Extinction risk assessment as a tool for biological conservation

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Abstract of the Dissertation

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Effective conservation of biological diversity requires accurate assessments of species extinction risks. Both under- and over-estimating extinction risks can have serious consequences. Overlooking species that are in need of conservation management can result in extinction or expensive recovery efforts. Misidentifying species which have stable populations as threatened can misdirect limited conservation resources or unnecessarily halt economic activity and development. I used a retrospective multi-modeling framework to explore the extinction of a once abundant and wide-spread North American species, the Passenger Pigeon (*Ectopistes migratorius*). I simulated three different types of anthropogenic impacts: harvest, habitat loss, and nest disturbance. I explored the effect of these impacts in conjunction with a range of life-history parameters through a global sensitivity analysis. I found that over-harvest and accompanying nest disturbance, rather than habitat loss were the primary impact factors driving this species to extinction. I extended this analysis by looking at the population trajectories generated by the model to illustrate how the International Union for the Conservation of Nature (IUCN) Red List criteria, a globally recognized method of assessing extinction risk, might have been used as an early warning system to identify the threats the species was facing well before extinction was imminent. I demonstrate that data collection and monitoring the population trends through time would have been necessary to identify the threat early on. Waiting until population sizes were reduced to critical thresholds would likely have only provided a few years of advance warning before the extinction of this species. In a related study, to gain a better understanding of how the IUCN Red List criteria may perform in the future under the threat of global climate change, I applied the Red List criteria to an ensemble of models representing endemic North American reptile and amphibian species, with a wide range of life-history characteristics, range sizes, and habitat types. Overall, I found that the Red List criteria reliably provided a sensitive and precautionary way to assess extinction risk due to climate change. Together, these case-studies demonstrate the ability of currently used methods to assess extinction risks under a variety of threats, and highlight the need for data collection and monitoring of wildlife species, particularly when simultaneously facing multiple impact factors. Heading into the future, preventing further loss of species will require much vigilance. The process of ranking species according to their threat status can provide an organized framework to help identify gaps in knowledge and guide data collection and conservation effort.

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1 Introduction

> We no longer destroy great works of art. They are treasured, and regarded as of priceless value; but we have yet to attain the state of civilization where the destruction of a glorious work of Nature, whether it be a cliff, a forest, or a species of mammal or bird, is regarded with equal abhorrence.
>
> - *William Temple Hornaday, 1913*

W.T. Hornaday was among the first to advance a philosophy and approach to species conservation that would be familiar to conservation biologists today. Hornaday's 1913 book, *Our Vanishing Wild Life: Its Extermination and Preservation*, has been called a precursor to Red Data Books which catalog threatened and endangered species at national or global levels (Scott et al. 1987). Hornaday (1913) highlights a number of recent extinctions in the Americas, and implores his readers to rally for the immediate protection of a number of additional birds and mammals whose extinctions he saw as imminent (Table1-1). At the time of its writing the last known individual passenger pigeon (*Ectopistes migratorius*) was still living in captivity at the Cincinnati zoo, a female specimen who would die the year following the publication of Hornaday's call to action (Herman 1948).

Of the 25 North American bird species named by Hornaday (1913) as threatened with extinction, only one was eventually lost. The heath hen (*Tympanuchus cupido cupido*), a once abundant and wide-ranging species was reduced to a single remnant population that was eventually lost altogether in 1932 after recovery efforts failed (Simberloff 1986, Johnson and Dunn 2006). An additional 4 of Hornaday's species are currently listed by the International Union for the Conservation of Nature (IUCN) as threatened, 2 are near threatened, and the remainders are not considered to be in immediate danger (Table 1-1).

Table 1-1 North American bird species identified as threatened with extinction by Hornaday (1913) with their status today as classified by the IUCN.

Common name (current, if different)	Scientific name	Current IUCN Red List status
Whooping crane	*Grus americana*	Endangered
Trumpeter swan	*Cygnus buccinator*	Least Concern
American flamingo	*Phoenicopterus ruber*	Least Concern
Roseate spoonbill	*Platalea ajaja*	Least Concern
Scarlet ibis	*Eudocimus ruber*	Least Concern
Long-billed curlew	*Numenius americanus*	Least Concern
Hudsonian godwit	*Limosa haemastica*	Least Concern
Upland plover (Upland sandpiper)	*Bartramia longicauda*	Least Concern
Buff-breasted sandpiper[A]	*Tryngites subruficollis*	Near Threatened
Golden plover (American golden plover)	*Pluvialis dominica*	Least Concern
Dowitcher (Short-billed dowitcher)	*Limnodromus griseus*	Least Concern
Willet	*Catoptrophorus semipalmatus*	Least Concern
Pectoral sandpiper	*Calidris melanotos*	Least Concern
Black-capped petrel	*Pterodroma hasitata*	Endangered
American egret (Great egret)	*Casmerodius albus*	Least Concern
Snowy egret	*Egretta thula*	Least Concern
Wood duck	*Aix sponsa*	Least Concern
Band-tailed pigeon	*Patagioenas fasciata*	Least Concern
Heath hen	*Tympanuchus cupido cupido*	Extinct[B]
Sage grouse (Greater sage grouse)[C]	*Centrocercus urophasianus*	Near Threatened
Prairie sharp-tail (Sharp-tailed grouse)	*Tympanuchus phasianellus*	Least Concern
Pinnated grouse (Greater prairie-chicken)	*Tympanuchus cupido*	Vulnerable
White-tailed kite	*Elanus leucurus*	Least Concern
California condor	*Gymnogyps californianus*	Critically Endangered
Woodcock (American woodcock)	*Scolopax minor*	Least Concern

[A] Hornaday had this species labeled as 'Knot: Red-Breasted Sandpiper' which is an anachronistic common name for *Calidris canutus*. It's not clear which species he intended, however, he did comment that shorebirds in general were in danger.

[B] IUCN does not have a separate designation for this subspecies of the greater prairie-chicken, *Tympanuchus cupido*, but its extinction is well documented (Simberloff 1986).

[C] The Gunnison sage grouse, *Centrocercus minimus,* was recently recognized as a separate species. Its IUCN Red List status is Endangered.

Hornaday (1913) assembled this list based on his own observations and expert opinion. Very little was available at the time in terms of data collected specifically for assessing the status of these species. Observations of declining trends in wildlife were based primarily on casual observations and records for numbers captured or killed for sport or commerce. The fact that the majority of Hornaday's threatened birds are no longer considered imperiled, is not necessarily evidence that his assessments were overly precautionary. All of the species named are currently legally protected or managed to some degree or another either through the Migratory Bird Treaty Act (http://www.fws.gov) or through other state and/or federal management. Some of these species have benefited greatly from these protection efforts in conjunction with restoration of critical habitat. The trumpeter swan for example, while not nearly as numerous as it was historically, has rebounded from very low population numbers (Denson Jr. 1970). Still others, such as the California condor, remain imperiled despite decades of intensive recovery efforts (Finkelstein et al. 2012).

In the last several decades the trend in IUCN species risk assessment has moved away from expert-opinion and moved toward more objective and transparent data-driven measures (Mace et al. 2008). This refinement of the assessment criteria not only increases the accuracy and credibility of the classifications, but guides the public, policy makers, and conservation organizations in setting goals and priorities. Just as a century ago, often the first step toward illustrating the urgency of conservation action is through highlighting the individual species which may be forever lost without immediate protection (Cart 1973, Smith 1976). Therefore it is important to have the most precise and defensible risk assessments as possible.

The list of species in Table 1-1 illustrates a common problem encountered when evaluating the accuracy of risk assessment. The majority of those species that were identified a century ago as being immediately imperiled not only did not to go extinct but are no longer considered in immediate danger of doing so. Was this change due to protections that occurred after the recognition that they may be at risk or because the prediction was inaccurate?

One way to address this question is by taking a detailed look at a species for which the fate is known without the potentially confounding factor of conservation action. I do this here with a retrospective analysis of the decline and extinction of the passenger pigeon (*Ectopistes migratorius*). Industrial and agricultural expansion throughout the 19th century heavily impacted the forests on which the passenger pigeon relied. At the same time, their breeding colonies were harvested heavily for sport and commercial markets. The population numbers began to fall dramatically in the latter half of the 19th century and it is believed they were extinct in the wild by the dawn of the twentieth (Hodge 1911, 1912). The extremely rapid decline of this species from extreme abundance to extinction in such a short period of time has drawn much speculation.

This species makes an excellent case-study to explore risk-assessment because the extinction event is recent enough that there are numerous eye-witness accounts available in the historic record, yet far enough in the past that it pre-dated most conservation laws. This species is also of interest because it was wide-ranging and extremely abundant, two characteristics that usually indicate a lower extinction risk. In Chapter 2 I describe a retrospective multi-model approach I used to quantitatively reconstruct this extinction event. I simulated three different types of anthropogenic impacts on the passenger pigeon: harvest, habitat loss, and nest disturbance. I explored the effect of these impacts in conjunction with a range of life-history parameters through a global sensitivity analysis. This approach allowed me to generate thousands of possible trajectories to examine the range and interaction of parameters that result in extinction-level declines within a timeframe commensurate to the historical period of decline. For the first time, I am able to quantitatively demonstrate that that over-harvest, rather than habitat loss was the primary impact factor driving this extinction event. The level of harvest mortality implied by the models is likely beyond what would have been successfully shipped, stored, and sold in the marketplace. This reinforces historical accounts of large amounts of waste in this largely unregulated market where there was little incentive for harvesting sustainably.

In Chapter 3 I applied some of the IUCN Red-listing criteria to the simulated trajectories generated by the passenger pigeon population model. I did this to both test how well the criteria performed in terms of identifying the risk of extinction, and also to determine how much time might have been available for conservation action had appropriate monitoring data and a tool like the Red List criteria been available. I found that had there might have been several decades in which to take conservation action, had the proper monitoring data and tools been available. By examining simulated model trajectories, I found the strongest indicator of extinction risk would likely have been in the observed rate of decline, as opposed to low population sizes. In most extinction trajectories, the species only becomes rare a few years prior to extinction. This is consistent with witness accounts of the species seeming to vanish. These results are particularly relevant for modern conservation where for some species rapid declines are observed, but may still be relatively abundant. Together these two chapters highlight the need for collecting data and carefully monitoring species even when high population numbers seem to imply low risk of extinction.

In Chapter 4 I look to the future and examine IUCN Red List criteria in the face of a modern challenge to species conservation, global climate change. Recently, the concern has been raised that the IUCN Red List criteria may not be sufficient to address the types of conservation challenges posed by climate change. I addressed these questions with a set of models developed to predict extinction risk over the coming century for a number of reptiles and amphibians endemic to North America. I found that the IUCN Red List does appropriately identify models when there is a high risk of extinction due to climate change. I also found that for the modeled species I examined it seems unlikely that a species would go from a non-threatened status to extinct between recommended re-evaluation intervals. However, whether the amount of warning the IUCN Red List provides will be sufficient to implement the kind of conservation actions that might be needed to prevent extinctions due to climate change is a larger question.

Together, this dissertation provides further evidence that extinction risk assessment and threat rankings can be a useful framework for setting conservation priorities and assessing species in need. The process of assessing extinction risk can be helpful in identifying critical gaps in knowledge and directing future investigations and data gathering. Finally, preventing further anthropogenic species extinctions will require vigilance for the foreseeable future.

2 How a common species went extinct: a case study of the passenger pigeon, *Ectopistes migratorius*

2.1 INTRODUCTION

Next year will mark the 100 year anniversary of the passing of the last known passenger pigeon (*Ectopistes migratorius*). At one time the most abundant bird species in North America, the passenger pigeon was so numerous that even after decades of intensive commercial harvesting and habitat modification many people did not believe it to be at risk of extinction[1] (Brewster 1889). This misconception remains a risk for many species even in the era of modern conservation biology, especially when commercial harvest is involved (Hutchings 2001). It is clear that hunting of adults and young from nesting colonies played a role in decreasing abundance, yet the precise cause of the extinction of *E. migratorius* remains a mystery. Throughout the 19th century human population growth and migration, as well as agricultural and industrial development, reduced and fragmented the hardwood forests which were primary nesting habitat for *E. migratorius* (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 1911, 1912). The species was possibly 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).

Presently, there are two leading theories to explain how this species could have declined from extreme abundance to extinction so rapidly; hunting pressure and habitat loss. Blockstein & Tordoff (1985) argue that direct harvest of adults and young combined with the disturbance of the nesting colony from hunters resulted in a loss of recruitment sufficient enough on its own to be the primary causal factor to explain the extinction event. However, Bucher (1992) counters that the persecution from professional hunters eased somewhat as the

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[1] Newspaper commentary from the late 1800's often expressed incredulity over concern that the species was headed toward or had already reached extinction. Examples include: 'The extinct wild pigeon'. Daily Press, December 21, 1896. Newport News, VA; 'The wild pigeon's fate'. The True Democrat, January 29, 1898. Bayou Sara, LA.; 'Where wild pigeon went'. The Sun, March 4, 1900. New York, NY.

population declined and the colonies became harder to find, thus making it unlikely that hunting alone was the primary causal factor. In addition, he argues that other species of Columbiformes with similar reproductive strategies are heavily harvested, yet maintain viable populations. Other theories have been proposed such as climate change, disease, environmental disasters, and competition with livestock; however there is a lack of evidence to support any of these alternative theories (Bucher 1992). While both Blockstein and Tordoff (1985) and Bucher (1992) argue their cases convincingly and present some quantitative evidence to support their theories, to date no one has explicitly modeled possible impacts of habitat loss, hunting, and intrinsic life history characteristic on the population dynamics of this species.

An important first step to exploring the history of the decline and extinction of species during the 19th century in North America is to quantify how the landscape changed during this time. Rapid and widespread deforestation is thought to have been a major contributing factor in the decline of the passenger pigeon. These changes were largely the result of the westward advance of human settlement and transportation infrastructure as well as increases in the extraction of natural resources. However, as this time period is well before the advent of modern technologies for monitoring changes in the landscape such as remote sensing, 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 the information that is available and inferences about the likely progression of the landscape transformation.

Approaches to map historic range for extinct species or species that have experienced significant range declines due to anthropogenic habitat disturbance usually only map, at most, two time-steps; one for the historic or pre-disturbance, and a second for the present-day or post-disturbance (Channell and Lomolino 2000, Donald and Greenwood 2001, Schulte et al. 2005, Farnsworth and Ogurcak 2006, Aldridge et al. 2008). This approach does not supply a sufficient level of information for constructing a spatially explicit population model if habitat loss is a potential causal factor. With no information about the availability of habitat between the first and last time-steps it is difficult to infer the trajectory that a population may have taken. For many species, spatial parameters such as the number, size, and distribution of suitable habitat patches have major impacts on population dynamics (Naujokaitis-Lewis et al. 2009).

Here I approximate the effect of habitat loss on carrying capacity by reconstructing the available nesting habitat for the passenger pigeon at annual time-steps. Through the analysis of environmental and landscape variables thought to have been important for habitat suitability, I first construct a model of potential nesting habitat then sequentially account for disturbance (i.e. human settlement patterns). I then construct a temporally dynamic model of potential breeding habitat for the passenger pigeon in the Eastern and Midwestern United States through the 19th century.

By combining this habitat model to a population model incorporating historical records of life history traits, abundance, human predation, and spatially-explicit trends in deforestation, I test extinction scenarios for the passenger pigeon. This approach allows me to address whether a given factor alone such as harvest, or a combination of factors such as harvest and habitat loss, can explain the observed decline and eventual extinction. This is essentially a population viability analysis (PVA) – a common and effective tool used in conservation planning for single species (Brook et al. 2000). PVA is normally used to forecast possible risks of decline or extinction, evaluate possible management actions, or plan future research (Stanton and Akcakaya 2013). Here, I apply a PVA approach to hindcast rather than forecast in order to explore the possible driving factors behind this extinction event. A similar approach was recently used (Prowse et al. 2013) to illuminate another recent anthropogenic extinction event, that of the thylacine (*Thylacinus cynocephalus*) in Tazmania.

2.2 METHODS

2.2.1 Estimating available nesting habitat through time

Occurrence Locations

I constructed an occurrence-only species distribution model (SDM) for the breeding range of the passenger pigeon. In total, I used 79 occurrence locations for model building (55 historic accounts and 24 museum collections). The historical accounts were descriptions of nesting sites encountered by settlers, naturalists, explorers and other travelers who observed breeding colonies in the 19th century and recorded those encounters in journals, letters, news articles, sportsman journals and were subsequently collated by (Schorger 1955). Location information on these accounts were descriptive in nature with varying levels of specific geographical details. For example, some of the descriptions gave estimates of the length and width of the area covered by the colony along with distance and bearing from known and extant landmarks such that a rough outline of the colony could be mapped. In other instances, the accounts were less precise, only giving the state and county where the colony was observed with few other details. For these I placed latitude and longitude coordinates at the described location or the midpoint of the location if it was an area.

The additional 24 occurrence locations were museum specimen records I accessed through the Global Biodiversity Information Facility (GBIF; http://data.gbif.org). These records represent museum specimens collected during the breeding season (March – June) with spatial information for the location of where the collection was made (Table 2-1 and Figure 2-3). For these I used the coordinates reported by GBIF.

I collected an additional 21 occurrence locations to use for model evaluation. This evaluation set consisted of 19 locations of breeding colony encounters not previously included by Schorger (1955) from the Auk, Wilson Journal, and early newspapers; and 2 passenger pigeon egg collection records accessed through GBIF (Table 2-1 and Figure 2-3). All descriptive historical accounts for both the testing and training sets were included only if the account specifically implied that the birds were breeding or attempting to breed. I included these criteria to exclude accounts of migratory flights or roosts.

Table 2-1 Geographic coordinates used for habitat model training and testing sets.

Model Training Locations

State/Provence	Location	Lat	Long	Source
Pennsylvania	Montrose	41.8	-75.9	Schorger 1955; pg 88
Kentucky	Green River	37.3	-85.5	Schorger 1955; pg 89
Kentucky	between Shelbyville and Frankfort	38.2	-85.0	Schorger 1955; pg 89
Michigan	Petoskey	45.5	-85.0	Schorger 1955; pg 89
Michigan	Crooked Lake, Emmet county	45.4	-84.8	Schorger 1955; pg 90
New York	Allegheny River north toward Collins	42.3	-78.9	Schorger 1955; pg 90
New York	Annsville to Watertown	43.3	-75.6	Schorger 1955; pg 90
Wisconsin	La Crosse	43.8	-91.2	Schorger 1955; pg 91
Wisconsin	Black River Falls	44.1	-90.3	Schorger 1955; pg 91
Pennsylvania	McKean and Potter counties	41.8	-78.3	Schorger 1955; pg 91
Oklahoma	Potawatomi Reservation	39.3	-95.8	Schorger 1955; pg 93
Mississippi	Tombigbee River	33.3	-88.4	Schorger 1955; pg 93
Wisconsin	Prescott Island	44.7	-92.8	Schorger 1955; pg 95
Wisconsin	Nine Mile Island	44.7	-91.9	Schorger 1955; pg 95
Minnesota	Chatfield	43.8	-92.2	Schorger 1955; pg 96
New York	Bell's Run	42.0	-78.3	Schorger 1955; pg 96
New York	Moose River	43.6	-75.1	Schorger 1955; pg 96
Wisconsin	Pine River	43.4	-90.4	Schorger 1955; pg 97
Wisconsin	Wautoma	44.1	-89.3	Schorger 1956; pg 97
Michigan	Grand Haven	43.1	-86.2	Schorger 1955; pg 97
Ontario	Guelph	43.5	-80.2	Schorger 1955; pg 97
New York	Tupper's Lake	44.2	-74.5	Schorger 1956; pg 97
New York	Wood Creek	43.1	-75.2	Schorger 1955; pg 98
New York	Altona	44.9	-73.7	Schorger 1955; pg 98
Michigan	Benzie County	44.6	-86.2	Schorger 1955; pg 115
Michigan	Platte River, Benzie County	44.7	-85.8	Schorger 1955; pg 124
Indiana	Decatur County	39.3	-85.5	Schorger 1955; pg 124
New York	Plattsburg	44.7	-73.5	Schorger 1955; pg 145
Michigan	Grand Rapids	43.0	-85.7	Schorger 1955; pg 146
Michigan	Shelby, Oceana County	43.6	-86.4	Schorger 1955; pg 149
Wisconsin	Sparta, Monroe county	43.9	-90.8	Schorger 1955; pg 152
Wisconsin	Kilbourn, Adams County	43.7	-89.8	Schorger 1955; pg 152
Michigan	Van Buren County	42.2	-86.0	Schorger 1955; pg 154
Wisconsin	Langlade/Oconto County	45.2	-88.6	Schorger 1955; pg 218
Pennsylvania	Forest and Warren counties	41.6	-79.3	Schorger 1955; pg 218
Michigan	Lake City	44.3	-85.2	Schorger 1955; pg 219
Pennsylvania	Potter County	41.7	-77.9	Schorger 1955; pg 219
Pennsylvania	Blossburg	41.7	-77.1	Schorger 1955; pg 219
Michigan	Au Sable headwaters	44.8	-84.8	Schorger 1955; pg 221
Montana	Fort Benton	47.8	-110.7	Schorger 1955; pg 264
Kansas	Neosha Valley	37.7	-95.5	Schorger 1955; pg 264
Mississippi	Choctaw	32.0	-89.0	Schorger 1955; pg 264
Georgia	Wayne County	31.5	-81.9	Schorger 1955; pg 264
Georgia	St. Simon Island	31.2	-81.4	Schorger 1955; pg 264
Georgia	McIntosh County	31.5	-81.4	Schorger 1955; pg 264
North Dakota	Berthold	48.3	-101.7	Schorger 1955; pg 265
South Dakota	Fort Pierre	44.4	-100.4	Schorger 1955; pg 265
Manitoba	Waterhan River	52.2	-99.5	Schorger 1955; pg 265
Manitoba	Portage la Prairie	50.1	-98.3	Schorger 1955; pg 265
Oklahoma	Atoka	34.4	-97.4	Schorger 1955; pg 265
North Dakota	Pembina	49.0	-97.2	Schorger 1955; pg 265
Ontario	Lake of the Woods	49.0	-94.3	Schorger 1955; pg 266
Ontario	Nipion	49.0	-88.3	Schorger 1955; pg 266
Ontario	Smokey Falls	50.1	-82.2	Schorger 1955; pg 266

New Brunswick	Grand Falls	46.9	-67.7	Schorger 1955; pg 266
Quebec	Fort George	53.8	-79.0	Canadian Museum of Nature
Vermont	Fair Haven	43.6	-73.3	Denver Museum of Nature & Science
Wisconsin	Platteville	42.7	-90.5	Field Museum
Wisconsin	Oakfield	43.7	-88.5	Field Museum
Illinois	Chicago Grand Crossing	41.7	-87.6	Field Museum
Maine	Westbrook	43.7	-70.4	Field Museum
Minnesota	Lake City	44.4	-92.3	James R. Slater Museum of Natural History
Wisconsin	Tomah	44.0	-90.5	Los Angeles County Museum of Natural History
Minnesota	Marshall County	48.5	-95.9	Museum of Vertebrate Zoology, CA
Michigan	Ypsilanti	42.2	-83.6	Museum of Vertebrate Zoology, CA
Manitoba	Oak Lake	49.7	-100.7	Royal Ontario Museum
Manitoba	Riding Mountain National Park	50.8	-100.3	Royal Ontario Museum
Minnesota	Big Lake	45.3	-93.8	Royal Ontario Museum
Wisconsin	Berlin	44.0	-89.0	Royal Ontario Museum
Indiana	Oak Forest	39.4	-85.1	Royal Ontario Museum
Ontario	Coe Hill	44.9	-77.8	Royal Ontario Museum
Ontario	Trenton	41.1	-77.6	Royal Ontario Museum
Pennsylvania	Milford	41.3	-74.8	Royal Ontario Museum
Michigan	Escanaba	45.8	-87.1	University of Michigan Museum of Zoology
Michigan	Kalamazoo	42.3	-85.6	University of Michigan Museum of Zoology
Indiana	Waterloo	39.6	-86.2	Yale University Peabody Museum

Model Testing Locations

State/Provence	Location	Lat	Long	Source
Illinois	North of Waukegan	42.37	-87.83	Coale 1922
illinois	West of Waukegan	42.36	-87.91	Coale 1922
Michigan	Muskegon	43.23	-86.25	Coale 1922
Indiana	English Lake	41.26	-86.82	(Deane 1895)
Pennsylvania	Columbia	40.03	-76.50	(Deane 1931)
Michigan	South Oceana County	43.53	-86.29	Jackson daily citizen 1872
Michigan	West of Traverse City	44.76	-85.93	Jackson daily citizen 1880
Pennsylvania	Forest county	41.53	-79.24	Macon Telegraph 1880
Iowa	Marquoketa	42.58	-90.68	(McGee 1910)
Pennsylvania	Upper Potter County	45.50	-84.85	The Sun 1899
Pennsylvania	Pike county	41.56	-76.06	The Sun 1899
Pennsylvania	Monroe county	41.91	-77.92	The Sun 1899
New Jersey	Cumberland	41.33	-75.06	The Sun 1899
New Jersey	Cape May	41.04	-75.25	The Sun 1899
New Jersey	Atlantic County	39.35	-75.06	The Sun 1899
Pennsylvania	Mehoopany Creek, Wyoming county	39.20	-74.80	The Sun 1899
Michigan	Straights of Mackinac	39.53	-74.67	The Sun 1899
Michigan	Northport	45.13	-85.62	(Wilson 1934)
Missouri	Salt River	39.61	-91.06	(Wright 1910)
New York	Albany	42.69	-73.75	(Wright 1911)
Vermont	Clarendon settlement	43.52	-72.97	Wright 1911
Pennsylvania	Indiana County	40.42	-79.12	Museum of Vertebrate Zoology, CA
Ohio	Holmes County	40.56	-81.92	Museum of Vertebrate Zoology, CA

I conducted the distribution modeling at a spatial resolution of 2.5 minutes (approximately 4.5 km by 4.5km) covering a spatial extent including the continental United States and a southern portion of Canada below approximately 55°N latitude. There is inherent spatial uncertainty in assigning location data to nest site locations coming from the historic record and museum collections. However, the nesting colonies themselves could be quite large. Schorger (1955) calculated the average of 47 nesting colonies that report length and width as

80 square kilometers. The vast spatial requirements of the breeding colonies and the coarseness of the spatial resolution should compensate somewhat for the inherent uncertainty of the location data.

