STATUS, DISTRIBUTION, AND POPULATION MODELING OF RED-CROWNED PARROTS AND CONSERVATION OPPORTUNITIES OF NATURALIZED PARROTS

A Dissertation

by

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ABSTRACT

Urbanization and the global transport of animals are interconnected aspects of ecology that play significant roles in the conservation of species. Both scenarios are viewed in a mostly negative light – in part, urbanization can destroy habitat while the establishment of animals outside their native range can wreak havoc on ecosystems. In contrast, these urban landscapes may provide unique opportunities for some species which can take advantage of highly modified environments. Red-crowned Parrots are an Endangered species of *Amazona* parrot which are native to northeastern Mexico and the lower Rio Grande Valley of Texas, but also have naturalized populations in urban regions of southern California and Florida. My research sought to discover a timeline of the bird's arrival in south Texas, determine current population size and productivity, as well as determine habitat use and threats. Species distribution modeling was also utilized to determine Red-crowned Parrot's levels of dependency on urban areas throughout the United States. Besides Red-crowned Parrots, upwards of 59 parrot species have established naturalized populations outside their normal ranges, and while much has been written about the real and potential negative aspects of these populations, little effort has been made to describe the real or potential positives. In that essence, I set to review the benefits of naturalized parrot populations with a focus on conservation, research, and societal impacts. My work found a healthy and growing population of Red-crowned Parrots in south Texas which is heavily reliant on urban and suburban areas. In addition, populations found in southern California and Florida showed similar urban dependencies. Threats to these populations include poaching and hybridization with other naturalized and closely related *Amazona* parrots; after quantifying levels of hybridization and modeling the future of the south Texas population relative to this threat, I found that management actions may be needed to ensure the genetic integrity of this threatened population. Naturalized populations of threatened and endangered parrots hold potential to help mitigate population declines elsewhere and could represent valuable genetic reservoirs. When these populations are located within highly modified habitats, they may also help mitigate the potential biodiversity loss created by urbanization. Whether the birds were purposefully introduced or accidentally released or escaped captivity, those that do become naturalized may provide unique opportunities for researchers and conservation.

CONTRIBUTORS AND FUNDING SOURCES

Contributors

This work was supervised by a dissertation committee chaired by Dr. Donald J. Brightsmith of the Department of Veterinary Pathobiology and included members Dr. Hsiao-Hsuan Wang, Dr. William E. Grant, and Dr. Thomas E. Lacher of the Department of Ecology and Conservation Biology.

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1. INTRODUCTION

Urbanization is one of the leading causes of biodiversity loss and often results in habitat degradation and fragmentation (Ceballos et al., 2015; Schmidt et al., 2020). Despite this, many organisms can thrive in highly modified environments and hold close associations with people and include commonly known species like the Rock Pigeon (*Columba livia*), European Starling (*Sturnus vulgaris*), and the House Mouse (*Mus musculus*). These species are termed synanthropes and have benefitted from the spread of urbanization across the globe (McKinney, 2006). Understanding the dynamics of synanthropes, including how and when they are transported and introduced to new ecosystems and how they take advantage of novel environments, is crucial to efficient management of a species. Much of the time synanthropes are considered as pests and management seeks to limit their spread or eradicate them where they have become naturalized as in the cases of Norway Rats (*Rattus norvegicus*) and Monk Parakeets (*Myiopsitta monachus*)(Feng & Himsworth, 2014; Senar et al., 2021). But in some rare instances, synanthropic species also happen to be threatened or endangered within their native range and habitats (Shaffer, 2018). One such species is the Red-crowned Parrot (*Amazona viridigenalis*), an endangered species of parrot native to northeast Mexico where their populations have suffered precipitous declines over the past century (Enkerlin-Hoeflich, 1995). My work sets out to understand more thoroughly the associations that Red-crowned Parrots have with their urban environment to better manage and predict the future of this endangered parrot as well as to better understand the role that urban areas may play in conserving threatened species.

For over 2000 years parrots have been transported by humans as pets and sources of food (Calzada Preston & Pruett-Jones, 2021). Most of the almost 400 species of parrots have been subjected to the pet trade, and while there is rarely intent to introduce these birds into novel environments outside of their native ranges, some individuals may escape or are otherwise released giving them the opportunity to become established in novel areas (Calzada Preston & Pruett-Jones, 2021). Propagule pressure plays an important role in the ability for a species to become established, since the higher number of individuals and release events that take place, the higher the chance at successful colonization (Lockwood et al., 2005). Propagule pressure with parrots is high - since 1975, tens of millions of parrots have been traded globally representing almost 25% of all legal bird trade – the real number of parrots being transported is undoubtedly much higher when including illegal trade (Senar et al., 2021). As a result of this trade, roughly 60 species of parrot have become naturalized and are successfully breeding and maintaining populations outside of their native ranges (Calzada Preston & Pruett-Jones, 2021). The United States plays host to at least 28 of these species, one of which is the Red-crowned Parrot with naturalized populations in Florida, California, Hawaii, and Puerto Rico in addition to their native population in the southern tip of Texas. South Texas also plays host to populations of six nonnative parrot species: namely Monk Parakeet, Green Parakeet (*Psittacara holochlorus*; native/nonnative status in dispute), White-fronted Parrot (*Amazona albifrons*), Yellow-headed Parrot (*Amazona oratrix*), Red-lored Parrot (*Amazona autumnalis*), and Lilac-crowned Parrot (*Amazona finschi*).

As human activities have brought together previously isolated taxa, the opportunities for hybridization increase – especially so when these taxa are closely related, as in the case with the previously mentioned *Amazona* parrots in south Texas. During my field work it became apparent that hybridization between Red-crowned Parrots and other *Amazona* parrots was taking place – especially with their sister species the Lilac-crowned Parrot which originates from the Pacific coast of Mexico. We describe this as anthropogenic hybridization and it can have both positive and negative impacts on populations and on conservation efforts (Allendorf et al., 2012).

Hybridization can lead to increased genetic variation which may benefit conservation efforts by increasing adaptive potential and fitness in small populations (Whiteley et al., 2015). However, hybridization can also result in a loss of genetic integrity and decreases in fitness in hybrid offspring, and can lead to genetic swamping or even species extinctions (Abbott et al., 2013). From a conservation perspective, it's important to consider the specific context in which anthropogenic hybridization is occurring and the potential impacts it may have on the populations involved (Muhlfeld et al., 2014). This becomes especially paramount when the hybridizing species are species of conservation concern, as is the case for both Lilac-crowned and Red-crowned Parrots in south Texas.

Red-crowned Parrots are a range-restricted *Amazona* parrot species endemic to northeast Mexico and the extreme southern tip of Texas, normally inhabiting tropical lowland forests, deciduous woodlands, and gallery forests centered on the Atlantic slope of Tamaulipas and San Luis Potosi (Enkerlin-Hoeflich & Hogan, 2020; Monterrubio-Rico et al., 2016). Populations in Texas were declared to be native around 2014 owing to somewhat ambiguous records of parrots in the late 19th century from Brownsville to Corpus Christi; this declaration allowed avenues of funding through the State of Texas to study current populations in the Texas counties of Hidalgo and Cameron. During this time, it was especially prudent to study the species as they were listed as a Candidate Species for listing under the Endangered Species Act through the United States Fish and Wildlife Service (U.S. Fish and Wildlife Service, 2019). The species apparent successes in south Texas, as well as the successful naturalized populations in Florida and California, have ran counter to populations in Mexico where populations have been declining for decades (Enkerlin-Hoeflich, 1995). The ability to succeed in highly modified habitats in the southern United States is not clearly understood, and little information on these populations is available. My dissertation sets out to better understand dynamics of urbanized and naturalized species using Red-crowned Parrots as a model system, as well as to better understand the possible benefits and drawbacks of naturalized populations of parrots in general.

Chapter two of this dissertation reviews the history of Red-crowned Parrots in the Lower Rio Grande Valley of Texas to better understand the origins and establishment of the species within the state. I also use past data from eBird and Christmas Bird Counts as well as current data from field work collected from 2016 through 2019 to better understand the current population status and trends. This chapter was published in *Bird Conservation International* with the title “History, status, and productivity of the Red-crowned Amazon *Amazona viridigenalis* in the Lower Rio Grande Valley of Texas”.

Chapter three produced coarse-scale national level species distribution models of the three continental Red-crowned Parrot populations in the United States. Four models were created: one using all presence points within the continental USA and one each using only presence points within either California, Texas, or Florida. The intent was to (1) describe the current geographical range of Red-crowned Parrots within the United States and to analyze their potential for future spread; (2) determine whether the models produced predict Red-crowned Parrot presence similarly to one another; (3) determine important climatic and environmental variables that are determining Red-crowned Parrot presence; and (4) to determine whether Red-crowned Parrots throughout the contiguous United States are responding to climatic and environmental variables similarly. This chapter has been published in the journal *Diversity* and is titled “Presence of Endangered Red-Crowned Parrots (*Amazona viridigenalis*) Depends on Urban Landscapes”.

The fourth chapter of this dissertation takes a closer look at the consequences of hybridization between Red-crowned Parrots and similar species in south Texas including Yellow-headed Parrots, Red-lored Parrots and the Red-crowned Parrots sister species, Lilac-crowned Parrots. During field studies in south Texas, it became apparent that Red-crowned Parrots were occasionally hybridizing and raising young, mainly with Lilac-crowned Parrots; many intermediate phenotype individuals were also being seen. For this chapter, I utilized data collected by my team in south Texas as well as information collected through literature searches to build a population viability model using Stella Architect to examine the potential population level impacts of anthropogenic hybridization among populations of *Amazona* parrots in south Texas. This study will shine a light on a potential threat to populations of naturalized animals which may negate some of the positive aspects of these populations.

The fifth chapter analyzed the potential conservation and research opportunities of naturalized parrots more generally to offset the more numerous studies that have focused on the real and perceived negative economic, ecological, or societal issues that naturalized parrot populations have caused. The goal was to take a more holistic look at an issue that is generally seen in a negative light. This chapter was included as a chapter in a book published by Princeton University Press titled “Naturalized Parrots of the World: Distribution, Ecology, and Impacts of the World's Most Colorful Colonizers”.

Naturalized populations of parrots throughout the United States have not received much attention from researchers, even though some of these populations consist of species of conservation concern. The idea that the birds “do not belong” in these areas strikes me as irrelevant when it comes to trying to understand or manage for or against these populations, and this is especially true considering the lack of knowledge we have in general about *Amazona* parrots, or Psittaciformes more generally. As the world is becoming more urbanized and human populations are growing exponentially, our understanding of how taxa survive and coexist alongside and within highly modified landscapes is becoming more crucial. This dissertation creates a body of work that is foundational for not only the future of Red-crowned Parrots, but of naturalized parrots more generally and even beyond the realm of Psittaciformes. It is my hope that this research spurs attention to the plight of naturalized species and encourages researchers to look more critically at taxa living in our backyards.

2. HISTORY, STATUS, AND PRODUCTIVITY OF THE RED-CROWNED AMAZON *AMAZONA VIRIDIGENALIS* IN THE LOWER RIO GRANDE VALLEY OF TEXAS[1]

2.1. Summary

Newly established populations of endangered species can help mitigate declines elsewhere and can be a valuable genetic reservoir. When these populations are located within anthropogenic habitats, they may also help mitigate the potential biodiversity loss created by urbanization. The Red-crowned Amazon (*Amazona viridigenalis)* is an endangered species that has become naturalized in multiple urban areas throughout the United States and Mexico, and these populations may currently outnumber the population within their historical habitat. While these urban populations may hold the majority of this endangered species, very few studies have analyzed the status and trends of this species, or of threatened parrots in general, in urban areas. Our study focuses on an urban Red-crowned Amazon population in the Lower Rio Grande Valley (LRGV) of Texas: the only parrot population currently recognized as native to the United States. To determine a timeline of Red-crowned Amazon arrival and growth in the LRGV, we reviewed published literature and online citizen science databases. To quantify current

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population levels and trends, we conducted 412 surveys at all known roost sites throughout the LRGV from January 2016 through April 2019.We also quantified the ratio of adult and juvenile parrots at roosts. Our data suggest the species has been present in the LRGV consistently since the 1970s and showed rapid growth from the mid-1990s through roughly 2016. Roost counts suggest there is currently a minimum LRGV population of about 680 and the population has been relatively stable over the last 3.5 years. Productivity averaged 19% over three breeding seasons, suggesting successful internal reproduction. This study provides important baseline information for the management and conservation of Red-crowned Amazons in the region and provides a valuable timeline on the beginnings and trends of this recently established urban population of *Amazona* parrot.

2.2. Introduction

Red-crowned Amazons *Amazona viridigenalis* (hereafter RCAM) are a range-restricted species inhabiting north-eastern Mexico and extreme southern Texas (BirdLife International, 2023). Throughout the 20th century, the species was eliminated from 50–85% of its already limited native range largely due to habitat conversion for agriculture and harvest for the pet trade (Enkerlin-Hoeflich, 2000; Enkerlin-Hoeflich & Hogan, 2020; Monterrubio-Rico et al., 2016; Ríos-Muñoz & Navarro-Sigüenza, 2009). Since the early 1900s, the population is estimated to have decreased by c.95%, from over 100,000 to a currently estimated 3,000–6,500 (BirdLife International, 2023; Enkerlin-Hoeflich, 2000). Because of this large and rapid decline in population and habitat, Red-crowned

Amazons are currently designated as ‘Endangered’ by IUCN and by the Mexican government (BirdLife International, 2023).

Since the 1960s in the United States, the legal and illegal pet trade has helped Red-crowned Amazons establish naturalized populations in urban areas of California, Florida, Puerto Rico, and Hawaii (Uehling et al., 2019). However, the origin of the population in the Lower Rio Grande Valley (LRGV) of south Texas has been a topic of debate among ornithologists for decades (Webster, 1974, 1977). Some authors maintain that the birds arrived naturally during hard winters of the mid-1980s, as the LRGV is roughly 175 km north of the historically described range for Red-crowned Amazons and the species regularly undergoes long-range dispersal during the winter season in search of food (Enkerlin-Hoeflich & Hogan, 2020; Webster, 1982). This scenario is supported by habitat maps which suggest the LRGV is at the northern edge of the species’ range and that parrots were reported in south Texas sporadically from the late 1800s throughout the mid-20th century (Casto, 2010; Monterrubio-Rico et al., 2016). However, other authors (Enkerlin-Hoeflich & Hogan, 2020) maintain that the population is likely not native, as Red-crowned Amazons were commonly traded across the Rio Grande into Texas during the 1970s and early 1980s (Iñigo-Elias & Ramos, 1991). Some authors believe that the current LRGV population of Red-crowned Amazons consists of both naturally dispersed birds and those released from the pet trade (Neck, 1986). Regardless of how the birds arrived, the State of Texas and United States Fish and Wildlife Service (USFWS) consider, for legal purposes, that the LRGV population of Red-crowned Amazon is native to the USA (U.S. Fish and Wildlife Service).

Although the Mexican population of RCAM has declined precipitously since the 1970s, the LRGV population and the introduced populations in the U.S.A. have been stable or growing over the past five decades and together may currently outnumber the native populations in Mexico (Uehling et al., 2019). As a result, these populations are an important reservoir for this endangered species, but a lack of protection and management of these populations means that poaching, habitat change, and hybridization could prove detrimental to their future existence.

The RCAM is protected by city ordinances throughout its range in the LRGV (Harlingen §90.03, Brownsville Ordinance No. 92-1249). These laws protect nest sites and the birds against poaching and harassment. At the state level they are considered a native species, but their protection is ambiguous due to conflicting state laws (Parks and Wildlife Code §§ 67.001(1985), 64.002(d) (2009)). Recently, the species was listed as threatened by the State of Texas (Parks and Wildlife Code §65.175). At the federal level, the USFWS had considered the species for listing under the Endangered Species Act (ESA) but it was denied listing and removed from consideration in 2019. The species is also not listed on the Migratory Bird Treaty Act (see 50 CFR § 10.13 for a complete list of protected species) and as a result, it receives no protection at the federal level.

The likely native origin of some birds, and close proximity to the native population in Mexico, make the south Texas population of the globally 'Endangered' Red-crowned Amazon a valuable conservation resource. Its presence outside Mexico is also valuable, as parrot species occurring in more than one country have a lower risk of extinction (Olah et al. 2016). Usually, residential and commercial development are a threat to parrots globally (Olah et al., 2016). However, Red-crowned Amazons in the United States seem to be dependent on human-modified habitats (Garrett, 2018; Mabb, 2003; Meseck, 2013; Uehling et al., 2019). Besides those considered to be invasive (Monk Parakeet *Myiopsitta monachus* and Rose-ringed Parakeet *Psittacula krameri*) there has been little research on urbanized parrots, and those in south Texas are no exception, with only one detailed study taking place over three decades ago (Neck, 1986).

In this study, we review the history of the species in the LRGV to look for new insights into the origins of the population. We also use online databases of bird sightings (CBC and eBird) to document the establishment and growth of the population in south Texas. We use three years of fieldwork on RCAM in the LRGV to estimate the current population status and the proportion of young in the population. Our results help us understand the history surrounding the species in the LRGV and provide a baseline that gives managers important information on how to conserve this valuable population of Red-crowned Amazons.

2.3. Methods

2.3.1. Study Area

This study focuses on historical and current records of RCAM in the LRGV in Cameron and Hidalgo counties, Texas, USA. This is the northern extent of the RCAM's native range, which is centered on the Atlantic slope of Tamaulipas and San Luis Potosi in north-eastern Mexico (Enkerlin-Hoeflich & Hogan, 2020; Monterrubio-Rico et al., 2016; Ríos-Muñoz & Navarro-Sigüenza, 2009). The LRGV population is thought to have little to no current exchange with populations in Mexico, so no records in Mexico were taken into consideration for this study. There are also a few records of RCAM from Texas north of the LRGV, but these are likely from released or escaped pets and were not included in our analyses with the exception of mentions in historical narratives.

The LRGV contains four known RCAM roosts – one each in the cities of Brownsville, Harlingen, Weslaco, and McAllen. These roosts are separated by an average of about 30 km. Roosts were found in suburban neighborhoods in all cities except Brownsville, where the roost was always in a 24-acre (9.7 ha) city park. In Harlingen, Weslaco, and McAllen the exact roost locations varied within a radius of about 1.5 km but were always located in the same type of suburban neighbourhood. For our data collection and analyses we divided the LRGV into four sections with each section containing one of the four roosts (Figure 1). The Lower Rio Grande Valley is generally flat, with the main habitats including coastal wetlands, remnant riparian forests along the Rio Grande and its oxbow lakes, and Tamaulipan thorn scrub (Brush, 2005; Monterrubio-Rico et al., 2016). Although some natural habitat does exist, RCAM inhabit urban and suburban areas almost exclusively. The neighbourhoods containing RCAM roosts and nests generally consist of small (0.1 to 0.5 ha) properties. These plots usually contain a home and moderately landscaped yards. Yards contain turf and a wide variety of native and nonnative shrubs and small citrus trees. Larger trees were usually mesquite (*Prosopis* sp.), live oak (*Quercus virginiana*), *Washingtonia* spp. palms, ash (*Fraxinus* sp.), and other native and non-native trees to a lesser extent. The LRGV consists of a humid subtropical climate in the east which transitions to a hot semiarid climate in the west and annual rainfall averages 697 mm in Brownsville to the east and 564 mm in McAllen in the west (NOAA 2018). Much of the LRGV has been converted to agriculture and the metro areas are urbanizing rapidly (U.S. Census Bureau, 2011).

2.3.2. Historical presence in South Texas

To determine when RCAM first appeared in Texas we reviewed the published literature by searching Google Scholar for the terms “Red-crowned Amazon AND Texas”, and “Amazon viridigenalis AND Texas” while replacing the term “Red-crowned Amazon” with other common names such as “Red-crowned Parrot” and “Green-cheeked Amazon”. All resulting publications mentioning parrots in Texas were reviewed. Many of the earliest records mention “parrots” or “green parrots” and provide no scientific or common names. Green Parakeets *Psittacara holochlorus*, Yellow-headed Amazons *Amazona oratrix*, and Red-lored Amazons *Amazona autumnalis* share similar color and characteristics with Red-crowned Amazons and occur naturally in northern Tamaulipas, Mexico. The possibility that these early accounts were of these other species cannot be discounted. However, owing to the large population of RCAM in the late 1800s, their propensity to wander during the non-breeding season, and their close proximity to the Rio Grande (Enkerlin-Hoeflich, 2000), it is reasonable to presume that at least some of the birds mentioned were Red-crowned Amazons.

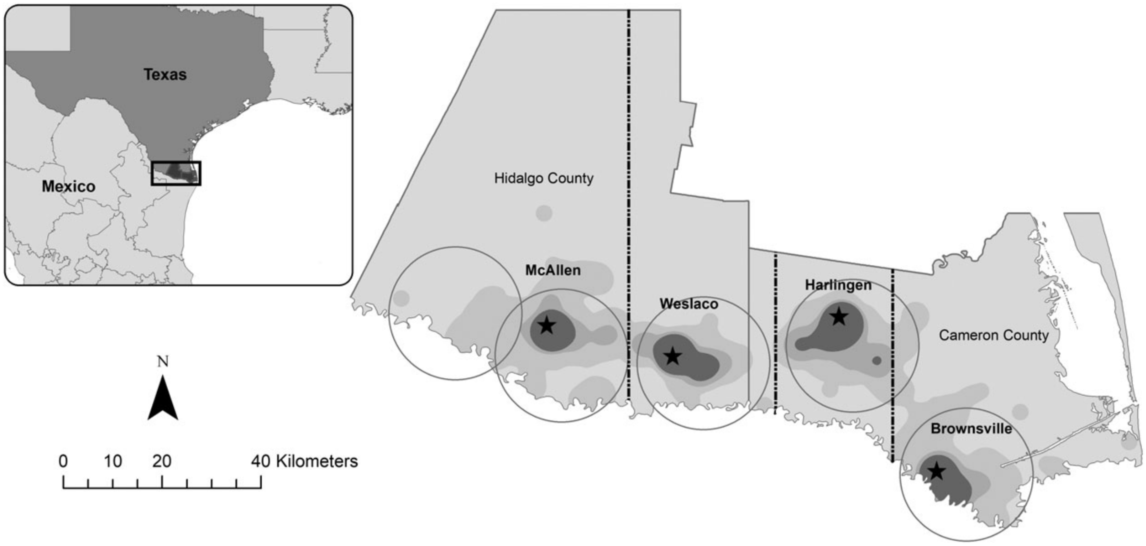

Figure 1. Red-crowned Amazon range map throughout the Lower Rio Grande Valley of Texas. Dotted lines separate eBird, iNaturalist, and Christmas Bird Count locations used in this study by longitude to coincide with their respective roosting areas. Shaded areas represent where Red-crowned Amazons were seen most often from June 2016 through May 2019 and were created in ArcMap 10.6.1. Roosts occurred in the areas marked by stars. The five circles represent the 24-km diameter Christmas Bird Count circles that recorded Red-crowned Amazons at least once in their history. Reprinted with permission from (Kiacz et al., 2021).

To analyse trends of Red-crowned Amazons in the LRGV, we downloaded the eBird Basic Dataset through April 2019 and filtered sightings using the auk R package (eBird Basic Dataset, 2019; Strimas-Mackey et al., 2017). Sightings were confined to only Cameron and Hidalgo counties. All bird checklists submitted to eBird containing sightings of Red-crowned Amazons were analysed and duplicate sightings and checklists were removed. To avoid data duplication, the first author's (S. Kiacz) personal eBird submissions were removed from the analyses since many of the checklists contain the same counts used in the "Roost Counts" section of our study. After data filtering, 8,362 eBird reports of RCAM were left for analysis. In order to establish the geographic origins and spread of RCAM across the LRGV, we report the earliest eBird records for each major LRGV city. To determine whether RCAM were being reported more often over time, we analysed the percentage of checklists (complete and incomplete) which registered RCAM presence each year. In order to illustrate overall population trends, the 10 highest eBird counts per year since RCAM arrival in the LRGV are reported as a three-year moving average.

To provide another independent view of the arrivals and trends of RCAM, we used Christmas Bird Count (CBC) data, which includes wintering (December–January) bird count data from 24-km diameter count circles (National Audubon Society, 2010). Counts are conducted by local volunteers and the number of participating volunteers and execution of different counts is variable among years. To analyse overall trends, we combined and graphed the total number of RCAMs from all LRGV count circles reporting them through time as a three-year moving average. Six count circles have reported RCAM in the LRGV, including counts centered near Brownsville, Harlingen, Weslaco, and McAllen (Figure 1). These counts encompass the main areas in which RCAM roost and nest. One count circle, centered on Brownsville, was discontinued in the 1980s but started anew from the same location during the same time although it used a different count code, so only five count circles are shown in Figure 1.

