



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



Jessica C. Stanton¹

Ecology and Evolution, Stony Brook University, Stony Brook, NY, United States

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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.

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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

¹ Current address: US Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, WI, United States.

E-mail address: jcstanton@usgs.gov

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 (i.e. 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 decennially 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

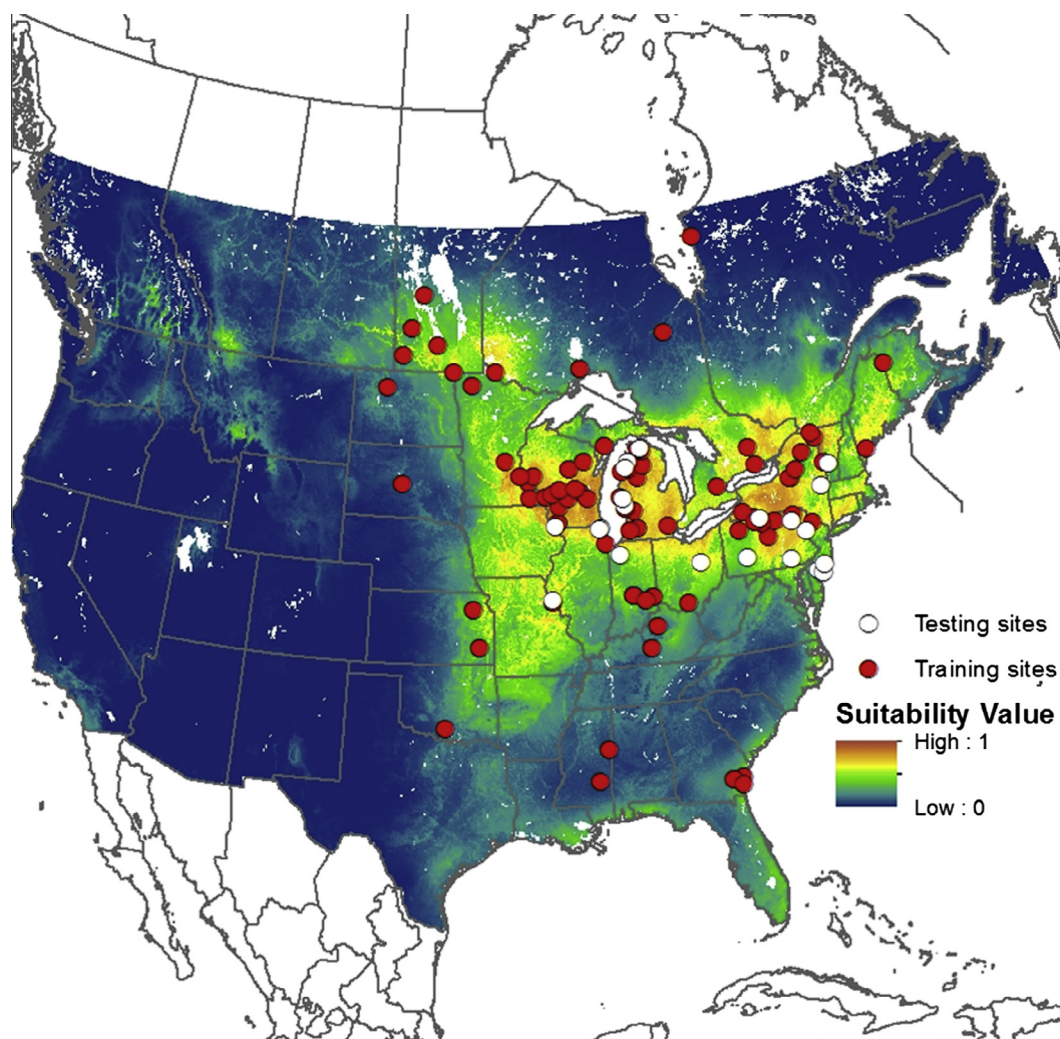


Fig. 1. Predicted breeding habitat of passenger pigeon without anthropogenic land use showing locations of occurrences used for model training and model testing.

Table 1
Predictor variables included in passenger pigeon pre-settlement breeding habitat model.

Variable ^a	Rationale for inclusion	% Contribution to final model
April temperature range	Mast regulation	30.9
Max July temperature	Beech distribution	26.9
Total precipitation growing season	Beech distribution	20.1
Start growing season	Mast preservation	11.1
Total precipitation coldest quarter	Mast preservation	3.6
Potential natural vegetation	Forest type	3.2
Slope variation	Forest type	3.1
Temperature seasonality	Beech distribution	0.5
Mean temp. coldest quarter	Mast preservation	0.5

^a Additional details on predictor variables are available in [Appendix A](#).

the parameterization of the population model are available in [Supplementary Information](#)).