Predictor Variables

In selecting predictor variables to include in the habitat model, I elected to include those that primarily relate to the distribution of food resources utilized by the nesting colony. The species preferred the high quality nuts of American beech (*Fagus grandifolia*) but also were known to feed on the nuts or acorns of oaks (*Quercus sp.*), chestnut (*Castanea dentata*), and hickory (*Carya sp.*) (Cook 1903, Schorger 1955, Bucher 1992). Therefore I included variables important to American beech distribution and deciduous forests with a high percentage of these species. A characteristic of many of these tree species is highly variable year-to-year nut production or having 'masting seasons'. Similar to many social species that are dependent on a highly variable food resource, passenger pigeons were 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 rotting or germinating before the spring migration (Bucher 1992). In fact, it had been observed that passenger pigeons could be reliably predicted to occur in the spring where a sizable fall beech mast was covered continuously over the winter by snow (Cook 1903). Table 2-2 summarizes the variables included in the model.

I obtained the climate variables from Natural Resources Canada (McKenney et al. 2006). The climate variables were ANUSPLIN gridded layers from weather station data for the period 1901-2000. Although this time period does not perfectly align with the era being modeled, weather station data for this region prior to 1900 do not exist at enough locations to generate reliable gridded layers (D. McKenney *pers. com*). Further, including data post 1950 would begin to incorporate records from the current warming trend. Summarizing over this timeframe of records spans enough years to incorporate year-to-year climatic variation while still representing conditions very similar to those experienced by the passenger pigeons and the forests within which they nested.

To characterize the distribution of *Fagus grandifolia* in North America, I selected temperature seasonality, total precipitation through the growing season, and maximum July temperature for inclusion on the model because similar variables have been shown to be important in previous studies for this tree species (Prasad et al. 2007, 2009). I included April temperature range in the analysis because there is evidence that it may be relevant to the regulation of mast production in *Fagus* species (Kon et al. 2005). I selected mean temperature in the coldest quarter, total precipitation in the coldest quarter, and Julian date of the beginning of the growing season as variables related the overwinter preservation and spring availability of tree mast.

Table 2-2 Predictor variables included in passenger pigeon breeding habitat model.

Variable	Rationale	Data Source	% Contribution to final model
Temperature seasonality*	Beech distribution	Natural Resources Canada	0.5
Mean temp. coldest quarter	Mast preservation	Natural Resources Canada	0.5
Total precipitation coldest quarter	Mast preservation	Natural Resources Canada	3.6
Start growing season	Mast preservation	Natural Resources Canada	11.1
Total precipitation growing season	Beech distribution	Natural Resources Canada	20.1
Max July temperature	Beech distribution	Natural Resources Canada	26.9
April temperature range	Mast regulation	Natural Resources Canada	30.9
Potential Natural Vegetation	Forest type	Ramankutty and Foley 1999	3.2
Slope variation	Forest type	SRTM 90m	3.1

* Climate variables are based on data from 1900-1950 (see text)

I incorporated a land cover layer in the model derived from the potential natural vegetation map from Ramankutty and Foley (1999) which is a 5 min. resolution categorical map of 15 potential natural land cover types. Potential natural vegetation is not necessarily equivalent to pre-settlement vegetation; however the categories from this dataset are sufficiently broad that in the model they essentially function to distinguish forested area from non-forested areas.

In order to characterize the dominant pattern in elevational changes over the landscape, I smoothed a 90m digital elevation model (Jarvis et al. 2008) by finding the mean of a 10 pixel by 10 pixel window. I then calculated the maximum difference in the mean slope values within each 2.5 minute resolution grid cell.

Model Construction

I modeled habitat suitability using the program Maxent (v.3.3.3; Phillips et al. 2006). Maxent uses a maximum entropy approach to predict the geographic location of suitable habitat. Maxent takes as input locations where the species has been observed (presence locations) and a set of environmental predictors layers. Because the program does not require the user to specify locations that were known to have been surveyed but where the species was not detected (absence locations), Maxent is characterized as a 'presence-only' or 'presence-background' model as it does not require the specification of known absence locations (Phillips et al. 2006, Phillips and Dudík 2008). Comparisons among a number of frequently used presence-only approaches showed Maxent to have reliably high predictive performance (Elith et al. 2006). Since the environmental predictor variables I selected for the model were related to the distribution of the primary food and structural resource the species depended on for reproduction, I treated the suitability value predicted by Maxent as proportional to the quantity of breeding habitat available, and thus proportional to the carrying capacity of each area unit.

I used the output from the habitat model as a spatial template of the breeding habitat which was modified through land use change (described below). I then scaled the carrying capacity at each time-step to the corresponding total habitat suitability dependent on a stochastic colony movement process and the strength of colony cohesion (both processes described below).

I evaluated the habitat model fit by the area under the receiver operating characteristic curve (area under curve, or AUC) calculated from the 21 occurrence locations retained for model testing (Table 2-1 and Figure 2-3). AUC is a measure of model fit based on the area under a curve that plots the true positive rate vs. false positive rate at multiple threshold values. A model that fits no better than random would be expected to have an AUC value close to 0.5, while a model with perfect predictive accuracy would have an AUC value of 1.

Habitat Loss and Fragmentation

I treated the output from the distribution model as a baseline-level, maximum possible habitat without anthropogenic disturbance. To estimate the quantity of habitat available at each time step, I reduced the habitat suitability based on anthropogenic disturbance. For each decade from 1800-1900, I modified the baseline habitat map to account for human settlement land use 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. I then linearly interpolated the maps between decades to produce a habitat map for each year.

The cropland and pasture land use maps I 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 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. These land use areas are mapped by considering how much land area would have been needed to support the estimated human population density levels. The HYDE models then spatially allocate the needed land area based on information about landform, soil, climate, and access to water. Each grid cell in the HYDE database is the proportion of land area within that grid cell estimated to be in cropland or pasture. To downscale the resolution of the HYDE layers to the baseline habitat layer I assumed that the proportions in each land use type remained constant.

2.2.2 Linking nesting habitat to population dynamics

I constructed a stage-based matrix model to simulate population abundances from 1800 through 1900 plus a 20 year burn-in period to allow the model to calibrate. Because the passenger pigeon was nomadic and irruptive with no major physical barriers to dispersal within its range, it was unlikely that there was any form of metapopulation structure. Therefore, I modeled the species as a single panmictic population. I only modeled females in the population. Passenger pigeons formed monogamous pairs with shared parental duties during the breeding season. However, because population sizes were very large, it is unlikely that demographic stochasticity would result in either sex becoming limiting until the species was very close to extinction. Limiting the analysis to a single sex allowed me to speed calculation times and avoid computational memory limitations with little impact on model results or conclusions.

I constructed the model with discrete time-step, birth-pulse model with the entire female population calculated once annually pre-breeding. I configured the model with two life stages, hatch year (HY) and after hatch year (AHY). I calculated fecundity values for HY and AHY birds as the product of maternity for each stage and chick survival from hatching to the next pre-breeding census.

I parameterized the model using both qualitative historic descriptions of the life history characteristics of passenger pigeon and quantitative information from related species. Based on accounts of both wild and captive passenger pigeons, they were similar biologically to members of the genus *Patagioenas* and other Columbid species (Bucher 1992, Blockstein 2002). True estimates of some model parameters can never be known. However, given that there is nothing to suggest they were not biologically similar in many respects to other pigeons, it is justifiable to look at studies of related species for some estimated life history parameter values. Given the inherent uncertainty of this approach, I conducted a global sensitivity analysis to assess the impact of parameter uncertainty on model outcomes. Further details of the global sensitivity analysis are described below.

Survival and Fecundity

The genus *Patagioenas* is the sister genus to *Ectopisties* based on ecological, morphological (Bucher 1992), and genetic evidence (Pereira et al. 2007, Johnson et al. 2010).

The most thoroughly studied species in this genus and one of the closest extant relatives to the passenger pigeon is the band-tailed pigeon (*Patagioenas fasciata*). Jarvis & Passmore (1992) estimated average adult survival of band-tailed pigeon at 0.64 (CV = 0.23) based on a mark-recovery study of over 23,000 band-tailed pigeons banded between 1950 and 1973 in Oregon (though survival estimates are only averaged over the years 1965-1973). Although the authors did not attempt to estimate survival over the first year after hatching, a rough estimate can be made based on data presented. Ratios of juvenile to adult birds based on wings surrendered by hunters for the years 1966-1976 have a mean of 0.21 (CV=0.09). The hunting season extended from September 1 through September 30. In the spring another estimate of juveniles to adults in the population is presented for the years 1968-1969 and 1976-1977 based on birds captured for the banding study. The mean for the springtime ratios was 0.16 (CV=0.30). Assuming that both juvenile and adult survival probabilities are constant over a single calendar year, the fall to spring survival estimates for juveniles can be estimated from the fall to spring ratios using the following formula:

$$\frac{N_{juv(Spring)}}{N_{adult(Spring)}} = \frac{N_{juv(Fall)} * S_{juv(fall\ to\ spring)}}{N_{adult(Fall)} * S_{adult(fall\ to\ spring)}}$$

This calculation is possible because the birds breed within a relatively discrete breeding season that takes place after the spring banding data are collected, and concludes before the fall hunting season. Therefore there is no influence of reproduction in the fall versus spring ratios.

The spring and fall juvenile to adult ratios were the means as reported above. The adult survival from fall to spring was estimated by breaking down the annual adult survival into the approximately 37 weeks between the midpoint of the fall hunting season and the midpoint of the spring banding season. The fall to spring juvenile survival rate was then extrapolated to a full year as 0.45. Kautz & Braun (1981) estimate adult survival of band-tailed pigeons at 0.73 (CV = 0.24) and juvenile survival as 0.66 (CV = 0.49) from marked birds in Colorado from 1969 to 1974. The adult survival rates estimated from these two studies may be on the lower end for this species. It was not uncommon for individuals greater than 10 years old to be recaptured in the Oregon study, especially prior 1968 when dramatic population declines were observed (Jarvis and Passmore 1992). However, given the survival estimates from these two studies, the probability of any individual surviving to 10 years of age is between 0.01 and 0.04. It is possible that whatever conditions were driving the population estimates downward were also reflected in the estimated survival rates.

Jarvis & Passmore (1992) do not directly estimate maternity or nesting success and instead rely on knowledge of band-tailed pigeon biology and breeding phenology. By monitoring the production of crop milk for feeding nestlings and egg development of birds captured during the breeding season, they estimate that most adult pairs attempt 2-3 nestings per season of single-egg clutches, resulting in an average of 1 fledgling per breeder or 1 daughter per mother. Yearling birds will sometimes attempt to reproduce in their first year, but typically later in the season and at a lower rate than adult birds. Jarvis & Passmore (1992) estimate yearling maternity to be 0.33 of the adult rate. Other studies estimate an annual reproductive rates as 1.14-1.26 juveniles/pair or 0.63 daughters/mother (Keppie and Braun 2000).

Although there was some early debate about whether passenger pigeons laid one-egg or two-egg clutches (Brewster 1889, Schorger 1952, 1955), there was later general agreement largely from observing captive birds that the clutches were strictly single-egg and any observed two-egg nests must have been from multiple females depositing in the same nest (Deane 1908, Coale 1922, Schorger 1955). This is consistent with the band-tailed pigeon, which also invariantly lays a single-egg clutch (Blockstein 2002).

There remains some debate as to how many nestings were attempted by each pair of passenger pigeons within a season. Schorger (1952, 1955) and Brewster (1889) strongly argued that there was only a single successful nesting colony per season and colonies were only assembled long enough to accomplish a single round of nesting. That is not to say that a second nesting would not be attempted in the case of a failed attempt. However, Bucher (1992) and Ellsworth & McComb (2003) counter that if passenger pigeon survival estimates and single-egg clutches were similar to band-tailed pigeons, population growth rates would be unrealistically low without at least regular attempts for at least two rounds of nesting per season. Iterative nesting would also have been consistent with other irruptive colonial avian species. However, I found little evidence to support multiple nestings within a season, at least for the very large colonies. Out of approximately 100 nesting records spanning from 1749 to 1896 with both location and year, there is only one year where distances between reported observations of large colonies was great enough that they couldn't be considered part of the same colony. This occurred in 1880 when there were colonies reported in both northwestern Michigan and central Pennsylvania, a distance of over 650km. In addition, there was only a short window of time to complete the nesting cycle between snowmelt in the early spring and the ground being warm enough to allow the mast to germinate which would effectively eliminate the primary food source for the breeding colony (Schorger 1955). That is not to say that re-nesting after a failed attempt or small colonies or single pairs wouldn't nest multiple times on occasion. I contend that the (albeit scant) evidence supports the theory that the majority of pairs in the main colony only attempted a single breeding cycle per season. I constructed my model and parameterized fecundity estimates based on this assumption. Although a range of both survival and fecundity values were fully explored through global sensitivity analysis (see below) to account for these kinds of uncertainty.

Constructing a 2-stage matrix based on the survival and fecundity values as described above for a band-tailed pigeon describe populations with generation times of 4 to 4.6 years (calculated by the method described in Caswell 2001), These estimates are lower than expected for band-tailed pigeons (as well as most New World columbids) which are thought to be relatively long-lived birds with high annual survival rates (Keppie and Braun 2000). This discrepancy is possibly due to adult survival being artificially low in these studies because of harvesting, which can have measurable impacts on a population's demography (Langvatn and Loison 1999). I surveyed the Bird Life International database (www.birdlife.org) for average generation times of columbiformes in general, and birds in the genus *Patagioenas* in particular, to establish a likely range of values for the passenger pigeon assuming they were a long-lived species (on average, 15 years in captivity; Blockstein 2002) with a generation time similar to other columbids. I calibrated the estimated stage matrix by adjusting the survival and fecundity values to generate two population matrices, one with a lower-bound generation time of 5.1 years and one with an upper-bound generation time of 6.5 years. Generation time was calculated for each matrix using the popbio package in R (Stubben et al. 2012) which uses the calculation described by (Caswell 2001). Both upper and lower-bound matrices have a lambda value near 1 at carrying capacity and will vary in a density dependent manner depending on the difference between total population size and carrying capacity at each time step. I used these population matrices as the upper and lower bound matrices in the global sensitivity analysis.

The lower-bound matrix has a generation time of 5.1 years and is as follows:

$$\begin{bmatrix} 0.10 & 0.32 \\ 0.70 & 0.75 \end{bmatrix}$$

The upper-bound matrix has a generation time of 6.5 years and is as follows:

$$\begin{bmatrix} 0.0 & 0.22 \\ 0.82 & 0.82 \end{bmatrix}$$

I estimated temporal variability in survival and fecundity initially by estimating the standard deviation of estimated annual survival rates observed in the Oregon population of band-tailed pigeons (Jarvis and Passmore 1992). I then tuned these values in RAMAS Metapop (Akçakaya and Root 2007) to produce population trajectories with CV values similar to what was observed in this population between 1950 and 1968 before the population began to decline.

Density Dependence

I modeled the population with a scramble-type density dependence (Ricker 1954) calculated on the abundance of both HY and AHY birds. I justify this density dependence structure because of the extremely gregarious nature of this species. Nesting and flocking birds were non-territorial and therefore it is expected that resources for food and space would have been equally shared. I modeled the effects of density dependence as only impacting fecundity values. 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 (Bucher 1982, 1992, Allen and Saunders 2002).

I estimated a maximum growth rate (Rmax) value by constructing a matrix with maximum survival (0.82 for HY and AHY) and fecundity (0.3 HY and 0.48 AHY) estimates and calculating the lambda on this matrix, which was 1.24. To test the effect of uncertainty in this parameter in the global sensitivity analysis I set a lower bound on Rmax as 1.04 which would be a modest positive annual increase.

Nomadic colonial nesting and carrying capacity

Because of the nomadic and irruptive manner in which this species utilized mast resources, it would not be reasonable to treat the habitat suitability across the breeding range equally across years. I modeled this process by generating random trajectories of 'masting areas' for each model replicate. I modeled the masting process by selecting a random location within the breeding range, drawing a 250km radius buffer around that location, and summing the habitat suitability values that fall within the buffer area. In the following timestep a new random location was selected with the restriction that it may not fall within the masting area from the previous timestep, as large colonies rarely nested in the same area two years in a row. I parameterized the radius of the masting area based on the records for the passenger pigeon nesting of 1871 in Wisconsin. That single year provides the best record for the possible spatial extent and arrangement of a nesting colony as multiple observations were made across the entire state that year and are mapped in Schorger (1955).

I used the simulated masting trajectories to generate trajectories of variable carrying capacity. Passenger pigeons were famous for their highly social breeding colonies; at the same time, it was not uncommon to see single pairs or smaller flocks nesting away from the main colony (Brewster 1889, Coale 1922). While there is much evidence that they were a highly social species, there is no mention in the literature of the existence of non-reproductive 'helpers' which would be evident of them being obligately social breeders (Stephens and Sutherland 1999). Therefore it is clear they were facultatively social, but it is unknown to what degree or what proportion of the total population would have been nesting in the main colony in a given year. I parameterized this variable as the degree of coloniality, defined as the proportion of the total population within the masting radius. I modeled this at 3 levels, 40, 60, or 80% of the total population. I used the assigned degree of coloniality to set a weighting constant for total habitat suitability within versus outside of the mast radius at each time step. As the degree of coloniality increases, it essentially has the effect of increasing the year-to-year variation in carrying capacity.

Harvest

I parameterized two different forms of harvest in the models; background and commercial harvest. The background level of harvest was meant to simulate utilization of passenger pigeons by the indigenous people and settlers that would come into contact with local breeding colonies. Passenger pigeons were utilized for food and feathers whenever they were encountered. The fledglings in particular were heavily harvested as they were more easily captured than adult birds yet weighed as much or more (Brewster 1889), provided an accessible source of protein and fat, and could be processed for medium-term food storage.

Once a breeding colony was located, the harvest of large numbers of fledglings could be accomplished with no more sophisticated tools than long sticks or poles to knock them from the nests or gather them from the ground before they could fly. Adult birds were also taken, but required more skill and either guns or nets to capture. Small numbers of birds were shipped short distances by boat and/or sold in local markets prior to the 1840’s but the majority of birds were utilized by the individuals or family groups that captured them. There are no historic records to estimate mortality from this opportunistic, subsistence-level harvest. I set the range of harvest values for the global sensitivity analysis as a proportional harvest of 0.05 – 0.5% of all HY and 0.01 – 0.1% of all AHY birds. This background harvest is simulated in all models throughout the entire duration of the simulation.

The commercial harvest model simulates the effects of the commercial market in passenger pigeons that developed with the expansion of the rail and telegraph lines in the mid 1800’s. The railroads provided a means to ship harvested birds from the breeding colonies in remote or rural areas to the urban population centers. The adult and juvenile birds were shipped fresh and minimally processed for consumption. Adult birds were also live-trapped and transported for use in sport-shooting. The first commercial shipments of passenger pigeons began in the 1840’s, but did not take off as a regular market until continuous rail lines spanned the distance from the east coast to the Mississippi in the early to mid-1850’s.

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 range of estimates that I used to parameterize the model. Most estimates put the total harvest at 1.2 to 3 million birds per season. One of the highest estimates comes from Cook (1903) who participated in a pigeon hunt as a young man and calculates a rough estimate around 7.5 million birds from a nesting in Michigan in 1869. However, Martin (1915), a game dealer, strongly contradicted that account on the grounds that it would have far exceeded the shipping and storage capacity available at the time. I parameterized the commercial harvest 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 (Figure 2-1). These estimates exceed the reported total harvest range to account for the fact that estimates based on rail shipping records do not include birds that were killed but not harvested, birds that spoiled before they were shipped, and birds that were sold in local markets or shipped via waterway. For model runs that include commercial harvest, I modeled it to begin in year 1845 and run until the end of the simulation. The density-dependent shape of the commercial harvest function (Figure 2-1) allows the maximum harvest levels to decrease with declining population sizes as would be expected with a commercial market.

In comparison, it is estimated that approximately 10,000 and 30,000 band-tailed pigeons are currently harvested annually in North America (Sanders 2013). It is not clear what proportion of the total population this represents because the total population size is unknown. Making a rough calculation based on estimates of population sizes ranging from 1 to 3 million individuals (Jarvis and Passmore 1992, Sanders 2013) this is possibly 0.2 to 3.0% of the total North American population annually. On several occasions over the last century, unusually large harvests have occurred when the birds aggregated at lower elevations to take advantage of masting events. Following one of these large harvests in 1972, the population index the next year was observed to be only half as large (Jarvis and Passmore 1992).