2.3.3. Roost Counts

To quantify current LRGV population size, we collected roost attendance data from each of the four known roosts from June 2016 to May 2019 (n = 412). Counts were conducted during the spring (March–May; n = 104), summer (June–August; n = 137), fall (September–November; n = 50), and winter (December–February; n = 121).

Here we report results from two different, but similar, types of counts. The Tejano Parrot Project (TPP), a group consisting of the lead author and local volunteers trained by the lead author, conducted most counts (n = 356). One or two TPP members conducted a single roost count per night, covering all four roosts over a one-week period. To calculate weekly aggregates of the total roosting population across the LRGV, counts from each roost within a seven-day span were added together (these will be referred to as "TPP" counts hereafter). Weekly aggregates during which RCAM were likely double counted because birds moved from their home roost to a neighbouring roost (roost switching) were omitted from our analyses. Roost switching was evident when one roost would have limited or no RCAM attendance while a neighbouring roost had an unusually high number of RCAM within a one-week span. Additionally, we report results from quarterly counts organized by the Texas Parks and Wildlife Department conducted in January, April, July, and October (n = 56). TPWD counts were conducted at all four roosts simultaneously by an average of 42 volunteers per count (range = 28–71; these counts will be referred to as "TPWD" counts hereafter). The TPWD counts gave LRGV minimums without the chance of roost switching biases but required a large contingent of volunteers. Both TPP and TPWD counts used the methodology explained in the following paragraph.

Surveyors arrived in the general roost areas an average of 60 minutes before sunset to count the parrots as they arrived at the roosts. Roosts were not surveyed during thunderstorms or other severe weather because sighting birds became difficult and parrots may not attend roosts during such weather (Cougill & Marsden, 2004). Surveys were not done in the morning because parrots left the roosts quickly and in large flocks making counting difficult and inaccurate. Additionally, parrots at three of the four sites did not consistently roost at the same location so surveyors were unlikely to find the roosts before the parrots left in the morning. In Brownsville, Red-crowned Amazons roosted in the same park every night during this study, so all observers waited in the park and counted parrots as they arrived. At the other three sites, RCAM regularly roosted within the same neighbourhoods, but not in the same location. For TPP counts, observers drove through these neighbourhoods until they found the parrots and once found, parrots were followed, counted, and photographed. For TPWD counts, observers were stationed at different points around the city and reported groups as they flew in, then followed the main group once it was located. Final counts were usually obtained just before sunset when the majority of the birds flew as a single flock or perched as a group on power lines. If photos were obtained, exact counts were acquired by counting individual RCAM on the photos, otherwise counts were determined by counting flock size by groups of 5–10 individuals.

2.3.4. Historical and current nesting in South Texas

Nesting data were gathered from previous RCAM accounts reported in various outlets as well as from online databases such as the Texas Breeding Bird Atlas (Benson & Arnold, 2001) and iNaturalist. Additional nesting data were collected by our team during the breeding seasons (March–May) of 2017 and 2018. We found nests by surveying suburban areas throughout the LRGV by car and searching for duetting pairs of RCAM and locating trees with potential cavities. Some RCAM pairs were followed until nesting locations were found. Locations of trees with cavities were noted and revisited multiple times throughout the breeding season to determine whether cavities had active nests. Nesting activities were considered “likely” if a cavity was large enough for a parrot and RCAM were heard/seen duetting nearby (<50 m). Nests were considered active if RCAMs were seen emerging from the cavity when the base of the tree was gently knocked on, RCAM were seen entering the cavity, or RCAM were seen in the nest cavity using a camera probe on a telescoping pole.

2.3.5. Productivity

Juvenile attendance at roosts was estimated by counting the number of adults and juveniles while conducting TPP roost counts. During our roost counts, we detected juveniles as early as mid-June and as late as February. However, we report productivity from July and August when the majority of fledglings that were attending roosts still had obvious physical features separating them from adults (eye colour, overall size, tail length) in addition to begging behaviour and poorer flight skills. During each TPP roost count, we checked as many RCAM as possible for adult/juvenile status. To avoid double-counting individuals during roost counts we only counted groups of birds as they flew into the roost and landed, and avoided as much as possible any individuals moving within the roost. When possible, we would count adults and juveniles when large groups lined up on power lines. To avoid biased estimates due to small sample sizes in our estimates of overall juvenile percentages, we excluded from our analyses counts when we checked <10%of the total roost or <20 individuals for adult/juvenile status. Fifty-two counts met our threshold and on average we were able to check 38% (60 ± 32) of parrots attending the roosts for adult/juvenile status.

2.3.6. Data analysis

Individual roost counts (n = 412) and aggregated roost counts (n = 80) were tested for normality using Shapiro-Wilk goodness-of-fit tests; both were non-normal ($P < 0.0001$, $P < 0.0075$ respectively). We therefore conducted Kruskal-Wallis tests and Dunn's post-hoc tests to examine the effect of season on attendance for aggregated roost counts, and season, year, and city on attendance at individual roost counts. To determine if productivity varied among cities, we tested the effects of year, city, and city by year on juvenile percentage (juvenile/adult ratio) using a two-way ANOVA. Productivity data were tested for normality ($P < 0.05$) using a Shapiro-Wilk goodness-of-fit test ($P = 0.7509$). All statistical analyses were calculated using JMP Pro 14. Alpha level for all tests was 0.05 and data are presented as mean ± standard deviation unless otherwise noted.

2.4. Results

2.4.1. Historical presence in the Lower Rio Grande Valley

2.4.1.1. Narrative accounts

Reports of parrots in south Texas start during the late 19th century when drought and severe winter weather were affecting northeast Mexico and south Texas (Stahle et al., 2016). In 1885, the Galveston Daily News reported that travellers were seeing flocks of parrots as close as 34 km south of Brownsville, Texas (Anonymous, 1885a; Casto, 2010). Also in 1885, a south Texas newspaper reported flocks of parrots north of Brownsville and noted this as the first instance of these birds being seen in Texas (Anonymous, 1885b; Casto, 2010). In March 1899, during another severe cold front, "100s" of parrots were reported just south of Corpus Christi, Texas, roughly 190 km north of Brownsville (Anonymous, 1899; Casto, 2010). Skins of "Mexican parrots" taken near Corpus Christi (likely from the same flock witnessed in 1899) were noted by Florence Merriam Bailey in 1900 at a ranch just south of Corpus Christi (Bailey, 1916; Casto, 2010), approximately 175 km north of the Texas-Mexico border.

Few reports exist during the early and mid-1900s; it was reported that Red-crowned Amazons roosted in a pump house in La Feria during the 1920s and a home movie taken in 1956 was described by Walker and Chapman (1992) as showing four RCAM feeding in a pecan tree somewhere in south Texas. It is not until the 1970s that Red-crowned Amazons were identified with regularity and accuracy in south Texas with field notes from reliable observers (Walker & Chapman, 1992; Webster, 1977). John Arvin reported RCAM at Anzalduas Park on the Rio Grande, near McAllen, during September 1973 and 10 RCAM were seen continuously during the winter (December–February) of 1976 in Brownsville (Neck, 1986; Webster, 1974). RCAM were then seen regularly only during winter months (December–March) until 1985 when they started being noted year-round in the LRGV (Burgess, 2006; eBird Basic Dataset, 2019; U.S. Fish and Wildlife Service, 2019; Walker & Chapman, 1992).

2.4.1.2. eBird

As of April 2019, 193,816 eBird checklists (complete and incomplete) had been entered for the LRGV, with 8,483 (4.3%) of those reporting sightings of RCAM. The first eBird record of RCAM in Texas is of an individual in Hidalgo County at Santa Ana National Wildlife Refuge (Santa Ana NWR) in March of 1973. The next record is from Brownsville in May 1976 and then an almost six-year gap occurs until the next record of a pair flying along the Rio Grande at Santa Ana NWR in April of 1982. From 1982 on, yearly records of RCAM occur in the LRGV, with annual occurrences reported in Brownsville starting in 1984, McAllen in 1985, Harlingen in 1995, and Weslaco in 1999.

RCAM are reported in all LRGV roost areas during the 1981-1985 timespan except Weslaco, where reports began during 1991-1995. In the LRGV area, the number of checklists entered increases greatly since the 1980s but the percentage of checklists containing RCAM stays relatively consistent since the 1986–1990 period. The total number of entered checklists and the number of checklists including RCAM were not dispersed uniformly through the LRGV. Overall, the McAllen area had 71,817 checklists with 2% reporting RCAM, Brownsville 70,275 (3.4%), Weslaco 36,869 (7.7%), and Harlingen 14,755 (12%). In Brownsville and McAllen, checklists including RCAM hover around 2–6% of all checklists entered from 1981 until present. However, in Harlingen and Weslaco, large increases of checklists including RCAM occur from 1991-2000 and drop to about 11% and 6% respectively in the last five years.

Throughout the four roost cities of the LRGV, eBird data suggest that the populations of RCAM show little or no growth from the 1970s through the late 1990s

(Figure 2). Very small increases occur in Brownsville and McAllen during the 1980s into the 1990s. Starting in 1998, the number of birds in Weslaco and Brownsville increases but it is not until 2008 to 2011 that the numbers in all four cities begin to show major and sustained growth. Over the past five years, RCAM in all four cities have continued to increase, but there is some indication that this growth is starting to level off in all cities except Weslaco.

2.4.1.3. Christmas bird counts

Six Christmas Bird Count circles within the LRGV area have reported RCAMs at least once throughout the history of the count. The earliest CBC record of RCAM in the LRGV was in 1976 in Brownsville’s TX10 circle when six birds were reported. At least one but fewer than six RCAM were reported yearly from 1976 through 1986 in the LRGV (Figure 2). Since 1986, the annual numbers of birds reported has been highly variable but increasing overall. The CBC counts over the last five years have been too variable to determine if the population is continuing to increase or if it has levelled off.

2.4.2. Current populations

2.4.2.1. Roost Counts

The three largest TPP aggregate counts were 680, 670, and 665 occurring during January 2017, July 2018, and Dec 2016, respectively. The largest TPWD counts were similar with 659, 650, and 648 RCAM counted in October 2018, January 2016, and October 2016, respectively. TPP counts at individual roosts ranged from 0 to 435 RCAM (mean = 112 ± 78.6, n = 356), while TPP aggregated counts ranged from 151 to 680 (mean = 447.5 ± 139.3, n = 66). TPWD counts at individual roosts ranged from 0 to 350

RCAM (mean = 132 ± 85.8, n = 56), while aggregates ranged from 251 to 659 (mean = 527 ± 138.8, n = 14). In total, 91% of all roost count attempts registered at least one RCAM, whereas in Brownsville roosts had 100% site fidelity and RCAM were registered on 100% of count attempts.

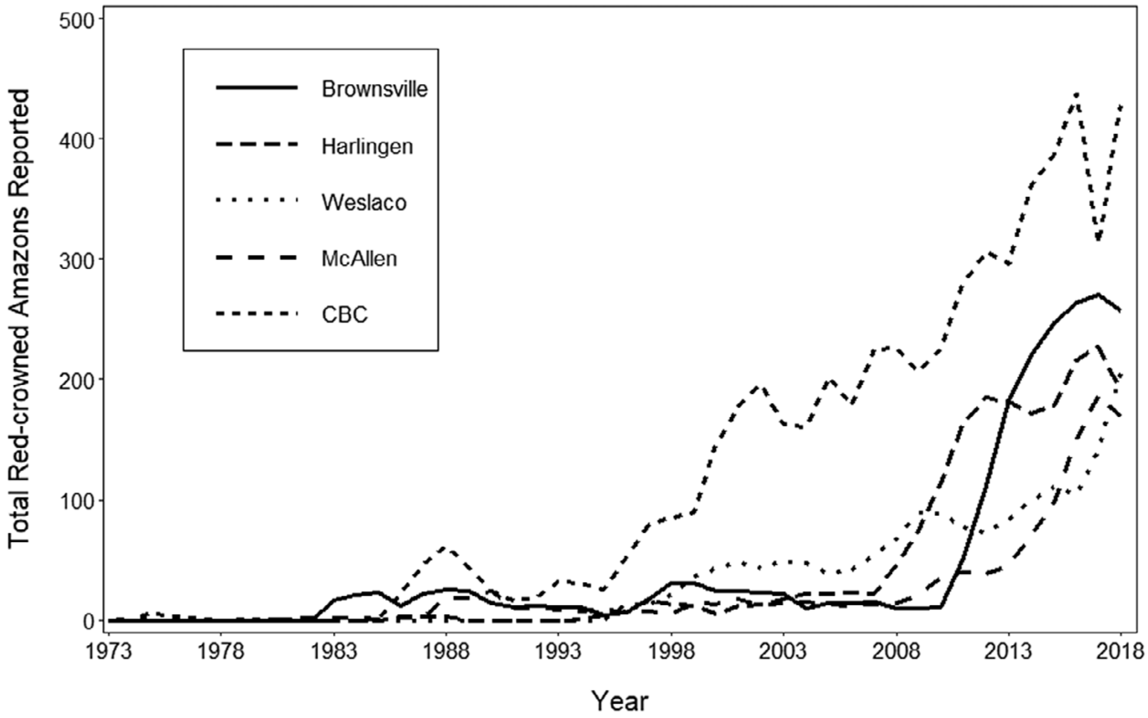

Figure 2. Moving three-year averages of the top-ten (if available) highest reported numbers of Red-crowned Amazons on eBird checklists in the Lower Rio Grande Valley of Texas. Data are reported as coinciding with the four main roosting areas of Brownsville, Harlingen, Weslaco, and McAllen. Also included is the three-year moving average of the total number of Red-crowned Amazons counted yearly throughout all five Christmas Bird Count circles in the LRGV, labeled as 'CBC'. Data are from January 1973 through December 2018. Reprinted with permission from (Kiacz et al., 2021).

Roost switching at a large scale, when at least one of the four roosts was roughly twice its normal size and another roost has little or no attendance, only occurred during the winter months (December–February). From December 2016 through January 2017, Brownsville and McAllen had extremely high attendance (counts of 300 and 380, respectively) while no parrots were located in Weslaco and Harlingen during this time. A similar pattern occurred the following year during January 2018, and then from December 2018 through early February 2019 high counts in Weslaco (350) and Brownsville (250) coincided with an absence of parrots being found in Harlingen and McAllen.

Seasonal fluctuations in roost attendance (TPP and TPWD counts) were apparent with fewer birds attending individual roosts during the spring (March–May) versus summer (June–August), fall (September–November), and winter (December–February; Kruskal-Wallis; χ^2= 19.0, P = 0.0003; Figure 3). Aggregate LRGV-wide count totals (TPP and TPWD counts) were also significantly less during the spring (mean = 327 ± 143.6) compared to summer (mean= 473 ± 113.2), fall (mean= 502.9 ± 133.8), or winter (mean= 539 ± 94.9; χ^2 = 20.3, P <0.0001; Figure 3). Roosts were significantly smaller in McAllen (mean = 66) than at all other sites, while Brownsville averaged the largest (mean= 173; χ^2 = 109.6, P <0.0001). There was no significant difference in average roost size by year (χ^2 = 5.9, P = 0.1156). Overall, roost counts averaged 128 birds in 2018, slightly more than the average of 111 birds during 2016, and 109 birds in both 2017 and 2019. The increase in 2018 was likely due to fewer counts in McAllen (the smallest roost) relative to other years rather than a real difference in roost attendance.

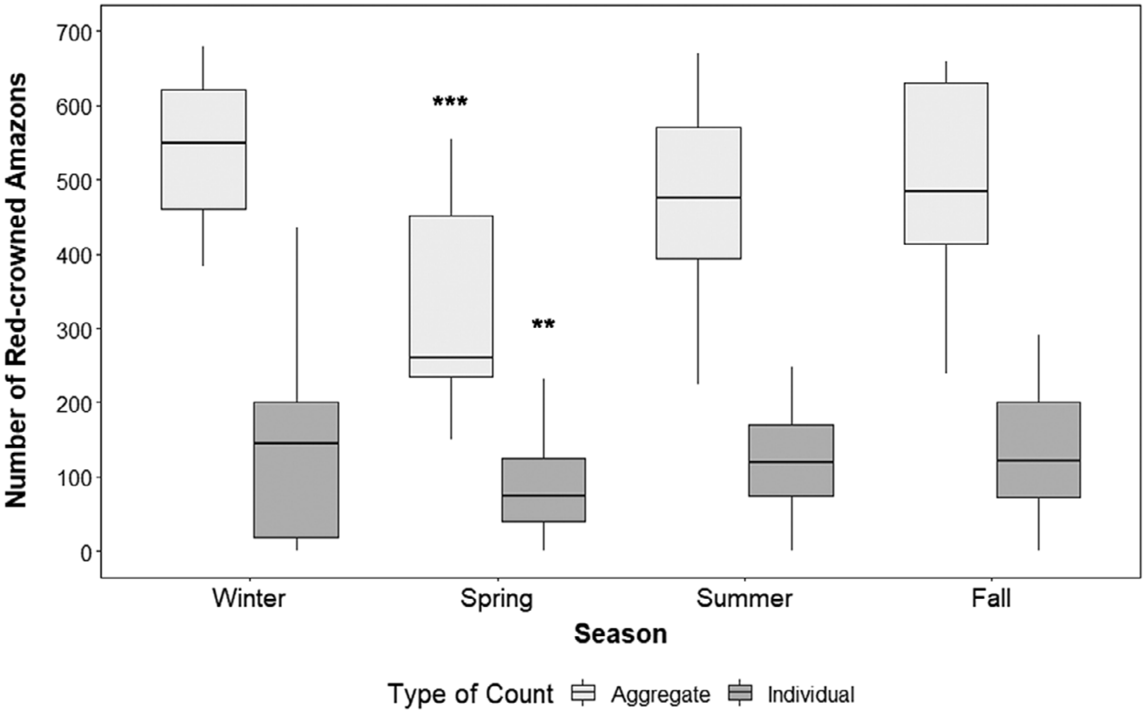

Figure 3. Average roost count size by season for both individual counts (dark gray) and total aggregate counts (light grey) from both Tejano Parrot Project and Texas Parks and Wildlife Department roost counts. Individual roost counts (n = 412) were significantly less during spring (March–May) compared to all other seasons, while summer, fall, and winter did not differ statistically (; Kruskal-Wallis; $\chi2$= 19.0, P = 0.0003). Aggregate counts (n = 80) were also significantly less during spring compared to all other seasons, while summer, fall, and winter did not differ statistically (***; Kruskal-Wallis; $\chi2$ = 20.3, P < 0.0001). Data are from January 2016 through April 2019. Reprinted with permission from (Kiacz et al., 2021).**

2.4.2.2. Nesting

Before 1980, most records of RCAM in the LRGV were during the non-breeding season, suggesting that the birds did not breed in Texas at this time. The first substantiated LRGV records of RCAM during the breeding season consisted of a flock of six reported throughout the year in 1976 in Brownsville (Webster, 1977) and one RCAM at Bensten-Rio Grande Valley State Park in June of 1978 (Webster, 1978). These records may indicate either escaped pets or natural wanderers, but no breeding activity was reported for these birds. The first known nesting in Texas was observed in Harlingen in 1985 when a pair successfully fledged one young (Lasley & Sexton, 1985). The Texas Breeding Bird Atlas reports the earliest nests in Brownsville, Weslaco, and McAllen from the early 1990s (Burgess, 2006). Reports of RCAM nesting in San Marcos, Texas (~425 km north of the Texas-Mexico border) from 1990–1993 and in Victoria, Texas (~315 km north of the border) in 1989 are presumably of escaped pets. A nesting parrot survey by B. McKinney in 1995 found 10 nests in Brownsville, three in Harlingen, and three in McAllen (Burgess, 2006).

iNaturalist's earliest nesting records are from 1995 in San Benito (near Harlingen) and a 2010 record in the McAllen area (iNaturalist.org, 2019). Additional breeding records are posted from Brownsville (20 since 2016), Harlingen (one in 2016), and McAllen (one in 2015).

During our study, we found 72 likely nest cavities (defined as a cavity of the correct size and shape with RCAM duetting within earshot) throughout the LRGV, excluding Brownsville. Twenty (28%) of these cavities were on commercial properties in urban or suburban areas, while the majority (51; 72%) were on residential properties in neighborhoods. Of these, at least 34 were active for one or more years over the three-year study (i.e. RCAMs were seen spending at least 10 minutes inside the cavity). Most active nests were found in the Harlingen area, including neighbouring San Benito (21 of 34; 62%), seven (21%) were found in Weslaco and the surrounding areas, and six (18%) in the McAllen region. Twenty-one (62%) nests were in dead non-native palm trees, with the majority of those (86%) in *Washingtonia* spp. palms. Six (18%) were in living *Fraxinus* sp., while three (9%) were found in living *Populus* sp.

2.4.2.3. Productivity

The number of parrots checked for adults/juvenile status averaged 60 ± 32 (range = 20–165), and the number of juveniles detected averaged 126.8 (range = 0–34) per roost. The number of RCAM attending these roosts averaged 159 ± 49 (range = 45–225) per roost count (n = 52). The maximum of 34 juveniles was seen in Harlingen in July 2018.

The average percentage of juveniles at roosts throughout the LRGV was 19% across the three years of the study (2016–2018; Table 1). Overall, productivity by city ranged from 10% in Brownsville in 2017 to 25% in Harlingen in 2016. However, these differences in juvenile percentage did not vary significantly among cities, years, or city by year (two-way ANOVA; $r^2 = 0.21$, $F_{(10,41)} = 1.12$, MSE = 0.01, $P = 0.37$).

Table 1. Overall juvenile percentages for Red-crowned Amazons recorded at roosts during July and August from 2016 through 2018 in the Lower Rio Grande Valley of Texas. Data are reported for the four regions shown in Figure 1. "N counts" is total number of roost counts per year combined across all cities. "Total # of RCAMs checked" is the sum of all juvenile and adults checked for adult juvenile status per year. "Average per roost" is the "Total number of RCAMs checked" divided by the "N counts" conducted that year. Reprinted with permission from (Kiacz et al., 2021).

Year	Brownsville	Harlingen	McAllen	Weslaco	Grand Total	N counts	Average per roost	Total # of RCAM checked
2016	25%	25%	N/A	19%	24%	13	145	1,885
2017	10%	21%	19%	14%	15%	22	166	3,660
2018	19%	24%	15%	24%	22%	17	159	2,706
Combined	16%	23%	15%	19%	19%	52	159	8,251

2.5. Discussion

2.5.1. Origins

RCAM have likely been entering south Texas from northern Mexico since at least the late 1800s. Most early records (<1980s) occur during the non-breeding season from September to March, which coincides with previously reported large-scale movements in Mexico and California (Enkerlin-Hoeflich & Hogan, 2020). Many of the early records also coincide with major winter weather events when food supplies were likely disrupted in their normal range, forcing large movements in search of food (Casto, 2010).

By the 1970s, RCAM were being regularly reported, mostly during the winter months, throughout the LRGV. eBird and CBC data confirm the occasional reports during the 1970s, with an increase of sightings during the 1980s. By the mid-1980s, the population was established in the LRGV seemingly through multiple points of entry, from Anzalduas Park in the west to Brownsville in the east (roughly 87 km apart).

It is uncertain if the currently established population of RCAM in the LRGV was founded by birds brought to the area as part of the pet trade or through natural dispersal events. Given the historical 1800s records, close proximity of their Mexico range, habitat destruction in Mexico, and the time of year of the earliest records it is likely that at least some of the founding birds dispersed naturally from Mexico into the United States (Casto, 2010; Neck, 1986; Walker & Chapman, 1992; Webster, 1974, 1977, 1978, 1982). However, during the 1970s and 80s, RCAM were being harvested in large numbers in Mexico and exported to the USA en masse (Cantu et al., 2007; Enkerlin-Hoeflich & Hogan, 2020). In addition, other parrot species with established populations in the LRGV (Lilac-crowned Amazon *Amazona finschi*, White-fronted Amazon *Amazona albifrons* and Red-lored Amazon) most likely originated from escaped pets given the large distance to their native ranges. Both lines of evidence suggest that at least some of the LRGV RCAM population came from captive origins (Enkerlin-Hoeflich & Hogan, 2020; Neck, 1986). Our review of RCAM in the LRGV has provided no evidence that shows conclusively where the founders of the LRGV population originated, but it is likely that both birds from the pet trade and natural dispersal played a role in the establishment of the species in south Texas.

Both eBird and CBC datasets show the population grew little from 1973 to 1983 and again from ~1985 to 1995. These lags follow a well-known pattern seen during species establishment (Crooks, 2005; Crooks & Soulé, 1999; Runde et al., 2007; Sakai et al., 2001; Valéry et al., 2009). Although populations with few founders have inherently low rates of increase during the immediate years following establishment (Crooks & Soulé, 1999), an additional factor likely playing a role in these lags is the Allee effect which correlates small population sizes with low or negative population growth rates (Collazo et al., 2013; Stephens & Sutherland, 1999; Wang et al., 1999). Small population sizes can negatively affect predator avoidance, mate choice, and information exchange and may limit population growth especially in gregarious species (Beissinger, 2008; Buhrman-Deever et al., 2008; Courchamp et al., 2008; Stephens & Sutherland, 1999; Wright et al., 2019). Additionally, poaching in the LRGV during this establishment period certainly could have hampered potential growth.