2.3. Nomadic colonial nesting and carrying capacity

Because of the nomadic and irruptive manner in which this species utilized highly variable tree mast resources, it was not reasonable to treat the habitat suitability throughout the breeding range equally across years. Variability in food resources for the nesting colony was simulated by generating a random trajectory of 'mast

areas' for each model replicate. The radius of the mast area was set at 250 km based on the records for the passenger pigeon nesting of 1871 in Wisconsin. That single year provided the best record for the possible spatial extent and arrangement of a nesting colony as multiple observations were recorded across the entire state ([Schorger, 1955](#)). For each model year, a random mast location within the breeding range was generated to serve as the location of the main breeding colony for that year. The following year, a new location was selected at random with the restriction that it may not fall within the boundary of the previous year's breeding

colony. This process was repeated to generate 1000 random trajectories based on the pre-settlement habitat suitability map (no habitat loss) and 1000 random trajectories based on the annual maps of available habitat with settlement disturbance to the landscape (habitat loss scenario).

For each model year habitat suitability values within and outside of the radius of the breeding colony were summed. The total carrying capacity of the landscape (within and outside the main colony) for each simulation year was determined by applying a weighting constant to the total habitat suitability within the main area. The weighting constant corresponded to the percentage of the total population breeding annually within the main nesting colony. It was not uncommon to encounter smaller colonies or individual pairs nesting away from the main colony (Brewster, 1889; Coale, 1922), but it is not known what proportion of the total population in any given year would have been engaged in this practice. This parameter was defined as the 'degree of coloniality' and modeled it at 40%, 60%, or 80% of the total population breeding within the main colony. As the degree of coloniality increases, it essentially has the effect of increasing the year-to-year variation in carrying capacity.

The population was modeled with a scramble-type density dependence (Ricker, 1954) impacting fecundity values. Nesting and flocking birds were non-territorial and therefore it is expected that resources for food and space would have been equally shared. Density dependence was modelled by modifying fecundity values of the stage matrix as a function of total population abundance.

In descriptive accounts of captive birds, adults could persist for long periods of time on low-quality food sources but rarely produced viable young in captivity despite frequent attempts at reproduction (Deane, 1908). This could possibly be evidence that nutrient requirements for adult maintenance were less stringent than for successful reproduction. Like most other columbids, passenger pigeons fed young with a high-protein, high-fat crop milk after hatching which resulted in very rapid growth rates. Nestling mass paralleled adult mass within 14 days of hatching (Schorger, 1955). Further, for many other nomadic colonial nesters such as the red-billed quelea (*Quelea quelea*) and eared dove (*Zenaida auriculata*), breeding attempts are also thought to be closely tied to food availability (Allen and Saunders, 2002; Bucher, 1992, 1982).

2.4. Harvest

Two different forms of harvest were parameterized in the models: background and commercial harvest. The background level of harvest was meant to simulate utilization of passenger pigeons by indigenous people and settlers that came into contact with local breeding colonies. There are no historic records to estimate mortality from this opportunistic, subsistence-level harvest. The range of harvest values for the global sensitivity analysis were set as a proportional harvest of 0.05–0.5% of all hatch year and 0.01–0.1% of all after hatch year birds. This background harvest is simulated in all models throughout the entire duration of the simulation.

The commercial harvest model simulated the effects of the commercial market in passenger pigeons that developed with the expansion of the rail and telegraph lines in the mid 1800s (Schorger, 1955). Precise mortality estimates imposed on the population from the commercial harvest are not available. However, shipping records and estimates recorded by local observers and professional hunters at the time provide a rough range of estimates used to parameterize the model with added mortality to account for waste and spoilage. The commercial harvest was parameterized as a density-dependent function with maximum harvests ranging from 1 to 5 million females per year. Because the model is female only, this range represents total harvests of 2 to 10 million birds total (Supplementary Fig. C2). Model runs that include commercial

harvest were modeled to begin in year 1845 and to run until the end of the simulation. The density-dependent shape of the commercial harvest function (Supplementary Fig. C2) allows the maximum harvest levels to decrease with declining population sizes, as would be expected with a commercial market.

