** The sighting record for *C. c.*

294 *ludovicianus*. For panels a and b, the top row represents specimen records (purple), the middle

295 row represents confirmed observations (blue), and the bottom row represents unconfirmed or

296 controversial records (green). For each year, we used data with the highest certainty. **c.** The

297 estimates of likely extinction dates for *C. c. ludovicianus* (green), *C. c. carolinensis* (orange), and

298 for all records (yellow).

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