To negate Allee effects or other population suppressors, population size must reach a certain threshold. The small increase in the population during the mid-1980s, shown in both eBird and CBC datasets, may have provided the boost in numbers needed to break the cycle. There are two possibilities that may have caused the increase. A natural dispersal event from Mexico is possible, as there was an unprecedented freeze during the winter of 1983–1984 which may have driven RCAMs to disperse north from Mexico (Walker & Chapman, 1992). Additionally, this freeze killed many non-native *Washingtonia* palm trees in the LRGV which became suitable nesting habitat for RCAM (see (Lasley & Sexton, 1985)) perhaps leading the way to the rapid increase in population during the mid-1990s. The second possibility is that the population increase in the mid-1980s was driven by increased releases or escapes from the pet trade. Throughout the 1970s and early 1980s, 16,490 Red-crowned Amazons were legally imported to the United States, and roughly the same number was estimated to have been imported illegally (Enkerlin-Hoeflich & Hogan, 2020; Iñigo-Elias & Ramos, 1991). Although not all these imports entered the U.S. through Texas, it is likely the majority did because of the close proximity to where the birds were harvested. It seems very possible that a combination of natural dispersal and escaped individuals led to the initial increase that allowed the population to escape the Allee effect and begin the growth documented during the mid-1990s.

2.5.2. Current Status

Using two separate but similar roost count methodologies, we found a minimum of 659–680 RCAM across the roosts in the LRGV. The actual population could be slightly higher if we missed roosts during our counts or if our assumption that all RCAM attend roosts nightly during the nonbreeding seasons does not hold. It seems unlikely we would miss large roosts since RCAM roost in residential areas and are loud and conspicuous, even to non-birdwatchers. In addition, the LRGV is one of the most heavily birded areas in the entire U.S. (Mathis & Matisoff, 2004), leading us to believe that over the course of multiple years it is unlikely that a decent sized roost could persist undetected. We have occasionally found “mini-roosts” of 10–15 RCAM separated from the main roosts by over 8 km, but these events were confined to the breeding season and were not known to take place during the post-fledging season when our high counts occurred. Roost attendance by *Amazona* parrots is known to be variable from day to day (Cougill & Marsden, 2004) but our large number of roost counts (n = 412) over all four seasons likely negates any effect that small daily fluctuations would have. Recent VHF radio-tracking in this population has shown that birds do switch roosts occasionally (Kiacz and Brightsmith unpubl. data) but since our counts are LRGV-wide and we surveyed all suspected roosts, when roost switching did occur, we were still able to detect all tracked birds and likely negate any effect from roost switching on our estimated minimum population size.

Our counts suggest that the population has apparently remained stable from 2016 through 2019, which may signal that the rapid population growth of the past two decades is slowing. This is somewhat surprising; although the population appears healthy overall, it could be reaching carrying capacity in the LRGV. Cavity availability is often a limiting factor for secondary-cavity nesters like RCAM, especially in human-modified habitats (Cockle et al., 2010; Cornelius et al., 2008). Although we did not specifically collect cavity availability data, we did notice that residential and commercial landscaping commonly removes nest structures across the LRGV (S. Kiacz pers. obs.). Homeowners regularly remove dead palm trees on their properties because they are not visually appealing and may be hazardous. The same is true for any large tree (*Fraxinus* sp., *Populus* sp., *Carya* sp.) that is weak or dying and presents a hazard to homes, roads, or walkways. This is unfortunate since most nests found during this study were in dead non-native *Washingtonia* spp. palm trees, and all were located on private commercial or residential property. Because these birds are rarely utilizing protected state and federal lands, initiatives which only affect these types of property will have a reduced impact. Poaching can also destroy cavities for future use by felling nest trees or enlarging the cavity entrances to reach the chicks inside (Cantu et al., 2007). Nest cavities destroyed by poachers were regularly seen over the course of our study. Although urbanization and ornamental planting may increase the amount of nesting structures desirable to RCAM, poachers, property owners, and commercial landscapers may well be destroying these structures at a similar rate. Further studies are warranted to determine whether nesting cavities are a limiting factor for this RCAM population.

Productivity (19% LRGV-wide over the course of our study) seems to be at levels comparable to other studies of *Amazona* parrots. Red-tailed Amazons *Amazona brasiliensis* were found to have 31.6% and 4.6% juveniles in protected and non-protected populations, respectively (Martuscelli, 1995). During another Red-tailed Amazon study, researchers found that 18% of groups flying to a roost consisted of three or more birds (Cougill & Marsden, 2004). Similarly, two studies of Yellow-naped Amazon showed a 24% (Wright et al., 2019) and 18% (Matuzak & Brightsmith, 2007) rate of groups of three or more attending roosts. If we assumed these groups of three or more were successfully fledgling two young apiece (as RCAM average; (Enkerlin-Hoeflich, 1995)), these three populations would be averaging about 19% (Red-tailed Amazon), 15%, and 15% (Yellow-naped Amazon) juveniles, respectively. Clearly, this analysis is crude at best, but it offers a comparative glimpse of *Amazona* populations. Our LRGV population of Red-crowned Amazons was stable over the course of our study, the Red-tailed Amazon populations were likely stable or declining, and the

Yellow-naped Amazon population was likely declining. If valid, this comparison suggests that there may be a fine line between stable and declining populations. Productivity rates should continue to be monitored in the LRGV population on a yearly basis and compared to the current trend. If rates continue to drop, more active conservation measures should be considered.

2.6. Acknowledgements

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3. PRESENCE OF ENDANGERED RED-CROWNED PARROTS (*AMAZONA VIRIDIGENALIS*) DEPENDS ON URBAN LANDSCAPES[2]

3.1. Overview

Many species of plants and animals thrive in urban habitats and stand to gain from the global trend in increased urbanization. One such species, the Red-crowned Parrot (*Amazona viridigenalis*), is endangered within its native range but seems to thrive in urban landscapes. While populations of endangered synanthropic species may be uncommon, they can act as genetic reservoirs and present us with unique conservation and research opportunities. We sought to determine the Red-crowned Parrot's level of dependency on urban areas, as well as the climatic and anthropogenic drivers of their distribution throughout the United States. We built national level species distribution models for the USA using Maxent and correlated presence points derived from field work and citizen science databases to environmental variables for three Red-crowned Parrot populations: two naturalized (California and Florida) and one native (Texas). We found current occupancy to be 18,965 km^2 throughout the three states. These three states also contained 39,429 km^2 of high- and medium-quality habitats, which, if occupied, would represent a substantial increase in the species range. Suitable habitat showed a

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strong positive correlation with urbanization in areas where average monthly temperatures were at least 5 °C. The current and predicted distributions of Red-crowned Parrots were closely aligned with urban boundaries. We expected populations of Red-crowned Parrots and other synanthropic species to grow due to a combination of factors, namely, continued urbanization and the effects of climate change, which increase the size and connectivity of a suitable habitat. For some imperiled species, urban habitats could prove to be important bastions for their conservation.

3.2. Introduction

Urbanization is one of the leading causes of biodiversity loss and can result in habitat degradation and fragmentation (Ceballos et al., 2015; Schmidt et al., 2020; United Nations et al., 2019). However, many species of plants and animals can thrive in urban habitats and stand to gain from this conversion (Kowarik, 2011). The global trend in increased urbanization is likely to continue for the foreseeable future (United Nations et al., 2019). Species that thrive in urban areas (synanthropes) are generally viewed as neutral or invasive in terms of their ecological or economic impacts (McKinney, 2006). Synanthropes can be intentionally brought to urban areas (i.e., ornamental plants), can be accidentally introduced (i.e., escaped pets), or can be species naturally expanding their ranges into these novel habitats (Thompson & McCarthy, 2008; Uehling et al., 2021; Veech et al., 2011). They rarely have declining populations within their native ranges, are infrequently considered to be threatened or endangered, and, as such, are not usually considered to be conservation priorities (Brightsmith & Kiacz, 2021; Kowarik, 2011). But, when endangered species are synanthropic and thrive in urban landscapes, we are presented with unique conservation, research, and social opportunities (Kiacz & Brightsmith, 2021; Shaffer, 2018).

While populations of endangered synanthropic species are uncommon, they can provide valuable information on the natural history of the species and can act as genetic reservoirs or backup populations for possible translocations (Kiacz & Brightsmith, 2021; Shaffer, 2018). One endangered synanthropic species, the Red-crowned Parrot (*Amazona viridigenalis*), is a medium-sized parrot endemic to northeastern Mexico and southern Texas. It has been popular in the domestic and international pet trade (Enkerlin-Hoeflich, 2000; Enkerlin-Hoeflich & Hogan, 2020; Kiacz et al., 2021), and, like many other parrot species, Red-crowned Parrots have declined in their native range due to threats from the pet trade and habitat destruction (Enkerlin-Hoeflich & Hogan, 2020). However, three significant populations occur within the United States. Two of these populations, one in southern California and another in southern Florida, are considered naturalized and owe their origins to released or escaped pets. Roughly 3700 individuals make up the California population, whereas a smaller population of an unknown size is found in Florida (Garrett, 2020; Uehling et al., 2019). The third US population is recognized as native by the State of Texas and the United States Fish and Wildlife Service and consists of roughly 675 birds located in the two southernmost Texas counties Hidalgo and Cameron (Kiacz et al., 2021).

Some authors have equated urban areas to “arks”, in which endangered species could persist while the drivers of their declines in their native range are remedied (Garcia-Gonzalez & Garcia-Vazquez, 2012; Shaffer, 2018). However, different species likely depend on urban areas with unique conditions (Beninde et al., 2015; Faeth et al., 2011; Jokimäki et al., 2018). To determine the Red-crowned Parrots' levels of dependency on urban areas, as well as the drivers of their distribution throughout the United States, we utilized the Species Distribution Modeling (SDM) algorithm Maxent which estimates likelihoods of presence under different environmental conditions (Phillips et al., 2006).

Understanding habitat use of threatened species is a prerequisite for identifying where and how to manage and maintain populations, as well as to ascertaining a population's level of synanthropy (IUCN, 2020; Pacifici et al., 2015). Species distribution models correlate climatic and environmental data with areas of known species presence and are useful in determining the drivers that may influence a species' potential distribution and in predicting geographic regions where a species may occur (Austin & Van Niel, 2011; Pearson, 2007; Randklev et al., 2015; Wang et al., 2015). Although climate is usually considered the main driver of species distributions (Bellard et al., 2012), many ecologically relevant variables, e.g., land-use variables (Sohl, 2014) or edaphic factors (Wang et al., 2019), have been added to SDMs to increase the predictive abilities of species distributions. As land use has been shown to influence the distribution of animals, we also include land use/cover variables in our models (Illán et al., 2010; Martin et al., 2013). Frequently, SDMs are used to identify critical habitat for species with reduced ranges and predict areas where these species might expand their ranges (Mainali et al., 2020; Wang et al., 2019). Coupled with expert knowledge, SDMs have played an important role in determining protected areas for target species important to the maintenance of biodiversity (Austin & Van Niel, 2011; IUCN, 2020).

In this study, we produce coarse-scale, national level SDMs for three isolated populations of the Red-crowned Parrot (*Amazona viridigenalis*) to answer the following questions:

(1) What is the current geographical range of Red-crowned Parrots in the USA, and what is the potential for range expansion?

(2) Does a combined model that includes all populations predict presence similarly to individual population models?

(3) What are the important climatic and environmental (anthropogenic) drivers for Red-crowned Parrot presence in the USA?

(4) Are all populations of Red-crowned Parrots in the contiguous USA responding to climate and environmental (anthropogenic) variables similarly?

3.3. Methods

3.3.1. Occurrence Data

We obtained occurrence data (presence-only records) for Red-crowned Parrots from two sources: sightings entered into the citizen science database eBird (Sullivan et al., 2009) and locations from four years of field work in South Texas (2016–2019). Records obtained through eBird and other citizen science databases have been shown to be valuable for building accurate SDMs (Dickinson et al., 2010).

The eBird presence records (n = 36,680) were from March 1973 through February 2020. Only the states of California (n = 23,717), Texas (n = 11,956), and

Florida (n = 1,007) contained presence points for Red-crowned Parrots. We included points from both “complete” and “incomplete” checklists but excluded “random” and “historical” checklists due to their potential inaccuracies. All travelling checklists over 10 km in distance were removed, as were all points with duplicate coordinates and all points located over water. Additionally, we removed all locations of single birds located over 20 km from another presence point, as these likely represented released or escaped pets that were not part of established populations. We then scrutinized the points individually as a final quality check and removed any point that was likely from list-building checklists or placed at a county level. After data refinement, we retained a total of 4784 eBird presence points for use in modeling (n = 2740 California; n = 1826 Texas; n = 217 Florida). We also included 415 presence locations gathered during field work in South Texas from June 2016 through February 2020. These points consisted of foraging, roosting, and nesting locations and were obtained throughout all four seasons (Kiacz et al., 2021). For the purpose of this nationwide study, all points were lumped and considered as presence only. A fine-scale study comparing specific habitat use of foraging, roosting, and nesting of Red-crowned Parrots in South Texas is currently in preparation.

3.3.2. Environmental Data

The environmental data we used as potential drivers in our SDMs included climatic variables commonly regarded as important, such as rainfall and temperature data (Abellán et al., 2017; Hayes & Barry, 2008), as well anthropogenic variables frequently suspected to drive species distribution, including land-use and human density data (Blair & Launer, 1997; Lemoine et al., 2007).

As variables used in Maxent must have identical cell sizes, we resampled all datasets to a resolution of ~300 m × 300 m using bilinear interpolation for continuous data layers, and nearest neighbors for categorical data, calculated with QGIS V3.12.0. The cell size chosen represented a balance of the original datasets' grid sizes, which ranged from 1 km to 30 m, and allowed us to easily detail the range of Red-crowned Parrots. Previous studies on parrot distributions generally used rather coarse grid sizes (>1 km) (Molloy et al., 2020; Monterrubio-Rico et al., 2010), so, while 300 m^2 may not have been detailed enough to specify tree species or microhabitats, it could adequately describe important drivers of distribution at a broad scale.

3.3.2.1. Climatic Variables

We used 19 world bioclimatic layers (30 arc-second resolution) that included variables that represented minimum, maximum, and average temperatures and precipitation throughout the seasons, as well as indexes of climatic variance. The bioclimatic variables used were averages from the years 1970–2000 and represented biologically meaningful environmental data (Fick & Hijmans, 2017) (see complete list in Table 2).

Table 2. Climatic and environmental variables included in all Maxent models, including a description of the variable and units, if applicable. Variables and descriptions of climatic data from Fick and Hijmans (2017). All bioclimatic data (Bio"xx") are representative of the averages from the years 1970-2000. Reprinted with permission from (Kiacz et al., 2023).

Variable	Description	Detailed Description	Unit
Bio1	Annual Mean Temperature.	The annual mean temperature.	°C
Bio2	Mean Diurnal Range (Mean of monthly (max temp–min temp)).	The mean of the monthly temperature ranges (monthly maximum minus monthly minimum).	°C
Bio3	Isothermality (BIO2/BIO7) (×100).	Isothermality quantifies how large the day to-night temperatures oscillate relative to the summer to-winter (annual) oscillations.	%
Bio4	Temperature Seasonality (standard deviation × 100).	The amount of temperature variation over a given year (or averaged years) based on the standard deviation (variation) of monthly temperature averages.	%
Bio5	Max Temperature of Warmest Month.	The maximum monthly temperature occurrence over a given year (time-series) or averaged span of years (normal).	°C
Bio6	Min Temperature of Coldest Month.	The minimum monthly temperature occurrence over a given year (time-series) or averaged span of years (normal).	°C
Bio7	Temperature Annual Range (BIO5-BIO6).	A measure of temperature variation over an annual period.	°C
Bio8	Mean Temperature of Wettest Quarter.	This quarterly index approximates mean temperatures that prevail during the wettest season.	°C
Bio9	Mean Temperature of Driest Quarter.	This quarterly index approximates mean temperatures that prevail during the driest quarter.	°C
Bio10	Mean Temperature of Warmest Quarter.	This quarterly index approximates mean temperatures that prevail during the warmest quarter.	°C
Bio11	Mean Temperature of Coldest Quarter.	This quarterly index approximates mean temperatures that prevail during the coldest quarter.	°C
Bio12	Annual Precipitation.	This is the sum of all total monthly precipitation values.	mm
Bio13	Precipitation of Wettest Month.	This index identifies the total precipitation that prevails during the wettest month.	mm
Bio14	Precipitation of Driest Month.	This index identifies the total precipitation that prevails during the driest month.	mm
Bio15	Precipitation Seasonality (Coefficient of Variation).	This is a measure of the variation in monthly precipitation totals over the course of the year. This index is the ratio of the standard deviation of the monthly total precipitation to the mean monthly total precipitation (also known as the coefficient of variation) and is expressed as a percentage.	%
Bio16	Precipitation of Wettest Quarter.	This quarterly index approximates total precipitation that prevails during the wettest quarter.	mm
Bio17	Precipitation of Driest Quarter.	This quarterly index approximates total precipitation that prevails during the driest quarter.	mm
Bio18	Precipitation of Warmest Quarter.	This quarterly index approximates total precipitation that prevails during the warmest quarter.	mm
Bio19	Precipitation of Coldest Quarter.	This quarterly index approximates total precipitation that prevails during the coldest quarter.	mm
Population_ Density	Human population density.	Human population density during 2015 as 30 arc-second resolution.	Persons /km^2

Table 2 Continued

Variable	Description	Detailed Description	Unit
GAP/ LANDFIRE	Thematic land cover map representing ecological systems throughout the continuous US.	The map legend includes types described by NatureServe's Ecological Systems Classification (Comer et al., 2003) as well as land use classes described in the National Land Cover Dataset 2011 (Homer et al., 2015). These data cover the entire continental U.S. and are a continuous data layer. These raster data have a 30 m × 30 m cell resolution. (U.S. Geological Survey Gap Analysis Program, 2016)	
NLCD_2016_ LandCover	Details land cover throughout the continuous US. Includes layers for open water, urban intensities, barren land, forest types, shrublands, grassland types, wetlands, and agriculture.	The National Land Cover Database (NLCD) provides nationwide data on land cover and land cover change at a 30 m resolution with a 16-class legend based on a modified Anderson Level II classification system.	
NLCD_2016_ Impervious	Details impervious surfaces (roads, homes, etc.) throughout the continuous US.	NLCD imperviousness products represent urban impervious surfaces as a percentage of developed surface over every 30-meter pixel in the United States.	
NLCD_2016_ TreeCanopy	Details tree canopy coverage throughout the continuous US.	These data contain percent tree canopy estimates, as a continuous variable, for each pixel across all land covers and types and are generated by the United States Forest Service (USFS). The USFS derives tree canopy cover from multi-spectral Landsat imagery and other available ground and ancillary information.	
NDVI_2020	Details living vegetation throughout the continuous US.	A normalized difference vegetation index assessing living vegetation throughout the continuous United States in early 2020.	

3.3.2.2. Anthropogenic Variables

As a proxy of anthropogenic activity at a landscape level, we included an estimation of human population density during 2015 (30 arc-second resolution, represented as per-sons per km^2) (CIESIN, 2018). We also included three land cover layers: (Williams et al.) the GAP/LANDFIRE National Terrestrial Ecosystems data layer, (2) the National Land Cover Databases (NLCD) land cover data layer, and (3) an urban imperviousness layer (Comer et al., 2003; Homer et al., 2020; Homer et al., 2015; U.S. Geological Survey Gap Analysis Program, 2016). These layers represent land cover and vegetation at a 30 m × 30 m scale and detail the level of developed surfaces such as roads and core urban areas throughout the contiguous United States. Finally, we included percent tree canopy cover estimates from the NLCD (Coulston et al., 2012) as well as a Normalized Difference Vegetation Index (NDVI) derived from early 2020. See Table 2 for a detailed list of all variables used in the modeling process.

Many naturalized parrot populations have been shown to be at least partially reliant on urban parks and the diversity of flora that is associated with human settlements (Davis et al., 2014; Strubbe & Matthysen, 2009; Uehling et al., 2019). To analyze this phenomenon in our current study, we use post hoc analysis to detail land use (urban vs. nonurban) where presence, foraging, nesting, and roosting sites occurred. We utilized a data layer denoting urbanization that considered areas urban if over 50% of land cover consisted of non-vegetated human constructed elements (CIESIN, 2019; Liu et al., 2019). We did not use this binary layer in the SDMs since urban imperviousness and land cover layers provided a more detailed image of urbanization for modeling.

3.3.3. Species Distribution Modeling

We determined the relationships between environmental variables and Red-crowned Parrot presence using maximum entropy modeling (Maxent V3.4.0) (Phillips et al., 2006). Maxent is widely used with presence-only data (Baldwin, 2009) and for modeling nonnative species distributions (Elith et al., 2010; West et al., 2016).

3.3.3.1. Model Settings

To detail any potential differences in habitat use among the three US populations, we also created SDMs analyzing each population independently (Koralewski et al., 2015; Smith et al., 2019). We parameterized four models using presence points from only (1) California (California model), (2) Texas (Texas model), and (3) Florida (Florida model), and (4) using presence points from all three states (combined model).

Maxent considered any cell with at least one presence point within its bound as a “presence” cell, which helped to reduce spatial autocorrelation of presence points. After Maxent removed spatially correlated presence points, the final combined model used 2922 presence locations (eBird and field data combined), including 1995 in the California model, 779 in the Texas model, and 148 in the Florida model.

All models utilized 75% of presence records for training and 25% for testing, which exceeded the minimum recommended number of presence locations (30) for accurate model production (Wisz et al., 2008). We used default Maxent parameters for all other options. We did not spatially bias background data for pseudo-absence point creation since the presence of Red-crowned Parrots was not limited by any physical or geographical barriers because they are popular in the pet trade and moved by humans throughout the United States (Uehling et al., 2019). We ran five replicates for each model, utilizing random seeds and bootstrapping during each run. We reported the averages of the 5 replicates (±1 SD) for each of the four models unless otherwise stated below.

3.3.3.2. Model Evaluation

As a measure of model validity, we used the area under the receiver operating characteristic curve (AUC), which is commonly used for Maxent and other ecological distribution models (Merow et al., 2013). Interpretation of the AUC measurements ranged from random (0.5) to perfect (1.0), with values >0.9 considered very good, >0.8

considered good, and <0.8 considered poor (Hosmer Jr. et al., 2013). To analyze variable importance and to determine the correlations among similar variables, we used jackknifing (Elith et al., 2011; Phillips, 2005).

3.3.3.3. Distribution

We use Maxent's default Cloglog output to estimate occurrence probability (Phillips et al., 2017). For analyses, including map creation and calculating the area of predicted Red-crowned Parrot presence, we divided habitat suitability into three categories consisting of "High-quality", "Medium-quality", and "Unsuitable". We defined a high-quality habitat as all areas ranking at or above the Cloglog threshold, denoting the 10th percentile training presence (P10). The P10 threshold excluded the bottom 10% of training occurrence points with the lowest predicted habitat suitability. We defined medium-quality habitat as areas with values half of P10 up to P10. We defined all areas below half of the P10 threshold as unsuitable. (High-quality habitat $\geq$ P10; $0.5\times P10 \leq$ medium-quality habitat $<$ P10; unsuitable $< 0.5\times P10$)

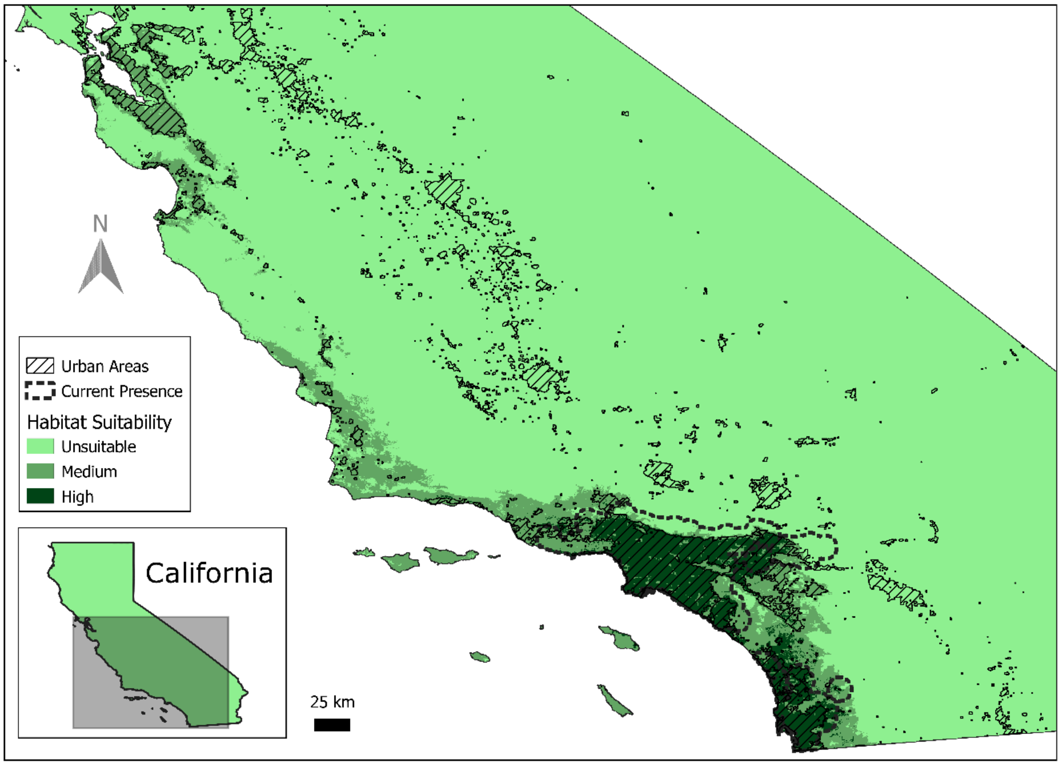
We determined actual distribution by applying a 10 km radius buffer to all presence points. Red-crowned Parrots are known to make daily flights from roost to foraging or nesting areas of roughly 10 km one-way (Kiacz pers. obvs.). Although Red-crowned Parrots can undergo much longer flights (Enkerlin-Hoeflich & Hogan, 2020), we used 10 km to represent a normal daily use range, which excluded long-distance winter foraging flights.