Probability of a failed colony

Late winter storms and disturbance by man often resulted in failed nesting attempts or abandonment (Schorger 1955). It was believed that many of the birds would attempt to re-nest after a failed attempt, but it is unclear how successful these subsequent attempts were. Also unknown is the degree to which a failed attempt impacted the recruitment that year or how often these failed attempts took place. I parameterized the model to include a simulated nesting colony collapse that would result in a 70% reduction in the number of HY birds for that time step. I modeled colony collapse 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 advance of human settlement and commercial hunting activity into the main breeding range.

2.2.3 Exploring parameter uncertainty and extinction scenarios

Global sensitivity analysis

Because of uncertainty in model parameters, I conducted an extensive sensitivity analysis that fully explores the parameter space both within and across three primary anthropogenic impact factors: commercial harvest, habitat loss, and colony disturbance (probability of colony failure). I used Latin hypercube sampling (LHS; McKay et al. 1979) to generate 500 models for each of the 12 unique combinations of anthropogenic impact factors (Figure 2-2) for a total of 6,000 separate models. LHS sampling divides each parameter into equally spaced strata. Unique models are generated by randomly sampling within each parameter's strata without replacement. This sampling scheme, when used in population modeling allows a full 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). Random variables selected by LHS for each parameter were held constant across the anthropogenic impact factors (see discussion below) to directly make paired comparisons between the effects of the impact factors on model outcome while holding the rest of the parameters constant. Models were run in RAMAS Metapop (Akçakaya and Root 2007) each with 1,000 replicates to incorporate environmental and demographic stochasticity. I ran all models for 100 time steps (years) plus 20 time steps at the beginning to allow the model to calibrate (spin-up). All models started with an initial abundance of 600 million females at spin-up.

To characterize the impact of commercial harvest, I analyzed two modes; either commercial harvest was conducted or there was no commercial harvest (although background, subsistence-level harvest was modeled regardless). The functional shape of the commercial harvest for the models when it was included was determined by the LHS by randomly selecting the maximum harvest value between the upper and lower bounds and fitting the function as described in Figure 2-1.

To measure the impact of habitat I also analyzed two modes for habitat loss in the impact factor analysis; carrying capacity either decreased with increasing anthropogenic land use, or maintained a consistent average through time. In either case the carrying capacity was variable according to the simulated nomadic nesting and degree of coloniality as described above. In other words, the habitat loss factor simply determined whether the stochastic carrying capacity process had a decreasing or a flat trend.

I analyzed the impact of disturbance at the breeding colony by modeling three modes; the probability of a failed colony increasing to 0.1, 0.2, or 0.3 (low, medium, or high) after 1830.

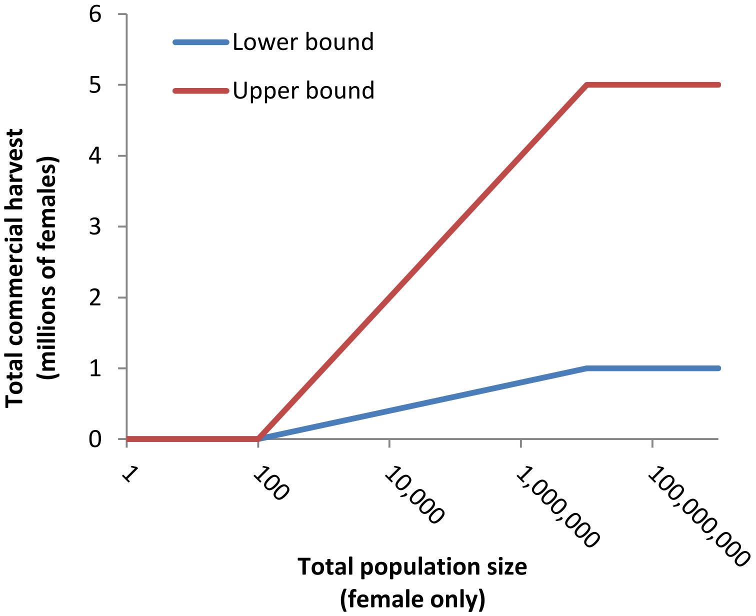

Figure 2-1 Upper and lower bound functions for commercial harvest model.

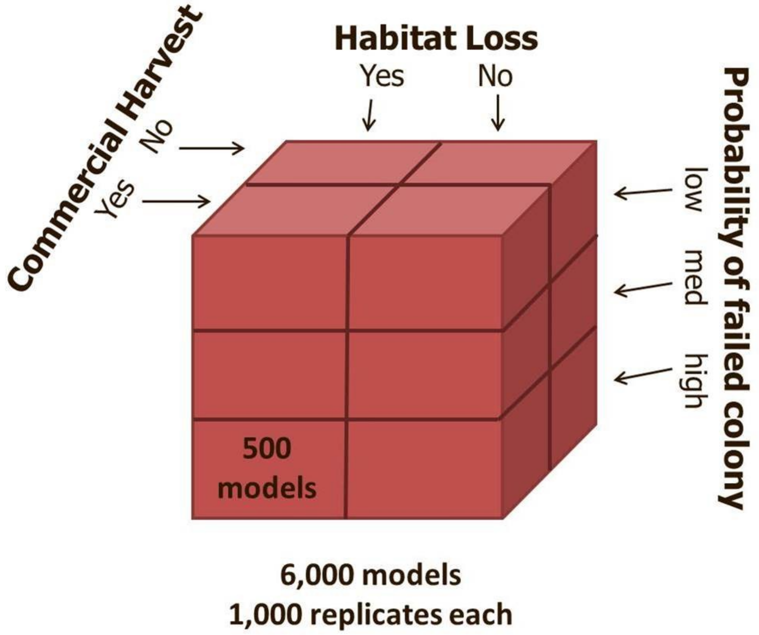

Figure 2-2 Schematic illustrating analysis structure used to explore parameter uncertainty and impact factors.

2.2.4 Analysis of factors contributing to decline and extinction

I analyzed the influence of model parameters on predicting decline and/or extinction of passenger pigeons using boosted regression trees (BRT). BRT build a succession of regression (or decision) trees in a forward fashion such that each new tree in the sequence is built from the residual deviance from the tree before (Elith et al. 2008). I implemented the BRT in R using the 'gbm' and 'dismo' packages (Hijmans et al. 2012, Ridgeway 2013). Under this implementation tree complexity (number of splits) and learning rate (maximum contribution of each tree) are controlled by the user (Elith et al. 2008, Elith and Leathwick 2013). Here, I allowed a tree complexity of 3 and tuned the learning rate such that at least 1,000 trees were created.

I focused on two simulation results as response variables: (1) expected minimum abundance; and (2) probability of decline to a quasi-extinction threshold of 1,000 females at any point before the end of the simulation. 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. I specified a Gaussian distribution for the residuals of this parameter in the BRT analysis.

Probability of decline to 1,000 is a way to measure whether the simulations approach extinction-risk levels before the end of the simulation. I chose a threshold of 1,000 females for two reasons. First, 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 (Schorger 1955, Jovani and Grimm 2008) it is likely that there would have been Allee effects as the population declined (Halliday 1980, Reed 1999, Stephens and Sutherland 1999, Cook and Toft 2005). However, there are no data available to parameterize this within the model. In this instance a threshold at 1,000 females can be regarded as a de-facto extinction. Probability of decline to 1,000 is expressed in the BRT 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), I specified a Poisson distribution of the residuals in the BRT analysis.

I selected 6 predictor variables in the BRT models to explore the effects of parameter uncertainty and the impact of anthropogenic factors. (1) Maximum growth rate (Rmax), which determines the shape of the density dependence curve and the rate of population increase when population levels are far below carrying capacity. (2) Generation time (GT), which is determined by the matrix of survival and fecundity values. (3) Coefficient of variation of total population size over the first 10 years after model spin-up (CV10). Variation in this parameter across models is due largely to the effect of colonial nesting and the degree of coloniality in the population. I use it here because it is correlated with, but more informative than, degree of coloniality. (4) Habitat loss (HL), which is included in the model as a categorical variable. (5) Maximum commercial harvest (CH), which is the maximum harvest level selected by the LHS (see Figure 2-1 and description above). For models without commercial harvest this parameter is zero in the analysis because it is ignored by RAMAS Metapop. (6) Probability of colony failure (Pfail), which is a categorical variable corresponding to probability levels of 0.1, 0.2, or 0.3.

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

2.3 RESULTS

2.3.1 Available habitat through time

The breeding range habitat suitability without anthropogenic disturbance is shown in Figure 2-3. Model fit AUC was 0.897 on the training set and 0.947 on the testing set. Accounting for habitat loss through time by subtracting the area estimated to be in crops or pasture resulted in a 52.8% decrease in the total summed habitat suitability between 1800 and 1900 across the breeding range. A sample of maps illustrating the pattern of habitat loss is shown in Figure 2-4.

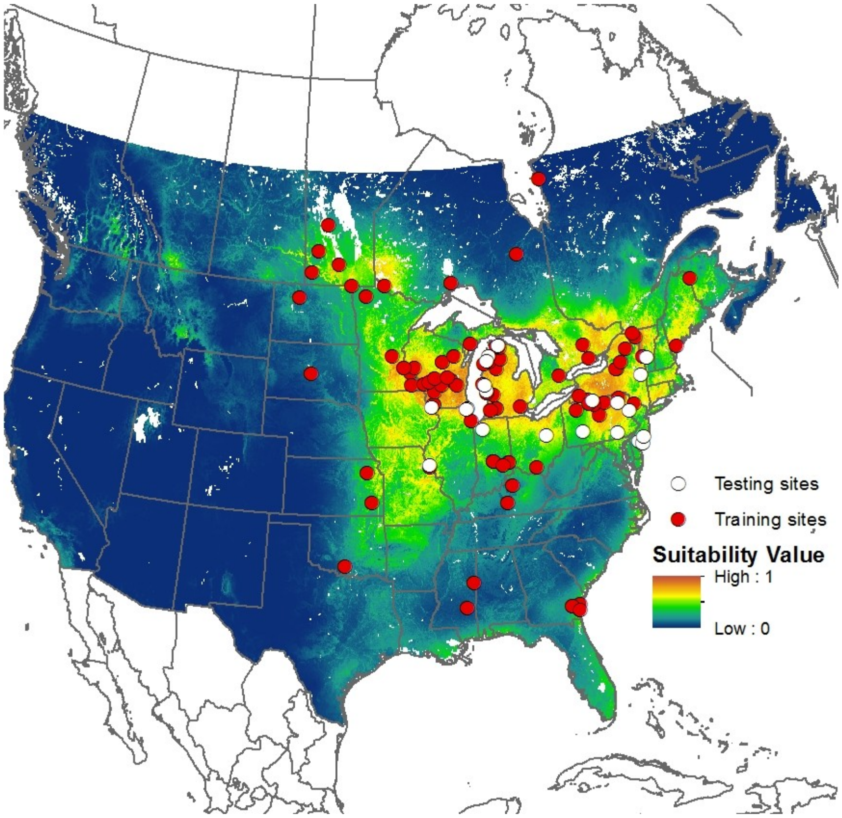

Figure 2-3 Modeled breeding habitat of passenger pigeon prior to anthropogenic land use changes.

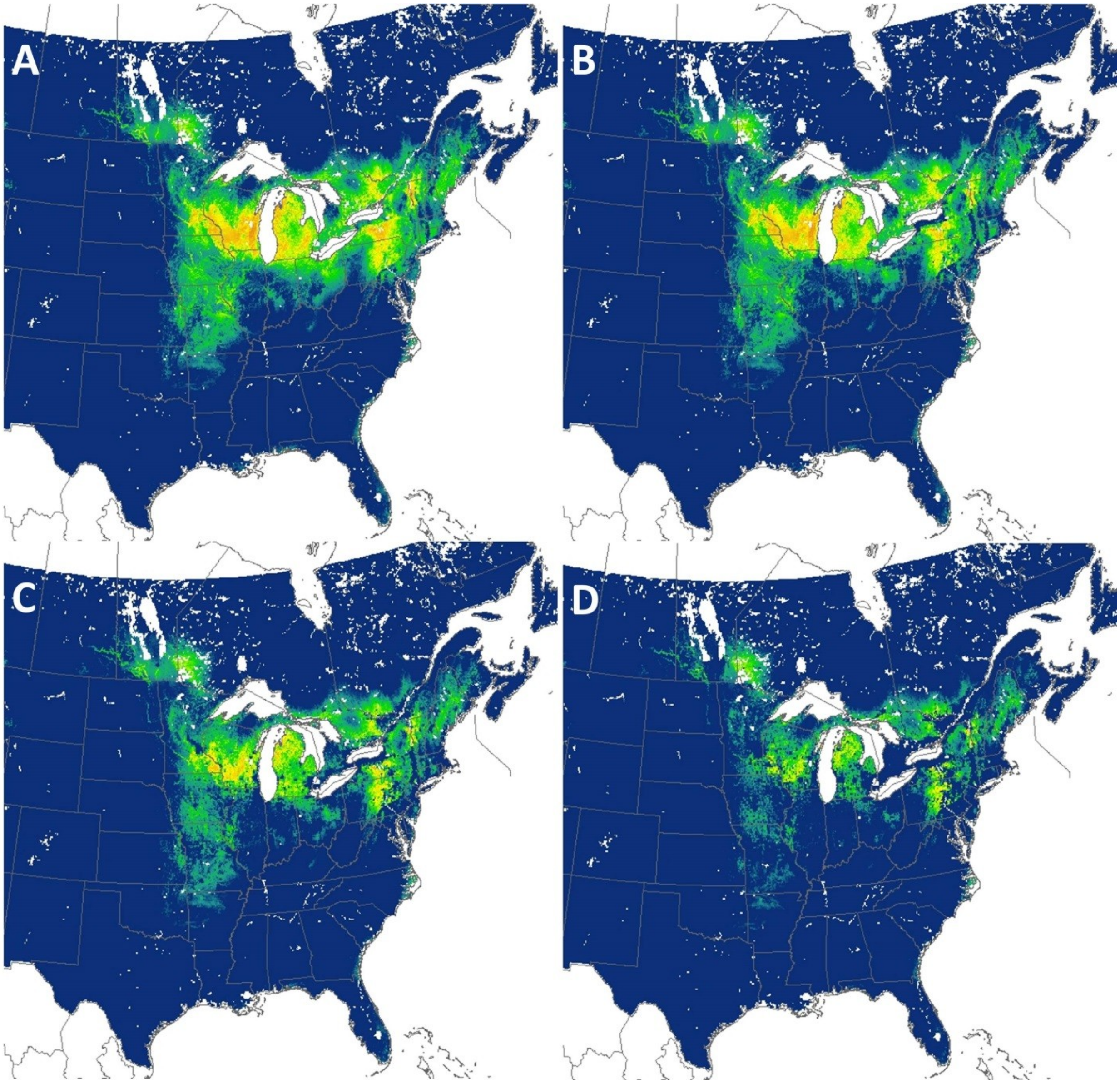

Figure 2-4 Available breeding habitat at four selected time steps; 1810 (A), 1840 (B), 1870 (C), and 1900 (D). Warmer colors indicate higher suitability.

2.3.2 Analysis of decline and extinction

Predictably, increasing the number and severity of anthropogenic threats resulted in greater expected population declines. Habitat loss had the single largest effect on decreasing the expected minimum abundance, calculated as the mean minimum abundance achieved across all 1,000 replicates of a model (Figure 2-5). Paired comparisons of models across threat factors with all other variables held constant allowed for directly measuring the impact of each threat factor without confounding variance due to random sampling in parameter space. In direct paired comparisons, including habitat loss in the model resulted in a 38.3 ± 0.1% (standard error) decrease in expected minimum abundance. Commercial harvest decreased expected minimum abundance by 17.7 ± 0.3%. Going from a low probability of colony failure (0.1 after 1830) to a high probability (0.3) results decreases the expected minimum abundance by 34.4 ± 0.4%.

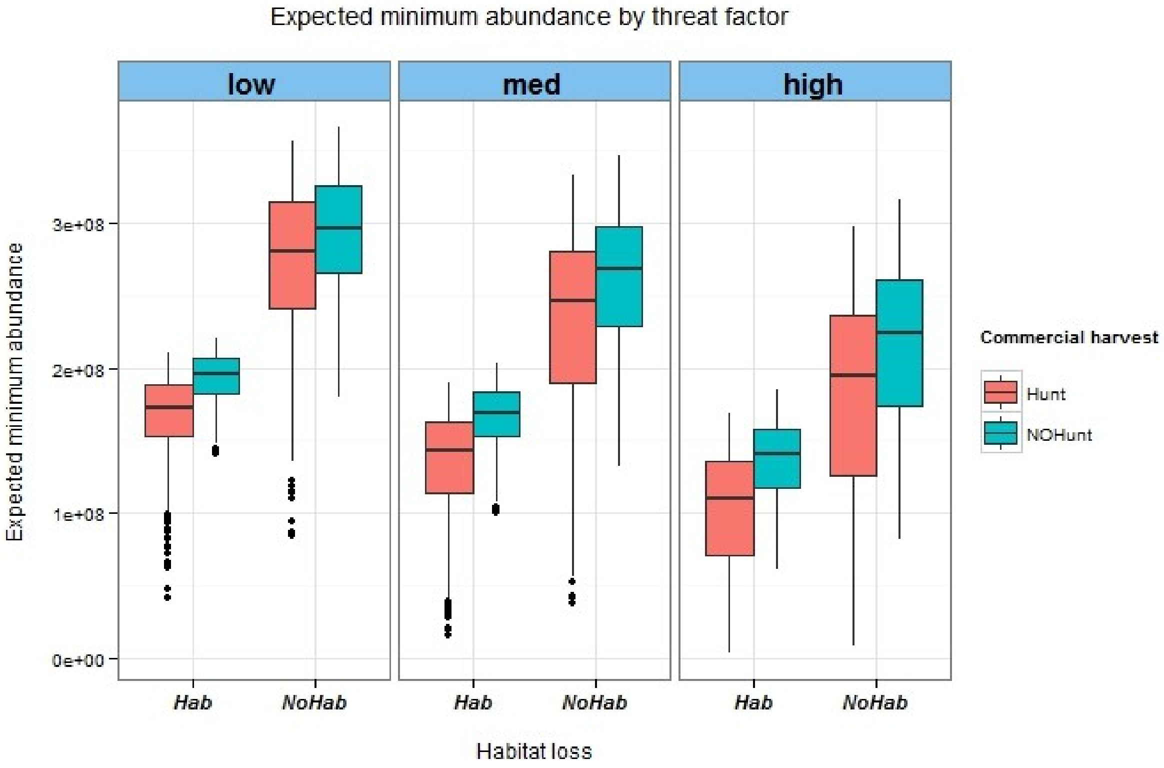

Figure 2-5 Distribution of expected minimum abundance values for the model sets under each anthropogenic threat factor combination. Expected minimum abundance is calculated as the mean minimum abundance achieved across model replicates. Panels 'low', 'med', and 'high' refer to probabilities of colony failure of 0.1, 0.2, and 0.3 per year, respectively. Commercial harvest categories refer to models that included a commercial harvest at some level ('Hunt') or no commercial harvest ('NOHunt'). Habitat loss categories refer to models with a declining trend in carrying capacity due to land use change ('Hab') or a constant average carrying capacity through the duration of the model ('NoHab').

The most important variable predicting expected minimum abundance in the boosted regression tree analysis was 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. BRT 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.

Probability of the population falling below 1,000 females was most sensitive to the presence of a commercial harvest. Only models which included a commercial harvest resulted in probabilities greater than zero. The mean probability of falling to 1,000 females over all the models including a commercial harvest was only 0.01 (range 0 to 0.67). Figure 2-6 shows the probability of falling below 1,000 individuals for all models with a commercial harvest. The probability of crossing this threshold increased with increasing probability of nest failure, but was only slightly positively influenced by the effect of habitat loss in the model.

To analyze the boosted regression tree model for the probability of falling to 1,000 females I only included the 467 models that achieved this threshold in at least one replicate. I limited the analysis in this way to more effectively explore the parameter space where this phenomenon occurred. In essence, I drilled down to the collection of models of the most interest in terms of determining which variables were important to reconstruct 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 at 1.2%. The strongest interaction terms were CH vs. Rmax and CH vs.

CV10 (Figure 2-7). Model fit assessed through the 10-fold cross validation had a mean DE across folds of 0.89.

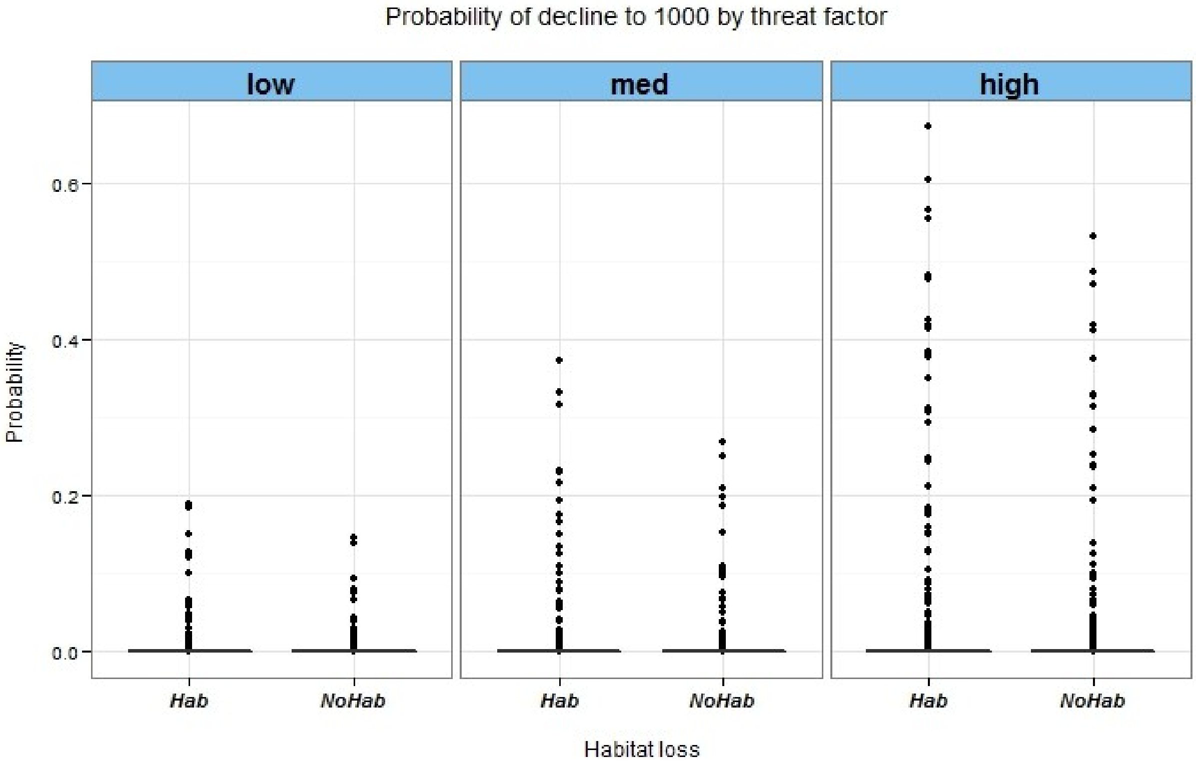

Figure 2-6 Probability of decline to 1,000 females for models with commercial harvest (all models without commercial harvest have probability values of zero). Panels 'low', 'med', and 'high' refer to probabilities of colony failure of 0.1, 0.2, and 0.3 per year, respectively.