2.5. Probability of a failed colony

Late winter storms and disturbance by hunters and trappers often resulted in failed nesting attempts or abandonment (Schorger, 1955). The models include a simulated nesting colony collapse that would result in a 70% reduction in the number of new recruits to the population for that time step. Colony collapse was modeled as a random process with a probability of 0.05 in the years prior to 1830 and either 0.1, 0.2, or 0.3 thereafter. This stepped function was meant to simulate primarily weather-related effects in the early years and an increased frequency of disturbance later with the encroachment of human settlement and commercial hunting activity into the main breeding range.

2.6. Global sensitivity analysis

To examine the effects of uncertainty in model parameters on population trajectories an extensive sensitivity analysis was carried out to explore the parameter space both within and across three primary anthropogenic impact factors: commercial harvest, habitat loss, and colony disturbance (probability of colony failure). Latin hypercube sampling (McKay et al., 1979) was used to generate 500 models replicated across each of the 12 unique combinations of anthropogenic impact factors (Supplementary Fig. C1) for a total of 6000 separate models. This sampling scheme, when used in population modeling, allows for extensive sampling of the parameter space while still allowing tests for interactions between parameters, which is not possible in one-at-a-time sensitivity analysis (Conroy and Brook, 2003). Models were run in RAMAS Meta-pop (Akçakaya, 2012), each with 1000 replicates to incorporate environmental and demographic stochasticity.

2.7. Analysis of factors contributing to decline and extinction

The influence of model parameters on predicting decline and/or extinction of passenger pigeons was analyzed using boosted regression tree analysis implemented in R (R Core Team, 2013) using the *gbm* and *dismo* packages (Hijmans et al., 2012; Ridgeway, 2013). Two simulation results were used as response variables: expected minimum abundance, and probability of decline to a threshold of 1000 females at any point before the end of the simulation (quasi-extinction). Expected minimum abundance is the natural log of the lowest abundance of each trajectory averaged across all replicates, and its difference from the initial abundance is a measure of overall population reduction. Probability of decline to a quasi-extinction threshold is a way to measure whether the simulations approach extinction-risk levels before the end of the simulation. Using an extinction threshold (decline to zero) can sometimes be less informative than using a higher threshold if few model replicates decline to extinction. Second, as a highly social, colonial species with high apparent intra-specific attraction that also exhibited signs of synchronized egg laying (Jovani and Grimm, 2008; Schorger, 1955) it is likely that there would have been Allee effects as the population declined (Cook and Toft, 2005; Halliday, 1980; Reed, 1999; Stephens and Sutherland, 1999). However, there are no data available to parameterize this within the model. In this instance a threshold of 1000 females can be regarded as a de facto extinction. Probability of decline to 1000 is expressed in the boosted regression tree analysis as the number of replicates per model that decline to the threshold.

Because this variable is heavily left-skewed count data (most replicates never reach the threshold).

Six predictor variables were selected in the boosted regression tree analysis to explore the effects of parameter uncertainty and the impact of anthropogenic factors: (1) Maximum growth rate (Rmax); (2) Generation time (GT); (3) Coefficient of variation of total population size over the first 10 years after model spin-up (CV10); (4) Habitat loss (HL), treated as a categorical variable; (5) Maximum commercial harvest (CH), as the maximum harvest level selected by the Latin hypercube sampling; and (6) Probability of colony failure (Pfail), as a categorical variable corresponding to probability levels of 0.1, 0.2, or 0.3. Maximum growth rate determines the shape of the density dependence curve and the rate at which the population will increase when population levels are far below carrying capacity. Generation time was calculated from the matrix of survival and fecundity values. Variation in CV10 across models is due largely to the effect of colonial nesting and the degree of coloniality in the population (see 2.3 Nomadic colonial nesting and carrying capacity above). However, CV10 was used as a predictor in the boosted regression tree analysis because it is correlated with, but more informative than degree of coloniality.

For both response variables, I conducted a 10-fold partition cross-validation on the boosted regression tree analysis to validate model fit. This cross-validation method repeats the analysis 10 times, each time leaving out 10% of the models as a testing set and using the other 90% for model building. Model performance was then estimated as the average deviance in the testing set that can be explained by the model.

2.8. Hindcast annual IUCN Red List assessment

IUCN Red List criteria was applied separately at each time step to individual stochastic replicate model runs for all models that demonstrated a decline to 1000 females in at least one replicate. Details of the listing criteria and guidelines for their use are available from the IUCN (2012; for summary table see http://www.iucnredlist.org/documents/2001CatsCrit_Summary_EN.pdf).