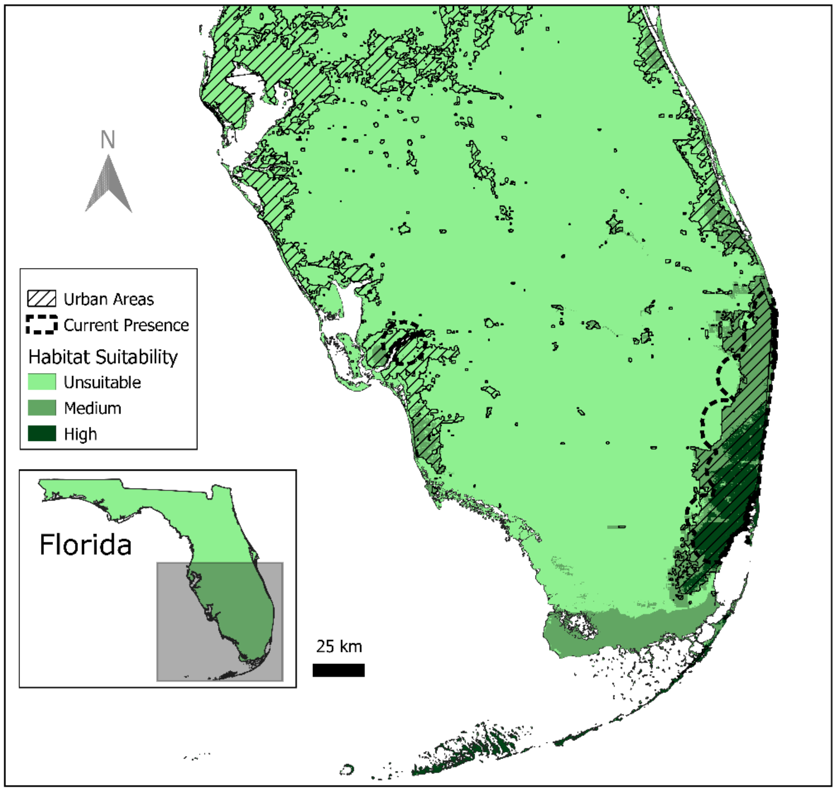
To determine the percent of each habitat class that was currently occupied (high-quality, medium-quality, and unsuitable), we used the predicted presence of the combined model overlaid with current (actual) presence. We made all calculations using RStudio Version 1.2.5033.

3.4. Results

3.4.1. Current Red-Crowned Parrot Distribution

The current distribution of Red-crowned Parrots in the United States was estimated at 18,965 km^2 – 11,890 km^2 (2.9% of state) in California, 3573 km^2 (0.5%) in Texas, and 3502 km^2 (2.4%) in Florida (Figure 4). Using the combined model, 57% of the current Red-crowned Parrot distribution in California was classified as high-quality habitat, 29% as medium-quality habitat, and 14% as unsuitable habitat. In Texas, 39% of the current distribution was classified as high-quality habitat, 55% as medium-quality habitat, and 6% as unsuitable habitat. In Florida, 37% of the current distribution was classified as high-quality habitat, 39% as medium-quality habitat, and 24% as in unsuitable habitat.


N
Urban Areas
Current Presence
Habitat Suitability
Unsuitable
Medium
High
California
25 km


N
Urban Areas
Current Presence
Habitat Suitability
Unsuitable
Medium
High
Florida
25 km

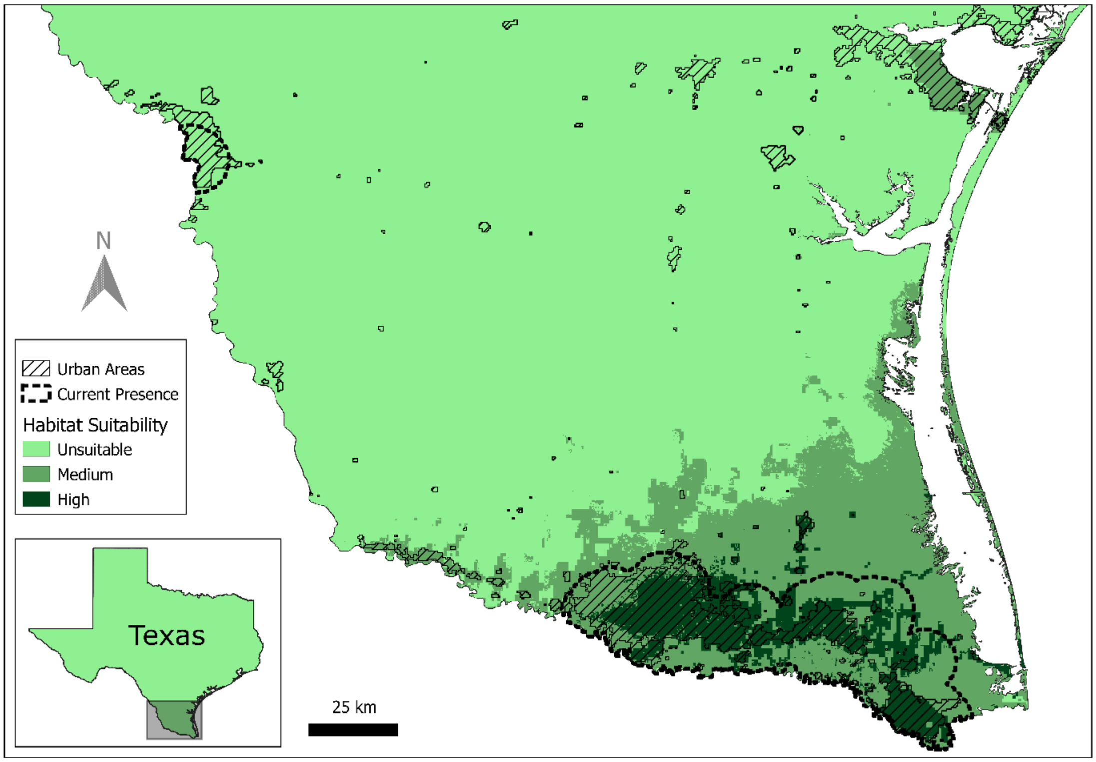


Figure 4. Maxent predicted high-quality, medium-quality, and unsuitable habitat for Red-crowned Parrots (*Amazona viridigenalis*) in (a) California, (b) Florida, and (c) Texas. High-quality habitat is shaded dark green, medium-quality habitat is shaded medium green, and unsuitable habitat is shaded light green. Current Red-crowned Parrot presence is outlined in a dashed black line, and urbanized areas are outlined in solid black. Only the areas within each state that contain medium or high-quality habitat are shown. Reprinted with permission from (Kiacz et al., 2023).

In the combined model, 1950 km^2 of high-quality habitat and 21,199 km^2 of medium-quality habitat throughout the contiguous USA is unoccupied; 17% of high-quality habitat and 80% of medium-quality habitat in California is unoccupied, 9% of high-quality habitat and 65% of medium-quality habitat in Texas is unoccupied; and 23% of high-quality habitat and 72% of medium-quality habitat in Florida is unoccupied.

Presence points used by the models were distributed almost entirely in urban areas. In California, 92% of all presence points (n = 2740) were in urban areas, in Texas 96% (n = 2241), and in Florida 62% (n = 217). Almost all points not in urban areas were <1 km from the edge of land classified as urban.

3.4.2. Predicted Habitat Distribution

The combined model predicted 11,463 km^2 of high-quality habitat across the contiguous USA (8250 km^2 in California; 1523 km^2 in Texas; 1690 km^2 in Florida) and 27,966 km^2 of medium-quality habitat (17,489 km^2 in California; 5623 km^2 in Texas; 4854 km^2 in Florida; Table 3). Models created to predict nationwide habitat suitability by using only one state's presence locations (state-level models) each gave radically different results, as they predicted high- and medium-quality habitats only in the state from which the presence points originated. For each state-level model, all areas outside the state of origin were predicted as unsuitable. Of note is that the medium- and high-quality areas predicted by single-state models were similar to that state's predicted area using the combined model (Tables 3 & 4).

Table 3. Combined model area predictions of high-quality, medium-quality, and unsuitable habitat for Red-crowned Parrots (*Amazona viridigenalis*) in each state. The percentage of the state that each predicted habitat type covers is also included. Reprinted with permission from (Kiacz et al., 2023).

	Predicted High Quality (km^2)	% of State	Predicted Medium Quality (km^2)	% of State	Predicted Unsuitable (km^2)	% of State
California	8250	2%	17,489	4.30%	383,661	94%
Texas	1523	0.20%	5623	0.80%	677,208	99%
Florida	1690	1.20%	4854	3.30%	139,117	96%
Total	11,463		27,966		1,199,986	

Table 4. Model predictions of Red-crowned Parrot (*Amazona viridigenalis*) habitat availability using single-state models and the percent of the state that each habitat type covers. State models predicted only unsuitable habitat outside of their own state. Reprinted with permission from (Kiacz et al., 2023).

	Predicted High Quality (km^2)	% of State	Predicted Medium Quality (km^2)	% of State	Predicted Unsuitable (km^2)	% of State
California	7999	2%	14,577	3.60%	386,824	94%
Texas	1486	0.20%	4546	0.70%	678,322	99%
Florida	1986	1.40%	1722	1.20%	141,953	97%

3.4.3. Variable Importance

All three state-level models and the combined model had a very good AUC (>0.91), averaging 0.95 (Table 5). Variable importance for each model was similar, with colinear variables related to temperature playing a large role in three of the four final models produced, with the exception being the California model, where precipitation variables played a larger role (Appendix). With regard to permutation importance (found by randomly permuting values for each variable at presence locations and determining the resulting drop in AUC (Phillips, 2005)), temperature seasonality (Bio04_250; the difference between the warmest and coldest seasons) played the largest role in the combined model (93%) (Appendix). Human population density also played an important role in the combined model, precipitation-related variables were important in the California model, and temperature-related variables played important roles in the Florida model and Texas model (Appendix). Additionally, jackknifing results supported the conclusion that temperature seasonality, population density, and mean coldest temperature played important roles in all models, whereas precipitation variables (specifically Bio15_250; precipitation seasonality, Bio18_250; precipitation of the warmest quarter) were increasingly important in the California model. The percent contributions representing variable importance should be interpreted with caution since they are only heuristically defined and can express multi-collinearity with one another (O'Donnell & Ignizio, 2012; Phillips, 2005). However, Maxent accounts for variable correlation reasonably well, and excluding correlated variables does not significantly influence model performance (Feng et al., 2019).

Table 5. AUCs (Area under the ROC (receiver operating characteristic) Curve) for each model, using model performance standards defined by Hosmer Jr. et al. (2013). Reprinted with permission from (Kiacz et al., 2023).

Model	AUC Training Average	AUC Test Average	Model Performance
California	0.935	0.935	Very Good
Texas	0.972	0.973	Very Good
Florida	0.994	0.995	Very Good
Combined	0.91	0.91	Very Good

3.4.3.1. Response Curves

In Maxent, response curves depict model responses from changing each variable while holding other variables at their average sample values. Predicted habitat suitability generally showed a strong positive correlation with urbanized areas (Figure 4). In all models, ideal habitat suitability was mostly constrained to developed areas at a low-to-medium intensity (defined as 20–79% impervious surfaces, generally including single-family homes). Human population density was positively correlated with high habitat suitability in all models. However, this effect was limited in the Texas and Florida models where suitability dropped off at densities higher than ~2500 people/km^2. The decrease in habitat suitability was much more pronounced in the Florida model (Figure

5). The most suitable human population density in the Texas model was 500–2500 people/km^2, in the Florida model 1000–8000 people/km^2, and in the California model and combined model at densities greater than 1000 people/km^2.

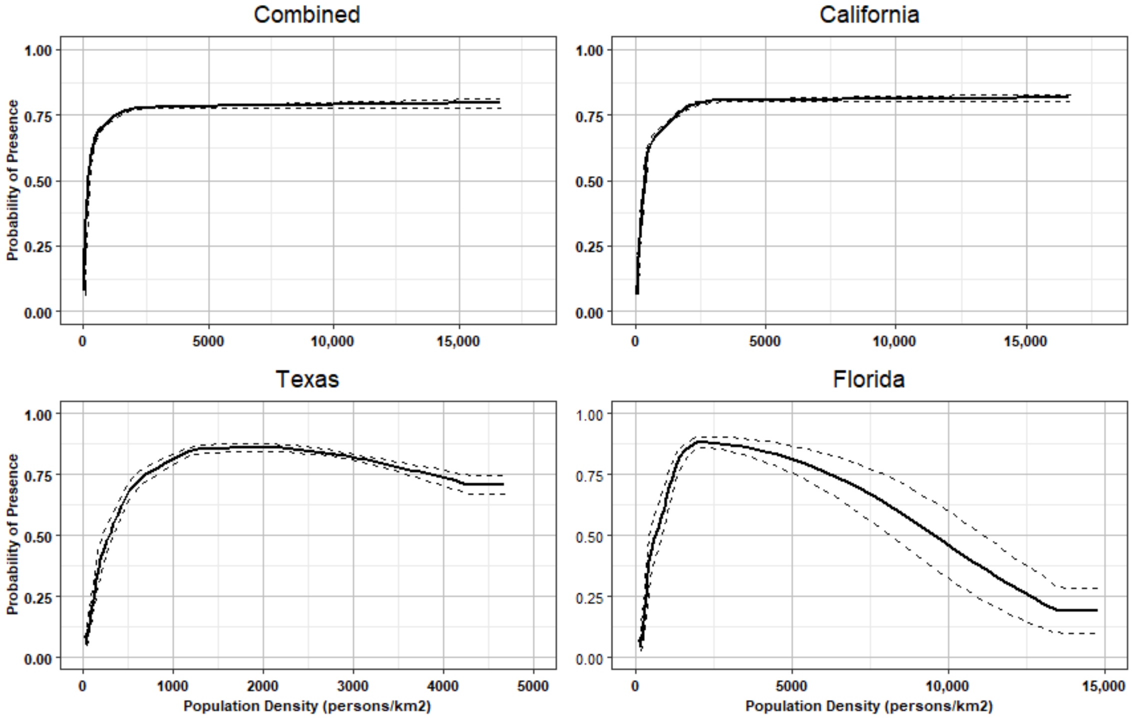


Figure 5. Response curves characterizing the probability of Red-crowned Parrot (*Amazona viridigenalis*) presence versus human population density from each of the four models. The response curves were created by Maxent using only human Population Density as a predictor variable. Solid lines represent the average response of five replicate models and dashed lines represent the mean ± one standard deviation. Reprinted with permission from (Kiacz et al., 2023).

Habitat suitability was positively correlated with the mean annual temperature in all models, with ideal minimum annual means of at least ~17 °C (Figure 6). Temperature seasonality (standard deviation of monthly values × 100) did not play a significant role in the state-level models, but, in the combined model, any variation above 5.5 °C showed a strong negative correlation with habitat suitability. Additionally, this negative correlation was noticeable in all models when building models using only temperature seasonality, and the correlation occurred at roughly the same temperature (5.5 °C). In all models, the mean temperature of the coldest month strongly suggested that temperatures below ~5 °C were unsuitable for Red-crowned Parrots. Annual precipitation showed no consistent correlation among all models, but ideal habitat suitability seemed to require at least ~400 mm.

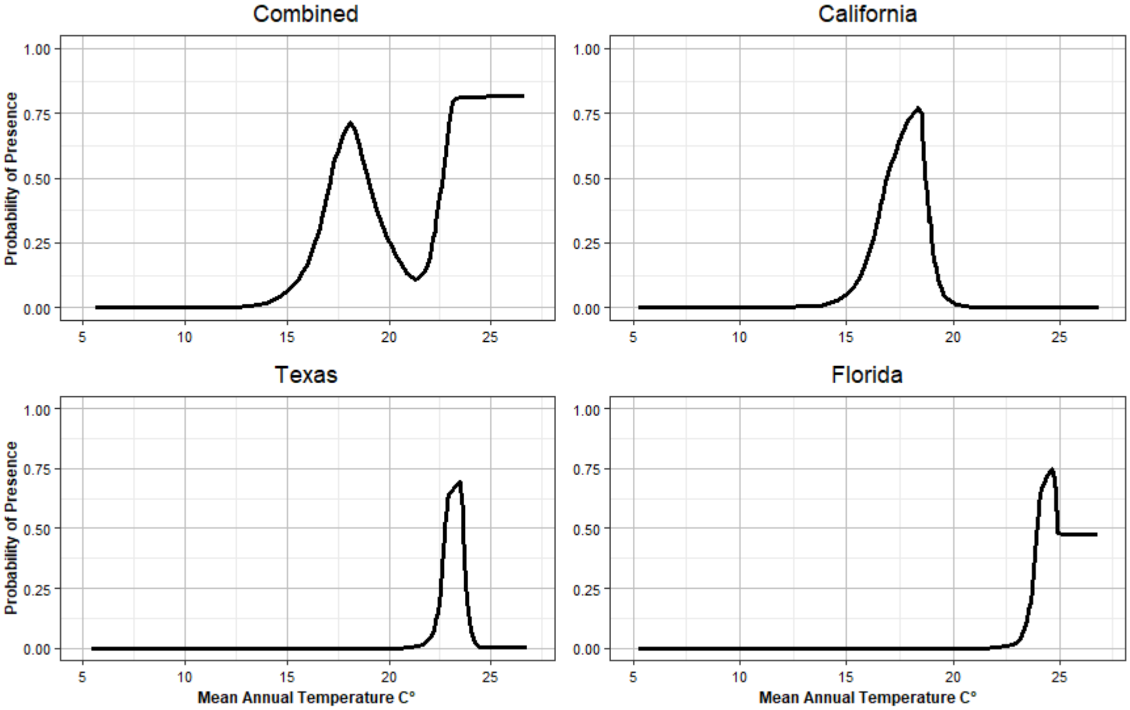


Figure 6. Response curves characterizing the probability of Red-crowned Parrot (*Amazona viridigenalis*) presence versus mean Annual Temperature from each of the four models. The response curves were created by Maxent using only mean Annual Temperature as a predictor variable. Solid lines represent the average response of five replicate models. Reprinted with permission from (Kiacz et al., 2023).

3.5. Discussion

3.5.1. Current Geographical Range and Potential for Expansion

Previous studies have indicated that Red-crowned Parrots in Mexico have lost an estimated 127,278 km^2 of habitat from 1995 through 2016, whereas the current amount of suitable habitat in Mexico is estimated to be 94,988 km^2 (Monterrubio-Rico et al., 2016). Our study shows that 39,429 km^2 of suitable habitat (occupied and unoccupied high- and medium-quality habitat) is available for Red-crowned Parrots within the contiguous United States. These data suggest that roughly 30% of the suitable worldwide range lies within the United States, and almost all high-quality habitat is in urban areas. Thus, similar to other endangered species like Sociable Lapwings (*Vanellus gregarious*) and *Rhinolophus* spp. bats, synanthropy may play an important role in the future conservation and recovery of Red-crowned Parrots (Kamp et al., 2009; Winter et al., 2020).

A large percentage of the high-quality habitat predicted by our models is currently inhabited by Red-crowned Parrots. Only 23% of high-quality habitat in Florida, 17% in California, and 9% in Texas are unoccupied. In Florida, most of the unoccupied high-quality habitat is south of the parrot's current range in recently urbanized areas and throughout the Florida Keys. Although our models identified high-quality habitat in the Florida Keys, individual islands are likely not large enough to maintain populations, owing to the large sizes of individual home ranges (Enkerlin-Hoeflich & Hogan, 2020). Frequent hurricanes, which destroy nesting, feeding, and roost resources and cause high mortality, may also limit use of the Keys (Renton et al., 2018; White et al., 2021).

In California and Texas, we predict range expansion into high-quality habitats neighboring currently occupied areas, but such expansion may not include large enough areas to significantly impact the overall populations within these states. However, California and Texas are urbanizing rapidly, and we expect recently developed urban and suburban areas will become high-quality habitat as urban vegetation matures (Kowarik, 1995).

Our model identified 21,200 km^2 of unoccupied medium-quality habitat, which, if occupied, would represent a 112% increase in range. Most medium-quality habitat is urbanized or abuts urban areas but lacks the mature vegetation and favorable climatic conditions to be classified as high-quality. Also, most medium-quality urban areas are smaller and more isolated than the currently inhabited metro centers in our three states and, therefore, have lower levels of propagule pressure and lower connectivity to current Red-crowned Parrot populations. Climate change may increase the suitability of these areas (Hitch & Leberg, 2007), and continued urban growth may decrease their isolation and increase connectivity to current populations. Thus, given climate change and urbanization, medium-quality habitats may represent important future resources and drive the future spread of the Red-crowned Parrot. However, increased propagule pressure, climate matching, and range connectivity alone will not guarantee spread and establishment success. Site-specific factors, such as availability of nesting and foraging substrate, as well as species-specific factors, such as behavioral flexibility and life history traits, will also play important roles in the success of the red-crowned parrot, as well as other synanthropic species (Colautti et al., 2006; McKinney, 2006; Sol et al., 2005).

3.5.2. Variation among Models

When building SDMs, it is assumed that species respond to environmental conditions similarly across their ranges. In our case, it was clear that the three disjunct populations of Red-crowned Parrots in the contiguous USA were responding to their environments in slightly different ways. State-level models predicted suitable habitats only within the states where presence locations originated, whereas the combined model predicted presence in all three states. This regional variability could have been caused by biological processes, including biotic interactions, genetic differentiation, or resource availability (Habibzadeh et al., 2019; Olson et al., 2021; Peterson et al., 2019). Additionally, models built with confined populations such as ours may not be easily generalized to novel environments because of the specificity of the species response to its surroundings or overfitting of the model (Boria & Blois, 2018), which was likely the situation in our case. Regardless, this finding suggested that Red-crowned Parrot populations were responding to their environments similarly but uniquely throughout the United States. The following discussion will explore these nuances.

3.5.3. Important Climatic and Environmental Drivers of Presence

All four of our models indicated the importance of minimum temperatures and minimum annual precipitation. They also showed that urbanization and population density were extremely important. However, they also indicated that Red-crowned

Parrots have a rather wide niche relative to other variables we explored. This pattern is similar to other nonnative birds, including parrots (Ancillotto et al., 2016; Mori et al., 2020; Pereira et al., 2020; Stohlgren et al., 2006; Strubbe et al., 2015). Red-crowned Parrots have established populations in the United States in regions that are similar but unique, so, while strict climate matching can increase spread rates of nonnative species, it is often not necessary for their successful establishment (Abellán et al., 2017; Pigot et al., 2010).

3.5.4. Temperature

Our data suggest that Red-crowned Parrots have a low tolerance for low temperatures, as the minimum temperature in suitable habitats is relatively constant among all models at roughly 5 °C, and all models indicate a high tolerance to high temperatures. Temperature plays an important role in predicting the establishment of other nonnative tropical birds, with minimum temperatures limiting the northward expansion of many species (Ancillotto et al., 2016; Davis et al., 2014; Monterrubio-Rico et al., 2016; Mori et al., 2020; Socolar et al., 2017). Our results suggest that warming trends associated with climate change will likely increase suitable areas for Red-crowned Parrots within the United States. Other authors have similarly suggested that climatically suitable areas likely will increase for subtropical and tropical synanthropes, especially nonnatives (Bellard et al., 2013; Hitch & Leberg, 2007).