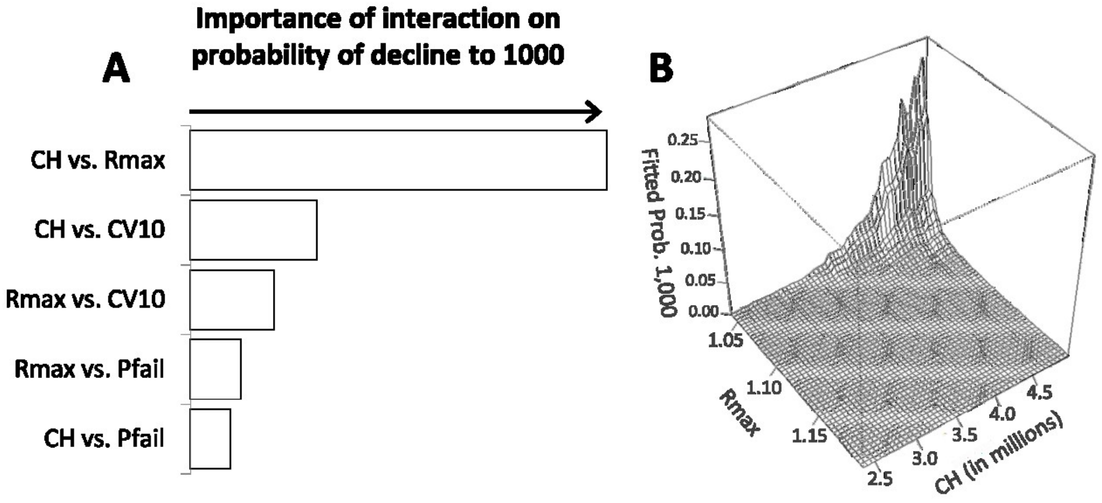

Figure 2-7 Interactions of variables predicting probability of decline to 1,000. (A) Relative importance of interaction terms, and (B) modeled response surface for interaction between maximum commercial harvest and maximum growth rate. Variables are maximum commercial harvest (CH), maximum population growth rate (Rmax), coefficient of Coefficient of variation in total population size over the first 10 years (CV10), and probability of colony failure (Pfail).

2.4 DISCUSSION

The results of this model indicate that 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 (2 million females in female-only model) and showed a strong positive relationship with increasing maximum harvest levels. 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 BRT 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. All of the models had expected minimum abundances much less than the initial abundance even in cases of no habitat loss. In the model this was primarily because of the year to year fluctuations in carrying capacity driven by the simulated mast and colonial nesting. The degree to which the expected minimum abundance was pushed downward was heavily influenced by the decrease in carrying capacity from habitat loss. However, this predictable level of overall decrease in population size did not necessarily drive the population to threshold-level (i.e. pseudo-extinction) declines within the timeframe of the model.

It is important to note that the duration of the model ended when the population was thought to have become extinct in the wild. It is conceivable that had the simulation run longer and continued to accumulate the effect of land conversion throughout this portion of the North American continent, habitat loss alone might have depressed the carrying capacity to the point where it might have become an important predictor of threshold-level declines. Forest loss in this region continued to outpace regeneration for several decades into the 20th century (Whitney 1996). Further, the mature beech trees on which this species depended are slow-growing shade-tolerant species that tend to only dominate in undisturbed old-growth forests. Even today, with much of the formerly-forested area in the Northeast and Midwestern United States returning once again to forest cover (Ramankutty et al. 2010); it is unlikely that the age and composition of these second-growth forest could provide much suitable habitat for large passenger pigeon colonies. In essence, although the model I presented does not indicate that habitat loss was a key driver on the time-scale of the observed extinction event, it is likely it would have become more problematic for the species eventually.

An important caveat to the issue of habitat loss is the fact that the model I constructed only included land conversion for settlement (crop and pasture) and did not account for the commercial timber harvest. Unfortunately, including this factor in the habitat loss model was beyond the scope of this study. Tackling a wide-ranging and detailed reconstruction of deforestation in North America, including the effects of commercial timber harvest is an important but exceedingly difficult undertaking. The different physical properties of each commercially harvested tree species meant they had different uses, market demand, and transportation systems (Boucher et al. 2009). Further, these factors changed and evolved throughout the 19th century as advances and innovations were made in transportation and technology. Timber was inexorably linked with a complex history of domestic and geopolitical economics driving demand for building supplies, ship masts, railroad ties, and fuel (Williams 1992, Whitney 1996). Timber in 18th and 19th century North America was a burgeoning and largely unregulated industry, and records which might have been used to reconstruct maps of cleared land are inconsistent or nonexistent for most areas in North America. There are additional challenges even in establishing accurate pre-settlement forest cover maps to use as a baseline. Reconstructions based on the original land surveys are fraught with challenges such as erroneous (and sometimes fraudulent) survey coordinates, misidentification of bearing and witness trees, and reconciling a patchwork of different agencies conducting surveys at different times using different approaches (Bourdo 1956, Waisanen and Bliss 2002, Wang 2005). Despite these challenges, there have been some notable attempts although they usually are conducted at either restricted spatial extents (Foster and O'Keefe 2000, Schulte et al. 2005, He et al. 2007, Rhemtulla et al. 2009, Boucher et al. 2009, Dupuis et al. 2011) or coarse spatial resolutions (Ramankutty and Foley 1999, Houghton and Hackler 2000, Steyaert and Knox 2008). If ever a reliable, detailed, and spatially-explicit reconstruction of deforestation including commercial timber harvest was made available, it would be worthwhile to revisit the conclusions of this study at that time.

In summary, only a narrow set of parameter values results in population trajectories from billions of individuals to extinction in less than a century, as was observed for this species. 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. Despite the fact that the shipping and storage capacity at the time was inadequate to handle this level of harvest, it was noted that there was very high levels of waste involved in this industry (Hornaday 1913, Schorger 1955). Young birds were often taken before they reached marketable size and were left on the ground. Birds that were improperly dressed or treated would spoil before they could be packed and shipped. While the harvest estimates based on rail shipments made at the time were imprecise and uncertain, it is possible that the harvest activity might have resulted in total mortality 2 to 10 times greater because of waste and improper handling.

This case study demonstrates the role of a weakly regulated commercial harvest in the extinction of the passenger pigeon, and illustrates the importance of data collection and monitoring of any harvested species. It is vitally important to have accurate estimates of total harvest including all avenues for mortality; commercial harvest, non-commercial harvest, as well as incidental takes and waste (such as bycatch). In addition, it is essential to have an accurate understanding of the underlying population dynamics of commercially important species and to use the proper model structures to characterize the systems. The conservation biologist assessing extinction risk and the resource manager setting catch limits may approach the same population with very different model structures and assumptions. Some traditional models of open access harvest do not allow for extinction as a possible outcome (Conrad 2005), do not consider the possibility of critical inflection points such as Allee thresholds (Reed 1999), or assume that market forces will ease hunting pressures sufficiently as populations decline (Halliday 1980). The collapse of any commercially managed or natural population resulting from over-harvest is cause for alarm and should be avoided; few would contest this point. The disagreement arises over the most appropriate way to avoid situations where population collapse or extinction becomes inevitable or very expensive to prevent. Many who participated in the harvest of passenger pigeons later lamented the role they played in causing their extinction, but at the time justified their activity because of mistaken notions about biology and the impact of their activities.

3 Red-listing analysis of the passenger pigeon

3.1 INTRODUCTION

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 is especially true when species are economically important or when protection of key habitat would hamper other economic activities. This is not meant as a cynical observation but is a consequence of the need of policy makers to balance multiple societal demands and a desire to avoid 'false alarms' where economic activity is curtailed for the protection of species when they are not actually imperiled. Therefore, it is important to evaluate not only how well extinction risk metrics perform at providing an early-warning system for identifying species in need of conservation intervention (avoiding 'missed opportunities'), but also how accurately the risk rankings translate to how imminent the threat is (avoiding 'false alarms').

Measuring the rate of 'missed opportunities' involves identifying species evaluated against the criteria, deemed not imperiled, but go extinct nonetheless. 'False alarms' are species identified as being on the verge of extinction, yet remain extant or recover on their own. This kind of objective evaluation is difficult because identifying a species as imperiled often (and rightly) brings conservation action which can change the trajectory the species was on. Since the goal of conservation actions would be to halt downward trajectories of imperiled species, a failure to go extinct as predicted is usually attributed to conservation actions (Hoffmann et al. 2010) rather than low specificity of the risk-assessment test.

Any test for which the false positive rate is difficult to evaluate runs the risk of being perceived as overly sensitive or overly precautionary. After all, if a test evaluates most species as being imperiled there will be no 'missed opportunities' (true positive rate is 100%). Substantial economic costs either directly (i.e. habitat restoration, monitoring, or captive rearing programs) or indirectly due to lost opportunity costs for activities (i.e. resource extraction, development, recreation) that might halt when species are listed as imperiled, will bring extra scrutiny. This is especially true when the criteria for which the species is listed is based primarily on past trends or predicted future trends and at present the species is still relatively abundant and extinction is not perceived as being an imminent threat. 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 (Punt 2000, Hutchings 2001, Hutchings and Reynolds 2004, Dulvy et al. 2005, Godfrey and Godley 2008). 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 (US Fish and Wildlife Service 2006).

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 1970's (Scott et al. 1987) and 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 (Mace et al. 2008, IUCN 2012). One approach that has been used to evaluate how well the IUCN Red List criteria assess extinction risk is to look for agreement between Red List categories and independent evaluations of population health. Dulvy et al. (2005) compared Red List status of harvested marine fisheries to the International Counsel on the Exploration of the Sea (ICES) evaluations of safe exploitation levels. They did not find any 'false alarms' where Red List criteria indicated a species was imperiled but ICES evaluated the harvest levels as safe (Dulvy et al. 2005). Hutchings & Reynolds (2004) found that Red List criteria based on observed percent declines are good indicators of ability for marine fish populations to recover if not probability of extinction, even when total abundances might still be high. Harris et al. (2012) found general agreement between the species listed under the United States Endangered Species Act (ESA) and IUCN Red List, although the ESA was generally found to be less precautionary. Species listed as vulnerable under IUCN were less likely to also be listed under ESA than species classified as endangered or critically endangered (Harris et al. 2012).

Another approach that can be used to evaluate rule-based risk assessment measures is by applying them retrospectively to populations for which the trajectory and fate is known. Keith et al. (2004) used this approach by comparing assessments of extinct and extant species pairs. Here I use simulated trajectories modeled after a recent extinction event and apply IUCN Red List criteria to trajectories that either resulted in extinction or remain extant by the end of the simulation. I used simulated population trajectories for a model based on the passenger pigeon (*Ecotopistes migratorius*) extinction in North America in the nineteenth century. I chose this species as a case study because it showed marked population declines but was reportedly still relatively abundant up to within a decade or two of its believed extinction in the wild (Schorger 1955). This species is also a relevant case study in this context because little was done in terms of management or conservation which might have impacted the trajectory. Therefore the trajectories can be examined for 'false alarms' without the confounding factor of recovery resulting from conservation actions.

In order 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. This kind of metric provides an estimate of how much time is available for mobilizing conservation action. Here, I also examine each trajectory in terms of when it is first recognized as imperiled and how long it spends in each category.

3.2 METHODS

3.2.1 Hindcast annual IUCN Red List assessment

I applied IUCN Red List criteria separately each time step to individual stochastic replicate model runs from stage-based matrix population models of passenger pigeon. 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).

The models analyzed here are described in Chapter 1. I treated each trajectory generated from the model as a possible realized truth. In other words, I regarded population numbers from each stochastically generated population trajectory as if they were field data collected without measurement error. I conducted this analysis 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. To avoid circularity, I did not consider any Red List criteria involving forecasts of future population trajectories or future risk analysis such as criteria A3, A4 or E.

I also did not consider 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 are still too large to trigger the thresholds for listing under criteria B or D2.

I analyzed the raw output of 467 separate models from RAMAS Metapop (Akçakaya and Root 2007). The models chosen for this analysis were the 467 out of 6000 possible passenger pigeon models that resulted in at least one replicate falling below a threshold of 1000. The models were developed to explore the parameter space and possible factors leading to the extinction of the passenger pigeon (see Chapter 1). The models used in this analysis all included a simulated commercial harvest beginning in the model year 1845 and continuing until the end of the simulation in 1900. The simulated harvest increased with population to a maximum harvest level between 1 and 5 million birds. Each model was run with 1000 replicates.

I analyzed this subset of models because I was interested in determining the amount of time that conservation workers of the day would have had to enact conservation actions had a diagnostic tool such as the Red List been available. Model trajectories that do not result in, or even approach, extinction are not representative of the actual trajectory of the population which is known to have been extinct in the wild before 1900.

To simulate Red List assessment of each trajectory, I used the "raw output" option of RAMAS Metapop, which gives the simulated population numbers for each time step of each replicate, instead of the results displayed by the program's user interface, which are summarized over replicates. The raw output also partitions the population data based on age or stage class and individual subpopulations if the model is structured as a Metapopulation. Therefore the raw output can be treated as if they were annually repeated full-population census data with each replicate being a possible time-series of such data.

I implemented the analysis in R (ver.3.0.0, R Core Team 2013) by coding a rule set based on the current IUCN Red List criteria rules and guidelines (IUCN 2012). The R script I developed for this purpose (see Appendix) reads the raw output for each replicate and calculates the Red List category (and the criteria that triggered the category) for each time step based on the information up to and including that time step (see details below). This R script also uses R functions for reading in results and model parameters from RAMAS Metapop (developed by M. Aiello-Lammens).

By applying the Red List criteria separately for each time step and each replicate I was able to track each population trajectory as it progressed through the threat categories towards extinction. I smoothed the results by giving each Red List category a numerical score and calculating a 5-year moving window average. I implemented this smoothing 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. I also ignored 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). This makes the simulated assessments more realistic, because most taxa are assessed for the IUCN Red List at 4 to 10 year intervals. All models include a 20 year spin-up period for model calibration which I excluded from the Red List analysis.

I recorded 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. I analyzed trajectories ending in extinction 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.

3.2.2 Calculation of Red List criteria

Criterion A

IUCN Red Listing under criterion A is met when there are substantial reductions in population size. Red List guidelines stipulate that these reductions should be independent of inter-annual variation or fluctuations (Red List guidelines). Criterion A1 is met when the cause of the reduction is known, reversible, and has ceased. In the case of passenger pigeon, the causes for the population reductions were driven by habitat loss and harvesting, neither of which ceased before extinction. Therefore, I did not consider criterion A1 in this study.

Criterion A2 is met when the cause of the reduction is either unknown, non-reversible, or ongoing. The criterion stipulates that the reduction is calculated over the past three generations or 10 years whichever is longer and can be based on direct observation of abundance, an appropriate index measure of abundance, decline in spatial measures (extent of occurrence, area of occupancy, or habitat quality), actual or potential harvest levels, or inferred population declines because of invasive species, hybridization, pathogens, pollutants, competitors, or parasites. Observed reductions of 80%, 50%, or 30% would qualify the species for classification as critically endangered (CR), endangered (EN), or vulnerable (VU), respectively. Classification as near threatened (NT) is less strictly prescribed, but observed population reductions of greater than 20%, but less than 30% would qualify the species for that status.

I determined if criterion A2 was met by calculating the slope of a linear function of the natural log of the number of mature individuals at each time step. The population trend each year was calculated for the timeframe of the 3 previous generations utilizing a moving window function. Generation time is calculated from the stage matrix and ranges from 5.1 to 6.5 years (see Chapter 1). I treated the population trend, or slope of the curve, as the observed population growth rate, *r*, and transformed this into percent reduction calculation using the formula 100-e^{rt} *100, where *t* is 3x generation time. I applied the thresholds described above for determining classification as CR, EN and VU. I used a threshold of 20% decline for classification as NT. Classification under criteria A3 or A4 both involve projections to future population trends and I therefore did not consider them for this analysis as discussed above.

Criterion C

IUCN Red Listing under criterion C can occur when the total population size is small and is coupled with observed declines. Population sizes of less than 250, 2,500, or 10,000 mature individuals would qualify the species as CR, EN, or VU, respectively, when the species is also experiencing a continuing decline. Each threat level has a specified severity of this continuing decline specified as 25% over 3 years or 1 generation for classification as CR; 20% in 5 years or 2 generations for EN; or 10% in 10 years or 3 generations for VU. Alternatively, declines of any level if also accompanied by extreme population fluctuations or a risk-prone distribution of individuals in sub-populations may also qualify the species to be listed as threatened under criterion C. To qualify as NT under Red List guidelines the species should be very near the thresholds described for listing as VU (IUCN Red List guidelines).

To determine if criterion C was met, I checked the number of mature individuals against the thresholds above, then determined if any of the sub-criteria were met. I defined extreme fluctuations for this criterion as the ratio between the maximum and minimum number of mature adults over the past 2 generations being greater than 10. It should be noted that under criterion C, continuing declines of any level, if coupled with risk-prone metapopulation structure (such as 95% or more of all mature individuals in a single sub-population), would qualify the species for listing if the thresholds for low abundance were met. In the case of this model of passenger pigeon, since it was modeled as a single panmictic population, any negative population trend by default would meet this sub-criterion. I defined the NT classification under criterion C as being met if the population size was estimated to be fewer than 15,000 mature individuals and declines were as described above for VU.

Criterion D

Species achieve threatened status under criterion D when population sizes are very small. The criterion for CR is met when the population falls to 50 or fewer mature individuals. Criterion for EN is met when the population falls to 250 individuals. Classification of VU under criterion D is met when either the population falls to 1,000 individuals or either of the following conditions are met: 1) the occupied area is less than 20km^2 or 2) there are 5 or fewer locations. Because the definition of location depends on the spatial distribution of threats, and such information is not available from simulation results, I only considered the population level thresholds for criterion D and ignored the spatial criteria under VU D2. I considered criterion D met for NT if the number of mature individuals fell to 1,500 individuals.

3.3 RESULTS

Out of the 467,000 model replicates (467 models with 1,000 replicates each) 21,297 result in extinction before the end of the simulation. Of these extinction replicates, the majority are 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) rises sharply with the onset of the simulated commercial harvest. By 1855, 10 years after the onset of the commercial harvest, more than 90% of replications are classified as threatened (Figure 3-1). The mean extinction year is 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 CR. On average 23 years were spent listed in the CR category, 12 years in EN, and 4 years in VU (Figures 3-2 and 3-3).

Trajectories that do not end in extinction show lower proportions of threatened status overall throughout the simulation compared with replications that end in extinction. Non-extinction trajectories show 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 are classified as non-threatened after this point. Relatively few trajectories are classified as CR even toward the end of the simulation (Figure 3-1).

In almost all cases, the listings were driven by meeting criterion A2 at the highest level. In 50 replicates, criterion C was also met briefly at the CR level. However, it should be noted that IUCN Red List criteria stipulate that the highest threat level achieved for any criterion determines the listing category. For example if criterion A2 was met at a CR level and criterion C or D was also met, but at a lower threat level (EN or VU) for a given time step, only the CR due to A2 was recorded as the threat classification.

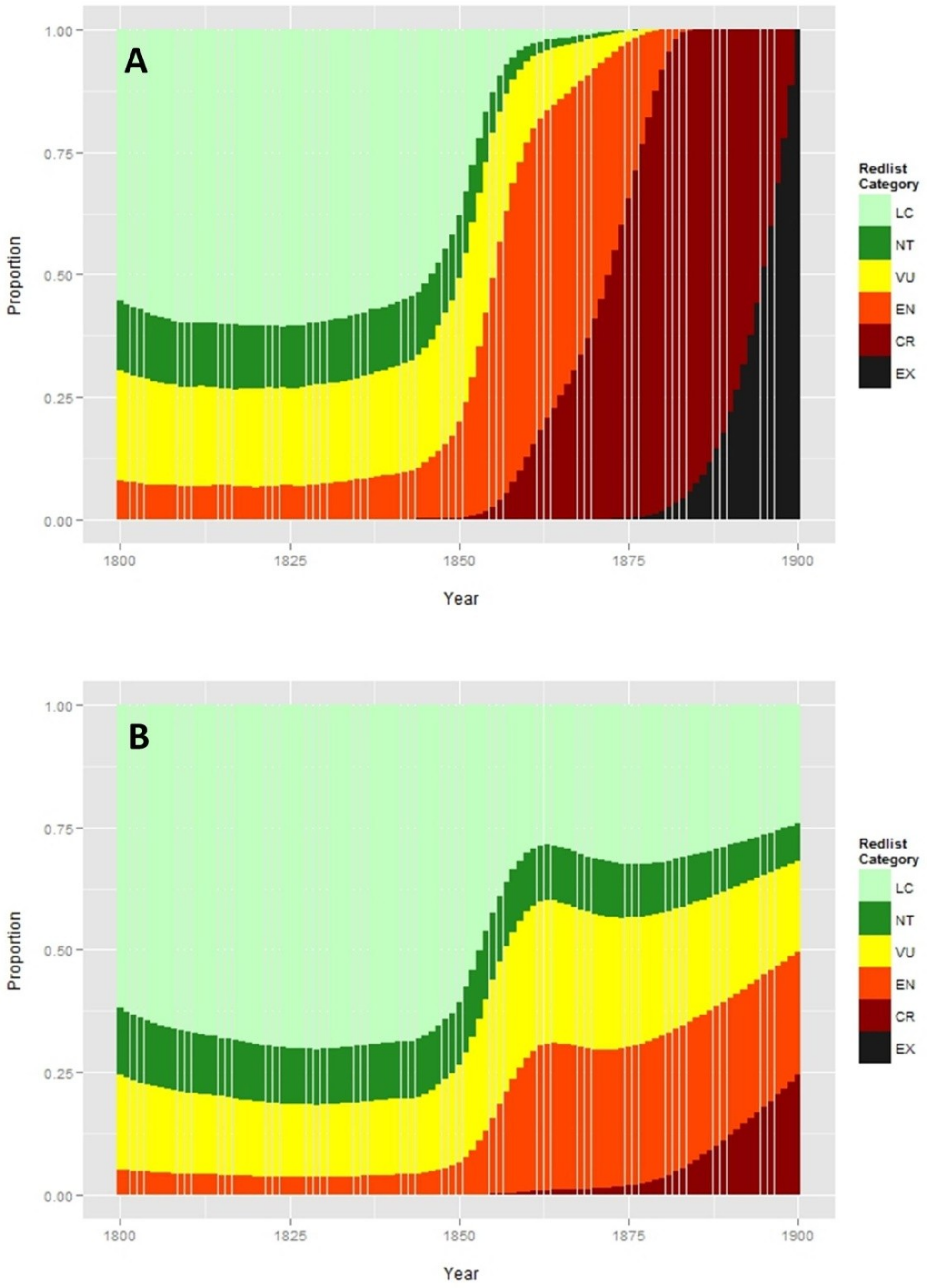

Figure 3-1 Proportion of replicates listed under IUCN Red List criteria each time step. A) replicates resulting in extinction and B) replicates without extinction

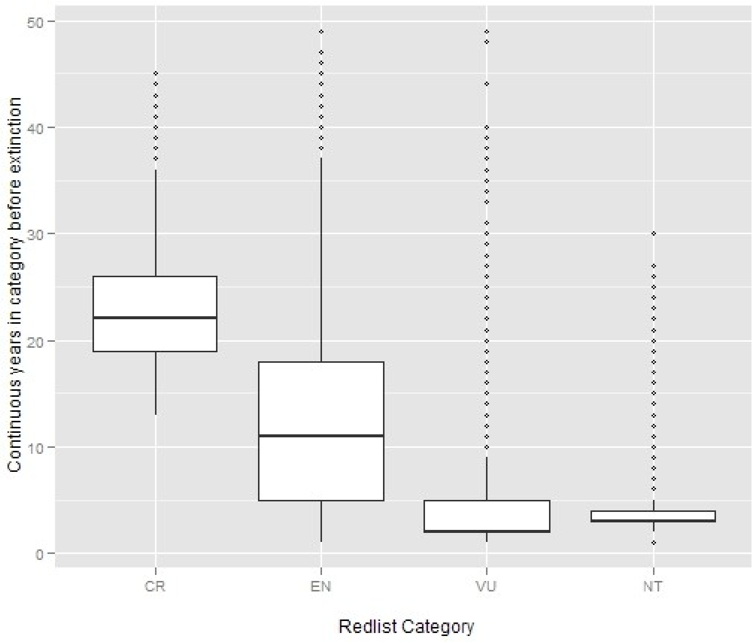

Figure 3-2 Number of years spent in each IUCN Red List category prior to extinction.