Each trajectory generated from the model was treated as a possible population trajectory. In other words, population numbers from each stochastically generated population trajectory was regarded as if they were field data collected without measurement error. This analysis was conducted independently for each year (i.e., model time step), using the data generated from the initialization of each model trajectory up to the time step being considered without knowledge or speculation of the future of that trajectory. The analysis was conducted in R (ver.3.0.0, R Core Team, 2013) by coding a rule set based on the IUCN Red List criteria rules and guidelines (IUCN, 2012). The Red listing category (and the criteria that triggered the category) was determined for each model replicate at each time step. To avoid circularity, any Red List criteria involving forecasts of future population trajectories or future risk analysis such as criteria A3, A4 or E were not considered.

Also not considered was Red List criteria based on geographic range or occupancy such as under criteria B or D2. Despite the fact that a considerable amount of total breeding habitat area is lost during the course of the simulation, the remaining habitat defining the area of occupancy (AOO) and extent of occurrence (EOO) at the end of the simulation were still larger than the thresholds for listing under criteria B or D2.

The time step at which the criteria were met for each Red List category and the number of years spent in each category before advancing to the next category or going extinct was recorded. By applying the Red List criteria separately for each time step and each replicate it was possible to track each population trajectory as it progressed through the threat categories towards extinction. Results were smoothed by giving each Red List category a numer-

ical score and calculating a 5-year moving window average. This smoothing was done to minimize the effects of stochastic year-to-year switching between categories which can happen when the trajectories approach the threshold boundaries between two threat categories. Short duration category switches (either upgrades or downgrades) of 3 years or less if the classification returned to the original category (for example going from Vulnerable to Near Threatened if it returns to Vulnerable within 3 time steps) were ignored. Most taxa are assessed for the IUCN Red List at 4–10 year intervals. However, a recent analysis of warning times for extinctions due to climate change found the length of the assessment interval to have little impact (Stanton et al., 2014).

Trajectories ending in extinction were analyzed separately from trajectories that did not result in extinction prior to the end of the simulation to see if they showed substantial differences in Red List categorization trends.

3. Results

Effects of habitat loss reduced the total summed habitat suitability of the breeding range by 52.8% between 1800 and 1900 (Figs. 1 and 2). In paired comparisons of models across each impact factor with all other parameters held constant, habitat loss had the largest direct impact on expected minimum abundance. Including habitat loss in the model resulted in a 38.3% (0.1 SE) decrease in expected minimum abundance. Commercial harvest decreased expected minimum abundance by 17.7% (0.3 SE) across all harvest levels. Nest disturbance decreased expected minimum abundance by 34.4% (0.4 SE) when the probability increased from 0.1 per year to 0.3 (Supplementary Fig. C3).

The boosted regression tree analysis on expected minimum abundance showed similar results with most important predictor variable being habitat loss (HL), accounting for 24.5% of the relative influence on the model. The next four variables, in order of importance, had roughly equal amounts of relative influence; they were maximum commercial harvest (CH) at 19.1%, coefficient of variation in total population size over the first 10 years (CV10) at 19.0%, probability of colony failure (Pfail) at 18.1%, and maximum growth rate (Rmax) at 17.9%. Generation time (GT) had the lowest influence on model prediction at 1.4% relative influence. Boosted regression tree models did not indicate any strong interactions between variables. Model fit as assessed through 10-fold cross-validation showed high performance with average deviance explained (DE) by the model across folds at 0.98.

However, models with low expected minimum abundance did not necessarily result in, or even approach, extinction. Only 467 models (out of 6000 total models run) resulted in quasi-extinction probabilities greater than zero, all of which included commercial harvest. The mean probability of quasi-extinction over the subset of models that included a commercial harvest was 0.01 (range 0–0.67). The probability of crossing this decline threshold increased with increasing probability of nest failure, but was only slightly positively influenced by the presence of habitat loss in the model (Supplementary Fig. C4).