3.5.5. Precipitation

The ideal annual precipitation was at least 400 mm in all four models. While the use of urban areas likely lessened dependency on precipitation due to increases in irrigation, otherwise suitable urban areas in drier regions, such as Phoenix, Arizona (204 mm/yr), Tucson, Arizona (294 mm/yr), and El Paso, Texas (250 mm/yr), may not maintain the vegetation required for foraging, roosting, and nesting. In Arizona, multiple naturalized populations of the Rosy-faced Lovebird (*Agapornis roseicollis*) inhabit urban areas, but its native desert distribution, high trade volume in aviculture (i.e., high propagule pressure), and small size likely explain its presence (Mori et al., 2020; Uehling et al., 2019). The presence of medium-to-large-sized cavity nesters may be precluded by the lack of precipitation sufficient for large tree growth. Although sizable Red-crowned Parrot populations exist in southern California, the areas of Los Angeles and San Diego are relatively dry (~300 mm precipitation annually), well below what our models indicated as ideal (>400 mm annually). Our California model was also the only model where precipitation variables played outsized roles in predicting parrot presence. It is likely that high levels of residential irrigation offset the lack of precipitation in this region. Southern California imports ~90% of their water supply from outside the region (Hogue & Pincetl, 2015), and residential areas in southern California utilize twice as much water for outdoor irrigation than northern California (Mayer et al., 2011; Mini et al., 2014a). Additionally, affluent neighborhoods irrigate landscapes at higher levels compared to less affluent areas (Mini et al., 2014b), which may help explain why these neighborhoods have increased numbers of large trees and more wildlife. In short, our results suggest that suitable Red-crowned Parrot habitats depend on a minimum level of at least 400 mm of precipitation and/or irrigation.

3.5.6. Urbanization and Population Density

Most high- and medium-quality habitats predicted by our models closely followed urban boundaries (Figure 4), which was consistent with some of the earliest observations of these birds in the United States (Meseck, 2013; Neck, 1986; Uehling et al., 2019). While the California model, Florida model, and combined model predicted high- and medium-quality habitats in areas that had at least 1,000 people/km^2, the Texas model predicted high- and medium-quality habitats in the Lower Rio Grande Valley at levels above 500 people/km^2, which was similar to previous models focused on San Diego County in California (Meseck, 2013). Overall, all models indicated a similar lower limit to human population density (500–1000 people/km^2), but upper limits were extremely variable (2500–15,000 people/km^2). In general, regions with Red-crowned Parrot populations in southern California, including Los Angeles and San Diego, and in the Miami area of southeastern Florida had much higher human population densities than South Texas, but these regions did not seem to harbor higher densities of Red-crowned Parrots (Garrett, 2018; Kiacz et al., 2021). These wide tolerance ranges may explain why our three state-level models did not predict suitable habitat outside of the state from which the presence points originated. The lower bounds for climatic and anthropogenic variables may have been suitable in many areas, but the upper bounds were overfit. Therefore, when modeling distributions for species that may have wider physiological constraints than realized or that may not be in equilibrium with their environment, it is important to include presence locations from as many viable populations as possible.

Human population density alone is not likely to be the driving factor of occupancy for this synanthropic species. Instead, density is likely a proxy for an array of anthropogenic changes (i.e., urban landscaping, irrigation, bird feeders, etc.) (Duncan et al., 2003; Meseck, 2013; Neck, 1986). Given that many Red-crowned Parrots were released or escaped pets, higher human density also correlated with higher levels of propagule pressure (Vall-Llosera & Cassey, 2017). Additionally, human density could be seen as a proxy of human activity or of socio-economic drivers, and studies have shown that these factors alter bird behavior, habitat selection, distribution, and IUCN status (Meager et al., 2012; Olah et al., 2016).

Previous studies have noted that wildlife presence in urban ecosystems can increase with the presence of resources such as bird feeders, large street trees, and berry-bearing plants—all of which are abundant in mature suburban areas of southern California, Tex-as, and Florida (Goddard et al., 2013; Wood & Esaian, 2020). Another well-noted pattern is that affluent neighborhoods harbor more and larger trees and thus a greater diversity of wildlife (Kuruneri-Chitepo & Shackleton, 2011; Wood & Esaian, 2020). While we did not integrate data on neighborhood income into our work in South Texas, it was evident that parrots favored areas with larger homes and more mature trees. As Red-crowned Parrots in South Texas were utilizing roughly 70% nonnative tree species for roosting, nesting, and feeding (Kiacz, personal communication), it was apparent that urban landscaping was a large driving force behind species occupancy, supporting previous observations and modeling outcomes (Meseck, 2013; Neck, 1986). While native trees are generally better for native birds in urban areas (Chalker-Scott, 2015; Pena et al., 2017; Wood & Esaian, 2020), nonnative trees in urban areas can be beneficial for native and nonnative birds alike (Martin A Schlaepfer et al., 2011), which appeared to be the case for the Red-crowned Parrots in our three US populations.

Although Red-crowned Parrots in Texas are considered native, they depend on a completely modified urban ecosystem similar to naturalized populations in California and Florida (Kiacz et al., 2021; Meseck, 2013). Urban and suburban areas with ample and mature landscaping on residential and commercial properties are likely the main non-climatic drivers of Red-crowned Parrot occupancy, which seems to be a dependence commonly exhibited by other synanthropic species, including other naturalized parrot populations (Runde et al., 2007; Uehling et al., 2019).

Urbanization was an extremely influential predictor for occupancy, and our presence locations contained few sightings in natural areas. These findings suggested that it was unlikely that Red-crowned Parrots would inhabit surrounding natural or wild areas in large numbers. While many "urbanized" species are dependent on remnant patches of native habitat within or adjacent to urban areas, Red-crowned Parrots do not seem to utilize these natural habitats often (Kiacz et al., 2021). The reasons why are unknown, but we suspect that populations learn to survive in these urban areas and pass this knowledge to subsequent generations since urban areas are generally where individuals or groups are initially released or escape into. This urban adaptation likely limits the species ability to disperse into and survive in more natural areas, leading to isolation by adaptation (Nosil et al., 2008). This has important implications for the future of populations of Red-crowned Parrots within the United States and should alleviate most threats they may represent as a potential invasive species. It also implies that synanthropic species like the Red-crowned Parrot are likely to persist as long as currently inhabited urban areas do not drastically change their vegetation structures or landscape mosaics. Moreover, if urbanization continues along its recent trajectory, and urban yards and landscaping are maintained at similar levels, populations of these and other synanthropes are likely to grow in California, Texas, and Florida.

3.6. Appendix

Percent contribution and permutation importance for all variables in all models. Percent contribution is found by keeping track of the importance that each variable is having during the model training process and should be interpreted with caution since it is heuristically defined and can be influenced by multicollinearity. Permutation importance is found for each variable by altering "…values of that variable on training presence and background data [and] are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages." (Phillips, 2005) Reprinted with permission from (Kiacz et al., 2023).

Combined Model			California Only			Florida Only			Texas Only		
Variable	**Percent Contribution**	**Permutation Importance**	**Variable**	**Percent Contribution**	**Permutation Importance**	**Variable**	**Percent Contribution**	**Permutation Importance**	**Variable**	**Percent Contribution**	**Permutation Importance**
Population_Density250	57.9	0.6	**Bio14_250—Precip. of Driest Month**	36.8	0.8	**Bio11_250—Mean Temp. of Coldest Quarter**	74.5	78.2	**Bio01_250—Annual Mean Temp.**	50.7	93.3
Bio15_250—Precipitation Seasonality	7.9	0.6	**Population_Density250**	27.8	0.7	**Bio01_250—Annual Mean Temp.**	7.2	5.3	**Population_Density250**	24.9	0.6
Bio01_250—Annual Mean Temp.	5.9	0.6	**Bio15_250—Precip. Seasonality**	17.5	4.7	**Population_Density250**	6.9	0.6	**Bio11_250—Mean Temp. of Coldest Quarter**	6.4	0.0
Bio04_250—Temp. Seasonality	5.1	93.2	**Bio18_250—Precip. of Warmest Quarter**	3.1	0.2	**Bio13_250—Precip. of Wettest Month**	2.4	0.5	**Bio18_250—Precip. of Warmest Quarter**	3.4	1.9

Combined Model			California Only			Florida Only			Texas Only		
Variable	**Percent Contribution**	**Permutation Importance**	**Variable**	**Percent Contribution**	**Permutation Importance**	**Variable**	**Percent Contribution**	**Permutation Importance**	**Variable**	**Percent Contribution**	**Permutation Importance**
Bio06_250—Min Temp.	5.1	0.5	**Bio02_250—Mean Diurnal Range**	2.5	0.0	**Bio18_250—Precip. of Warmest Quarter**	2.2	0.9	**Bio06_250—Min Temp.**	3.3	1.0
Bio07_250—Temp. Annual Range	4.1	0.3	**Bio05_250—Max Temp.**	2.1	0.0	**Bio06_250—Min Temp.**	1.3	1.8	**Bio07_250—Temp. Annual Range**	2.8	0.0
Bio11_250—Mean Temp. of Coldest Quarter	3.1	1.8	**Bio17_250—Precip. of Driest Quarter**	1.7	0.3	**Bio16_250—Precip. of Wettest Quarter**	0.7	0.0	**Bio05_250—Max Temp.**	1.9	0.0
Bio10_250—Mean Temp. of Warmest Quarter	2.5	0.1	**Bio04_250—Temp. Seasonality**	1.7	0.0	**Bio08_250—Mean Temp. of Wettest Quarter**	0.7	0.5	**Bio17_250—Precip. of Driest Quarter**	1.7	0.3
Bio02_250—Mean Diurnal Range	1.6	0.0	**Bio06_250—Min Temp.**	1.1	83.6	**NLCD_2016_Land Cover250**	0.6	0.2	**Bio08_250—Mean Temp. of Wettest Quarter**	1.3	0.0

Combined Model			California Only			Florida Only			Texas Only		
Variable	Percent Contribution	Permutation Importance	Variable	Percent Contribution	Permutation Importance	Variable	Percent Contribution	Permutation Importance	Variable	Percent Contribution	Permutation Importance
Bio05_250—Max Temp.	1.3	0.0	**NLCD_2016_LandCover250**	0.9	0.3	**Bio03_250—Isothermality**	0.6	0.0	**Bio02_250—Mean Diurnal Range**	0.6	2.3
Bio09_250—Mean Temp. of Driest Quarter	1.1	0.3	**Bio10_250—Mean Temp. of Warmest Quarter**	0.7	0.3	**Bio05_250—Max Temp.**	0.5	0.0	**Bio15_250—Precip. Seasonality**	0.6	0.3
NLCD_2016_LandCover250	1.3	0.1	**Bio19_250—Precip. of Coldest Quarter**	1.0	4.4	**Bio12_250—Annual Precip.**	0.6	11.5	**NLCD_2016_Impervious250**	0.6	0.0
Bio03_250—Isothermality	0.7	0.0	**Bio01_250—Annual Mean Temp.**	0.6	0.2	**Bio07_250—Temp. Annual Range**	0.3	0.0	**Bio10_250—Mean Temp. of Warmest Quarter**	0.5	0.0
NLCD_2016_TreeCanopy250	0.4	0.0	**Bio11_250—Mean Temp. of Coldest Quarter**	0.6	0.1	**Bio10_250—Mean Temp. of Warmest Quarter**	0.3	0.0	**Bio09_250—Mean Temp. of Driest Quarter**	0.3	0.0
Bio14_250—Precip. of Driest Month	0.4	0.0	**Bio03_250—Isothermality**	0.6	0.0	**Bio09_250—Mean Temp. of Driest Quarter**	0.3	0.0	**GAPlandfire250**	0.3	0.0

Combined Model			California Only			Florida Only			Texas Only		
Variable	Percent Contribution	Permutation Importance	Variable	Percent Contribution	Permutation Importance	Variable	Percent Contribution	Permutation Importance	Variable	Percent Contribution	Permutation Importance
Bio18_250—Precip. of Warmest Quarter	0.4	1.3	**NLCD_2016_Impervious250**	0.4	0.0	**Bio04_250—Temp. Seasonality**	0.3	0.0	**Bio03_250—Isothermality**	0.2	0.0
Bio12_250—Annual Precip.	0.2	0.0	**GAPlandfire250**	0.1	0.3	**GAPlandfire250**	0.1	0.2	**NLCD_2016_LandCover250**	0.1	0.0
GAPlandfire250	0.2	0.0	**Bio09_250—Mean Temp. of Driest Quarter**	0.3	0.1	**Bio14_250—Precip. of Driest Month**	0.1	0.0	**Bio04_250—Temp. Seasonality**	0.1	0.0
NLCD_2016_Impervious250	0.3	0.0	**Bio07_250—Temp. Annual Range**	0.3	0.0	**Bio02_250—Mean Diurnal Range**	0.2	0.0	**NLCD_2016_TreeCanopy250**	0.1	0.0
NDVI_2020_250	0.0	0.0	**NDVI_2020_250**	0.0	0.1	**NDVI_2020_250**	0.0	0.0	**Bio19_250—Precip. of Coldest Quarter**	0.0	0.1
Bio08_250—Mean Temp. of Wettest Quarter	0.1	0.0	**Bio08_250—Mean Temp. of Wettest Quarter**	0.1	0.6	**NLCD_2016_Impervious250**	0.1	0.1	**NDVI_2020_250**	0.0	0.0

Combined Model			California Only			Florida Only			Texas Only		
Variable	Percent Contribution	Permutation Importance	Variable	Percent Contribution	Permutation Importance	Variable	Percent Contribution	Permutation Importance	Variable	Percent Contribution	Permutation Importance
Bio16_250—Precip. of Wettest Quarter	0.1	0.3	**Bio16_250—Precip. of Wettest Quarter**	0.0	0.0	**Bio15_250—Precip. Seasonality**	0.0	0.1	**Bio14_250— Precip. of Driest Month**	0.0	0.0
Bio19_250—Precip. of Coldest Quarter	0.2	0.0	**Bio12_250—Annual Precip.**	0.1	3.3	**Bio17_250—Precip. of Driest Quarter**	0.1	0.0	**Bio13_250— Precip. of Wettest Month**	0.0	0.0
Bio17_250—Precip. of Driest Quarter	0.0	0.0	**Bio13_250—Precip. of Wettest Month**	0.0	0.0	**NLCD_2016_TreeCanopy250**	0.0	0.0	**Bio16_250— Precip. of Wettest Quarter**	0.0	0.0
Bio13_250—Precip. of Wettest Month	0.0	0.0	**NLCD_2016_TreeCanopy250**	0.0	0.0	**Bio19_250—Precip. of Coldest Quarter**	0.0	0.0	**Bio12_250—Annual Precip.**	0.0	0.0

4. ANTHROPOGENIC HYBRIDIZATION WITHIN A COMMUNITY OF MULTIPLE ENDANGERED PARROT SPECIES: WHAT DOES THE FUTURE HOLD?

4.1. Overview

Hybridization is recognized as a potential threat to rare species and can complicate conservation and management efforts. Anthropogenic hybridization, which results from the direct or indirect actions of humans, can complicate matters further by increasing the array of potentially hybridizing species. To show the possible conservation and management consequences of anthropogenic hybridization, we developed an age-structured compartment model representing a community of congeneric parrots in south Texas. Our model community consists of both native and naturalized populations of *Amazona* parrots, including the Endangered Red-crowned Parrot (*Amazona viridigenalis*) and Lilac-crowned Parrot (*A. finschi*). Our simulation results suggest that in the absence of outbreeding depression or reduced fitness of hybrids, even at low levels of hybridization, the future of the community is likely to resemble a hybrid swarm. Future management of these naturalized/native communities will need to explicitly consider the possible impacts of hybridization and its implications on genetic integrity and diversity. Our models serve as a foundation for building field testable hypotheses about hybridization broadly across these and other hybridization-prone communities to help us better predict the potential impacts of hybridization and inform conservation management decisions.

4.2. Introduction

Human activity has altered and fragmented landscapes, introduced hosts of non-native species, and has played a significant role in driving the current biodiversity crisis (Alvey, 2006; Chase et al., 2020). These events are also increasing the opportunities for previously isolated species to come into contact and potentially hybridize (Whiteley et al., 2015). This anthropogenic hybridization can have both positive and negative impacts on populations, as well as on efforts to preserve species (Allendorf et al., 2012). For example, genetic rescue is a useful tool used to increase genetic variation in threatened species, increasing their adaptive potential and fitness (Whiteley et al., 2015). However, anthropogenic hybridization can also result in the loss of genetic integrity in parent populations, potentially leading to genetic swamping or species extinctions (Abbott et al., 2013). Hybridization is a complex phenomenon that can also alter genetic and phenotypic variation, gene expression, and ecological interactions (Chan et al., 2019; Gompert & Buerkle, 2016; Todesco et al., 2016). Many factors influence hybridization - environmental conditions, reproductive barriers, hybrid fitness, and genetic distance between parental populations can all play significant roles (Abbott et al., 2013; Todesco et al., 2016).

From a conservation perspective, it is important to consider the specific context in which anthropogenic hybridization is occurring and its potential impacts when trying to maintain or preserve biodiversity (Muhlfeld et al., 2014). Defining the extent of hybridization can be challenging as it can be uncommon as well as difficult to detect in wild populations; even defining species boundaries can be a difficult philosophical endeavor (De Queiroz, 2007; Hedrick, 2013). The importance of hybridization depends on the specific goals of the conservation effort. Preserving species or populations may require limiting hybridization with closely related groups, whereas increasing or maintaining genetic diversity may necessitate some level of hybridization among populations (Allendorf et al., 2012).

To ensure effective conservation, it is essential to make informed decisions that can limit or reverse the current loss of biodiversity and predicting future scenarios based on current knowledge is crucial to making these decisions (Arlettaz et al., 2010; Geldmann et al., 2013). To that end, population viability models are useful tools to help predict future trends in species abundance and distribution which can inform and guide conservation planning and management to the best decisions (Guisan & Thuiller, 2005; Mantyka-pringle et al., 2012; Moilanen et al., 2009). Additionally, these models may consider population responses to management actions or changes in poorly known parameters that may influence population dynamics (Arlettaz et al., 2010).

To develop accurate models, we must identify and quantify the relevant demographic variables that influence population growth and structure (Boyce et al., 2006). While some demographic factors such as survival, fecundity, and predation can be relatively straightforward to quantify, others such as genetic diversity, disease prevalence, and hybridization are often more difficult to measure. Among these factors, hybridization can be tricky to identify visually, so expensive, invasive, and time-consuming techniques are often required (Fitzpatrick & Shaffer, 2007). Moreover, decisions regarding hybridization and management require context-specific considerations and well-defined objectives, in addition to a thorough understanding of the system (Chan et al., 2019; Fitzpatrick & Shaffer, 2007; Gompert & Buerkle, 2016). Active management can also be a difficult and expensive endeavor and can involve potentially controversial practices such as culling, the use of contraceptives, or translocations (Croft et al., 2021).

The rise of complex conservation situations involving closely related taxa and threatened species introduced into novel environments has created dilemmas for conservation practitioners (Fitzpatrick & Shaffer, 2007). In addition to considering the impacts on the ecosystem and determining whether the populations offer conservation opportunities or pose ecological or economic challenges, it is also necessary to evaluate the potential for beneficial or deleterious effects resulting from hybridization among populations.

Consequently, population modeling has become a valuable tool to simulate the consequences of varying demographic parameters and environmental variables on multiple populations simultaneously (Schaub & Abadi, 2011). In this study we utilize population modeling to examine the potential impacts of anthropogenic hybridization on a community containing native and nonnative parrot species in south Texas, providing a case study to illustrate possible future scenarios for this community and their implications for species conservation.

Our study focuses on a community of parrots in the genus *Amazona* in south Texas, consisting of one native species (Red-crowned Parrot, *Amazona viridigenalis*; RCPA) and four naturalized congeners (Red-lored Parrot, *A. autumnalis*; Yellow-headed

Parrot, *A. oratrix*; Lilac-crowned Parrot, *A. finschi*; White-fronted Parrot, *A. albifrons*). Red-crowned, Lilac-crowned, and Yellow-headed Parrots are considered Endangered by the IUCN, while only Red-crowned Parrots are considered native and Threatened by the State of Texas (IUCN, 2023; Kiacz et al., 2021). While Red-crowned, Yellow-headed, Red-lored, and White-fronted parrots share similar habitats and are sympatric in portions of northeastern Mexico, the native range of Lilac-crowned Parrots is allopatric to all others and endemic to the Pacific coast of Mexico. Although hybridization is possible among all these species, we exclude White-fronted Parrots from our model due to the observed rarity of hybrid pairings with Red-crowned Parrots. Our modeling approach should aid in the management of both endangered and naturalized species and help direct research towards the most pressing conservation needs.

4.3. Methods

4.3.1. Study Area

This study focuses on a Red-crowned Parrot population in the Lower Rio Grande Valley of south Texas, where the population utilizes four easy to access roost sites (Kiacz et al., 2021). To the best of our knowledge, the region's entire community of *Amazona* parrots utilize these four roosts and we have little reason to believe there are interactions between this community and native populations south of the US-Mexico border, as the closest population is at least 150km away. This makes it reasonable to assume the south Texas *Amazona* community is geographically isolated and makes it an ideal study community. It is also reasonable to expect that some parrot introductions still occur in the area through the escape or release of birds from the pet trade, but we have little evidence that this is occurring at demographically relevant rates.

The Lower Rio Grande Valley is primarily an alluvial flood plain of the Rio Grande, although strict flood control efforts along the river's corridor have resulted in a less dynamic ecosystem. Tamaulipan thornscrub, remnant riparian forests, and coastal floodplains make up most of the natural ecosystems, although the parrot community in the region occupies almost exclusively urban/suburban areas (Kiacz et al., 2021; Kiacz et al., 2023). Urban areas used by the parrots are generally landscaped and contain a wide array of native and nonnative flora including mesquite (*Prosopis* spp.), oaks (*Quercus* spp.), palms (*Washingtonia* spp.), and ashes (*Fraxinus* spp).

4.3.2. Model Description

Our model simulates the dynamics of three sympatric parrot populations: Red-crowned Parrots, *Amazona* spp. parrots (implicitly including Red-lored, Lilac-crowned, and Yellow-headed Parrots), and hybrid parrots. We formulated the model as an age-structured compartment model based on difference equations with a one-year time step. Within each of the three populations, age classes represent one-year-olds (fledglings that survived to age one), sexually immature two-year-olds, and sexually mature adults aged ≥3 years old (Fig. 7). Losses from each age-class result from natural mortality and poaching. Recruitment of one-year-olds is based on the number of nests initiated during the previous year and the success of those nests. The number of nests initiated depends on the proportion of adults that attempt breeding that year and the relative availability of nest sites, which depends on total parrot density in the community (Red-crowned plus

Amazona spp. plus hybrids). The relative availability of nest sites declines linearly as total parrot density increases. Nest success reflects losses due to unhatched eggs, predation, weather-related nestling morality, nest poaching, and (for Red-crowned Parrots and *Amazona* spp. parrots) hybridization. Hybridization reduces nest success of Red-crowned Parrots and *Amazona* spp. parrots because offspring from nests of mixed-species pairs are recruited as one-year-olds into the hybrid population. The proportion of nest losses due to hybridization increases linearly as the proportion of hybrids in the parrot community increases. Finally, successful nests are multiplied by average brood size and fledgling survival to determine yearly recruitment.