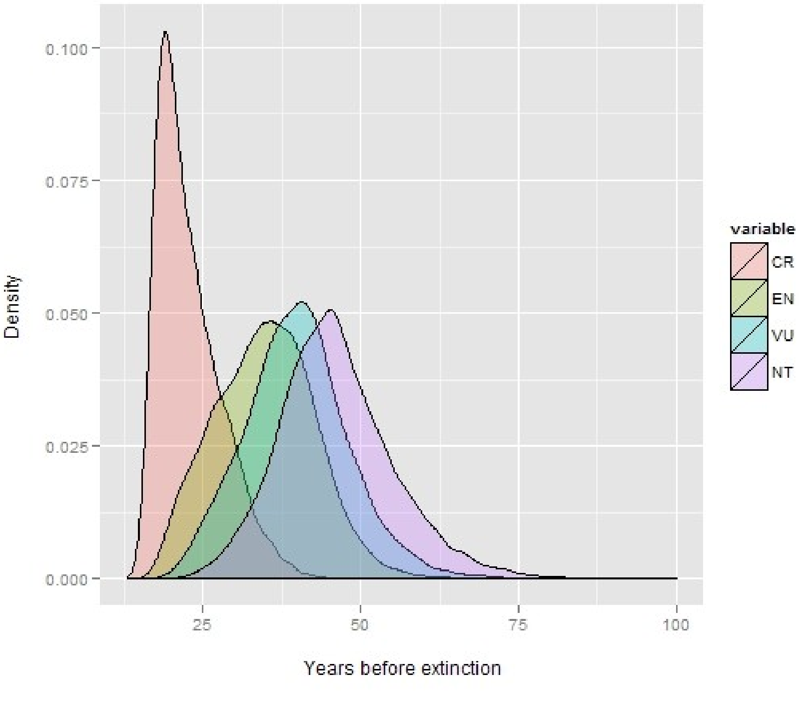

Figure 3-3 Frequency distributions of the number of years before extinction that trajectories first enter each IUCN Red List category. For example, trajectories that eventually went extinct were typically classified as VU for the first time about 40 years before extinction.

3.4 DISCUSSION

The results of this study highlight the essential roles that population monitoring and risk assessment play 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 reversing the extinction-bound trajectory. There were some who were sounding the alarms over the rate that the species was declining. Not co-incidentally, this was likely around the same time the species would have qualified as threatened under Red List criteria. Protection laws were passed by various states in the 1870's and 1880's 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.

If the extinction trajectories presented here are an accurate re-enactment of this extinction event, they demonstrate how the misperception that declining but still abundant species are at very low risk of extinction can lead to unintended consequences. Without accurate data collection and analysis of population trends through time, 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. Criterion C, small population size accompanied by continuing decline, is probably the criterion that is most accessible and easily perceivable to a general population where most observations of wildlife are casual. In this study, criterion C was only met rarely and the vast majority of listing criteria was met under criterion A2 (high rate of continued population decline). Without any data collection and analysis of abundance trends through time, the rate of decline was possibly not perceivable to the casual observer and therefore the true risk of extinction though most of the second half of the 18th century would have been obscured. The multiple criteria of the IUCN Red List allows different avenues for risk assessment. This fact might have been crucial for the passenger pigeon had it been available as a conservation tool in the 19th century. Different species might take different trajectories toward extinction and therefore should be assessed against as many criteria as possible.

All of the trajectories that resulted in quasi-extinction before the end of the simulation listed the species as imperiled under the Red List criteria (Figure 3-1A), meaning that there were no ‘missed opportunities’ or false negatives. Of the trajectories that do not reach the quasi-extinction threshold before the end of the simulation (Figure 3-1B), some proportion nonetheless are categorized as threatened at each time step. These can be thought of as being ‘false alarms’ or false positives. However, it should be kept in mind that those trajectories which did not reach quasi-extinction shared the same model parameters as those that did (only models that had at least one trajectory reaching quasi-extinction were included in this analysis). All were on declining trajectories; they just did not decline to the threshold before the end of the simulation. Looking at the trajectories prior to the onset of commercial harvest in the mid-1800’s when most of the habitat was still intact (see Chapter 1) gives a more accurate sense of the rate of ‘false alarms’ in the models. During this timeframe, random fluctuations primarily because of the species’ reliance on ephemeral food resources (tree mast) would occasionally result in multiple years of poor reproduction resulting in declining population trends. Approximately 1/3 of the time these trajectories met the criteria for ranking as VU or EN despite extinction not being imminent. However the overall patterns show a good discrimination between trajectories that did or did not result in quasi-extinction (Figure 3-1).

An important caveat to this study is that in real population studies it is very rarely possible to measure the true population size without error as I have assumed for the simulations I present here. Most population trend data are collected with various forms of measurement error that can obscure true population size. However, it is unlikely that measurement error will have much impact on estimates of population trends through time (Meir and Fagan 2000). If measurement error or missing data is of concern several different approaches are available to account for poor data problems (Holmes 2001, 2004, Holmes et al. 2012).

Had the appropriate data been collected and the appropriate analysis been conducted to recognize the threat level, this study suggests that there could have been several decades in which to enact appropriate conservation measures. For species threatened by agricultural activities and hunting, formal recognition of threat status (such as through Red Listing) can result in improvement in the status (Hayward 2011). Presumably this is possible because conservation measures and changes in legislation can relieve these types of threats more quickly than more diffuse or chronic threats such as hard infrastructure encroachment, invasive species or climate change. In an analysis of 37 mammal species that showed improved status between subsequent Red List assessments (Vié et al. 2009) more than half of the implemented conservation actions included hunting restrictions (Butchart et al. 2006, Hayward 2011). It is important to note that all of the simulations presented in this study included some level of commercial harvest, yet only a relatively small proportion of the replicates resulted in either CR threat status or extinction. The probability of the population declining to extremely low abundances is predicted by the highest levels of maximum commercial harvest (see Chapter 1). This suggests that commercial hunting *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 that there would have been room to increase the efficiency of the commercial harvest with minimal impact to those with financial interests.

It is impossible to know if enforcing regulations on the exploitation of passenger pigeons would have been enough to entirely prevent this extinction event. In addition to the mortality caused by hunting, the species was impacted by tremendous changes to the forested landscape. Total carrying capacity between 1800 and 1900 was possibly reduced by half because of land conversion related to pioneer settlement alone (see Chapter 1). This deforestation continued well into the 20th century. Even today, as much of that forest cover has regenerated throughout the Northeast and portions of the Midwestern United States, these second growth forests bear little resemblance to the late-successional deciduous and mixed-deciduous forests that passenger pigeons relied on (Whitney 1996). Had the crisis of over-harvest been averted, crisis levels of habitat-loss were still likely just a few years down the road for this species. The passenger pigeon went extinct in the wild around the same time that federal management and oversight of forested lands were first established under the Forest Reserve Act of 1891 (Williams 2000) . Whether or not the species would have been able to persist into the 20th century as smaller flocks in a disturbed and fragmented landscape is purely speculation. What can be said with some degree of certainty is that recognizing that a species is at risk of extinction is a crucial first step toward averting that outcome.

4 Extinction risk assessment and Red-listing of species threatened with climate change

4.1 INTRODUCTION

IUCN Red List criteria has been shown to work well for identifying the current compendium of factors threatening species today (Hutchings and Reynolds 2004, Keith et al. 2004, Dulvy et al. 2005, Hayward 2011, Harris et al. 2012) and provides ample warning for action (Chapter 2) even if recognition of threat status doesn't always halt deterioration of populations (Butchart et al. 2004). The Red List has also proven to be a useful tool in tracking the status of global biodiversity (Hoffmann et al. 2010) and the effectiveness of conservation action (Butchart et al. 2006, Rodrigues 2006).

Although the IUCN Red List has proven to be a highly useful conservation tool for a number of threats encountered by species today, it has been suggested that the criteria as they stand may not provide sufficient warning to protect species impacted by 'slow acting and persistent' threats such as global climate change (Thomas et al. 2004). Red List threat classifications are made on the basis of either recent data indicating the species is already headed toward extinction (criteria A – D) or evidence that projects a high risk of extinction in the near future (criterion E). The concern is that climate change may already be impacting species, but so gradually that waiting until observable signs of decline are evident may prove to be too late to take conservation action (Hannah 2011). The implication is that the horizons over which the IUCN Red List operates are too short (Thomas et al. 2004) especially for short-lived species (Akçakaya et al. 2006). Several alternative methods for identifying species as vulnerable to climate change have been proposed recently (Thomas et al. 2011, Young et al. 2012, Foden et al. 2013).

To evaluate how climate change might influence the effectiveness of the IUCN Red List criteria as a tool for identifying species at risk, I used a set of models developed previously for forecasting extinction risk due to climate change for a number of endemic North American reptiles and amphibians. I evaluated individual stochastic model replicates run under a climate change scenario by applying IUCN Red List criteria at each model year. I calculated the length of time spent in each threat category prior to extinction. I also measured agreement among listing criteria as a measure of robustness of classification.

4.2 METHODS

In Pearson et al. (*in press*), ecological niche models (ENM) were coupled with demographic models to forecast risk of extinction under three climate change scenarios: no climate change; a reduced carbon emissions scenario (Policy model), and a business-as-usual carbon emissions scenario (Reference model). Pearson et al. (*in press*) generated ENM based on occurrence data for 36 North American endemics under current climate and landscape variables. Pearson et al. (*in press)* then projected those distributions to annual future climate modeled variables thus generating 36 unique spatial trajectories of suitable habitat to the year 2100. Those spatial models were then paired with age- and stage-structured generic life history (GLH) models designed to encompass the range of demographic parameters representing a typical snake, small salamander, large salamander, turtle, tortoise, or lizard. Pearson et al. (*in press*) sampled within the parameter space for each paired GLH and ENM to generate 40-50 different spatially explicit demographic metapopulation models for each habitat-by-GLH combination. This modeling framework generated thousands of individual models representing realistic species scenarios with annual time steps tracking the impact of climate change. This previous study was constructed to explore what measurable life history traits and recent trend indicators might be useful for identifying species most at risk of extinction under climate change. Here, I extend this analysis to test how well the IUCN Red List criteria might perform in predicting individual model trajectories resulting in extinction. 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).

To isolate the impact of climate change as the primary risk-factor for this analysis, I only included models that showed low probability of extinction under a "no climate change" scenario (with probability less than 0.1). I separated the remaining models depending on whether they showed an increased extinction risk due to climate change or not. Overall risk of extinction and increased risk due to climate change was determined running each model with 1,000 replicates. Note that any individual model replicate resulting in extinction would give that model a positive extinction risk, although individual replicates may or may not result in extinction. I determined the IUCN Red List status annually for 10 replicates of each model run under a reference (business as usual) CO_2 concentration of 750 ppm (WRE750; Wigley et al. 1996) climate scenario model. All together there were 1,680 models run for a total of 16,800 individual replicates analyzed.

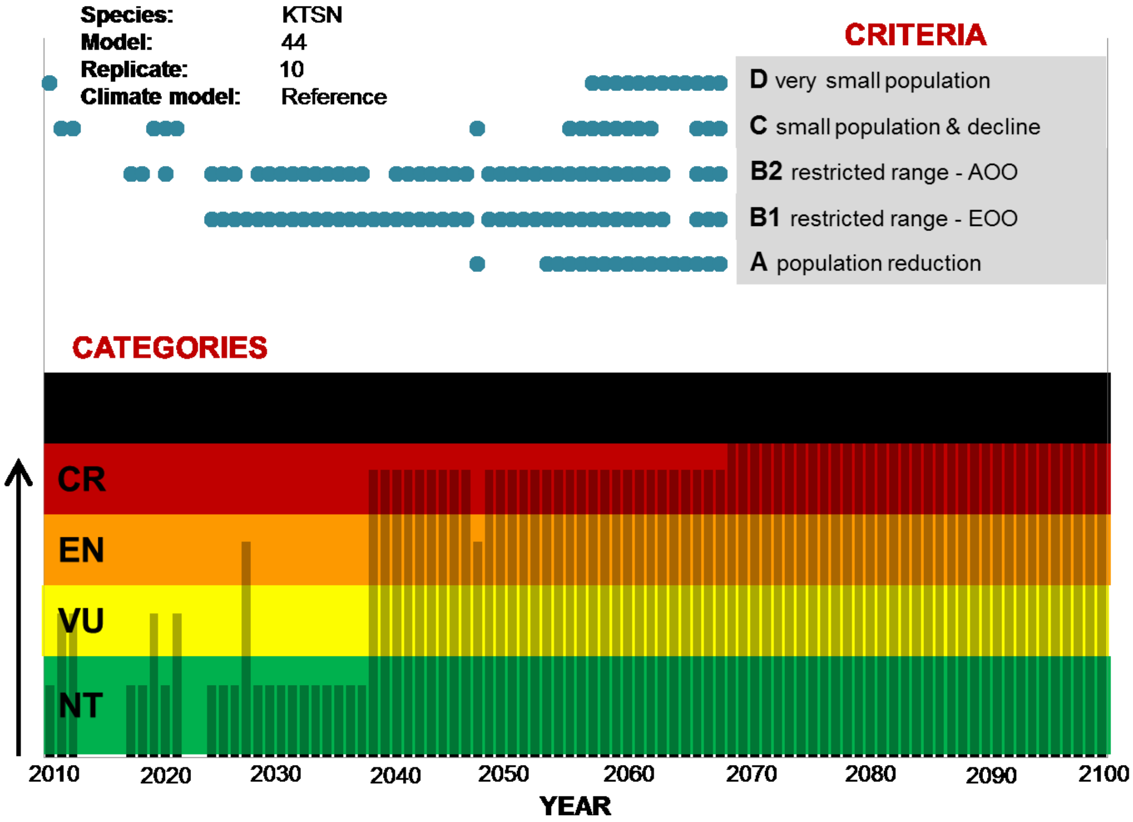

Figure 4-1 Schematic illustrating IUCN Red List analysis as applied to a single model replicate. Height of bars indicate the category the replicate would be classified under that model year considering data available up to and including that year. Blue dots indicate the criteria determining the Red List classification. Note that B1 and B2 are labeled separately for illustration purposes only; meeting either criterion would classify the replicate that year under criterion B. IUCN categories used in this analysis are: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), and Extinct (EX).

Similar to the approach described in Chapter 2, I evaluated each simulated trajectory separately against the IUCN Red List criteria. I applied the criteria at annual timesteps to generate a continuous time-line of Red List categories for each model replicate (see Appendix). Also as in Chapter 2, I only considered the information available in each time-line up to and including each time step under evaluation without consideration for the ultimate fate of the trajectory (Figure 4-1). I did not consider Red List criteria that involved making future projections such as criteria A3, A4, or E, in order to avoid circularity.

The details on the application of each individual Red List criterion are as described in Chapter 2. However, whereas I did not consider the criterion based on observed spatial parameters for the passenger pigeon (criteria B and D2), I do consider them here. The passenger pigeon as a nomadic breeder had a very unique and specialized manner in which it used its habitat, which made concepts such as area of occupancy (AOO) and extent of occurrence (EOO) problematic in the context of IUCN Red List criteria. Many of the species considered here have limited ranges and low dispersal. For these species, the spatial parameters EOO and AOO are relevant to the traditional definitions of how geographic constraints are thought to contribute to extinction risk (Gaston 1991, 1994).

Criterion B is met under IUCN Red List rules if EOO (B1) or AOO (B2) fall at or below threshold levels in conjunction with at least two of three additional aggravating circumstances. These additional circumstances are a) severe fragmentation or existing at a single location or few locations (depending on the threat category), b) continuing decline, or c) extreme fluctuations. The term severe fragmentation is used to identify conditions where most of a species total population is found in relatively small and isolated subpopulations (IUCN Standards and Petitions Subcommittee 2010). Here I define severe fragmentation as being met if more than half of the total adult population exists in populations of fewer than 100 total individuals that are isolated from the next closest population by a distance greater than 3 times the average dispersal distance. I determine the number of locations as the number of extant subpopulations. The definition for continuing decline under criterion B is slightly less strict than declines specified under criterion C because the designation is being made in conjunction with being spatially restricted (IUCN Standards and Petitions Subcommittee 2010). Here I define continuing decline as any negative trend in the total number of mature individuals, the total number of subpopulations, EOO, or AOO observed for at least the last generation or 3 years (whichever is longer). Extreme fluctuations or high variability in population sizes through time is associated with increased extinction risk. IUCN Red List criteria allows for taking a species biology, distribution, and dispersal patterns into account when establishing when this subcriterion is met (IUCN Standards and Petitions Subcommittee 2010). To establish a binary rule for determining if extreme fluctuations are occurring or not, I defined it as any 10-fold increase or decrease between the smallest and largest values in number of mature individuals, number of subpopulations, EOO, or AOO over the past 2 generations.

A species would be considered threatened under criterion B on the basis of EOO if any two of the conditions described above were met and EOO was less than 100km^2 for critically endangered, 5,000km^2 for endangered, or 20,000km^2 for vulnerable. The thresholds for AOO are 10km^2 for critically endangered, 500km^2 for endangered and 2,000km^2 for vulnerable. These threshold levels are as prescribed by IUCN standards (IUCN Standards and Petitions Subcommittee 2010). The near threatened category is less precisely defined by the IUCN. For this analysis I considered criterion B met if any of the above threshold requirements was met along with any one of the aggravating circumstances. I also considered criterion B met for near threatened if two of the aggravating circumstances were met, and EOO was less than 30,000km^2 or AOO was less than 3,000km^2.

Criterion D is reserved for identifying species whose population abundance has fallen to extremely low levels. The IUCN Red List allows for a special case of listing species as VU under a subcriterion D2 for species with severely restricted distributions, typically AOO less than 20km^2 or 5 or fewer locations. Criterion D2 is meant for cases where either the conditions that led to this severely restricted range are still actively threatening the species or the circumstances of the restriction could rapidly deteriorate and cause the species to become CR or EX (IUCN Standards and Petitions Subcommittee 2010). Although the IUCN does not necessarily advocate that these threshold levels to be applied as a strict rule-set for D2, I applied them in such a way here both for practicality and because within the context of these models climate change continues to be a threat. I also allowed listing at NT under criterion D2 if AOO was less than 30km^2.

4.3 RESULTS

Of the 1,680 models run, 1,069 did not demonstrate an increased risk of extinction due to climate change, 601 did show an increased risk, and the remainder (n=10) had extinction risk greater than 0.1 under the ‘no climate change’ scenario and were not analyzed further. Eighty-three percent (4,986 of 6010) of individual replicates from models that showed increased risk due to climate change resulted in extinction before the end of the simulation (Figure 4-2), whereas, only 3 out of 10,690 replicates from models not showing an increased risk from climate change resulted in extinction. For models that showed increased risk, 85% of model replicates were already classified as threatened (IUCN categories VU, EN, or CR) in simulation year 2010 compared with 54% of the replicates that did not show increased risk due to climate change. As the simulation progressed, nearly 100% of the replicates that showed increased risk were eventually classified as threatened if not already extinct (Figures 4-2 & 4-3). Models that did not show increased risk due to climate change eventually reached a relatively stable proportion where approximately 80-88% of replicates were classified as threatened (Figure 4-3). Many of the models that showed little to no risk of extinction under climate change nonetheless showed declining trends compared with the models run under a constant climate. Under the climate change scenario, 58% of these low extinction risk models showed decreases in total abundance over the course of the model with abundance in year 2100 only 0.25 of the abundance in year 2000 on average (s.d. 0.30).

All replicates that resulted in extinction were classified as threatened prior to that event. For these replicates, the final trajectory through the IUCN Red List categories toward extinction transitioned rapidly through the NT and VU categories and in general spent longer periods of time in the EN and CR categories (Figure 4-4). It should be noted that by model year 2010, few of the replicates were classified as LC or NT. Therefore, the number of years spent in these categories may have been truncated by the replicates beginning the analysis as already threatened, near-threatened, or extinct. However, examination of only the replicates that began the simulation as LC and ended in extinction showed a similar pattern of time spent in each category and total number of years threatened before extinction.

The criteria determining Red List classification varied by both Red List category and whether the model showed increased risk of extinction from climate change (Table 4-1). The criteria based partially on spatial parameters (B1, B2, as well as D for VU and NT) were strongly influential, particularly in determining the listing of models not under increased risk from climate change. However, the influence of these criteria varied across Red List categories.

In general there was stronger agreement between listing criteria in the determination of threatened categories (VU, EN, or CR) for replicates from models that demonstrated increased risk from climate change (Figure 4-5). By Red Listing rules, the criteria meeting the highest level of threat determines the listing category. Therefore, when a threat category is determined by a single criterion (for example CR by criterion C) it can be assumed that all other criteria displayed a lower threat level (criteria A, B, and D would have showed lower threat by this example). Seventy-four percent of replicates from models not showing an increased risk from climate change were listed as threatened on the basis of a single criterion, whereas this was the case for only 47% of replicates from climate risk models (Figure 4-5).

