Biological Conservation 180 (2014) 11–20

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Present-day risk assessment would have predicted the extinction of the passenger pigeon (*Ectopistes migratorius*)

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ARTICLE INFO

Article history:
Received 29 June 2014
Received in revised form 2 September 2014
Accepted 7 September 2014

Keywords:
Habitat loss
Hunting
IUCN Red List
Population fluctuations
Population modeling
Threat assessment
Threat status

ABSTRACT

The precipitous decline and extinction of the passenger pigeon one century ago helped galvanize implementation of national policies and international cooperation on wildlife management. Having a clear understanding of past conservation failures will aid in preventing future unanticipated extinctions. Simulations from a population model developed for this species indicate that while habitat loss contributed to decline, the main cause of the extinction was an unregulated commercial harvest. Hindcast application of the IUCN's Red Listing criteria to modeled population trajectories show that the species would have been listed as threatened for decades prior to extinction had the data and risk-assessment methods been available. Abundant populations can belie indicators of extinction-risk such as a high rate of population decline. Listing species as threatened based solely on rates of decline remains controversial; however this study demonstrates that this risk-indicator may have been the sole means by which the risk to the passenger pigeon could have been detected early enough for effective conservation measures.

1. Introduction

This year marks the 100 year anniversary of the passing of the last known individual passenger pigeon (*Ectopistes migratorius*), once the most abundant bird species in North America (Herman, 1948). For decades their relative abundance obscured the rapid rate of their decline (Brewster, 1889). Whether rapid decline rates ought to warrant threatened status for still-abundant species remains a controversial topic in conservation biology, especially when commercial harvest is a factor in management (Godfrey and Godley, 2008; Hutchings, 2001; Punt, 2000). Having a clear understanding of past conservation errors, and when and how they might have been avoided, is a critical exercise for meeting current obligations to slow the rate of biodiversity loss (Chandra and Idrisova, 2011).

Historically, passenger pigeons were a source of protein and lipids for both Native Americans and later European colonists (Schorger, 1955). The birds were nomadic, and therefore spatially and temporally variable as a food resource. However, when they were encountered, passenger pigeons tended to be abundant and relatively easy to harvest. In the mid-19th century a commercial market for passenger pigeon meat and live birds for sport shooting expanded rapidly (Blockstein and Tordoff, 1985; Schorger, 1955). At the same time, human disturbance was also reducing and fragmenting the hardwood forests which were the primary nesting habitat (Brewster, 1889; Bucher, 1992). Population numbers plummeted so dramatically that it was only a few decades after famously dense flocks were observed that cash rewards for evidence of a single wild individual went uncollected (Hodge, 1912, 1911). The species was likely extinct in the wild by the beginning of the 20th century, and the last known individual died in captivity in 1914 at the Cincinnati zoo (Herman, 1948).

For the past century, analysis of this extinction event has mostly concluded that overharvest combined with disturbance of the nesting colony was the primary causal factor (Blockstein and Tordoff, 1985). However, skepticism of that conclusion has been expressed since persecution from professional hunters ought to have eased as the population declined and colonies became harder to find and the role of habitat loss was proposed as an alternative (Bucher, 1992; but see Conrad, 2005). Recent work suggests that the species' reliance on tree mast made it prone to natural population fluctuations and unusually sensitive to anthropogenic disturbance (Hung et al., 2014). However, a quantitative analysis of the simultaneous impacts of anthropogenic impacts in conjunction with possible intrinsic life-history characteristics has not been done. I constructed a set of population models parameterized across a range of plausible species traits and anthropogenic impacts to find the driving factors and interactions that best simulate the observed population trajectory. Specifically, the anthropogenic impact factors I explored were direct mortality from

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http://dx.doi.org/10.1016/j.biocon.2014.09.023
0006-3207/

commercial harvest, reduction of reproductive success due to disturbance of nesting colonies, and habitat loss and fragmentation in the breeding range. In addition, I also conducted a global sensitivity analysis to assess the relative impacts of intrinsic life-history characteristics such as maximum growth rate, inter-annual population variability, generation time, and the strength of nesting colony cohesion.

To gain insight from this extinction event for the prevention of future extinctions, it is important to place this event in the context of how species are currently identified as threatened. This extinction occurred several decades before the widespread adoption of any organized systems for monitoring wildlife populations or broad-scale risk assessment (Fitter and Fitter, 1987; Hornaday, 1913). Currently, the most globally recognized system for identifying species as threatened is the International Union for the Conservation of Nature (IUCN) Red List. The IUCN first began to develop a comprehensive monitoring and data collection program for the world's flora and fauna and set out to define extinction risk in concrete biological terms in the 1970s (Scott et al., 1987). It adopted the first set of objective rule-based criteria in 1994 (IUCN, 2012). Since that time, the Red List criteria have undergone several revisions, with the most recent rules adopted in 2001 (IUCN, 2012; Mace et al., 2008).