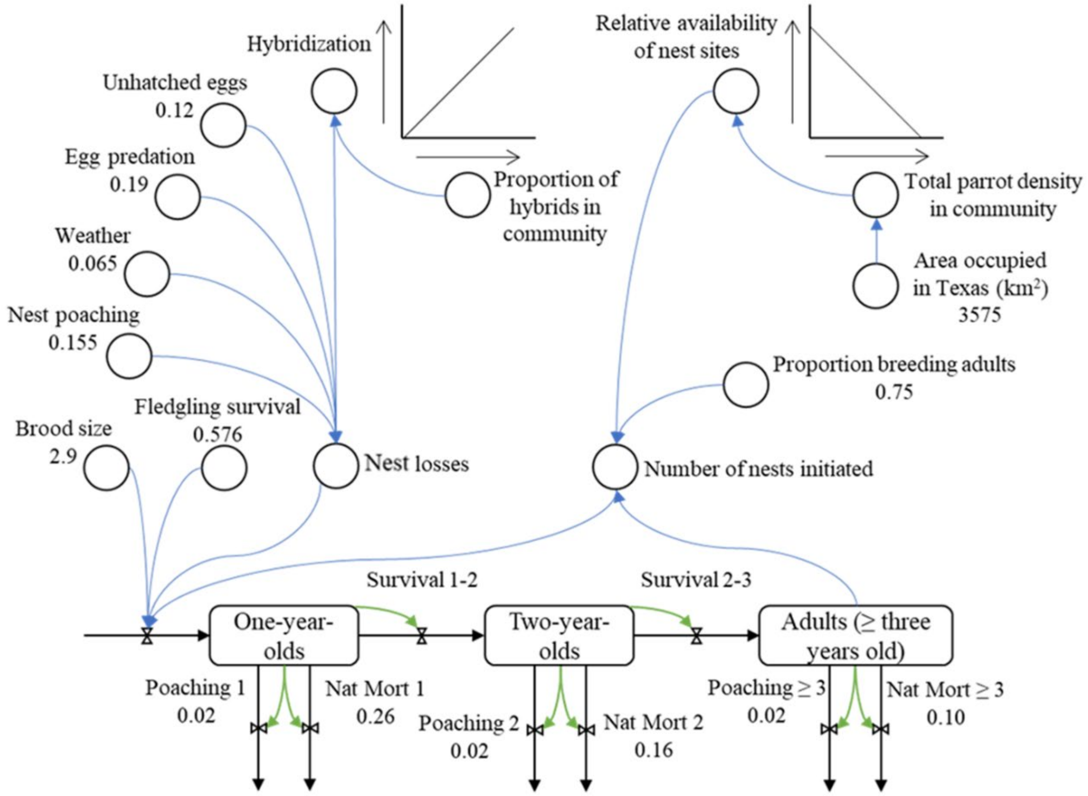


Figure 7. Diagram of the age-structured compartment model representing parrot population dynamics. Numbers represent values of the indicated parameters. See text for details.

4.3.3. Model Parameterization & Evaluation

We parameterized the model using our field data on Red-crowned Parrots from south Texas, published parameter values for Red-crowned and other parrot species, and parameter estimates suggested by species experts. We evaluated model performance by comparing model projections of abundance and annual productivity over a seven-year period to observed abundance and annual productivity from 2016-19 and 2021-22 (missing one year of productivity data in 2020 due to the pandemic). We initialized the simulated Red-crowned Parrot population with 434 adults, 126 two-year-olds, and 140 one-year-olds based on our 2016-17 survey results. We used the proportion of hatch-year birds in the population as an indicator of annual productivity. Observed abundance and annual productivity averaged 710 (ranging from 656 to 890) and 19% (ranging from 14% to 25%), respectively. Simulated abundance and annual productivity averaged 759 (ranging from 700 to 885) and 18% (ranging from 17% to 20%), respectively. We provide parameter values and functional relationships included in the baseline model, as well as information sources, in Table 6. In the Appendix we describe the rationale underlying our parameterization of the model which we programmed in Stella Architect® V3.2.1 (isee systems).

Table 6. Parameter values and functional relationships included in the baseline model and the information sources upon which they were based.

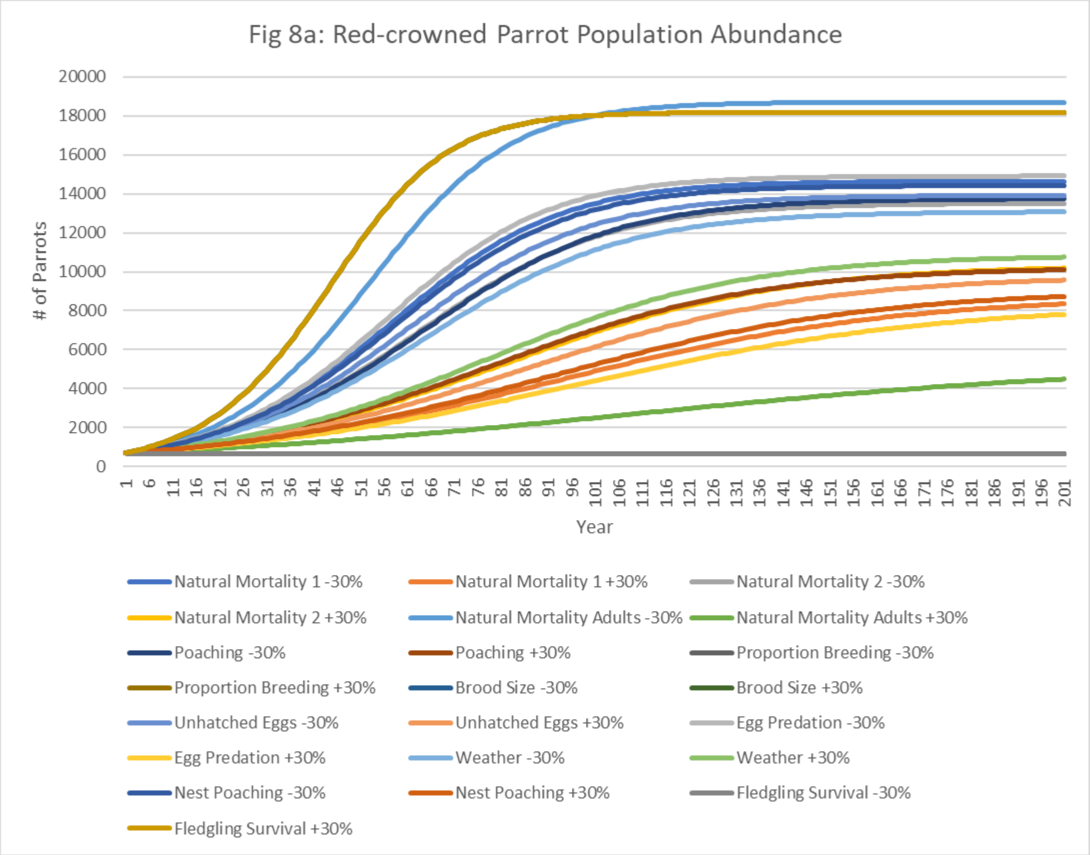
Parameters	Value	Source
Natural mortality one-year-olds	0.26	Expert Opinion
Natural mortality two-year-olds	0.16	(Koenig, 2008; Smith & Rowley, 1995)
Natural mortality adults ≥3 years old	0.10	(Koenig, 2008)
Poaching mortality one-yr-olds, two-yr-olds, adults	0.02	Expert Opinion
Proportion breeding	0.75	(Wiley et al., 2004)
Brood size	2.9	(Enkerlin-Hoeflich, 1995; Gnam & Rockwell, 1991; Renton & Salinas-Melgoza, 2004; Rivera et al., 2014; Sanz & Rodriguez-Ferraro, 2006; Seixas & de Miranda Mourão, 2002; Snyder et al., 1987; Wiley et al., 2004)
Nest loss unhatched eggs	0.12	(Enkerlin-Hoeflich, 1995; Renton & Salinas-Melgoza, 2004; Sanz & Rodriguez-Ferraro, 2006; Seixas & de Miranda Mourão, 2002; Wiley et al., 2004)
Nest loss predation	0.19	(Berkunsky et al., 2016; Renton & Salinas-Melgoza, 2004; Rivera et al., 2014)
Nest loss weather	0.065	(Berkunsky et al., 2016; Rivera et al., 2014; Sanz & Rodriguez-Ferraro, 2006)
Nest loss poaching	0.155	Field studies by Kiacz

Table 6 Continued

Parameters	Value	Source
Fledgling survival	0.576	(Koenig, 2008; Salinas-Melgoza & Renton, 2007; Smith & Rowley, 1995)
Functional Relationships		
Relative availability of nest sites (y) = f(total parrot density per km^2) (x)	$y = 1 - 0.0752 * x$	(Aragón-Tapia, 1986; Castro, 1976; Enkerlin-Hoeflich, 1995; Koenig, 2008; Monterrubio-Rico et al., 2021; Perez & Eguiarte, 1989; Rivera-Milán et al., 2018)
Nest loss hybridization (y) = f(proportion of hybrids in parrot community) (x)	$0.02 + 0.2 * x$	Field studies by Kiacz

4.3.4. Sensitivity to Parametric Uncertainty

To examine the sensitivity of model projections of abundance and annual productivity of the Red-crowned Parrot and *Amazona* spp. populations to parametric uncertainty, we ran a suite of 200-year simulations in which we altered the values of each of the 11 demographic parameters in Table 6, one at a time, by ± 30%. We assumed no hybridization was occurring. Abundances increased in 19 of the 22 simulations and remained stable when percent breeding, fledgling survival, and brood size were reduced by 30% (Fig. 8a). Abundance increased fastest when fledgling survival was increased by 30% and next fastest when natural mortality of adults aged ≥3 years old was decreased by 30%. At year 50, 30% increases in breeding percent, fledgling survival, and brood size all increased the Red-crowned Parrot population by at least 200% above the baseline model. Annual productivities declined as abundances increased, with the highest productivities occurring during the early growth phase of the simulation in which fledgling survival was increased by 30% (Fig. 8b). The lowest productivity occurred in the latter phase of the simulation in which natural mortality of adults aged ≥3 years old was decreased by 30%. Both the Red-crowned Parrot and *Amazona* spp. populations followed similar patterns.



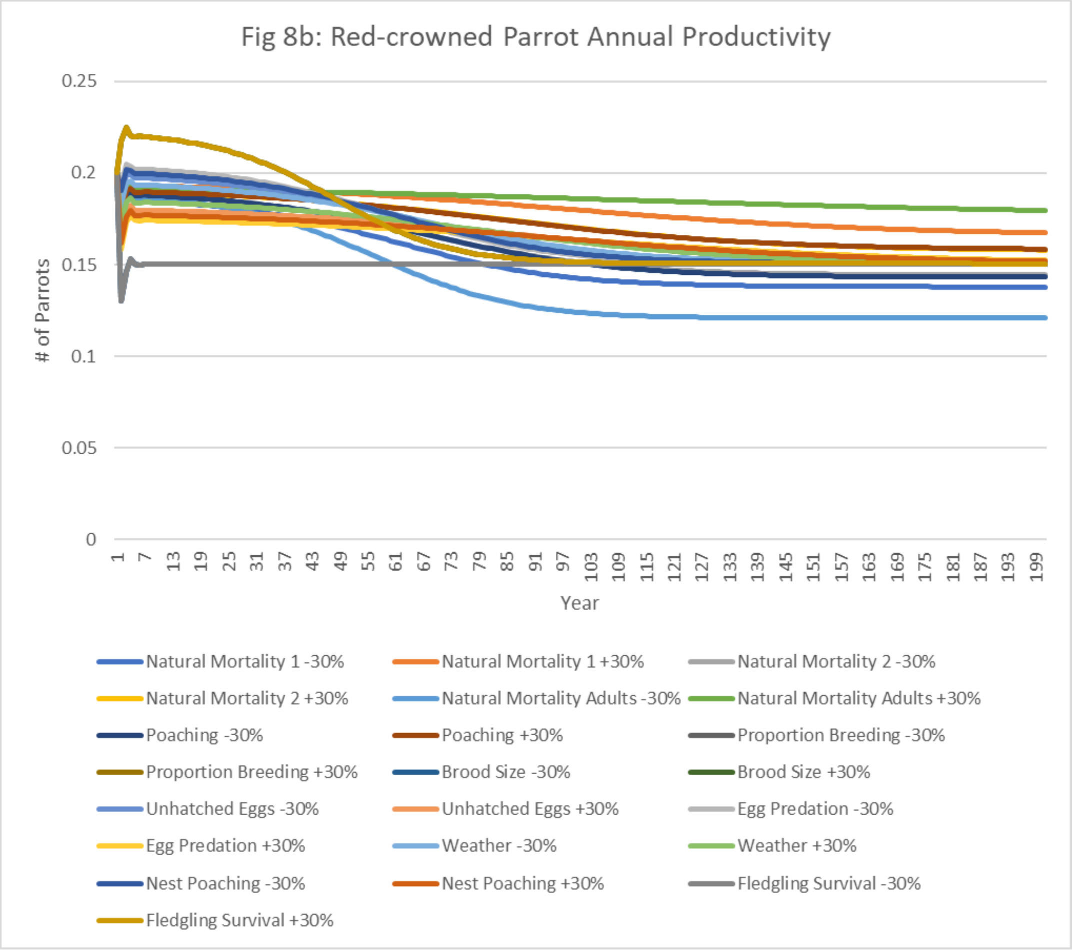


Figure 8. Sensitivity of model projections of (a) abundance and (b) annual productivity of Red-crowned Parrot populations to parametric uncertainty. Different colored lines represent values from the suite of simulations in which each of the 11 demographic parameters in Table 6 were altered, one at a time, by ± 30%. Productivity is (# of 1 yr olds / total population). See text for details.

4.3.5. Simulated Effects of Anthropogenic Hybridization

To explore the potential long-term impacts of anthropogenic hybridization on the parrot community in south Texas, we ran three suites of simulations. In the first suite, we simulated each of three different levels of nest losses due to hybridization. More specifically, we altered the baseline value of the y-intercept of the functional relationship between nest loss due to hybridization and the proportion of hybrids in the parrot community by ± 30% (i.e., from 0.02 to 0.026 and to 0.014, see Table 6). We fixed all other parameters at their baseline values. We initialized the simulated *Amazona* spp. parrot population with 110 adults, 20 two-year-olds, and 20 one-year-olds based on our 2016-17 survey results on Lilac-crowned Parrots, Yellow-headed Parrots, and Red-lored Parrots. We initialized the hybrid population at zero. We assumed no hybrid vigor or adaptive introgression and no outbreeding depression. For these simulations, we monitored abundance of each of the three sympatric parrot populations and noted the year in which hybrids became more abundant than Red-crowned Parrots (i.e., the time to hybrid dominance). Under all three levels of hybridization, the abundance of each population increased initially. However, the abundances of Red-crowned Parrots began to decline after 79, 72, and 89 years, with hybrid dominance occurring after 86, 76, and 102 years, under baseline, high, and low levels of hybridization, respectively (Fig. 9). The total number of Red-crowned Parrots after 200 years was 57, 24, and 160 under baseline, high, and low levels of hybridization, respectively. Productivity measures for Red-crowned and *Amazona* spp. populations remained above 15% in all three scenarios until at least year 71.

Fig. 9a: Baseline Nest Losses to Hybrid. (0.02)

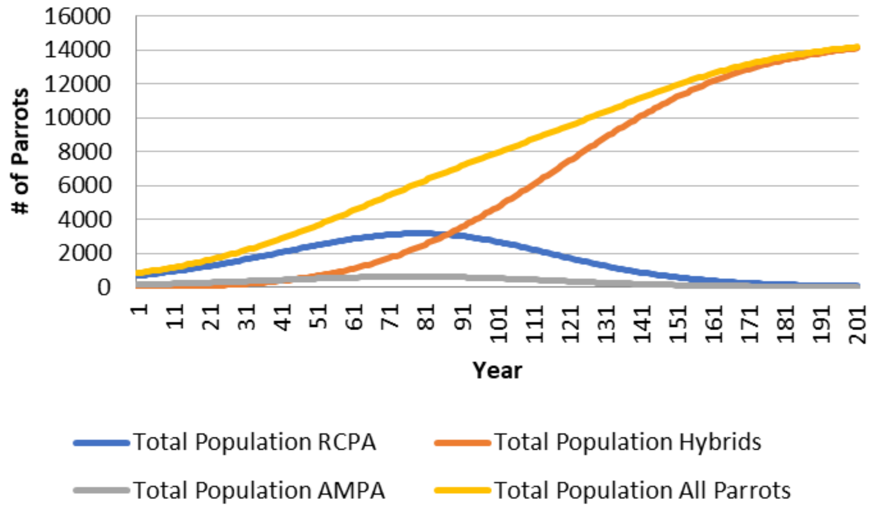
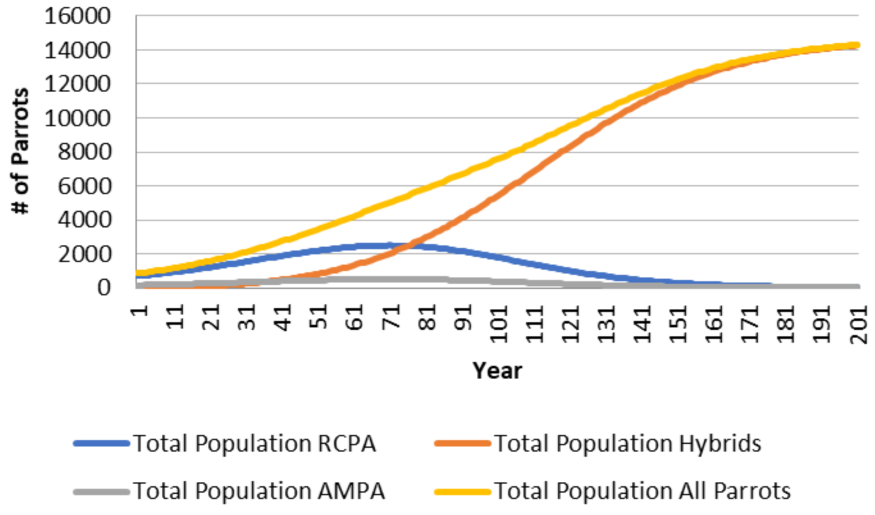


Fig. 9b: High Nest Losses to Hybrid. (0.026)



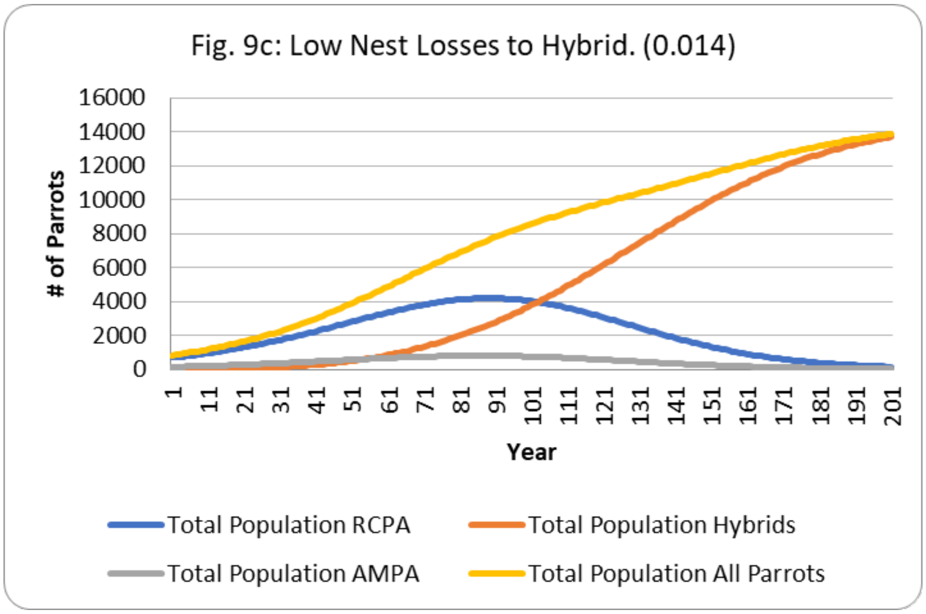


Figure 9. Model projections of abundance of the three sympatric parrot populations assuming (a) baseline, (b) high, and (c) low levels of nest losses due to hybridization. See text for details.

In the second suite of simulations, we explored in more detail the relationship between the level of nest losses due to hybridization and time to hybrid dominance. We sequentially reduced the rates of hybridization (the values of the y-intercept referred to above) from 0.040 to 0.001 in increments of 0.001. Once again, we fixed all other parameters at their baseline values, and we assumed no hybrid vigor or adaptive introgression and no outbreeding depression. For these simulations, we noted the time to hybrid dominance. As levels of hybridization increased above our baseline level, time to hybrid dominance decreased approximately linearly (from 86 to 59 years). However, as hybridization decreased below the baseline level, the time to hybrid dominance increased supra-exponentially (from 86 to 234 years, Fig. 10).

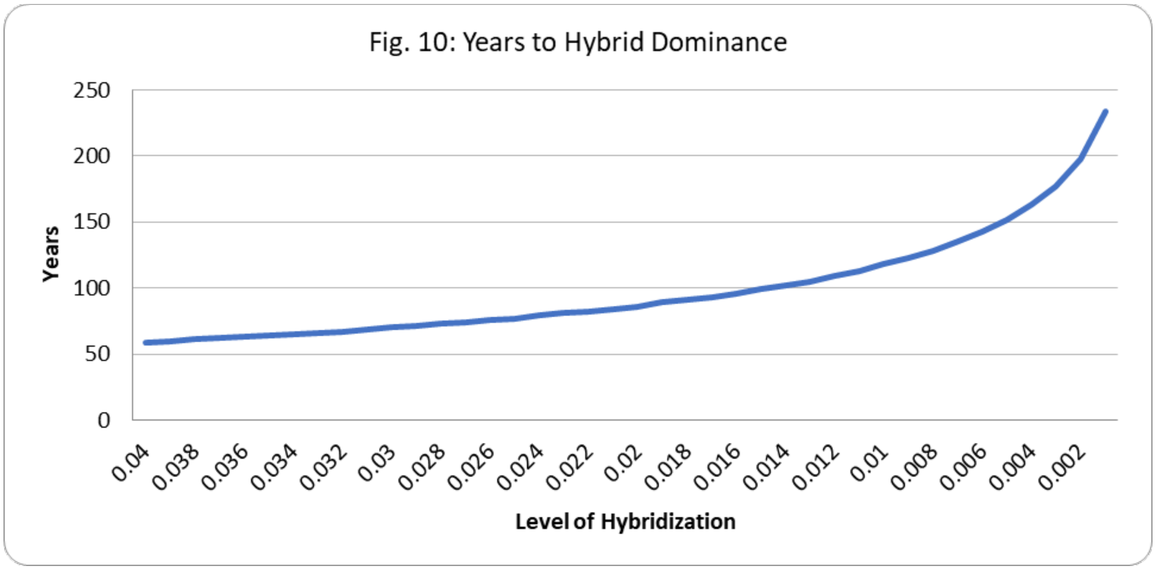
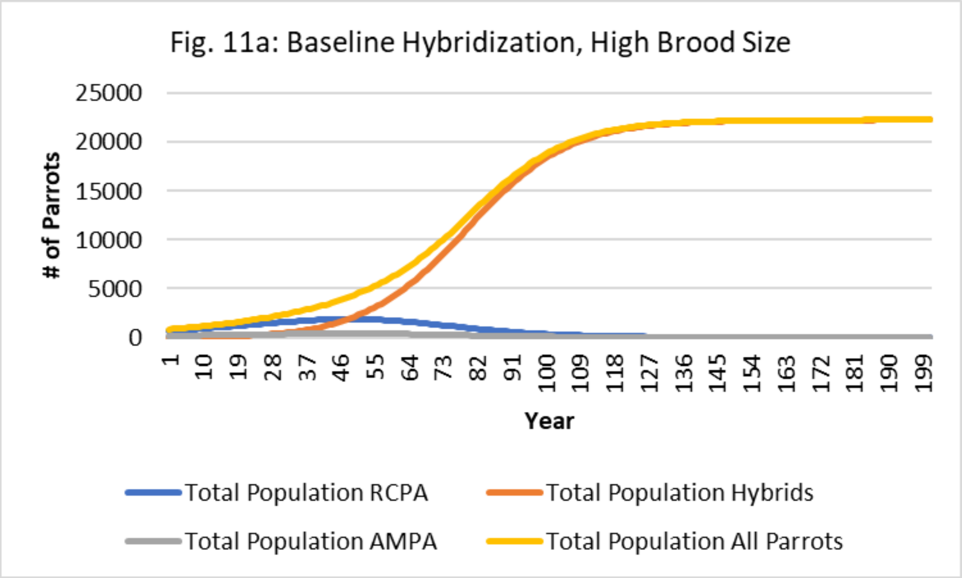


Figure 10. Relationship between levels of nest losses due to hybridization and years to hybrid dominance. On the x-axis are values of the y-intercept of the functional relationship between nest loss due to hybridization and the proportion of hybrids in the parrot community. Values > 0.02 (baseline value) represent increasing levels of nest loss due to hybridization. Values < 0.02 represent decreasing levels of nest loss due to hybridization. See text for details.