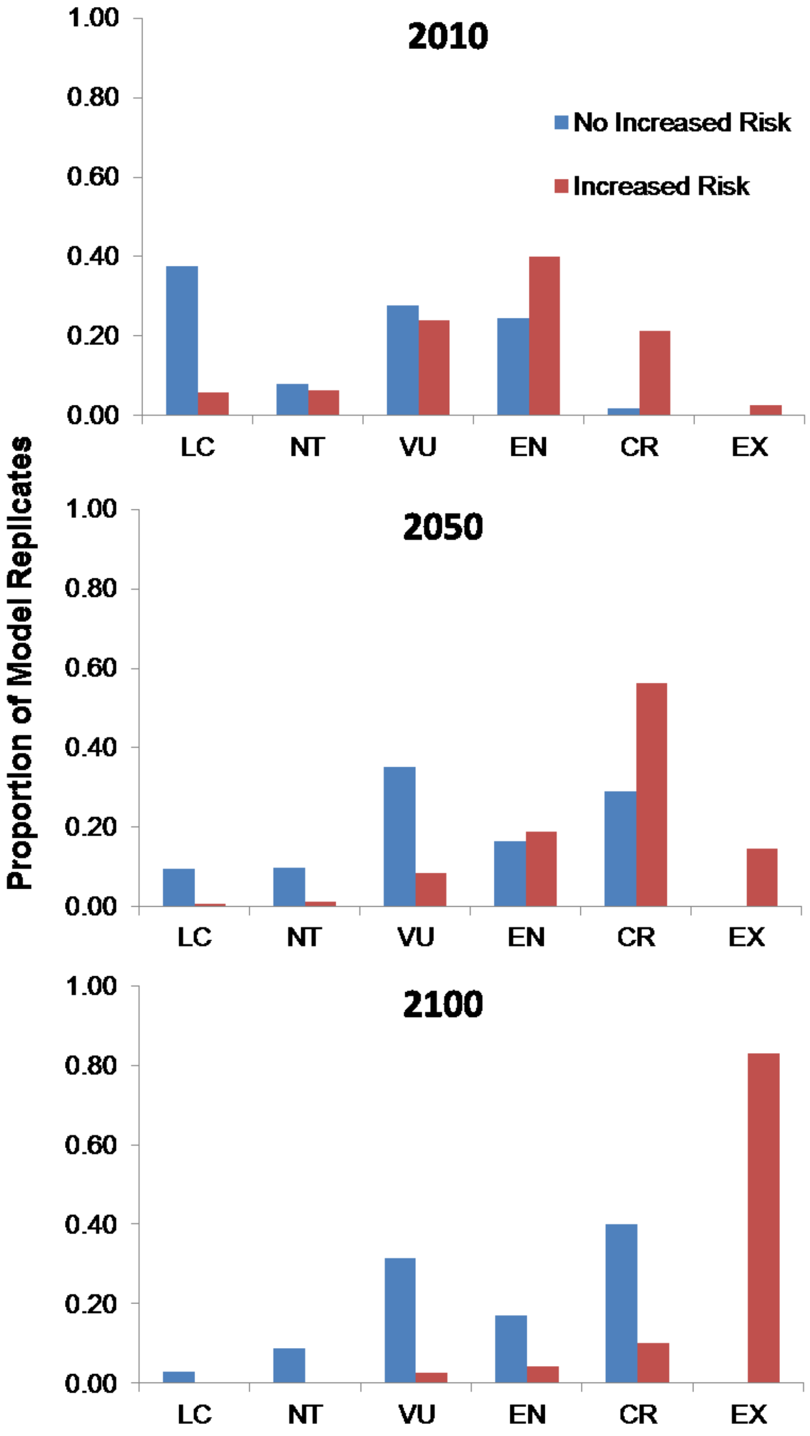

Figure 4-2 Distribution of IUCN Red List classification of model replicates in simulation years 2010, 2050, and 2100 for models that either do or do not demonstrate an increased risk of extinction due to climate change. IUCN categories used in this analysis are: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), and Extinct (EX).

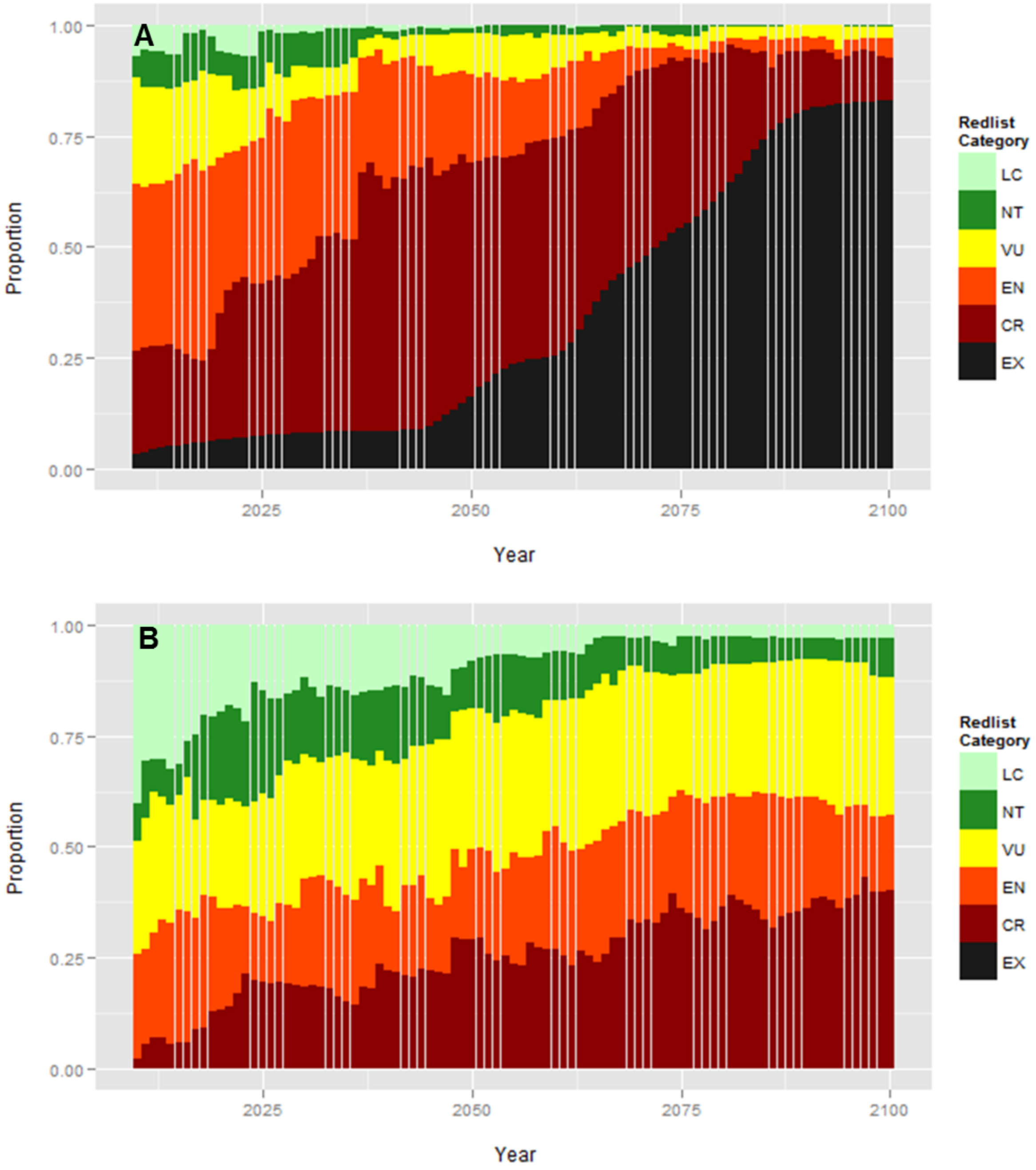

Figure 4-3 Proportion of model replicates in each IUCN Red List category by year. A) shows replicates from models that showed an increased risk of extinction due to climate change and B) shows replicates from models that did not exhibit an increased risk attributable to climate change.

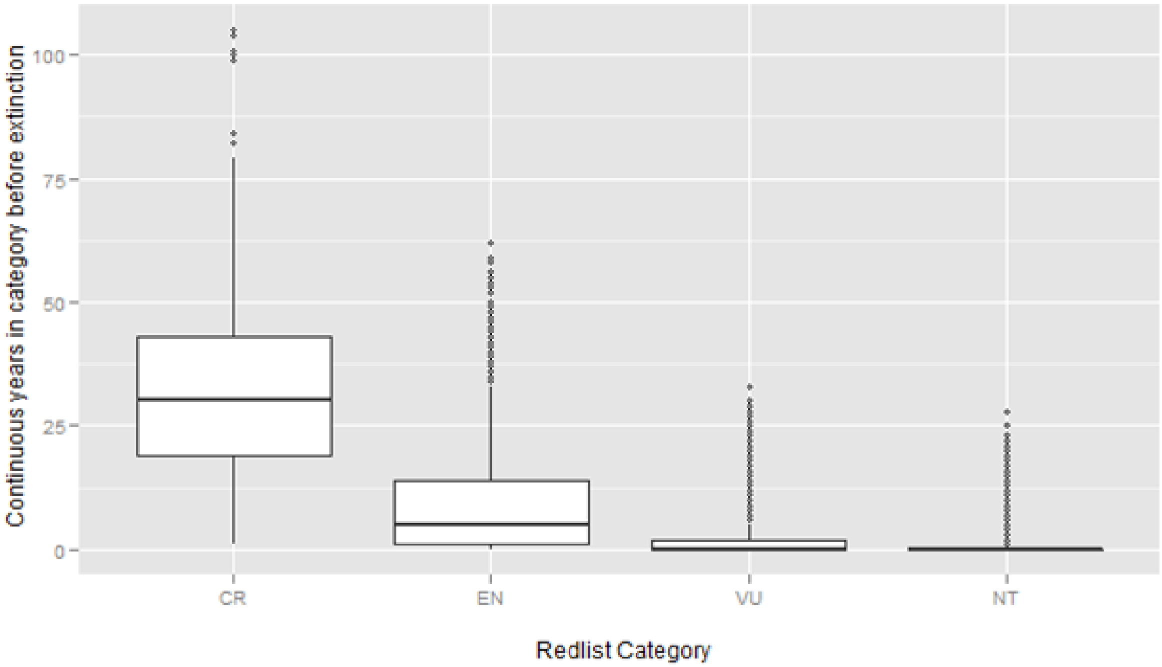

Figure 4-4 Number of continuous years spent in each IUCN Red List category prior to extinction for the 4,986 replicates that end in extinction.

Table 4-1 Proportion of each IUCN Red List category that met each listing criterion in any model year. Note that totals for each category do not sum to one because criteria are not mutually exclusive and often multiple criteria are met.

	No increased risk due to climate change					Increased risk due to climate change				
IUCN Red List Category	**A2**	**B1**	**B2**	**C**	**D**	**A2**	**B1**	**B2**	**C**	**D**
CR	0.25	0.88	0.68	0.22	0.10	0.43	0.62	0.58	0.61	0.44
EN	0.42	0.43	0.43	0.39	0.04	0.43	0.37	0.47	0.66	0.15
VU	0.22	0.14	0.15	0.34	0.53	0.17	0.52	0.50	0.45	0.46
NT	0.12	0.78	0.80	0.10	0.17	0.03	0.85	0.92	0.08	0.10

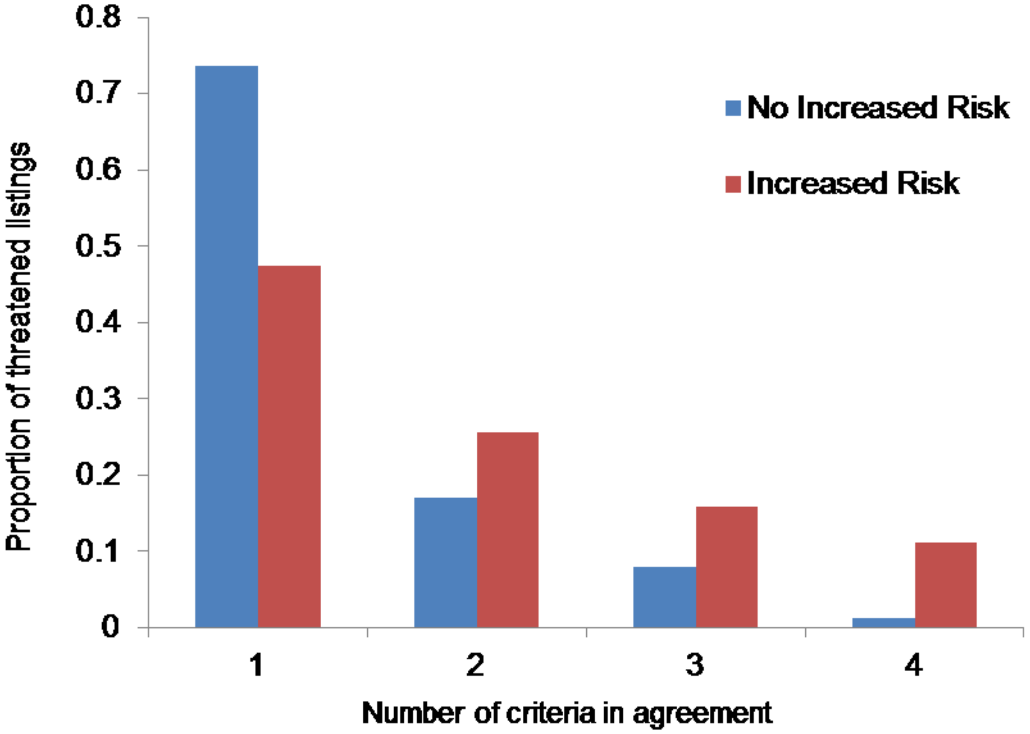

Figure 4-5 Agreement of Red List criteria when a threatened category (VU, EN, or CR) was assigned. Listing criteria considered here were criteria A – D. Note that by Red List assessment rules criteria not in agreement would have assigned a lower threat category.

4.4 DISCUSSION

The early warning time necessary for effective conservation of species threatened with extinction is difficult to determine, as it depends on the specific mechanisms through which climate change is affecting the species, the nature of conservation actions that are feasible, and social, institutional and economic constraints, among other factors. However, for most situations, a warning time of several decades might be considered sufficient. For replicates which ultimately resulted in extinction, the Red List criteria considered here did provide advanced warning and did not miss any replicates. It would be unlikely for a species to go from a non-threatened category to extinction between recommended re-evaluation intervals when climate change is a major threat. However, the progression through the NT, and VU categories were rapid with more time spent in EN and CR prior to extinction. In general, it is more desirable to take conservation action toward species recovery before a species is critically endangered. The costs of recovery generally increase while the likelihood of success generally decreases as a species becomes more imperiled. The short duration of time spent in lower-risk categories may result in species headed toward imperilment being overlooked as candidates for conservation until the situation is dire.

It is difficult to predict or anticipate how long a species is likely to spend in any given risk category. It is highly dependent on the rate and shape of the decline curve which can be influenced by the type of threat, whether impacts are proportional to population size, increasing or decreasing in intensity, are on-going, or happening all at once (Mace et al. 2008, Di Fonzo et al. 2013). Aside from listings based on criterion E (projected probability of 50% in 10 years for CR, 20% in 20 years for EN, and 10% in the next 100 years VU), IUCN Red List criteria A through D do not make assertions about probabilities of extinction within any specific timeframes (Akçakaya et al. 2006, Mace et al. 2008). This is despite the common assumption that they are (Crosby et al. 1994, Thomas et al. 2004, Sekercioğlu et al. 2004), or at least ought to be (Brooke et al. 2008, Brooke 2009), roughly equivalent. Assuming that the trajectory toward extinction is sequential through all categories and that the rate of extinction is constant, (Brooke et al. 2008) estimated that the number of years spent in each category should decrease with increasing threat level. Here I found the opposite pattern, implying that the assumptions outlined for this estimation were not met. This raises an important issue since failure to conform to the anticipated timeline in terms of not advancing to a higher threat level or persisting longer than a predicted extinction might be attributed to the effects of conservation actions when it's possible there was little impact of conservation – only a mistaken assumption of how long the progression toward extinction should take. I point out that in the models presented here there were no conservation actions represented. The changing quantity, quality and spatial arrangement of habitat patches caused by climate change interacting with the life history characteristics, density dependence, and dispersal of the modeled species often resulted in fluctuating rates of decline (and sometimes periods of increasing abundance) in individual model trajectories. This in turn caused some replicates' transitions through the Red List categories to include reversals to lower risk categories and long residence times. In the absence of knowledge about the details of a particular species, the specific threats it is facing, and the measured results of conservation actions taken (Butchart et al. 2006, Rodrigues 2006), the more conservative approach of not assuming an expected trajectory or timeline (Hoffmann et al. 2010) may be advisable, particularly when the primary threats include climate change.

A large proportion of the replicates from models that did not show high risks of extinction from climate change were nonetheless categorized as threatened (Figures 4-2 & 4-3). This would imply that the Red List may occasionally do a poor job of discriminating between replicates that are threatened and those that are not. However, threat listings for replicates that did not result in extinction before the end of the simulation do not necessarily indicate, for several reasons, that the Red List is in general overly precautionary. First, it should be noted that a large proportion of the threatened listings for the lower risk models were listed under the spatial-based criteria (B1, B2, as well as D for VU and NT; Table 4-1). This may indicate a bias particular to the species these models were constructed after. Many of the species selected for inclusion in this study were done so because they are North American endemics, many with relatively small ranges. This may have predisposed these models toward meeting the criteria based in-part on spatial parameters (note that B1 and B2 also require additional indicators to also be present in addition to the spatial thresholds).

Second, the fate of these replicates beyond the time-frame of the simulation is not known. The models these replicates were drawn from may have had a low probability of extinction before the end of the simulation, but extinction risk is not always the most useful measure of population viability (Ginzburg et al. 1982, McCarthy and Thompson 2001, Reed et al. 2002, McCarthy et al. 2003). In this study I sorted the models based on whether climate change increased the risk of extinction because that was the ultimate outcome I was primarily interested in. Many of the models that did not demonstrate an increased risk of extinction did nonetheless show greater levels of decline overall compared to models run under a constant climate scenario (see Results). Given that the Red List was designed to be precautionary (Mace et al. 2008) it is to be expected that it should have some difficulty distinguishing between replicates headed toward extinction and replicates merely declining (Keith et al. 2004).

The third reason why these results don't necessarily cast the Red List as overly precautionary is that in this modeling scenario I had perfect information on all aspects of the populations with which to apply the criteria, which is not the reality for most species assessment. The Red List takes the generally precautionary approach of allowing the criterion which meets the highest threat level to determine the overall listing category rather than seeking agreement over multiple criteria. Instances where data are insufficient to evaluate a species against all of the criteria generally results in listing species at lower threat levels if the data that is missing is that which would have met the criterion for a higher listing (Keith et al. 2000). In this study the vast majority (74%, Figure 4-5) of threatened status listings from models not showing increased risk of extinction are based on a single criterion. It is reasonable to assume that if a more realistic amount of information was used in this analysis the rate at which replicates were listed as threatened would be lower and at lower threat levels. Whereas for the models showing increased risk of extinction, more than half of the threatened listings showed agreement between at least two criteria (Figure 4-5). Therefore those results should be more robust to missing data.

Although this study goes beyond a simple climate envelope approach to risk assessment due to climate change by incorporating realistic life history and dispersal dynamics, there are still some notable avenues whereby species' extinction risks may be impacted by climate change that are not addressed here. Pearson et al. (*in press*) modeled climate change as altering the amount and physical configuration of habitat in the landscape gradually through time. The suitability values of the habitat patches were also impacted by the shifting bioclimate variables, which impacted the dynamics of the population by altering the carrying capacity. Thus climate change in this study influenced vital rates through the density dependence function rather than through physiological tolerances to specific temperature or precipitation extremes (Pörtner et al. 2006, Deutsch et al. 2008). In addition, changes in temperature or precipitation regimes may affect species in other complex and sometimes unpredictable ways such as by altering fire regimes (Keith et al. 2008), reducing the availability of pollinator (Memmott et al. 2007) or prey species (Fordham et al. 2013), or by increasing predation (Harley 2011) or disease (Pounds et al. 2006). Nor do the Pearson et al (*in press*) models used for this study address the possibility of genetic local adaptation. Incorporating these dynamics into the forecast of extinction risk due to climate change is best addressed on a species-specific basis rather than through a multi-species approach such as this. Still, many of these complex factors have already shown to be implicated in local extinctions (Cahill & Aiello-Lammens et al. 2013) and are likely to continue in the future.

5 Conclusions

The notion that natural resources and wild species are not inexhaustible is relatively new to this country and many other nations around the world, as are organized systems for monitoring and conservation. In the last century, risk assessment for individual species has become a dominant framework in which to organize conservation priorities (Scott et al. 1987). Only in the last few decades has the standard and goal become to set *a priori* quantitative thresholds and evaluate all known species into threat categories (Mace et al. 2008). As this framework has evolved, the utility of being able to identify and take action on individual or groups of species has become apparent (Cart 1973, Smith 1976). Going forward, the intensity of many of the known threats to species (e.g., resource extraction and land use change) will only intensify as the impact of new threats such as climate change become apparent. Having the most precise and defensible risk assessment tools is, and will continue to be, important for maintaining biodiversity.

Before looking forward, sometimes it is useful to first reflect on the past. I used the passenger pigeon (*Ectopistes migratorius*) as a case study for how an abundant and wide-spread species can rapidly decline to extinction. I conducted a retrospective population modeling analysis to quantitatively explore the interaction of anthropogenic impacts and intrinsic life-history characteristics that may have led to the extinction of this species. I found that high mortality and nest disturbance from the commercial harvest industry interacting with slow population growth rates and a high inter-annual variation due to the species' reliance on ephemeral food resources presented the most probable scenario. My models show that although habitat loss drove population levels downward throughout the 18th century, habitat loss does not explain the extinction event. Only commercial harvest at very intensive levels resulted in extinction-level declines in the model. This harvest intensity was likely beyond the capacity of what the rail-lines and processing facilities would have been able to process at the time (Martin 1915) implying that the waste in the system (Schorger 1955) cause a very high level of unnecessary mortality. These results have important implications for other species that are commercially harvested or are impacted as by-catch species especially if they have a propensity for high variability in either reproduction or survival rates.

The application of the IUCN Red-listing criteria to simulated trajectories of this passenger pigeon allowed me to determine how much time might have been available for conservation action had a tool like the Red List criteria and the appropriate monitoring data been available. I found that the Red List would probably have identified the species as endangered shortly after the expansion of the commercial industry and possibly decades before casual observers began to note that the species' seemed to be declining. I found that all simulated trajectories that resulted in extinction were identified at threatened by the Red List criteria prior to extinction. Most of those threat listings were made under criterion A2 (observed declines) rather than criteria based on small population sizes (criteria C and D). In the models, the population sizes only reached threatened-level thresholds in the last few time-steps before extinction after decades of decline. These results highlight the importance of data collection and monitoring. The extinction of the passenger pigeon was described at the time in terms of the species simply 'vanishing' and many were incredulous that a species once so abundant could go extinct. This study demonstrates how allowing different avenues for assessing risk is a precautionary approach that would have identified this species as at risk in a more timely manner than waiting until the population was at extremely low levels. This finding is highly relevant for modern conservation because there has been skepticism over basing risk assessments on observed declines when total population numbers imply a species is still abundant, this skepticism is especially relevant for species under commercial harvest. These results also highlight the fact that there are multiple avenues toward extinction and it should not be assumed that every species will display the same risk indicators.

I next turned my attention to the future to evaluate how the current IUCN Red List criteria might be used for conservation of species likely to be negatively impacted by global climate change. Because the effects of climate change are thought to be gradual but persistent there is concern that species may not manifest the threatened indicators within the time frames used by the IUCN Red List. Or once they do trigger the threshold criteria, conservation would be extremely challenging. I sought to address this by examining a set of modeled species under a climate change scenario. I found that for the models predicting extinction due to climate change the IUCN Red List provided advanced warning with no models going to extinction without first being classified as threatened. I also found that it would be unlikely for a species to go from a non-threatened category to extinction between recommended re-evaluation intervals when climate change is a major threat. However, I did find a general pattern where the models progressed rapidly through the lower threat level categories. This may indicate a potential problem because the costs of recovery generally increase while the likelihood of success generally decreases as a species becomes more imperiled. In the near future identifying extinction risk and taking action to prevent extinctions due to climate change will be a major challenge for conservation professionals. The most effective conservation methods and approaches have yet to be determined whether it be establishing corridors, protected area reserve networks, restoration, assisted migration, or a combination of the above. Therefore, how much time or advance warning risk assessment needs to provide is not clear.