By only including the 467 models that declined to the quasi-extinction threshold in at least one replicate, I limited the parameter space being analyzed to the most relevant portion in terms of reconstructing possible extinction scenarios. The variable with the highest relative importance for predicting probability of decline to threshold was maximum commercial harvest (CH) at 34.6%, followed by maximum growth rate (Rmax) at 26.5%, and probability of colony failure (Pfail) at 25.0%. Coefficient of variation in total population size over the first 10 years (CV10) and Generation time (GT) had relatively low relative influence values at 9.8% and 3.0%, respectively. Habitat loss (HL) had the lowest relative influence

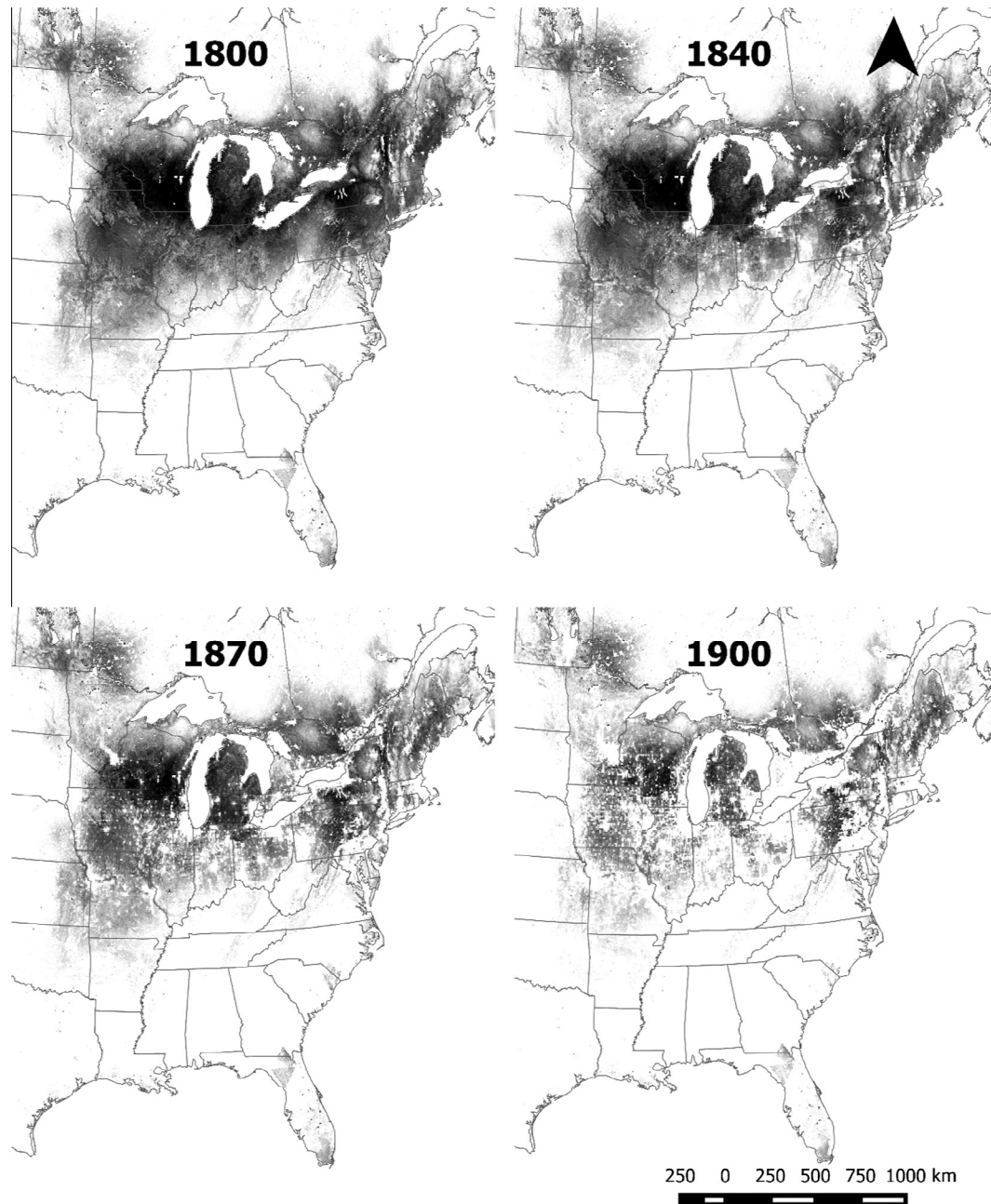


Fig. 2. Predicted available breeding habitat of the passenger pigeon at selected time steps during the 19th century. Darker shade indicates higher suitability score.

at 1.2%. The strongest interaction terms were CH vs. Rmax and CH vs. CV10 (Fig. 3). Model fit assessed through the 10-fold cross validation had a mean DE across folds of 0.89 (see Fig. 4).