In the third suite of simulations, we explored the effect of hybrid vigor and adaptive introgression and the effect of outbreeding depression on the time to hybrid dominance. We simulated hybrid vigor and adaptive introgression by altering two parameters in the hybrid population, one at a time, while maintaining baseline levels of hybridization. First, we assumed higher brood size for the hybrid population (brood size of hybrid population = baseline +30%), and secondly, we assumed higher hatching success (unhatched eggs of hybrid population = baseline -30%). Conversely, we simulated outbreeding depression by altering the same two parameters in the hybrid population in an opposing manner: low brood size for the hybrid population (brood size of hybrid population = baseline -30%) and low hatching success (unhatched eggs of hybrid population = baseline +30%). Once again, we fixed all other parameters at their baseline values. With an increase in the hybrid population brood size, hybrid dominance was achieved in 48 years (Fig. 11a), while an increase in the hybrid population hatching success resulted in hybrid dominance in 71 years (Fig. 11b). When decreasing the hybrid population brood size, hybrid dominance was not achieved within the 200-year simulation (Fig. 12a), while decreasing the hybrid population hatching success resulted in hybrid dominance in 114 years (Fig. 12b). When increasing hybrid brood size and hatching success, Red-crowned Parrot productivity dropped below 15% in year 49 and 68, respectively; when decreasing hybrid brood size productivity did not drop below 15%, but a decrease in hybrid hatching success resulted in productivity dropping below 15% at year 97.



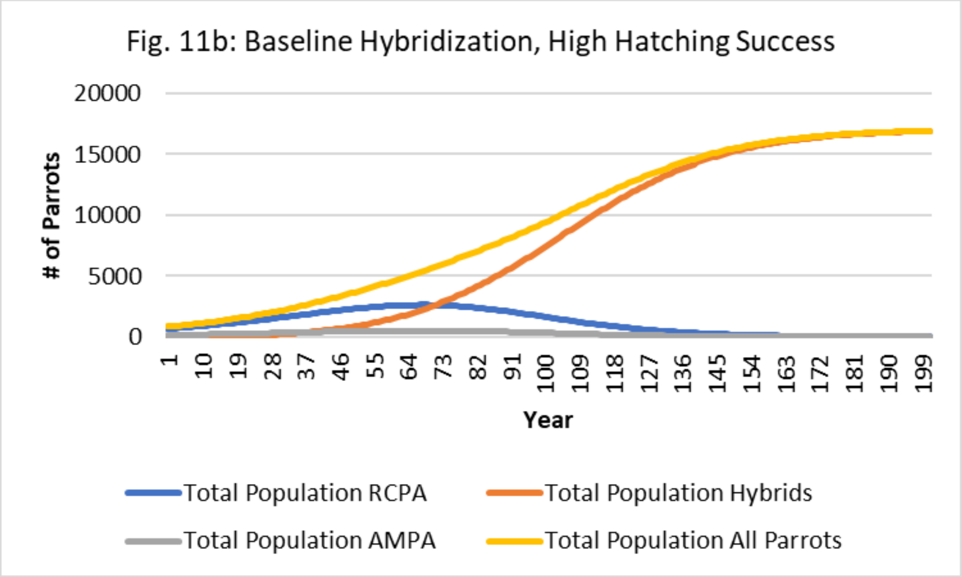
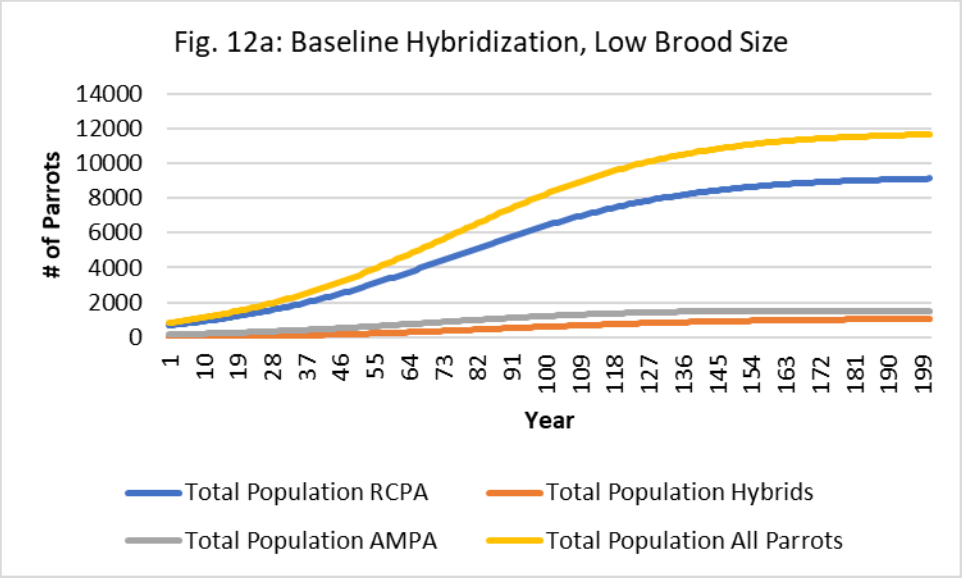


Figure 11. The effect of hybrid vigor and adaptive introgression on the number of years to hybrid dominance represented by (a) high brood size of hybrid population and (b) high hatching success of hybrid population relative to other parrot populations. See text for details.



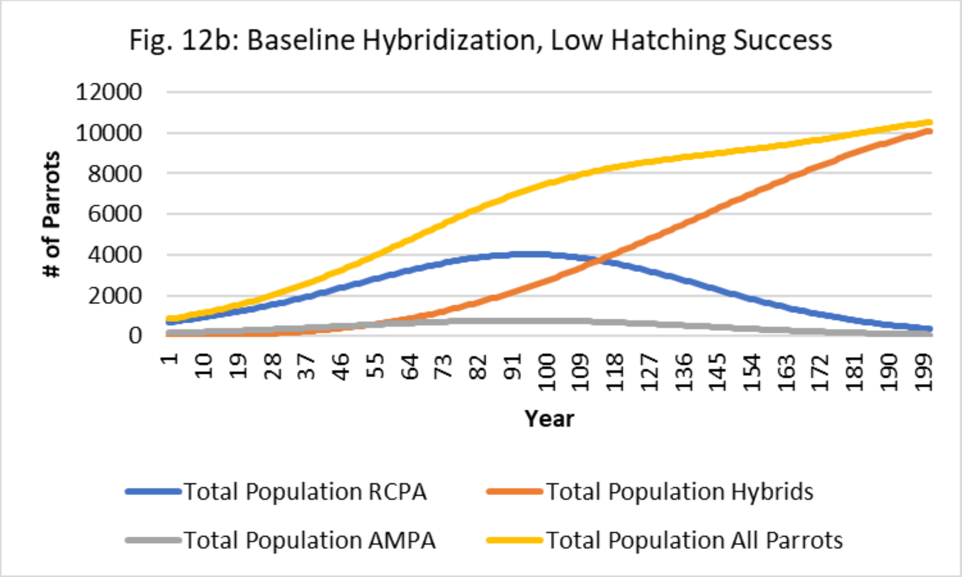


Figure 12. The effect of outbreeding depression on the number of years to hybrid dominance represented by (a) low brood size of hybrid population and (b) low hatching success of hybrid population relative to other parrot populations. See text for details.

4.4. Discussion

Hybridization is increasingly being shown to play major roles in evolution, ecology, and the conservation of rare species (Allendorf et al., 2004; Fitzpatrick & Shaffer, 2007; Wallis, 1999). But it is also a complicated issue – it can break down previously defined species delineations and introduce beneficial or deleterious genetic diversity that can lead to speciation or extinction (Quilodrán et al., 2020). These complications, paired with an increase in anthropogenic hybridization, have put a strain on Mayr's biological species concept by breaking down the binary notion of reproductive isolation and altering the relative fitness of hybrid offspring leading to differences in demographic parameters within populations. Hybridization can sometimes lead to relatively stable outcomes, such as the hybrid zones between Eastern and

Western Meadowlarks (*Sturnella magna & S. neglecta*) and their inviable offspring (Lanyon, 1979), or it can lead to total genetic or demographic swamping and drive taxa to extinction like a scenario involving iguanas in the Lesser Antilles (Vuillaume et al., 2015). To that end, we built our model with the intent to better understand how different hybridization scenarios may influence the population dynamics of multiple threatened species and to give researchers and other stakeholders a foundation to develop and test hypotheses concerning altered demographic values or potential management scenarios.

We developed a model that accurately simulated observed productivity and population growth for a mixed community of closely related *Amazona* parrots. Our sensitivity analysis on 11 demographic parameters suggested that, in the absence of hybridization, these populations demographics were robust; no 30% reduction of any individual demographic factor resulted in a decrease of the populations, although decreases in brood size, fledgling survival, or percent breeding limited population growth over the 200-year simulations. Likewise, 30% increases in parameters led to much larger populations over the baseline model, with increases in brood size, fledgling survival, percent breeding, and adult survival all leading to the largest gains. Similar demographic parameters have been shown to play outsized roles in modeling efforts and support prior results that *Amazona* parrots are on the slower end of the life history continuum (Beissinger et al., 2008).

Weather was shown to be the least important factor in determining population dynamics. This seems reasonable for our community's geographic location in south Texas since few major weather events occur that can reduce survival or fledging success at a large scale, although heavy rains have been noted to cause nesting failures in isolated patches (Kiacz, pers. observation). This is contrary to many island populations of *Amazona* parrots where hurricanes have been shown to play major roles in reducing adult populations and/or nesting resources (Thompson, 2004; White et al., 2005).

Changes in the mortality of second year birds also played a minimal role in our model, although this is likely because this parameter is affecting a single year of survival whereas rates of adult mortality are affecting individuals for the entirety of their breeding years.

When hybridization was included in our simulations, even at low levels (~2%), it played a dominant role in community dynamics and without any effects of outbreeding depression ultimately led to hybrid dominance and a reduced or non-existent population of pure Red-crowned Parrots. From an evolutionary perspective, this hybridization may lead to novel biodiversity with unique genetic variation that can produce a robust and resilient parrot population capable of withstanding changes in the climate or environment that either parent population may struggle with (Taylor & Larson, 2019). This adaptive introgression can happen quickly when strong selective forces are present or generation times are short and imbalances in population abundances are present, although populations of *Amazona* parrots may be cushioned from speedy allele fixation due to their longer generation times and lower reproductive output (Hedrick, 2013). Conversely, our models showed that large decreases in important demographic parameters of the hybrid population (i.e., outbreeding depression) can reduce their relative fitness low enough to allow parent populations to persist throughout our simulation. Depending on the strength of mate choice selection, this could lead to a weak or indiscernible decrease in productivity of parent populations (strong intraspecific selection) or a large enough drop in productivity that could drive this relatively small parrot community towards extinction (strong interspecific selection paired with low hybrid fitness). In our case, we have no reason to believe that interspecific selection is high – in fact, apart from a few individuals, flocks of Red-crowned and Lilac-crowned Parrots tend to separate outside of roosts. Even so, observed levels of hybridization within our community are still predicted to drive our community to resemble a hybrid swarm.

From a conservation perspective, maintaining genetic integrity is often viewed as an important management goal leading practitioners to shun hybridization; this is especially true in rare or charismatic taxa (Piett et al., 2015). This mindset results in a conundrum – rare species are inherently at-risk of inbreeding depression and may lack the standing genetic variation needed to withstand sudden changes in selective pressures, but hybridization may be the answer to these problems. Practitioners must decide in these situations – either let hybridization occur while risking the loss of genetic integrity and potential outbreeding depression that can be detrimental to both parental and hybrid populations or manage to reduce hybridization to preserve genetic integrity in parental species while trusting those populations can withstand changes in selective forces. In our scenario, there is no evidence of range connectivity between our study population and other parrot populations which provides a unique case where management may be able to allow hybridization to occur in this relatively small parrot community while supporting populations of the parent species within their native and isolated ranges. So even though our community involves rare and charismatic parrots, their isolation may allow management to take a hands-off approach while pure parental populations persist elsewhere. Of course, this scenario reduces the conservation value of these populations as rescue populations.

Results from our simulations and real-life examples show the importance of understanding the relative fitness of hybrid offspring and existing levels of genetic introgression to fully grasp the conservation implications and management needs of hybridizing populations. In addition to altering individual fitness, hybridization can indirectly lead to reduced demographic parameters of parental populations by wasting the breeding effort of individuals that raise hybrid offspring. This was shown in our models when even low rates of hybridization resulted in hybrid dominance over time. Indeed, large reductions in hybrid brood sizes or hatching rates were needed to simulate enough outbreeding depression to allow persistence of parental populations. Although outbreeding depression may help limit hybridization and introgression in our parrot community, genetic swamping may still occur from the comparatively large population of Red-crowned Parrots into the populations of Lilac-crowned, Red-lored, and/or Yellow-headed Parrot populations and may weaken the genetic integrity of the smaller populations. This asymmetric introgression is expected during natural range expansions or as populations become established in novel areas which is what is currently happening in our parrot community (Quilodrán et al., 2020). Although these smaller populations are nonnative, two species (Lilac-crowned and Yellow-headed Parrot) are IUCN

Endangered species and potentially important units of conservation. In cases where hybridization is occurring but unlikely to lead to a hybrid swarm, it may still prove useful to limit hybridization if maintenance of genetic integrity is the goal.

Hybrid vigor may be caused by multiple pathways (over-dominance, epistasis, complementation (Lippman & Zamir, 2007)) and was represented in our model by the increase in brood size and hatching rate in our hybrid population, but other routes are possible like an increase in survival of hybrid adults or fledglings. In our case, baseline hybridization resulted in eventual hybrid dominance, so any scenario including some form of hybrid vigor or adaptive introgression would achieve similar results but quicker. Increases in the hybrid average brood size in any version of our model (high, medium, low hybridization) resulted in hybrid swarms and the total loss of parental species, while decreases in the hybrid unhatched eggs resulted in hybrid swarms but not always the total loss of pure parental species. The rate of time until hybrid dominance was shortened by almost half when increasing the hybrid brood size by 30% over the medium model (from 86 to 48 years). From a conservation perspective, hybrid vigor results in a loss of time for management actions to take place if genetic integrity of parent populations is considered paramount, but it may also result in a more resilient hybrid parrot population that can withstand ongoing landscape and climate change in a novel environment better than the parental species (Fitzpatrick & Shaffer, 2007; Lippman & Zamir, 2007). In our scenario, the community is isolated from native parental populations so although we would not lose a species if genetic swamping and hybrid dominance occurs, we could lose a potentially important genetic reservoir of pure individuals of species of conservation concern. Similar situations are occurring; hybrid salamanders in California have shown increased fitness over their parental populations and this hybrid vigor is playing a role in the reduction of the native California Tiger Salamander population while producing a robust population of hybrids (Riley et al., 2003). As Fitzpatrick and Shaffer (2007) point out, this may be good or bad depending on the whether the main conservation goal is genetic purity or a robust population of salamanders to fill their ecological niche. In our case, conservationists must decide whether maintaining pure species and genetic integrity is the main goal and worth the costs of management versus allowing hybridization to occur and potentially creating a hybrid swarm.

4.5. Appendix

Below we describe the rationale underlying our parameterization and calibration of the model. (See Figure 7 and the text for relationships among model parameters and Table 6 for a summary of values and sources of model parameters.) We also present results of sensitivity analyses.

4.5.1. Rationale Underlying Model Parameterization

We found demographic parameters for RCPAs and *Amazona* parrots through a literature search and through previous field work in south Texas from 2016 through 2022. Few studies on life history demographics exist for *Amazona* parrots, so we used averages for most parameters with exceptions for nest poaching, hybridization, unhatched eggs, and poaching of immature and adult birds. We determined poaching and hybridization estimates, as well as poaching rates of first year, second year, and adult birds from previous RCPA field work in south Texas (Kiacz et al. 2021). We derived estimates for unhatched eggs from previous field work in northeast Mexico (Enkerlin-Hoeflich 1995).

4.5.1.1. Poaching

We estimated poaching rates in the south Texas population by monitoring local flea markets and online marketplaces (Craigslist), as well as opportunistically finding evidence of poaching while conducting field work during 2016-2018. Evidence of nest poaching included enlarged nest cavity entrances or fresh spike marks on active nest trees indicating recent climbing. Our initial value of 0.155 is lower than many published poaching estimates for parrots, which average 0.30 and can be as high as 0.90 (Wright et al. 2001), but social and economic factors within urban areas in the United States likely play an important role in facilitating lower poaching rates (Olah et al. 2016).

4.5.1.2. Hybridization

We obtained estimates of hybridization rates during 2017-19 field work in south Texas by noting hybrid phenotypes and mixed nesting pairs. We determined hybrid phenotypes by the presence of traits that were intermediate between RCPAs and other *Amazona* species, including but not limited to facial skin color, nare color, color of forehead feathers, extent of color on crown, iris color, and extent of black barring on chest feathers. We also noted mixed species pairs as evidenced by allopreening, copulation, and sharing of a nest cavity. We derived our initial (baseline) rate of 0.02 from the identification of 14 Red-crowned x Lilac-crowned hybrids from 2017-2019 in a total population of ~700; although we note that this estimate may be low owing to the difficulty of identifying hybrid phenotypes. Additional hybrids have been identified after field studies were completed, such as 2 Yellow-headed x Lilac-crowned individuals identified in 2021, but these individuals were not part of systematic searches for hybrids and thus are not included in our study.

4.5.1.3. Predation

Predation rates can vary widely across landscapes, and although our urban ecosystem likely has fewer traditional predators such as hawks and snakes, novel predators such as dogs and feral cats, and competition from cavity nesters (other parrots, House Sparrows, Starlings, etc.) exist in high numbers. Predation of eggs and chicks is more common than predation on adults, and we derived our estimate of 0.19 from previous studies on egg and nestling predation on Red-crowned Parrots and congenerics within their native range (Enkerlin-Hoeflich 1995; Seixas and de Miranda Mourão 2002; Renton and Salinas-Melgoza 2004; Sanz and Rodriguez-Ferraro 2006; Rivera et al. 2014; Berkunsky et al. 2016).

4.5.1.4. Weather

Weather can play important roles in chick and fledgling survival, as major storms can be a source of nest cavity flooding and can have direct impacts on fledglings and adults alike from high winds. Our initial value of 0.065 is an average of estimates from the literature for this parameter (Sanz and Rodriguez-Ferraro 2006; Rivera et al. 2014; Berkunsky et al. 2016).

4.5.1.5. Unhatched Eggs

We used data from nine sources to obtain an average of 0.12 for the unhatched eggs parameter which represents unviable or infertile eggs.

4.5.1.6. Age of Maturity

Age of first breeding is thought to be around 3-5 years for most *Amazona* parrots (Young et al. 2012). For our model, we considered birds 3 years of age and older to be sexually mature.

4.5.1.7. Average Brood Size

Estimates for average brood size at fledging varied from lows of 1 for Imperial Parrots (*A. imperialis*) to 3.6 for the Cuban Parrot (*A. leucocephala bahamensis*) and averaged 2.9, which is the estimate we used for our baseline model (Snyder et al. 1987; Gnam and Rockwell 1991; Enkerlin-Hoeflich 1995; Seixas and de Miranda Mourão 2002; Renton and Salinas-Melgoza 2004; Sanz and Rodriguez-Ferraro 2006).

4.5.1.8. Percent Breeding Per Year

Very few data exist for this parameter as it is extremely difficult to collect data pertaining to entire nesting populations, and percentages likely vary on a yearly basis due to weather and previous years nesting attempts/successes. We used an average of 0.75 for our medium model, just over half (0.525) for our low model, and 0.975 for our high model, which encompasses estimates encountered in the literature (Wiley et al. 2004; Berg and Angel 2006).

4.5.1.9. Survival Rates

As a result of the limited availability of survival data, we used 0.74 as the annual survival rate for first year birds, 0.84 for second year birds, and 0.9 for adults, which are similar to rates used previously for population modeling of an *Amazona* sp. (Koenig 2008). We estimated fledgling survival rates (survival from leaving the nest to the next breeding season) at 0.576, which was an average from published studies on *Amazona* spp. (Wiley et al. 2004; Salinas-Melgoza and Renton 2007; Koenig 2008) and two *Cacatua* spp. (Smith and Rowley 1995).

4.5.1.10. Density Dependence of Population Growth

Although the current parrot density in south Texas is extremely low (Kiacz et al., 2023), to guard against unrealistically high simulated parrot densities we established a density-dependent negative feedback on population growth by presuming an upper limit of 13.3 parrots/km^2. This density is the average of the previously published estimates from northwest Mexico (Enkerlin-Hoeflich 1995; Monterrubio-Rico et al. 2021). We represented density-dependent population growth by linearly decreasing the relative number of RCPA nests established in a given year from 1.0 toward 0 as the overall parrot density increased from 0 toward 13.3 parrots/km^2.

5. NATURALIZED PARROTS: CONSERVATION AND RESEARCH OPPORTUNITIES[3]

5.1. Introduction

Upwards of 60 of the world's 398 species of psittacines have established naturalized populations outside their normal ranges (Cassey et al., 2004; Menchetti & Mori, 2014; Runde et al., 2007). These populations vary in size from a few breeding pairs to thousands of individuals (Minor et al., 2012; Uehling et al., 2019). Much has been written about the real and potential negative ecological, economic, and social impacts caused by these naturalized populations ((Menchetti & Mori, 2014; Pimentel et al., 2005; Sax & Gaines, 2008); in this vol.: Crowley, chap. 3; Mori and Menchetti, chap. 6; Bucher, chap. 8). These negative impacts, coupled with the rate at which some of these populations have spread and grown, has led many to refer to these populations as invasive (Gonçalves da Silva et al., 2010; Newson et al., 2011; Russell & Blackburn, 2017). However, most literature on naturalized parrots has made little effort to describe and quantify the real or potential benefits of these populations. While most literature on naturalized parrots has focused on negative impacts, other authors have noted that in order to define a species as invasive, one must quantify the overall impact, both negative and positive, that these naturalized populations have on an ecosystem ((Goodenough,

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[3] Reprinted with permission from "Pruett-Jones, S. (ed.) (2021). Naturalized Parrots of the World: Distribution, Ecology, and Impacts of the World's Most Colorful Colonizers, Princeton University Press.

2010; Kueffer & Hadorn, 2008; Kumschick & Nentwig, 2010; M. A. Schlaepfer et al., 2011; Strubbe et al., 2011); Brightsmith and Kiacz, chap. 9 this vol.). While some benefits may be trivial and others more significant, a balanced review of these populations needs to look critically at both the positives and negatives. In this chapter, we will analyze the real and potential benefits of naturalized parrot populations, with a focus on conservation, research opportunities, and societal impacts. Table 7 summarizes the benefits of naturalized populations of parrots that we discuss in detail below.

Table 7. Challenges facing native and captive populations of parrots, and the benefits of naturalized populations when considering them for conservation initiatives. Reprinted with permission from (Kiacz & Brightsmith, 2021).

CHALLENGES FACING NATIVE AND/OR CAPTIVE PARROT POPULATIONS	BENEFITS OF NATURALIZED POPULATIONS
Populations decreasing in the wild due to habitat loss	Naturalized populations almost entirely use urban areas, which are expanding, representing potential areas of growth for backup populations
Populations decreasing in the wild due to poaching for the pet trade	Naturalized populations of nonthreatened parrots could be used as stock for the pet trade, possibly decreasing demand from native flocks
Loss of genetic variation in native populations due to stochastic events and genetic bottlenecking	Naturalized populations provide genetic reservoirs, free from the selection favoring captivity and from many of the stochastic pressures acting on native populations
Parrots held in captivity or in the wild can be susceptible to disease because they are held in close quarters or are in areas that lack easy access to management and veterinary care	Naturalized populations are free-living and not constrained in unsanitary conditions, and urban populations are accessible to biologists and veterinarians for monitoring and treatment
Rewilding techniques of captive populations are difficult, time consuming, and costly	Naturalized populations are able to forage and avoid humans and other predators, limiting any necessary rewilding before release
More parrot natural history studies are needed	Accessible urban parrot populations allow researchers and citizen scientists to easily study breeding, foraging, and nesting biology as well as other topics

Table 7 Continued

CHALLENGES FACING NATIVE AND/OR CAPTIVE PARROT POPULATIONS	BENEFITS OF NATURALIZED POPULATIONS
Designing and implementing new research techniques or equipment for parrots can be risky and expensive	Naturalized populations are useful for development of tracking techniques and new equipment, and could reduce the risks and cost of testing new techniques on threatened or inaccessible populations
Some parrot populations are considered invasive (Monk Parakeets and Rose-ringed Parakeets) and cause economic or ecological damage	Study of invasive populations can inform invasion biology and can also help develop techniques for control, which could be useful in case naturalized populations develop invasive tendencies

5.2. Naturalized Populations as Sources of Parrots for Conservation

The IUCN (International Union for Conservation of Nature) Red List data show that 55% (~227 species) of all parrot species are in decline, and roughly 28% of all parrot species are considered threatened (IUCN, 2019). Of the ~227 species in decline, at least 35 have naturalized populations (IUCN, 2019; Menchetti & Mori, 2014; Runde et al., 2007). In some cases, such as those of the Red-crowned Amazon (*Amazona viridigenalis*) and the Yellow-crested Cockatoo (*Cacatua sulphurea*), the species are listed as endangered, and the naturalized populations are, or may soon be, larger than the native populations (Gibson & Yong, 2017; Runde et al., 2007; Sullivan et al., 2009). Many of these native populations are continuing to decrease, and intensive management has yet to begin, signaling that these populations are likely years away from recovery (Berkunsky et al., 2017).