In general, I found further support for the conclusion that extinction risk assessment and threat ranking provides a clear, convenient, and accessible method for setting conservation priorities. This approach is also readily understood by the general public and policy makers. This aspect becomes very important when it comes to allocating resources or gaining support for conservation. The IUCN Red List threat categories have become a shorthand way of communicating extinction risk that is generally understood and broadly supported. Preventing further anthropogenic extinctions while balancing the needs of a growing human population will be a challenge for the foreseeable future

6 BIBLIOGRAPHY

Akçakaya, H. R., S. H. M. Butchart, G. M. Mace, S. N. Stuart, and C. Hilton-Taylor. 2006. Use and misuse of the IUCN Red List Criteria in projecting climate change impacts on biodiversity. Global Change Biology 12:2037–2043.

Akçakaya, H. R., and W. T. Root. 2007. RAMAS/GIS: linking spatial data with population viability analysis. Applied Biomathematics, Setauket, NY.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. Diversity and Distributions 14:983–994.

Allen, C., and D. Saunders. 2002. Variability between scales: Predictors of nomadism in birds of an Australian Mediterranean-climate ecosystem. Ecosystems 5:348–359.

Blockstein, D. E. 2002. Passenger Pigeon (*Ectopistes migratorius*). *in* A. Poole, editor. The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, NY.

Blockstein, D. E., and H. B. Tordoff. 1985. A contemporary look at the extinction of the Passenger Pigeon. American Birds 39:845–851.

Boucher, Y., D. Arseneault, and L. Sirois. 2009. Logging history (1820-2000) of a heavily exploited southern boreal forest landscape: Insights from sunken logs and forestry maps. Forest Ecology and Management 258:1359–1368.

Bourdo, E. A. 1956. A Review of the General Land Office Survey and of Its Use in Quantitative Studies of Former Forests. Ecology 37:754–768.

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 6:285–291.

Brook, B. W., J. J. O'Grady, A. P. Chapman, M. A. Burgman, H. R. Akçakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature 404:385–387.

Brooke, M. de L. 2009. A Necessary Adjustment of the Extinction Risk associated with the Red List Criteria? Avian Conservation and Ecology 4:1.

Brooke, M. de L., S. H. . Butchart, S. T. Garnett, G. M. Crowley, N. B. Mantilla-Beniers, and A. J. Stattersfield. 2008. Rates of Movement of Threatened Bird Species between IUCN Red List Categories and toward Extinction. Conservation Biology 22:417–427.

Bucher, E. H. 1982. Colonial breeding of the eared dove (*Zenaida auriculata*) in Northeastern Brazil. Biotropica 14:255–261.

Bucher, E. H. 1992. The Causes of Extinction of the Passenger Pigeon. *in* D. M. Power, editor. Current Ornithology. Plenum Press, New York.

Butchart, S. H. M., A. J. Stattersfield, L. A. Bennun, S. M. Shutes, H. R. Akçakaya, J. E. M. Baillie, S. N. Stuart, C. Hilton-Taylor, and G. M. Mace. 2004. Measuring Global Trends in the Status of Biodiversity: Red List Indices for Birds. PLoS Biol 2:e383.

Butchart, S., A. Stattersfield, and N. Collar. 2006. How many bird extinctions have we prevented? Oryx 40:266–278.

Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Y. Ryu, G. C. Sbeglia, F. Spagnolo, J. B. Waldron, O. Warsi, and J. J. Wiens. 2013. How does climate change cause extinction? Proceedings of the Royal Society B: Biological Sciences 280:20121890.

Cart, T. W. 1973. The Lacey Act: America’s First Nationwide Wildlife Statute. Forest & Conservation History 17:4–13.

Caswell, H. 2001. Matrix population models. Sinauer Associates Sunderland, MA, USA.

Channell, R., and M. V. Lomolino. 2000. Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. Journal of Biogeography 27:169–179.

Coale, H. K. 1922. On the Nesting of *Ectopistes migratorius* The Auk 39:254–255.

Conrad, J. 2005. Research Articles - Open Access and Extinction of the Passenger Pigeon in North America. Natural Resource Modeling. 18:501.

Conroy, S. D. S., and B. W. Brook. 2003. Demographic sensitivity and persistence of the threatened white- and orange-bellied frogs of Western Australia. Population Ecology 45:105–114.

Cook, L. F., and C. A. Toft. 2005. Dynamics of extinction: population decline in the colonially nesting Tricolored Blackbird *Agelaius tricolor*. Bird Conservation International 15:73–88.

Cook, S. 1903, March 14. What Became of the Wild Pigeon. Forest and Stream; A Journal of Outdoor Life, Travel, Nature Study, Shooting, Fishing, Yachting (1873-1930) LX:205.

Crosby, M. J., A. J. Stattersfield, N. J. Collar, and C. J. Bibby. 1994. Predicting Avian Extinction Rates. Biodiversity Letters 2:182–185.

Deane, R. 1895. Additional Records of the Passenger Pigeon in Illinois and Indiana. The Auk 12:298–300.

Deane, R. 1908. The Passenger Pigeon (*Ectopistes migratorius*) in Confinement. The Auk 25:181–183.

Deane, R. 1931. Abundance of the Passenger Pigeon in Pennsylvania in 1850. The Auk 48:264–265.

Denson Jr., E. P. 1970. The Trumpeter Swan, *Olor buccinator*: A conservation success and its lessons. Biological Conservation 2:253–256.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences 105:6668–6672.

Donald, P., and J. Greenwood. 2001. Spatial patterns of range contraction in British breeding birds. IBIS 143:593–601.

Dulvy, N. K., S. Jennings, N. B. Goodwin, A. Grant, and J. D. Reynolds. 2005. Comparison of threat and exploitation status in North-East Atlantic marine populations. Journal of Applied Ecology 42:883–891.

Dupuis, S., D. Arseneault, and L. Sirois. 2011. Change from pre-settlement to present-day forest composition reconstructed from early land survey records in eastern Quebec, Canada. Journal of Vegetation Science 22:564–575.

Elith, J., C. Graham, R. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. Hijmans, F. Huettmann, J. Leathwick, A. Lehmann, J. Li, L. Lohmann, B. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. Overton, A. Peterson, S. Phillips, K. Richardson, R. Scachetti-Pereira, R. Schapire, J. Soberon, S. Williams, M. Wisz, and N. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.

Elith, J., and J. Leathwick. 2013. Boosted Regression Trees for ecological modeling. CRAN.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77:802–813.

Ellsworth, J. W., and B. C. McComb. 2003. Potential Effects of Passenger Pigeon Flocks on the Structure and Composition of Presettlement Forests of Eastern North America. Conservation Biology 17:1548–1558.

Farnsworth, E., and D. Ogurcak. 2006. Biogeography and decline of rare plants in New England: Historical evidence and contemporary monitoring. Ecological Applications 16:1327–1337.

Finkelstein, M. E., D. F. Doak, D. George, J. Burnett, J. Brandt, M. Church, J. Grantham, and D. R. Smith. 2012. Lead poisoning and the deceptive recovery of the critically endangered California condor. Proceedings of the National Academy of Sciences 109:11449–11454.

Foden, W. B., S. H. M. Butchart, S. N. Stuart, J.-C. Vié, H. R. Akçakaya, A. Angulo, L. M. DeVantier, A. Gutsche, E. Turak, L. Cao, S. D. Donner, V. Katariya, R. Bernard, R. A. Holland, A. F. Hughes, S. E. O'Hanlon, S. T. Garnett, Ç. H. Şekercioğlu, and G. M. Mace. 2013. Identifying the World's Most Climate Change Vulnerable Species: A Systematic Trait-Based Assessment of all Birds, Amphibians and Corals. PLoS ONE 8:e65427.

Di Fonzo, M., B. Collen, and G. M. Mace. 2013. A new method for identifying rapid decline dynamics in wild vertebrate populations. Ecology and Evolution 3:2378–2391.

Fordham, D. A., H. R. Akçakaya, B. W. Brook, A. Rodríguez, P. C. Alves, E. Civantos, M. Triviño, M. J. Watts, and M. B. Araújo. 2013. Adapted conservation measures are required to save the Iberian lynx in a changing climate. Nature Climate Change advance online publication.

Foster, D. R., and J. F. O'Keefe. 2000. New England Forests Through Time: Insights from the Harvard Forest Dioramas. Harvard University Forest.

Gaston, K. 1991. How Large Is a Species Geographic Range. Oikos 61:434–438.

Gaston, K. J. 1994. Geographic Range Sizes and Trajectories to Extinction. Biodiversity Letters 2:163–170.

Ginzburg, L. R., L. B. Slobodkin, K. Johnson, and A. G. Bindman. 1982. Quasi-extinction Probabilities as a Measure of Impact on Population Growth. Risk Analysis 2:171–181.

Godfrey, M. H., and B. J. Godley. 2008. Seeing past the red: flawed IUCN global listings for sea turtles. Endangered Species Research 6:155–159.

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

Hancock, P. A., E. J. Milner-Gulland, and M. J. Keeling. 2006. Modelling the many-wrongs principle: The navigational advantages of aggregation in nomadic foragers. Journal of Theoretical Biology 240:302–310.

Hannah, L. 2011. Are a million species at risk? *in* L. Hannah, editor. Saving a Million Species: Extinction Risk from Climate Change. Island Press.

Harley, C. D. G. 2011. Climate Change, Keystone Predation, and Biodiversity Loss. Science 334:1124–1127.

Harris, J. B. C., J. L. Reid, B. R. Scheffers, T. C. Wanger, N. S. Sodhi, D. A. Fordham, and B. W. Brook. 2012. Conserving imperiled species: a comparison of the IUCN Red List and U.S. Endangered Species Act. Conservation Letters 5:64–72.

Hayward, M. W. 2011. Using the IUCN Red List to determine effective conservation strategies. Biodiversity and Conservation 20:2563–2573.

He, H., D. Dey, X. Fan, M. Hooten, J. Kabrick, C. Wikle, and Z. Fan. 2007. Mapping pre-European settlement vegetation at fine resolutions using a hierarchical Bayesian model and GIS. Plant Ecology 191:85–94.

Herman, W. C. 1948. The Last Passenger Pigeon. The Auk 65:77–80.

Hijmans, R. J., S. J. Phillips, J. Leathwick, and J. Elith. 2012. Package “dismo”: species distribution modeling. CRAN.

Hodge, C. F. 1911. The Passenger Pigeon Investigation. The Auk 28:49–53.

Hodge, C. F. 1912. A Last Word on the Passenger Pigeon. The Auk 29:169–175.

Hoffmann, M., C. Hilton-Taylor, A. Angulo, M. Böhm, T. M. Brooks, S. H. M. Butchart, K. E. Carpenter, J. Chanson, B. Collen, N. A. Cox, W. R. T. Darwall, N. K. Dulvy, L. R. Harrison, V. Katariya, C. M. Pollock, S. Quader, N. I. Richman, A. S. L. Rodrigues, M. F. Tognelli, J.-C. Vié, J. M. Aguiar, D. J. Allen, G. R. Allen, G. Amori, N. B. Ananjeva, F. Andreone, P. Andrew, A. L. A. Ortiz, J. E. M. Baillie, R. Baldi, B. D. Bell, S. D. Biju, J. P. Bird, P. Black-Decima, J. J. Blanc, F. Bolaños, W. Bolivar-G, I. J. Burfield, J. A. Burton, D. R. Capper, F. Castro, G. Catullo, R. D. Cavanagh, A. Channing, N. L. Chao, A. M. Chenery, F. Chiozza, V. Clausnitzer, N. J. Collar, L. C. Collett, B. B. Collette, C. F. C. Fernandez, M. T. Craig, M. J. Crosby, N. Cumberlidge, A. Cuttelod, A. E. Derocher, A. C. Diesmos, J. S. Donaldson, J. W. Duckworth, G. Dutson, S. K. Dutta, R. H. Emslie, A. Farjon, S. Fowler, J. Freyhof, D. L. Garshelis, J. Gerlach, D. J. Gower, T. D. Grant, G. A. Hammerson, R. B. Harris, L. R. Heaney, S. B. Hedges, J.-M. Hero, B. Hughes, S. A. Hussain, J. I. M, R. F. Inger, N. Ishii, D. T. Iskandar, R. K. B. Jenkins, Y. Kaneko, M. Kottelat, K. M. Kovacs, S. L. Kuzmin, E. L. Marca, J. F. Lamoreux, M. W. N. Lau, E. O. Lavilla, K. Leus, R. L. Lewison, G. Lichtenstein, S. R. Livingstone, V. Lukoschek, D. P. Mallon, P. J. K. McGowan, A. McIvor, P. D. Moehlman, S. Molur, A. M. Alonso, J. A. Musick, K. Nowell, R. A. Nussbaum, W. Olech, N. L. Orlov, T. J. Papenfuss, G. Parra-Olea, W. F. Perrin, B. A. Polidoro, M. Pourkazemi, P. A. Racey, J. S. Ragle, M. Ram, G. Rathbun, R. P. Reynolds, A. G. J. Rhodin, S. J. Richards, L. O. Rodríguez, S. R. Ron, C. Rondinini, A. B. Rylands, Y. S. de Mitcheson, J. C. Sanciangco, K. L. Sanders, G. Santos-Barrera, J. Schipper, C. Self-Sullivan, Y. Shi, A. Shoemaker, F. T. Short, C. Sillero-Zubiri, D. L. Silvano, K. G. Smith, A. T. Smith, J. Snoeks, A. J. Stattersfield, A. J. Symes, A. B. Taber, B. K. Talukdar, H. J. Temple, R. Timmins, J. A. Tobias, K. Tsytsulina, D. Tweddle, C. Ubeda, S. V. Valenti, P. P. van Dijk, L. M. Veiga, A. Veloso, D. C. Wege, M. Wilkinson, E. A. Williamson, F. Xie, B. E. Young, H. R. Akçakaya, L. Bennun, T. M. Blackburn, L. Boitani, H. T. Dublin, G. A. B. da Fonseca, C. Gascon, T. E. Lacher, G. M. Mace, S. A. Mainka, J. A. McNeely, R. A. Mittermeier, G. M. Reid, J. P. Rodriguez, A. A. Rosenberg, M. J. Samways, J. Smart, B. A. Stein, and S. N. Stuart. 2010. The Impact of Conservation on the Status of the World's Vertebrates. Science 330:1503–1509.

Holmes, E. 2001. Estimating risks in declining populations with poor data. Proceedings of the National Academy of Sciences of the United States of America 98:5072–5077.

Holmes, E. E. 2004. Beyond theory to application and evaluation: Diffusion approximations for population viability analysis. Ecological Applications 14:1272–1293.

Holmes, E. E., E. J. Ward, and K. Wills. 2012. MARSS: Multivariate autoregressive state-space models for analyzing time-series data. R Journal 4:11–19.

Hornaday, W. T. 1913. Our Vanishing Wild Life: Its Extermination and Preservation. Charles Scribner's Sons, New York, NY.

Houghton, R. A., and J. L. Hackler. 2000. Changes in terrestrial carbon storage in the United States. 1: The roles of agriculture and forestry. Global Ecology and Biogeography 9:125–144.

Hutchings, J. A. 2001. Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk. Canadian Journal of Fisheries & Aquatic Sciences 58:108.

Hutchings, J. A., and J. D. Reynolds. 2004. Marine Fish Population Collapses: Consequences for Recovery and Extinction Risk. BioScience 54:297 – 309.

IUCN. 2012. IUCN Red List Categories and Criteria: Version 3.1. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK.

IUCN Standards and Petitions Subcommittee. 2010, March. Guidelines for Using the IUCN Red List Categories and Criteria.

Jarvis, A., H. I. Reuter, A. Nelson, and E. Guevara. 2008. Hole-filled SRTM for the globe, CGIAR-CSI SRTM 90m Database.

Jarvis, R. L., and M. F. Passmore. 1992. Ecology of band-tailed pigeons in Oregon. U.S. Dept. of the Interior, Fish and Wildlife Service.

Johnson, J. A., and P. O. Dunn. 2006. Low Genetic Variation in the Heath Hen Prior to Extinction and Implications for the Conservation of Prairie-Chicken Populations. Conservation Genetics 7:37–48.

Johnson, K. P., D. H. Clayton, J. P. Dumbacher, and R. C. Fleischer. 2010. The flight of the Passenger Pigeon: Phylogenetics and biogeographic history of an extinct species. Molecular Phylogenetics and Evolution 57:455–458.

Jovani, R., and V. Grimm. 2008. Breeding synchrony in colonial birds: from local stress to global harmony. Proceedings of the Royal Society B: Biological Sciences 275:1557–1564.

Kautz, J. E., and C. E. Braun. 1981. Survival and Recovery Rates of Band-Tailed Pigeons in Colorado. The Journal of Wildlife Management 45:214–218.

Keith, D. A., H. R. Akçakaya, W. Thuiller, G. F. Midgley, R. G. Pearson, S. J. Phillips, H. M. Regan, M. B. Araújo, and T. G. Rebelo. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. Biology Letters 4:560–563.

Keith, D. A., T. D. Auld, M. K. J. Ooi, and B. D. E. Mackenzie. 2000. Sensitivity analyses of decision rules in World Conservation Union (IUCN) Red List criteria using Australian plants. Biological Conservation 94:311–319.

Keith, D. A., M. A. McCarthy, H. Regan, T. Regan, C. Bowles, C. Drill, C. Craig, B. Pellow, M. A. Burgman, L. L. Master, M. Ruckelshaus, B. Mackenzie, S. J. Andelman, and P. R. Wade. 2004. Protocols for listing threatened species can forecast extinction. Ecology Letters 7:1101–1108.

Keppie, D. M., and C. E. Braun. 2000. Band-tailed Pigeon (*Patagioenas fasciata*). The Birds of North America Online.

Klein Goldewijk, K., A. Beusen, and P. Janssen. 2010. Long-term dynamic modeling of global population and built-up area in a spatially explicit way: HYDE 3.1. The Holocene 20:565 – 573.

Klein Goldewijk, K., A. Beusen, M. de Vos, and G. van Drecht. 2011. The HYDE 3.1 spatially explicit database of human induced land use change over the past 12,000 years. Global Ecology and Biogeography 20:73–86.

Kon, H., T. Noda, K. Terazawa, H. Koyama, and M. Yasaka. 2005. Proximate factors causing mast seeding in *Fagus crenata*: the effects of resource level and weather cues. Canadian Journal of Botany 83:1402–1409.

Langvatn, R., and A. Loison. 1999. Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. Wildlife Biology 5:213–223.

Mace, G. M., N. J. Collar, K. J. Gaston, C. Hilton-Taylor, H. R. Akçakaya, N. Leader-Williams, E. J. Milner-Gulland, and S. N. Stuart. 2008. Quantification of Extinction Risk: IUCN's System for Classifying Threatened Species. Conservation Biology 22:1424–1442.

Martin, E. T. 1915. Letter in Response to Dr. Hornaday. Outing Magazine 66:727.

McCarthy, M. A., S. J. Andelman, and H. P. Possingham. 2003. Reliability of Relative Predictions in Population Viability Analysis. Conservation Biology 17:982.

McCarthy, M. A., and C. Thompson. 2001. Expected minimum population size as a measure of threat. Animal Conservation 4:351–355.

McGee, W. J. 1910. Notes on the Passenger Pigeon. Science 32:958–964.

McKay, M. D., R. J. Beckman, and W. J. Conover. 1979. A Comparison of Three Methods for Selecting Values of Input Variables in the Analysis of Output from a Computer Code. Technometrics 21:239–245.

McKenney, D. W., J. H. Pedlar, P. Papadopol, and M. F. Hutchinson. 2006. The development of 1901–2000 historical monthly climate models for Canada and the United States. Agricultural and Forest Meteorology 138:69–81.

Meir, E., and W. F. Fagan. 2000. Will Observation Error and Biases Ruin the Use of Simple Extinction Models? Conservation Biology 14:148–154.

Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price. 2007. Global warming and the disruption of plant–pollinator interactions. Ecology Letters 10:710–717.

Naujokaitis-Lewis, I., J. Curtis, P. Arcese, and J. Rosenfeld. 2009. Sensitivity Analyses of Spatial Population Viability Analysis Models for Species at Risk and Habitat Conservation Planning. Conservation Biology 23:225–229.

Pearson, R. G., J. C. Stanton, K. T. Shoemaker, M. E. Aiello-Lammens, P. Ersts, N. Horning, D. A. Fordham, C. J. Raxworthy, H. Y. Ryu, J. A. McNeely, and H. R. Akçakaya. *in press*. Life history and spatial traits predict extinction risk due to climate change. Nature Climate Change.

Pereira, S., K. Johnson, D. Clayton, and A. Baker. 2007. Mitochondrial and nuclear DNA sequences support a Cretaceous origin of columbiformes and a dispersal-driven radiation in the paleogene. Systematic Biology 56:656–672.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231–259.

Phillips, S. J., and M. Dudík. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31:161–175.

Pörtner, H. O., A. F. Bennett, F. Bozinovic, A. Clarke, M. A. Lardies, M. Lucassen, B. Pelster, F. Schiemer, and J. H. Stillman. 2006. Trade-Offs in Thermal Adaptation: The Need for a Molecular to Ecological Integration. Physiological and Biochemical Zoology 79:295–313.

Pounds, A. J., M. R. Bustamante, L. A. Coloma, J. A. Consuegra, M. P. L. Fogden, P. N. Foster, E. La Marca, K. L. Masters, A. Merino-Viteri, R. Puschendorf, S. R. Ron, G. A. Sánchez-Azofeifa, C. J. Still, and B. E. Young. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439:161–167.

Prasad, A., L. Iverson, S. Matthews, and M. Peters. 2009. Atlases of Tree and Bird Species Habitats for Current and Future Climates. Ecological Restoration 27:260–263.

Prasad, A. M., L. R. Iverson, S. Matthews, and M. Peters. 2007, ongoing. A Climate Change Atlas for 134 Forest Tree Species of the Eastern United States. Northern Research Station, USDA Forest Service, Delaware, Ohio.

Prowse, T. A. A., C. N. Johnson, R. C. Lacy, C. J. A. Bradshaw, J. P. Pollak, M. J. Watts, and B. W. Brook. 2013. No need for disease: testing extinction hypotheses for the thylacine using multi-species metamodels. Journal of Animal Ecology 82:355–364.

Punt, A. E. 2000. Extinction of marine renewable resources: a demographic analysis. Population Ecology 42:19–27.

R Core Team. 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramankutty, N., and J. Foley. 1999. Estimating historical changes in land cover: North American croplands from 1850 to 1992. Global Ecology and Biogeography 8:381–396.

Ramankutty, N., E. Heller, and J. Rhemtulla. 2010. Prevailing Myths About Agricultural Abandonment and Forest Regrowth in the United States. Annals of the Association of American Geographers 100:502–512.

Reed, J. M. 1999. The Role of Behavior in Recent Avian Extinctions and Endangerments. Conservation Biology 13:232–241.