Of the 467,000 model replicates generated from the 467 models with non-zero quasi-extinction probabilities (1000 replicates each), 21,297 result in extinction before the end of the simulation. IUCN Red List criteria (criteria A2, C, and D; IUCN, 2012) applied annually to individual model replicates showed the majority of replicates were categorized as non-threatened (least concern or near threatened) through most of the first half of the simulation. Around the mid-century mark, the proportion of trajectories classified as threatened (vulnerable, endangered, or critically endangered) increased sharply with the onset of the simulated commercial harvest. By 1855, 10 years after the onset of the commercial harvest, more than 90% of replicates were classified as threatened (Fig. 5). The mean extinction year was model year

1892, with the earliest extinction occurring in 1863. The mean number of years continuously listed in a threatened category before going extinct was 43 years, with the most time spent listed as critically endangered. On average 23 years were spent listed in the critically endangered category, 12 years in endangered, and 4 years in vulnerable (Fig. 3).

The remaining model replicates (drawn from the same 467 models, but not resulting in extinction), show lower proportions of threatened status overall throughout the simulation compared with replications that end in extinction (Fig. 5). Non-extinction replicates showed a similar spike in the proportion meeting threatened status shortly after the onset of the simulated commercial hunting, yet approximately 1/3 of the trajectories were still classified as non-threatened after this point.

The rate of population decline was almost exclusively the sole indicator of threatened status. In nearly all cases, the threat level

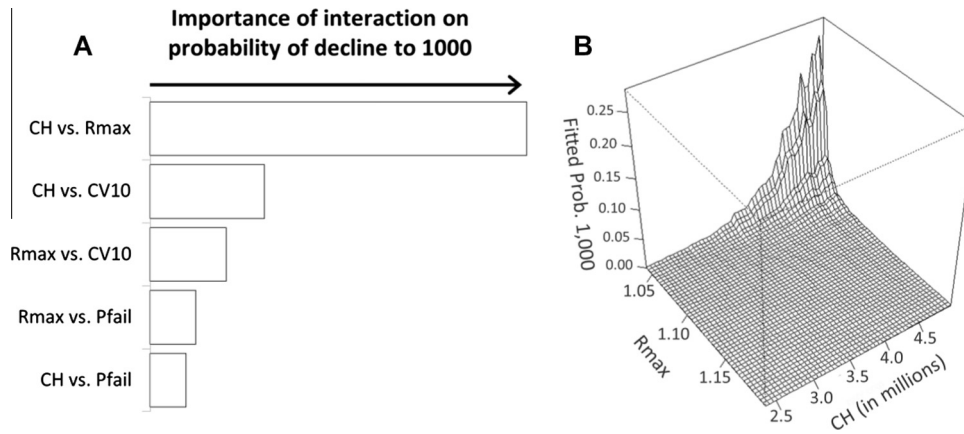


Fig. 3. Interactions of variables contributing to quasi-extinction (probability of decline to 1000 females) as assessed through boosted regression tree analysis. (A) Relative importance of interaction terms. Variables are maximum commercial harvest (CH), maximum population growth rate (Rmax), coefficient of variation in total population size over the first 10 years (CV10), and annual probability of colony failure (Pfail). (B) Modeled response surface for interaction between maximum commercial harvest and maximum growth rate.

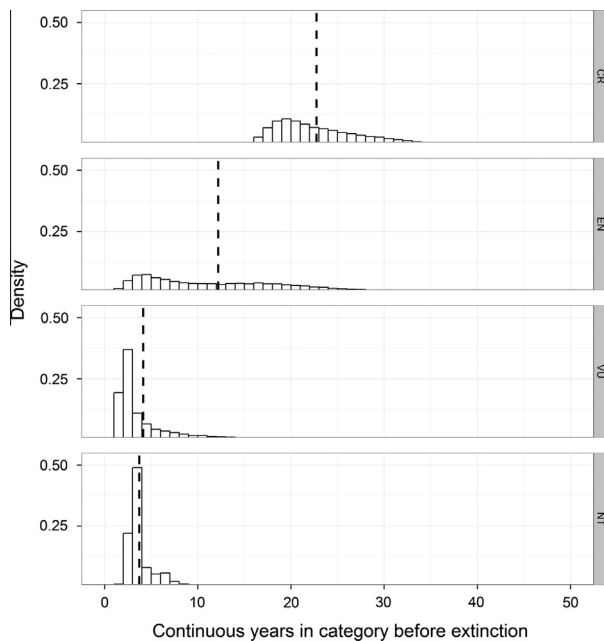


Fig. 4. Distribution of number of years continuously spent in each IUCN Red List category prior to extinction for model replicates resulting in extinction prior to the end of the simulation. Red List categories examined from highest to lowest threat level are critically endangered (CR), endangered (EN), vulnerable (VU), and near threatened (NT). Dashed lines indicate the location of the mean time spent in each category.

was determined by criterion A2, which is met when population sizes are reduced by 80, 50, or 30% over a period of 10 years or 3 generations (whichever is longer) for classification as critically endangered, endangered, or vulnerable, respectively (IUCN, 2012). In 50 replicates, criterion C (small population size plus decline) was also met briefly at the critically endangered level just prior to extinction.