Rule-based systems to assess risk of extinction, such as the IUCN Red List, can at times become contentious when species have experienced significant population declines but remain relatively abundant. This has been the case in fisheries where it has been argued that the thresholds of decline levels for commercial marine species under IUCN Red List criteria are overly precautionary (Dulvy et al., 2005; Godfrey and Godley, 2008; Hutchings and Reynolds, 2004; Hutchings, 2001; Punt, 2000). Similarly, when the United States Fish and Wildlife Service (USFWS) evaluated the cerulean warbler (*Setophaga cerulean*) for protection under the Endangered Species Act, they found listing not warranted despite longstanding and continuing declines, in part because the species remains relatively abundant (USFWS, 2006). The passenger pigeon is a relevant case-study in this regard since it was highly abundant prior to its extinction, yet little was done in terms of conservation to alter the trajectory of decline.

For a rule-based risk assessment approach to be useful as a conservation tool, it is important to establish the amount of time available from the point when imperiled status is first recognized to the point when the species is beyond recovery. I applied a selection of the IUCN Red List criteria to a subset of individual model trajectories that showed declines similar to what was observed for the passenger pigeon. From this I estimated how much warning time the IUCN Red List would have provided before extinction, what basis the evaluation would have been made on (ie. which criterion), and what type of data collection would have been necessary to make the assessment.

2. Methods

2.1. Estimation of available breeding habitat through time

Changes in the quantity and quality of habitat available to passenger pigeon through the 19th century were largely the result of the westward advance of American settlers and transportation infrastructure as well as increases in the extraction of natural resources. However a great deal of information is lacking about the location and availability of habitat through time (Wang, 2005). Therefore it is necessary to reconstruct potential habitat using limited available information and make inferences about the likely progression of landscape transformation.

The effect of habitat loss on carrying capacity was estimated through time by first constructing a baseline pre-settlement model of available nesting habitat. The pre-settlement habitat suitability was modeled using the program Maxent (v.3.3.3; Phillips et al., 2006) which uses a maximum entropy approach to predict the geographic location of suitable habitat. The model takes as input locations where the species has been observed (occurrence locations) and a set of environmental predictor layers. The occurrence locations used in the model were from 55 historical accounts of observed nesting colonies described in Schorger (1955) and 24 specimens collected during the breeding season (April–July) accessed through the Global Biodiversity Information Facility (GBIF; http://data.gbif.org) (Table B1 and Fig. 1).

Predictor variables were selected to reflect the potential distribution of food resources utilized by the nesting colony (Table 1). The species was known to feed on the nuts or acorns of oaks (*Quercus* sp.), chestnut (*Castanea dentata*), and hickory (*Carya* sp.), but preferred the high quality nuts of American beech (*Fagus grandifolia*) (Bucher, 1992; Cook, 1903; Schorger, 1955). A characteristic of many of these tree species is highly variable year-to-year nut production or having 'mast years'. Dependence on this highly variable food resource was a likely factor in passenger pigeons' habit of being nomadic or irruptive (Allen and Saunders, 2002; Hancock et al., 2006). The breeding range may also have been partially dictated by winter temperature and precipitation patterns as there was asynchrony between the fall production of tree mast and the spring arrival of the nesting colony. Early snowfall covering the forest floor was thought to both conceal the mast from possible forest-dwelling competitors and prevent the mast from decomposing or germinating before the spring migration (Bucher, 1992).

Habitat loss (i.e. human settlement patterns) was simulated by reducing the quantity available habitat at each time step. The baseline habitat map was modified decanally by reducing the proportion of breeding habitat available within each grid cell by the amount of land estimated to have been cleared for growing crops or pasturing animals. Maps were linearly interpolated between decades to produce a habitat map for each year. The cropland and pasture land use maps used were from the HYDE History Database of the Global Environment (HYDE 3.1; Klein Goldewijk et al., 2010; 2011). The HYDE database is a set of global gridded time series maps of modeled historic land use and population density. The land use layers include decadal time-steps at a 5 min-by-5 min resolution of area in crop and pasture for each decade. Each grid cell in the HYDE database is the proportion of land area within that grid cell estimated to be in cropland or pasture.

2.2. Construction of population model

A two-stage matrix model was constructed to simulate population abundances from 1800 through 1900 plus 20 years prior to the application of any anthropogenic impact factors to allow the population abundance of each age class to stabilize and also to calculate the natural interannual population variability. The model was a discrete time-step, birth-pulse reproduction model with the entire female population calculated pre-breeding. The modeled stages were hatch year and after hatch year. The model was parameterized using both qualitative historic descriptions of the life history characteristics of passenger pigeon and quantitative information from related species to set probable upper and lower bounds on parameter ranges. Based on accounts of both wild and captive passenger pigeons, they shared many life-history characteristics with members of the genus *Patagioenas* and other Columbid species (Blockstein, 2002; Bucher, 1992). However, true estimates of some model parameters can never be known. Given the inherent uncertainty of this approach, a global sensitivity analysis (Supplementary Fig. C1) was conducted to assess the impact of parameter uncertainty on model outcomes (additional details on