Reed, J., L. Mills, J. Dunning, E. Menges, K. McKelvey, R. Frye, S. Beissinger, M. Anstett, and P. Miller. 2002. Emerging issues in population viability analysis. Conservation Biology 16:7–19.

Rhemtulla, J. M., D. J. Mladenoff, and M. K. Clayton. 2009. Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s–1930s–2000s). Ecological Applications 19:1061–1078.

Ricker, W. E. 1954. Stock and Recruitment. Journal of the Fisheries Research Board of Canada 11:559–623.

Ridgeway, G. 2013. Package “gbm”: Generalized Boosted Regression Models. CRAN.

Rodrigues, A. S. L. 2006. Are Global Conservation Efforts Successful? Science 313:1051–1052.

Sanders, T. A. 2013. Band-tailed pigeon population status, 2013. U.S. Department of the Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Washington, D.C.

Schorger, A. W. 1952. The Number of Eggs Laid by the Passenger Pigeon, *Ectopistes migratorius*. The Auk 69:201.

Schorger, A. W. 1955. The Passenger Pigeon: Its natural history and extinction. University of Wisconsin, Madison.

Schulte, L., A. Pidgeon, and D. Mladenoff. 2005. One hundred fifty years of change in forest bird breeding habitat: Estimates of species distributions. Conservation Biology 19:1944–1956.

Scott, P., J. A. Burton, and R. Fitter. 1987. Red Data Books: The Historical Background. Pages 1–6 *in* R. Fitter and M. Fitter, editors. The Road to Extinction: Problems of Categorizing the Status of Taxa Threatened with Extinction�: Proceedings of a Symposium Held by the Species Survival Commission, Madrid, 7 and 9 November 1984. IUCN.

Sekercioğlu, C. H., G. C. Daily, and P. R. Ehrlich. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences of the United States of America 101:18042–18047.

Simberloff, D. 1986. The Proximate Causes of Extinction. Pages 259–276 *in* D. M. Raup and D. Jablonski, editors. Patterns and Processes in the History of Life. Springer Berlin Heidelberg.

Smith, R. L. 1976. Ecological Genesis of Endangered Species: The Philosophy of Preservation. Annual Review of Ecology and Systematics 7:33–55.

Stanton, J. C., and H. R. Akcakaya. 2013. Conservation planning to ensure viability of populations and metapopulations. *in* L. Craighead and C. L. Convis, editors. Conservation planning: shaping the future. ESRI Press.

Stephens, P., and W. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology & Evolution 14:401–405.

Steyaert, L., and R. Knox. 2008. Reconstructed historical land cover and biophysical parameters for studies of land-atmosphere interactions within the eastern United States. Journal of Geophysical Research-Atmospheres 113:D02101.

Stubben, C., B. Milligan, and P. Nantel. 2012. popbio: Construction and analysis of matrix population models. CRAN.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. Townsend Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. Nature 427:145–148.

Thomas, C. D., J. K. Hill, B. J. Anderson, S. Bailey, C. M. Beale, R. B. Bradbury, C. R. Bulman, H. Q. P. Crick, F. Eigenbrod, H. M. Griffiths, W. E. Kunin, T. H. Oliver, C. A. Walmsley, K. Watts, N. T. Worsfold, and T. Yardley. 2011. A framework for assessing threats and benefits to species responding to climate change. Methods in Ecology and Evolution 2:125–142.

US Fish and Wildlife Service. 2006. 12-Month Finding on a Petition To List the Cerulean Warbler (*Dendroica cerulea*) as Threatened with Critical Habitat. Federal Register 71:70717 – 70733.

Vié, J.-C., C. Hilton-Taylor, and S. N. Stuart (Eds.). 2009. Wildlife in a Changing World – An Analysis of the 2008 IUCN Red List of Threatened Species. IUCN, Gland, Switzerland.

Waisanen, P. J., and N. B. Bliss. 2002. Changes in population and agricultural land in conterminous United States counties, 1790 to 1997. Global Biogeochemical Cycles 16:1137.

Wang, Y. 2005. Presettlement land survey records of vegetation: geographic characteristics, quality and modes of analysis. Progress in Physical Geography 29:568–598.

Whitney, G. G. 1996. From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America from 1500 to the Present. Cambridge University Press.

Wigley, T. M. L., R. Richels, and J. A. Edmonds. 1996. Economic and environmental choices in the stabilization of atmospheric CO2 concentrations. Nature 379:240–243.

Williams, G. W. 2000. The USDA Forest Service; The First Century. USDA Forest Service, Washington, D.C.

Williams, M. 1992. Americans and Their Forests: A Historical Geography. Cambridge University Press.

Wilson, E. S. 1934. Personal Recollections of the Passenger Pigeon. The Auk 51:157–168.

Wright, A. H. 1910. Some Early Records of the Passenger Pigeon. The Auk 27:428–443.

Wright, A. H. 1911. Other Early Records of the Passenger Pigeon. The Auk 28:346–366.

Young, B. E., K. R. Hall, E. Byers, K. Gravuer, G. A. Hammerson, A. Redder, and K. Szabo. 2012. Rapid Assessment of Plant and Animal Vulnerability to Climate Change. *in* J. F. Brodie, E. S. Post, and D. F. Doak, editors. Wildlife Conservation in a Changing Climate. University of Chicago Press.

Appendix

Application of IUCN Red List assessment criteria from RAMAS output in R

The following is a portion of the code developed to apply IUCN Red List criteria (A2, B1, B2, C, and D; (IUCN 2012) from RAMAS population model output (Akçakaya and Root 2007) in the computing software R (R Core Team 2013). Red List categories are determined for each timestep of each stochastic model replicate.

Definition of parameters:

Nmature – total number of individuals of reproductive age.

percentreduction – percent reduction calculated from the slope of the natural log of the linear trend in number of mature individuals. Calculated as a moving window function with an interval width the longer of [1] one generation or three years, [2] two generations or five years, [3] three generations or 10 years.

EOO **–** extent of occurrence calculated as the area in km^2 within the minimum convex polygon surrounding all occupied patches.

AOO **–** area of occupancy in km^2 calculated as either the sum of the area of occupied patches or 4 x the number of mature individuals (whichever value is less).

SevereFrag – severe fragmentation condition is met when more than half of the total adult population exists in small and isolated subpopulations. A subpopulation is considered small if there are fewer than 100 mature individuals. A subpopulation is considered isolated if it's closes neighboring patch (whether occupied or not) is more than 3 x the average dispersal distance away.

singleLoc, fiveLoc, tenLoc, and ***fifteenLoc*** - number of occupied subpopulations is equal to or less than 1, 5, 10, or 15 respectively.

ContDecline – continuing decline determined as any current negative trend in number of mature individuals, extent of occurrence, or area of occupancy.

ExFluc2gen – extreme fluctuations condition is met when the ratio of maximum abundance to minimum abundance over the previous 2 generations is equal to 10 or greater.

LargestPopSize – number of mature individuals in the largest subpopulation.

PropInLargestPop – proportion of the total mature population contained in the largest subpopulation.

```
## IN FINAL TABLE:
##   1 - Extinct (EX)
##   2 - Critically Endagered (CR)
##   3 - Endangered (EN)
##   4 - Vulnerable (VU)
##   5 - Near Threatened (NT)
##   6 - Least Concern (LC)
#########################################Extinct################################
# population is zero
Extinct <- Ntotal == 0
EX<-Extinct*1
EX[EX==0]<-NA
################################Critically Endangered#######################
                                                    ## CriterionA ####
# Criterion A here is applied as if the observed trajectory from the beginning of the simulation
```

```
# up to the year for which the criteria is being applied is regarded as direct observation.
# Potential declines (future timesteps) are not considered.
# The criterion of threats being understood,  reversible,
# and ceased are assumed to not be met for simulations. Criteria A1, A3, and A4 are not considered.
#
# CR.A.2 80% reduction over 3 generations or 10 years whichever is longer
CRA2<-apply(percentreduction[[3]],2,function(x){ x >= 80})*1
CRA2<-replace(CRA2, is.na(CRA2),0)
CRA<-CRA2
                                                   ##Criterion B ##
### Criterion B is met if B1 OR B2 is met
# CR.B.1 extent of occurrence (EOO) is less than 100km2 AND at least two a-c criteria
CRB1.part1 <- apply(EOO,2,function(x) { x < 100})*1
#### a-c criteria calculated below (same for B2)
# CR.B.2 area of occupancy (AOO), is less than 10km2 (part1) AND two of a-c criteria (part2)
#Part 1:AOO is less than 10km2
CRB2.part1<-apply(AOO,2,function(x){x < 10 })*1
#Part 2: At least two of a-c:
#CR.B Part 2 a: Severely Fragmented OR known to exist at only a single location
CRB.part2.a<-(SevereFrag+singleLoc >=1)
#CR.B Part 2 b: Continuing decline (Calculated above combined to single var)
#CR.B Part 2 c: Extreme fluctuations (Calculated above combined to single var)
#NOTE: This is for Extreme fluctions over 2 generations - 3 gen is option
#Determine if 2 of a-c is met
CRB.part2<-(CRB.part2.a+ContDecline+ExFluc2gen >= 2)*1
# CR.B1 and CR.B2 (combine parts 1 and 2)
CRB1<-CRB1.part1*CRB.part2
CRB2<-CRB2.part1*CRB.part2
CRB<-CRB2 + CRB1 >=1

                                                ###Criterion C ######
### To meet this criterion Part 1 AND Part 2 most both be met
### Criterion C - Part 1: Population size estimated to number fewer than 250 mature
CRC.part1<-apply(Nmature,2,function(x){ x < 250 })*1
#Criterion C - Part 2:  Contdition 1 OR condition 2
#Cond 1. Continuing decline of at least 25% within 3 years
#or one generation whichever is longer OR
#Cond 2. Continuing decline in N mature AND sub condition a or b:
#a: popualtion structure such that condition (i) OR (ii)
# (i) there are no subpopulation with at least 50 mature
# (ii)  at least 90% of mature indv. in single pop
#b: Extreme fluctuations in N mat (calculated over 2 generations change for 3)
CRC.part2.cond1<-apply(percentreduction[[1]],2,function(x){ x >= 25 })*1
CRC.part2.cond1 <- replace(CRC.part2.cond1, is.na(CRC.part2.cond1),0)
CRC.part2.cond2.ai<-apply(LargestPopSize,2,function(x){ x<=50 })*1
CRC.part2.cond2.aii<-apply(PropInLargestPop,2,function(x){ x >= .90})*1
CRC.part2.cond2.a <- (CRC.part2.cond2.ai + CRC.part2.cond2.aii >= 1)*1
CRC.part2.cond2.b <- ExFluc2gen.Nmature *1
CRC.part2.cond2 <- (CRC.part2.cond2.a + CRC.part2.cond2.b >=1)
CRC.part2.cond2 <- (CRC.part2.cond2*ContDecline.lnNmat)*1
CRC.part2 <- (CRC.part2.cond1 + CRC.part2.cond2 >=1)*1
CRC<-CRC.part1*CRC.part2

                                                ###Criterion D ######
### Population size estimated fewer 50 mature
CRD<-Nmature < 50
```

```
CRD <-CRD*1
                                        ####Criterion E Not Calculated #####
                                   #####  Determine Critically Endangered   #######
CR<-(CRA+CRB+CRC+CRD)>=1
CR <- CR*1
#change 0's to NA's
CR[CR==0]<-NA
CR<-CR+1
#In the next step (i.e for Endangered" change 1 to 3, to create hierarchy)

##############################Endangered######################

                                                ## Criterion A ####
# EN.A.1 70% reduction where cause is understood and ceased - not modeled
# EN.A.2 50% reduction over 3 generations or 10 years (and possibly ongoing)
ENA2<-apply(percentreduction[[3]],2,function(x){ x >= 50 })*1
ENA2<-replace(ENA2, is.na(ENA2),0)
ENA<-ENA2

                                                 ##Criterion B ##
### Criterion B is met if B1 OR B2 is met
#EN.B.1 extent of occurrence (EOO) is less than 5000km AND at least two a-c criteria
ENB1.part1<-apply(EOO,2,function(x){  x < 5000 })*1
#EN.B.2 area of occupancy (AOO), is less than 500km (part1) AND *two* of a-c criteria (part2)
#ENB2 Part 1:AOO is less than 500km
ENB2.part1<-apply(AOO,2,function(x){x < 500 })*1
#Part 2: At least two of a-c:
#ENB Part 2 a: Severely Fragmented OR known to exist at no more than 5 populations
ENB.part2.a<-(SevereFrag+fiveLoc >=1)
#ENB Part 2 b: Continuing decline (Calculated above combined to single var)
#ENB Part 2 c: Extreme fluctuations (Calculated above combined to single var)
#NOTE: This is for Extreme fluctions over 2 generations - 3 gen is option
#Determine if 2 of a-c is met
ENB.part2<-(ENB.part2.a+ContDecline+ExFluc2gen >= 2)*1
# ENB1 and ENB2 (including parts 1 and 2)
ENB1 <- ENB1.part1*ENB.part2
ENB2 <- ENB2.part1*ENB.part2
ENB<-ENB2 + ENB1 >= 1

                                              ###Criterion C ######
### To meet this criterion Part 1 AND Part 2 most both be met
### Criterion C - Part 1: Population size estimated to number fewer than 2500 mature
ENC.part1<-apply(Nmature,2,function(x){ x < 2500  })*1

#Criterion C - Part 2:  Contdition 1 OR condition 2
#Cond 1. Continuing decline of at least 20% within 5 years
#or two generations whichever is longer OR
#Cond 2. Continuing decline in N mature AND sub condition a or b:
#a: popualtion structure such that condition (i) OR (ii)
# (i) there are no subpopulation with at least 250 mature
# (ii)  at least 95% of mature indv. in single pop
#b: Extreme fluctuations in N mat (calculated over 2 generations change for 3)
ENC.part2.cond1<-apply(percentreduction[[2]],2,function(x){   x >= 20  })*1
ENC.part2.cond1 <- replace(ENC.part2.cond1, is.na(ENC.part2.cond1),0)
ENC.part2.cond2.ai<-apply(LargestPopSize,2,function(x){ x<=250  })*1
ENC.part2.cond2.aii<-apply(PropInLargestPop,2,function(x){ x >= .95 })*1
```

```
ENC.part2.cond2.a <- (ENC.part2.cond2.ai + ENC.part2.cond2.aii >= 1)*1
ENC.part2.cond2.b <- ExFluc2gen.Nmature *1
ENC.part2.cond2 <- (ENC.part2.cond2.a + ENC.part2.cond2.b >=1)
ENC.part2.cond2 <- (ENC.part2.cond2*ContDecline.lnNmat)*1
ENC.part2 <- (ENC.part2.cond1 + ENC.part2.cond2 >=1)*1
ENC<-ENC.part1*ENC.part2

###Criterion D ######

# D Population size estimated fewer 250 mature
END<-Nmature < 250
END <-END*1
####Criterion E Not Calculated #####
#####  Determine Endangered   #######

EN<-(ENA+ENB+ENC+END)>=1
EN <- EN*1
#change 0's to NA's
EN[EN==0]<-NA
EN<-EN+2

############################## Vulnerable ######################

## Criterion A ####
# VU.A.1 50% reduction where cause is understood and ceased - not modeled
# VU.A.2 30% reduction over 3 generations or 10 years (and possibly ongoing)
VUA2<-apply(percentreduction[[3]],2,function(x){  x >= 30 })*1
VUA2<-replace(VUA2, is.na(VUA2),0)
VUA<-VUA2

##Criterion B ##
### Criterion B is met if B1 OR B2 is met
#VU.B.1 extent of occurrence (EOO) is less than 20,000km (part1) AND *two* of a-c criteria (part2)
VUB1.part1<-apply(EOO,2,function(x){ x < 20000 })*1
#VU.B.2 area of occupancy (AOO), is less than 2,000km (part1) AND *two* of a-c criteria (part2)
#VUB2 Part 1:AOO is less than 2,000km
VUB2.part1<-apply(AOO,2,function(x){ x < 2000 })*1
#Part 2: At least two of a-c:
#VUB Part 2 a: Severely Fragmented OR known to exist at no more than 10 locations
VUB.part2.a<-(SevereFrag+tenLoc >=1)
#VUB Part 2 b: Continuing decline (Calculated above combined to single var)
#VUB Part 2 c: Extreme fluctuations (Calculated above combined to single var)
#NOTE: This is for Extreme fluctions over 2 generations - 3 gen is option
#Determine if 2 of a-c is met
VUB.part2<-(VUB.part2.a+ContDecline+ExFluc2gen >= 2)*1
# VUA1 and VUB2 (including parts 1 and 2)
VUB1<-VUB1.part1*VUB.part2
VUB2<-VUB2.part1*VUB.part2
VUB<-VUB2 + VUB1 >= 1

###Criterion C ######
### To meet this criterion Part 1 AND Part 2 most both be met
### Criterion C - Part 1: Population size estimated to number fewer than 10,000 mature
VUC.part1<-apply(Nmature,2,function(x){  x < 10000  })*1
  #Criterion C - Part 2:  Contdition 1 OR condition 2
#Cond 1. Continuing decline of at least 10% within 10 years
```

```
  #or three generations whichever is longer OR
  #Cond 2. Continuing decline in N mature AND sub condition a or b:
  #a: popualtion structure such that condition (i) OR (ii)
  # (i) there are no subpopulation with at least 1000 mature
  # (ii)  100% of mature indv. in single pop
  #b: Extreme fluctuations in N mat (calculated over 2 generations change for 3)
  VUC.part2.cond1<-apply(percentreduction[[3]],2,function(x){  x >= 10 })*1
  VUC.part2.cond1 <- replace(VUC.part2.cond1, is.na(VUC.part2.cond1),0)
  VUC.part2.cond2.ai<-apply(LargestPopSize,2,function(x){   x<=1000 })*1
  VUC.part2.cond2.aii<-apply(PropInLargestPop,2,function(x){   x >= 1 })*1
  VUC.part2.cond2.a <- (VUC.part2.cond2.ai + VUC.part2.cond2.aii >= 1)*1
  VUC.part2.cond2.b <- ExFluc2gen.Nmature *1
  VUC.part2.cond2 <- (VUC.part2.cond2.a + VUC.part2.cond2.b >=1)
  VUC.part2.cond2 <- (VUC.part2.cond2*ContDecline.InNmat)*1
  VUC.part2 <- (VUC.part2.cond1 + VUC.part2.cond2 >=1)*1
  VUC<-VUC.part1*VUC.part2

                                   ###Criterion D ######
#D Either (1) Population size estimated fewer 1000 mature  OR
  # (2) AOO < 20km or Number of locations <= 5
  VUD.1<-Nmature < 1000
VUD.2<-apply(AOO,2,function(x){   x < 20 })*1
    VUD.2<-(VUD.2 + fiveLoc)>=1
    VUD <-(VUD.1 + VUD.2 >=1)*1

                               ####Criterion E Not Calculated #####
                              #####  Determine Vulnerable   #######
  VU<-(VUA+VUB+VUC+VUD)>=1
  VU <- VU*1
  #change 0's to NA's
  VU[VU==0]<-NA
  VU<-VU+3

  ##############################Near Threatened######################

                                    ## Criterion A ####
  # NT - Decline over 3 generations of 20%
  NTA2<-apply(percentreduction[[3]],2,function(x){ x >= 20  })*1
  NTA2<-replace(NTA2, is.na(NTA2),0)
  NTA<-NTA2

                                     ##Criterion B ##
  ### Criterion B is met if B1 OR B2 is met
  #Near threatened category is less precisely defined. Here it is defined as meeting the
  #area requirement for threatned with only one (rather than 2) of a-c
  #OR
  #meeting a NT threshold of 30,000km2 for EOO or 3,000km2 for AOO and 2 of a-c
  #NTB1 Part 1:EOO is less than 30,000km
  NTB1.part1<-apply(EOO,2,function(x){ x < 30000 })*1
  #NTB2 Part 1:AOO is less than 3,000km
  NTB2.part1<-apply(AOO,2,function(x){ x < 3000})*1
  #Part 2: At least one of a-c:
  #NTB2 Part 2 a: Severely Fragmented OR known to exist at no more than 15 locations
  NTB.part2.a<-(SevereFrag+fifteenLoc >=1)
  #NTB Part 2 b: Continuing decline (Calculated above combined to single var)
  #NTB Part 2 c: Extreme fluctuations (Calculated above combined to single var)
```

```
#NOTE: This is for Extreme fluctions over 2 generations - 3 gen is option
#Determine if any 1 or at least 2 of a-c is met
NTB.part2.any<-(NTB.part2.a+ContDecline+ExFluc2gen >= 1)*1
NTB.part2.two<-(NTB.part2.a+ContDecline+ExFluc2gen >= 2)*1
# NTB1 (including parts 1 and 2)
NTB1a<-VUB1.part1*NTB.part2.any
NTB1b<-NTB1.part1*NTB.part2.two
NTB1<-(NTB1a+NTB1b>=1)*1
# NTB2 (including parts 1 and 2)
NTB2a<-VUB2.part1*NTB.part2.any
NTB2b<-NTB2.part1*NTB.part2.two
NTB2<-(NTB2a+NTB2b>=1)*1
NTB<-NTB2 + VUB1 >= 1

                    ###Criterion C ######
### To meet this criterion Part 1 AND Part 2 most both be met
### Criterion C - Part 1: Population size estimated to number fewer than 15,000 mature
NTC.part1<-apply(Nmature,2,function(x){ x < 15000 })*1

#Criterion C - Part 2:  Contdition 1 OR condition 2
#Cond 1. Continuing decline of at least 10% within 10 years
#or three generations whichever is longer (note: this is the same as VU) OR
#Cond 2. Continuing decline in N mature AND sub condition a or b:
#a: popualtion structure such that condition (i) OR (ii)
# (i) there are no subpopulation with at least 1500 mature
# (ii)  100% of mature indv. in single pop (note: this is the same as VU)
#b: Extreme fluctuations in N mat (calculated over 2 generations change for 3)
NTC.part2.cond2.ai<-apply(LargestPopSize,2,function(x){ x<=1500  })*1

NTC.part2.cond2.a <- (NTC.part2.cond2.ai + VUC.part2.cond2.aii >= 1)*1
NTC.part2.cond2 <- (NTC.part2.cond2.a + VUC.part2.cond2.b >=1)
NTC.part2.cond2 <- (NTC.part2.cond2*ContDecline.lnNmat)*1
NTC.part2 <- (VUC.part2.cond1 + NTC.part2.cond2 >=1)*1

NTC<-NTC.part1*NTC.part2

#D Either (1) Population size estimated fewer 1500 mature  OR
# (2) AOO < 30km or Number of locations <= 5
NTD.1<-Nmature < 1500
  NTD.2<-apply(AOO,2,function(x){ x <= 30})*1
  NTD.2<-(NTD.2 + fiveLoc)>=1
  NTD <-(NTD.1 + NTD.2 >=1)*1

                ####Criterion E Not Calculated #####
             #####  Determine Near Threatened   #######
NT<-(NTA+NTB+NTC+NTD)>=1
NT <- NT*1
#change 0's to NA's
NT[NT==0]<-NA
NT<-NT+4
################################################################################
redlist.cat <- pmin(EX,CR,EN,VU,NT, na.rm =TRUE) #combine categories into single table
redlist.cat <- replace(redlist.cat, is.na(redlist.cat), 6)
```