4. Discussion

Only a narrow set of parameter values result in population trajectories from billions of individuals to extinction in less than a

century (Fig. 3B). Although land-use changes throughout the 19th century likely caused substantial total area loss and disruption to the continuity of breeding habitat, it is possible to explain the extinction of passenger pigeons through overharvest alone. Model scenarios approaching extinction-level population thresholds always included maximum commercial harvest levels greater than 4 million birds per year (2 million females in female-only model) and showed a strong positive relationship with increasing maximum harvest levels. The model results indicated that the mortality leveled on the population by commercial harvests was on the high end of estimates made at the time (Cook, 1903; Martin, 1915; Schorger, 1955).

The relationship between threshold-level declines and habitat loss was much more tenuous. Model scenarios showed slightly higher probabilities of reaching these threshold population levels when commercial harvest was coupled with habitat loss, but this interaction was weak and habitat loss did not prove to be an important predictor in the boosted regression tree models, nor did it show a strong interaction with any other predictor variable. Model scenarios showing high likelihood of threshold-level declines were those having high maximum commercial harvest levels, low maximum growth rate, high inter-annual population fluctuations, and high frequency of nest disturbance leading to low recruitment years.

Despite the fact that habitat loss did not prove to be an important driver of declines in the final trajectory toward extinction, it was the most important predictor of expected minimum abundance across all models. This seeming contradiction is explained by the fact that habitat loss drove average overall carrying capacity down to half of the initial carrying capacity. However, this predictable level of overall decrease in population size did not necessarily drive the population to threshold-level (i.e. quasi-extinction) declines within the timeframe of the model.

High population variability showed moderately strong interactions with both maximum growth rate and commercial harvest in predicting quasi-extinction. This was consistent with the findings of Hung et al. (2014) who found ratios of genetic effective population size (based on DNA extracted from museum specimens) to estimated census population size for passenger pigeon similar to other species with highly variable populations. Extreme population fluctuations are known to be correlated with increased extinction risk when it occurs over short time frames (1–3 generations) and in association with other symptoms of endangerment (IUCN, 2012).

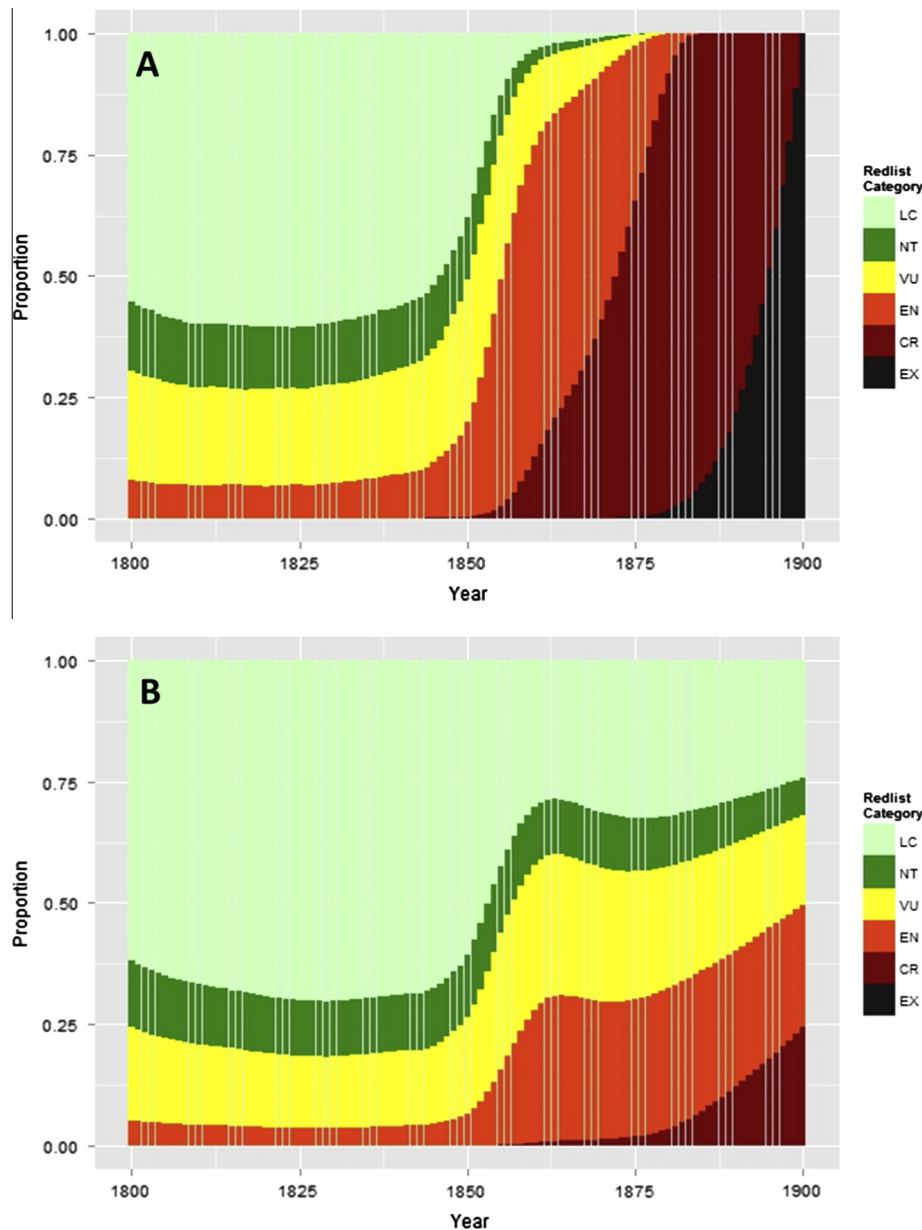


Fig. 5. Proportion of model replicates meeting criteria for IUCN Red List categories by time step. IUCN Red List criteria were applied separately to each stochastic model replicate. Only models with non-zero probability of quasi-extinction (at least one replicate reaches a decline to 1000 females) were analyzed. (A) Replicates resulting in extinction. (B) Replicates not resulting in extinction.

This study suggests that there could have been several decades in which appropriate conservation measures could have been enacted to preserve the passenger pigeon. It is important to note that of all the simulations that included a commercial harvest, only a small proportion of those replicates resulted in either critically endangered threat status or extinction. This suggests that commercial hunting of passenger pigeons *per se* was not unsustainable, only the intensity and manner (in terms of disrupting reproduction) in which it was carried out. In addition, the levels of commercial harvest in the models that induce the highest risk were at the limit of what could be shipped, stored, and marketed before spoilage (Martin, 1915). Both the commercial market and local harvests resulted in extremely high levels of waste, where birds were harvested but spoiled before shipping or were left uncollected to decompose on the forest floor (Schorger, 1955). All this suggests

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that there would have been room to increase the efficiency of the commercial harvest with minimal impact to those with financial interests.

5. Conclusions

Population monitoring and risk assessment play essential roles in preventing extinctions. Had a quantitative and objective evaluation tool, such as the IUCN Red List criteria, been available at the time it might have provided an early and evidence-based mechanism to focus the need for conservation. Protection laws were passed by various states in the 1870s and 1880s in an attempt to regulate the harvest (Hornaday, 1913), but the restrictions carried little weight or enforcement and were largely ignored.

The perception that passenger pigeon were still abundant masked the immediacy of the threat.

This analysis is predicated on the assumption that that accurate population data could have been collected for the passenger pigeon with which to conduct the IUCN Red List assessment. Without this data, a sense that flocks seem smaller, or nesting colonies do not cover the area they once did, might not be obvious or alarming until population sizes are extremely reduced. Reliance on casual observation is not likely to be a suitable monitoring strategy for many species, particularly while they are still relatively abundant. Organized, long-term data collection and monitoring is an essential mechanism for risk-assessment and should not be reserved for only those species known to be in decline or already at low population levels.

Presently in North America, avian populations are regularly monitored and assessed through several long-standing and organized programs (DeSante and Saracco, 2009; Hochachka et al., 2012; Sauer et al., 2013) making it unlikely that any future North American avian extinctions would come without a high degree of expectation or foreknowledge. However, globally most taxa are not nearly as well monitored; with many species too data deficient even for risk assessment. There is a great need for the expansion of global wildlife population monitoring programs and risk assessment based on population-level symptoms such as decline rates. We already have the necessary tools, such as the IUCN Red List assessment, for identifying species in need of protection before they go the way of the passenger pigeon.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.09.023>.

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