For threatened species, naturalized populations could act as backup populations or population reservoirs (Menchetti & Mori, 2014). Species with one or few populations are at higher risk of extinction (Boyd et al., 2017), so additional populations, naturalized or otherwise, can help reduce the overall risk of loss. Especially useful would be naturalized populations in countries outside the species' native range, because different social and political systems can play important roles in how native or naturalized fauna are perceived and/or protected (Dallimer & Strange, 2015), and parrot populations restricted to only one country are at a higher risk of endangerment (Olah et al., 2016). Naturalized population reservoirs could serve as tools for conservationists, biologists, and land managers by allowing them to address threats in native ranges without the threat of losing the entire species (Gibson & Yong, 2017). Although current naturalized populations of threatened parrots are not being actively managed to mitigate losses within their native range, they are still serving the important role of a backup population and genetic reservoir, including populations of Red-crowned Amazons and Yellow-crested Cockatoos.

Since many of the conservation benefits of naturalized parrots revolve around their potential usefulness in translocation programs, it is worth exploring the pros and cons of the usual methods. Translocations have allowed managers to establish new populations, bring species back from the brink of extinction, and maintain species' genetic viability for a wide variety of birds, including the California Condor (*Gymnogyps californianus*), Puerto Rican Amazon (*A. vittata*), Hawaiian Crow or ʻAlalā (*Corvus hawaiiensis*), Nene (*Branta sandvicensis*), and Black Robin (*Petroica traversi*) (Black, 1995; Butchart et al., 2006; Kuehler et al., 1994; Reed & Merton, 1991; Snyder & Snyder, 2000). If wildlife managers working with threatened parrots seek to create new wild populations or reinforce existing ones, they first need a source of birds. Birds are usually translocated directly from wild populations, obtained from wildlife confiscations, or bred in captivity (Lopes et al., 2018; Oehler et al., 2001; Plair et al., 2008; Sanz & Grajal, 1998; Snyder et al., 1994). When confiscated or captive individuals are not available, capturing birds from the wild is often needed, but justifying the take of an already threatened species from the wild to put into a captive-breeding or translocation program is often difficult, expensive, challenged legally, and logistically complicated (Kalmar et al., 2010; Nielsen, 2006). For species deemed in need of ex situ conservation, utilizing individuals from naturalized populations instead of native populations can remove or reduce many of these potential problems. Although naturalized parrots have not been utilized in this manner, this is a potentially valuable conservation benefit (Marchetti & Engstrom, 2016).

The source populations for translocations are normally held in captivity, either briefly when individuals are translocated directly from wild populations (Sisson et al., 2017) or permanently, as in many cases of captive breeding (Heinrichs et al., 2019; Snyder et al., 1996). But naturalized populations also maintain animals for the long term and could provide individuals useful for direct conservation actions. By definition, naturalized populations are breeding at a rate sufficient to maintain or grow the population (Colautti & MacIsaac, 2004), and this is accomplished usually without direct human involvement. Comparatively, captive breeding can be difficult, and while practices have advanced tremendously in the past decades and have succeeded in helping a number of plants and animals from perishing, captive breeding is not without its drawbacks (Comizzoli & Holt, 2019; Snyder et al., 1996; Yamamoto et al., 1989).

Having the correct environmental cues, maintaining proper health (i.e., exercise and diet), providing the proper breeding environment, and pairing birds correctly are all critical to maximizing successful breeding in captivity (Kalmar et al., 2010). In the sections that follow, we will provide a comparison between utilizing captive-breeding or naturalized populations as a source of parrots for conservation.

5.2.1. Costs and Time

Utilizing a naturalized population in place of captive breeding could save money. Costs for captive-breeding programs can exceed $1 million per year, as is the case for Black Stilts (*Himantopus novaezelandiae*) in New Zealand (Moran et al., 2005) and California Condors in the United States (US) (Snyder et al., 1996). Yearly costs for a captive population of about 170 Puerto Rican Amazons are over $700,000, which accounts for about 57% of the total costs of the endangered species program for that species (USFWS, 2009), and Kakapo (*Strigops habroptila*) recovery programs in New Zealand are in a similar situation (Moran et al., 2005). Initial funding for these efforts can be difficult to obtain, and many agencies, private and governmental, must work together to obtain the necessary funding and permits required (Garnett et al., 2018). Captive programs also compete for funding that could otherwise go to the conservation of wild (or naturalized) populations (Snyder et al., 1997).

Utilizing a naturalized population as a source for translocations also has associated costs, for items such as trapping teams, quarantine, veterinary care, disease testing, etc., but given the much shorter time in captivity, the overall cost of translocations should be much less than the cost of captive breeding.

Another limited resource that influences this debate is time. Legal restrictions, issuing of permits for capture, obtaining initial breeding stock, and housing threatened species can slow down captive conservation efforts (Marchetti & Engstrom, 2016). Practitioners and institutions also need time to build aviaries, get initial breeding stock, and learn how to breed captive individuals (Snyder et al., 1996). This is complicated by the fact that many parrot species have long generation times and take multiple years to reach sexual maturity (Young et al., 2012), and even after reaching maturity, many parrots have small clutch sizes and may not breed every year.

Some delays may occur when utilizing naturalized populations for translocation, such as the time it takes to obtain funding and permits for capture. Public relations and the societal implications of removing birds from urban areas need to be taken into consideration as well, as some members of the public may have a sense of ownership over birds that use their feeders or nest in their yards (Crowley et al., 2019).

Some costs would be the same, whether utilizing a naturalized population or a captive-breeding facility as a source for birds for conservation actions. These include costs for conserving or rehabilitating release sites, capture and release permits, health checks, release of birds, and protection of the release site and birds after release. However, all indications are that naturalized populations can maintain populations and produce cohorts for use in conservation in a more efficient manner than captive breeding.

5.2.2. Genetic Issues

The usually small populations held in captivity can suffer from negative genetic effects (Robert, 2009; Snyder et al., 1996) that can lead to health problems for individuals and reduced population growth. Furthermore, populations of organisms kept in captivity may experience unexpected selection pressures. Many times, individuals that are better adapted to life in a captive environment survive and reproduce better, passing on heritable traits such as neophobia, boldness, tameness, and sociability (Boissy, 1995; Faure & Mills, 2013; Grandin & Deesing, 2013; McDougall et al., 2006). Unfortunately, these adaptations to captivity may be detrimental to life in the wild (Carrete & Tella, 2015; McDougall et al., 2006; Shier, 2016).

Genetic issues can also arise in naturalized populations, although a continued supply of new escapees may help ameliorate this (Gonçalves da Silva et al., 2010; Kolbe et al., 2004; Simberloff, 2009). Naturalized parrots may also evolve or develop behaviors ideal for life in urban ecosystems but unsuitable for life in their native habitat. For example, birds may become reliant on food sources uncommon in their native environment, such as bird feeders or non-native flora. These birds would need to undergo at least some rewilding or a soft release during translocations.

5.2.3. Hybridization

In areas where congeners have become naturalized, individuals may hybridize readily (see summary by Mori and Menchetti, chap. 6 this vol.). Naturalized *Amazona* parrots are known to hybridize in California (Mabb, 1997a), and naturalized Lilac-crowned Amazons (*A. finschi*) are hybridizing with Red-crowned Amazons in Texas

(Kiacz and Brightsmith, unpubl. data). The population of Red-crowned Amazons in Texas is believed to be a combination of native birds, naturalized birds that escaped captivity, and their offspring (Enkerlin-Hoeflich & Hogan, 2020; Garrett, 1997; Mabb, 1997b; Neck, 1986; U.S. Fish and Wildlife Service, 2019; Uehling et al., 2019). Both Lilac-crowned and Red-crowned Amazons are endangered within their native ranges, which adds another layer of complexity to management of the naturalized populations (IUCN, 2019). Corruption of the gene pools for these species could reduce the value of these naturalized populations for use in future translocations or captive breeding programs (Mori et al., 2017; Rocha & Bergallo, 2012). Conversely, captive breeding programs have total control over breeding individuals, although genetic testing and organization can be costly.

5.2.4. Disease

Parrots are known to carry a variety of contagious diseases, including psittacine beak and feather disease (PBFD), exotic Newcastle disease (END), avian chlamydiosis (AC), parrot bornavirus, and polyomavirus (Harrison & Lightfoot, 2006; Lever, 2005; Raidal & Peters, 2018). Some of these diseases are of major conservation concern for wild parrots (PBFD) (Ortiz-Catedral et al., 2009), while others can impact a variety of avian taxa (END and AC) and even humans (AC) (Smith et al., 2011). Of note, different diseases affect parrot species differently, resulting in some species becoming healthy carriers of diseases that are highly virulent in others (Payne et al., 2011). All parrot populations are at risk from these diseases, including captive, naturalized, and wild populations, so disease control is a vital part of all parrot management, including translocations or captive breeding (Doak et al., 2013; Raidal & Peters, 2018).

Captive parrots are susceptible to disease from a variety of sources, including the founding stock of the population, the mixing of species in large facilities, and the addition of new individuals from a variety of sources (the wild, other breeding facilities, pet owners, etc.). In captive facilities, birds are usually kept in close quarters, fed from the same food sources, and handled by the same keepers, which can cause rapid spread of disease if infectious agents enter the facility. Common precautions to reduce this risk include maintaining single species in isolated facilities, high levels of biosecurity, regular disease testing, vaccination, and strict quarantine and testing of new stock—all costly procedures(Doak et al., 2013; Heritage, 2006; Raidal & Peters, 2018).

Diseases are unlikely to spread as quickly among naturalized populations as in captive breeding facilities due to lower densities of birds; however, where large communal roosts or use of bird feeders are common, this may not be the case (Bradley & Altizer, 2007; Robb et al., 2008). When taking individuals from a naturalized population, it is imperative to screen for diseases before housing them with other birds or releasing them into the wild. Screening for disease can be expensive and time consuming, but it is a necessary procedure for both captive and naturalized birds and has been done with positive results (Brightsmith et al., 2005; Collazo et al., 2003).

5.2.5. Rewilding and Release Preparation

Many conservation efforts utilizing captive-reared individuals have had very high losses post release: 59% mortality of Puerto Rican Amazons in 2002 (White Jr et al., 2005), 96% mortality of captive-reared Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*) after just two months in the wilds of Arizona (Snyder et al., 1994), and failure to establish a breeding population of Orange-bellied Parrots (*Neophema chrysogaster*), even after 423 birds were released in Australia over a 10-year period (OBPRT, 2006). In order to reduce these losses, many projects engage in rewilding of captive-bred birds in preparation for release. However, this activity is time consuming and costly and not always fully effective (Snyder et al., 1994; Stojanovic et al., 2017; White Jr et al., 2005). Unlike captive-bred populations, naturalized populations already have the ability to find food, avoid predators (including humans), and breed in the wild. This eliminates the need for most prerelease training and should greatly increase post-release survival (Carrete & Tella, 2015). Geographic and habitat similarity between the birds' naturalized and native ranges would be of concern in these situations, with individuals from peripatric naturalized populations presumably better equipped for translocation into their native ranges (Jeschke & Strayer, 2008), while naturalized birds from habitats dissimilar to their native range would need at least some prerelease training to help them identify local food sources and novel predation risks.

5.3. Naturalized Parrots for Conservation: Summary

Problems with captive breeding are not new and have been an issue for conservationists and wildlife managers for decades (Snyder et al., 1996). Nevertheless, over the last few decades, the breeding of rare species in captivity has been successful enough that it's no longer fringe science but a reliable method of species conservation (Griffiths & Pavajeau, 2008). The things that haven't changed over this time are the costs and time associated with breeding animals in captivity. Currently, ~227 species of parrots have declining populations, and 37 of those are listed as in need of ex situ conservation (IUCN, 2019). Of those 37, six have at least one naturalized population: Yellow-crested Cockatoo, Salmon-crested Cockatoo (*Cacatua moluccensis*), Grey Parrot (*Psittacus erithacus*), Red-crowned Amazon, Yellow-headed Amazon (*Amazona oratrix*), and Kuhl's Lorikeet (*Vini kuhlii*). Although no naturalized population is currently being utilized for conservation relative to its native populations, all six of these high-priority species have conservation programs within their native ranges that could benefit from the managed use of their naturalized populations. Additionally, 137 parrot species have declining populations and are listed as "near threatened" or "vulnerable" (IUCN, 2019), meaning that over the coming decades, many more species are likely to be in need of ex-situ conservation, and naturalized populations of those species could become very useful (Berkunsky et al., 2017). Although not completely free of costs or disadvantages, naturalized populations may be a viable alternative to captive breeding for long-term maintenance of parrots of conservation interest. Managers would still need to monitor for hybridization and disease, and genetic testing should be done in most cases, but utilizing naturalized populations for translocation should still be less expensive than captive breeding and provide individuals better prepared for life in the wild.

5.4. Opportunities for Research on Naturalized Parrots

Parrots are a greatly understudied portion of the world's avifauna (Collar, 1998), and there are critical gaps in our scientific knowledge of parrots as it relates to conservation of threatened and endangered species (Marsden & Royle, 2015; Renton et al., 2015). Even basic knowledge of psittacine natural history is still lacking for most parrot species worldwide. Naturalized populations can allow researchers to study the basic natural history traits important for conservation purposes (Marchetti & Engstrom, 2016; Uehling et al., 2019). Naturalized parrots also represent "natural experiments" that can be used to test adaptation of species to urban habitats as well as scientific hypotheses at spatial and temporal scales too large for controlled experiments. Research on naturalized parrots could further our understanding of autecology, ecosystem function, and biodiversity in ways that cannot be achieved easily with wild populations (Blackburn & Duncan, 2001; Richardson & Pyšek, 2008).

Research on naturalized bird populations has been conducted at least since the early 1900s, when Joseph Grinnell studied House Sparrows (*Passer domesticus*) in Death Valley, California (Grinnell, 1919). Since then, researchers have used naturalized birds to study a broad array of topics, including life history traits, genetics, adaptability, invasion biology, and disease (Blanvillain et al., 2017; Gonçalves da Silva et al., 2010; Martin-Albarracin et al., 2015; Moles et al., 2008). In this section, we will review some current research topics involving naturalized populations (including parrots and other birds) and highlight some potential avenues for future work with naturalized parrots.

5.4.1. Basic Natural History

Knowledge of basic parrot ecology and natural history is critical to help us conserve threatened species (Collar, 1998; Marsden & Royle, 2015; Masello & Quillfeldt, 2002). Naturalized populations of parrots can be studied to gain information on their life history traits, such as longevity, fecundity, number of eggs per brood, number of broods per season, nesting, dispersal, etc. (Blanvillain et al., 2017; Leech et al., 2008; Marchetti & Engstrom, 2016; Simberloff, 2009; Uehling et al., 2019). This is obviously most useful if the naturalized species itself is threatened, but it is also useful if congeners or other species that share similar traits are imperiled and lacking this general information.

5.4.2. Genetic Issues

Naturalized populations are ideal models with which to study the relationships of genetic bottlenecks and founding effects on allele frequency, heterozygosity, and polymorphic loci (Gonçalves da Silva et al., 2010; Kolbe et al., 2004; Simberloff, 2009). Baker and Moeed (1987) found that introduced populations of Crested Mynas (*Acridotheres cristatellus*)[4] had an 18% loss of alleles and lower heterozygosity than did native populations. The largest loss of diversity in mynas was in naturalized populations that had the smallest number of founders (Baker & Moeed, 1987). Other researchers have since shown similar losses in genetic diversity among naturalized or introduced populations (Fleischer et al., 1991; Jamieson, 2011). However, Simberloff (2009) points out that not all naturalized species suffer from genetic impoverishment if the propagule

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[4] The published copy of this chapter misstates this population as consisting of Common Mynas (*Acridotheres tristis*)

pressure is high, and Kolbe et al. (2004) were able to show this in naturalized populations of lizards, which actually have higher genetic variation than populations of their native counterparts. Additionally, Gonçalves da Silva et al. (2010) showed little loss of genetic variation in naturalized populations of Monk Parakeets (*Myiopsitta monachus*) in the USA, pointing to continued propagule pressure as the likely explanation. Barring high propagule pressure, genetic drift and fixation events could prove detrimental to a threatened species, so understanding the relationships between population numbers, genetic bottlenecks, and their possible effects is crucial to the design of effective translocations and captive breeding projects.

Naturalized populations also provide the opportunity to study adaptation and phenotypic change due to novel selection pressures as a result of living in novel ecosystems (Baker & Moeed, 1987; Cabe, 1998; Jackson et al., 2015; Ross, 1983; Suarez & Tsutsui, 2008). This type of work can also shed light on how organisms successfully invade new ecosystems and how they may respond in the face of changing climatic regimes and urbanization.

Genetic studies can also pinpoint source populations of naturalized populations, guiding where to focus poaching and trade control efforts (Jackson et al., 2015; Kirk et al., 2013; Perdereau et al., 2013). This genetic information can also help researchers understand the value of a naturalized population, since individuals with varying degrees of introgression or of a certain subspecies may be deemed undesirable for translocation projects (Amato, 1995; Sanz & Grajal, 1998).

5.4.3. Disease

Parrots and their associated diseases are moved at a global scale through the pet trade (Smith et al., 2009). Testing for disease, such as PBFD, on captive and wild individuals in native and naturalized ranges allows researchers to understand the spread of these infections and the susceptibility of populations and can guide conservation, management, and national policy (Fogell et al., 2018; Ha et al., 2007). Disease also has implications for translocation and breeding success (Tollington et al., 2015; Tollington et al., 2013) and, as such, is of major concern to conservationists and aviculturists alike (Harkins et al., 2014).

Vaccine testing and disease prevalence studies could be done using naturalized populations that have been deemed invasive and are suitable for removal (Kirkpatrick et al., 2011). Capture of these individuals and use in research that could potentially help their species or relatives in aviculture or in the wild could be a meaningful way to justify take. By using individuals from less critical, naturalized populations instead of pulling from native populations, we can limit the loss of native birds while gaining insight on possible methods to cure or prevent diseases.

Naturalized populations can also offer insight to potential environmental contamination. Naturalized *Aratinga* parakeets in California have been found to be affected by bromethalin toxicosis (Van Sant et al., 2019). Bromethalin is a common ingredient in rat poison; the source of this toxin in the environment is currently unknown but under investigation because of the studies performed by Van Sant and collaborators.

5.5. Development of Research Techniques

Naturalized populations can be useful when designing and implementing new research techniques or equipment. In the early 1990s, researchers tested multiple types of very high frequency (VHF) transmitters for fit and wear on naturalized *Amazona* parrots in Puerto Rico before using them on critically endangered Puerto Rican Amazons (Meyers, 1996). Naturalized Rose-ringed Parakeets were used to study hand-rearing and soft-release methodology of critically endangered Echo Parakeets (*Psittacula eques*) on Mauritius Island (Jones et al., 1998). Rose-ringed Parakeets were also used as surrogate fosters for raising some of the initial breeding crop of Echo Parakeets. Due to the possibility of future hybridization, no Echo Parakeets raised by Rose-ringed Parakeets were released into the wild but were instead kept and used for captive breeding and fostering of Echo Parakeets (Jones et al., 1998).

5.6. Invasion Biology

Parrots' repeated successes and failures to become established in different areas set up opportunities for researchers to test theories on how species successfully colonize new environments. Studies on naturalized parrots can look at the four major aspects of invasion biology: transport, introduction, establishment, and spread (Case, 1996; Duncan et al., 2003; Martin-Albarracin et al., 2015; Williamson, 1996), and in some cases the decline to extirpation. Two naturalized avian populations, Budgerigars (*Melopsittacus* *undulatus*) in Florida and Crested Mynas[5] in Vancouver, Canada, have gone through all four stages as well as extirpation in just a few decades. Roughly 7,000 Budgerigars and 20,000 Crested Mynas populated their respective naturalized ranges at their peaks, and both, without clear explanation, declined in number to virtually zero, and neither species is currently established where it was once common (Butler, 2005; Colautti & MacIsaac, 2004; Long, 1981). These events took place before scientists were actively engaged in invasion biology, but by studying the events that led to introduction, establishment, spread, decline, and extirpation of these populations, conservationists and managers could be better prepared to contain or manage naturalized populations.

Since naturalization events (especially introduction and establishment) mirror similar events that must take place during translocations, understanding the main factors in successful establishment of non-native species can be useful as a resource of ideology and theory for better understanding translocations (Royle and Donner, chap. 2 this vol.). Many studies place propagule pressure as the most significant factor correlated with establishment success (Brook, 2004; Duncan et al., 2001; Duncan & Forsyth, 2006; Lockwood et al., 2005; Simberloff, 2009; Veltman et al., 1996; Williamson, 1996). For example, Brook (2004) showed that number of introduction attempts and total number of individuals released predicted the successful establishment of almost 90% of 77 avian introduction cases in Australasia. Likewise, Veltman et al. (1996) showed that the

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[5] The published copy of this chapter misstates this population as consisting of Common Mynas (*Acridotheres tristis*)

highest correlate with naturalization success for 27 bird species in New Zealand was propagule pressure. By modeling the historical and current global trade of parrots, or the highest percentage of households with parrots as pets, researchers could predict areas with higher chances of establishment of non-native parrots, informing management and trade decisions at a worldwide scale (Uehling et al., 2019).

Species distribution models (SDMs) can greatly help our understanding of where an organism can successfully invade (Peterson, 2003; Yackulic et al., 2015). By developing models of naturalized parrot ranges, we can understand which regions across the globe could be successful points of introduction (Peterson, 2003; Strubbe & Matthysen, 2009). Modeling of these ranges can take into account urbanization and climate change for better predictive abilities (Bellard et al., 2013; Jeschke & Strayer, 2008; Strubbe & Matthysen, 2009). For most species, matching the naturalized environment (including climate) to that of their native environment can increase successful establishment (Daehler & Strong, 1993; Strubbe & Matthysen, 2009; Thuiller et al., 2005). However, this is not always the case, as with habitat generalists (Monk Parakeets, Rose-ringed Parakeets), which can survive in a wide range of habitats (Cassey et al., 2004; Strubbe & Matthysen, 2009). Additionally, climate change is predicted to create range shifts for many species both in native and non-native ranges (Bellard et al., 2013). These shifts include range shrinkage and enlargement and can cause extirpation of currently established non-natives or create new habitats for species to exploit.

5.7. Social Impacts of Naturalized Parrots

Although there are in-depth reviews of the societal impacts of naturalized parrot populations in this book (see Crowley, chap. 3, and Bucher, chap. 8), we provide a brief review of the conservation-related benefits of interactions between naturalized parrots and people. Fifty-five percent of humans live in urban areas, and as that figure continues to increase, human engagement with nature continues to decline (Soga & Gaston, 2016; Turner et al., 2004). This increasing disconnect from nature is termed “extinction of experience” (Miller, 2005; Pyle, 1978) or “nature deficit disorder” (Louv, 2008). Fortunately, most naturalized parrots occur in areas of high human activity, which offers opportunities for people to have interactions with groups of these sociable and noticeable birds. Research has shown that exposure to natural vs. urban environments can reduce blood pressure (Hartig et al., 2003) and increase happiness (MacKerron & Mourato, 2013; Shanahan et al., 2015) as well as change how the human population interacts with and views nature (Bixler et al., 2002; Miller, 2005). Participation in recreational activities, including birdwatching, has a positive influence on pro-environmental behavior, including contribution of money to conservation organizations (Nord et al., 1998). In order to increase support from the general public for biodiversity conservation, we urgently need to increase people’s interactions with the natural world (Miller, 2005). We argue here that naturalized parrots afford us with an opportunity to help connect urban human populations with nature.

Naturalized parrots have high visibility and great charisma, making them a natural attraction for many people (Avery et al., 2006; Crowley et al., 2019). Monk Parakeets that regularly nest on utility poles and palm trees in urban landscapes offer humans an opportunity to observe colorful “wild” birds courting, singing, and socializing in areas where the native fauna has been drastically reduced (Burger & Gochfeld, 2009). This opportunity is not unique to just a few cases—Monk Parakeets, Red-masked Parakeets (*Psittacara erythrogenys*), and Blue-and-yellow Macaws (*Ara ararauna*) have garnered enough public support in cities like Brooklyn, New York; San Francisco, California; and Caracas, Venezuela, respectively, to thwart attempts at removal. In Texas, local municipalities have passed laws that protect native and naturalized parrots from poaching and restrict destruction of trees used for roosting or nesting. This type of local support is important—public backing, perception, and education are critical to successful conservation initiatives, as shown in island nations with endemic parrots (Christian, 1993; Christian et al., 1996; White Jr et al., 2011). Dunn et al. (2006) argue that even non-native species, like naturalized parrots, can lead the way for conservation-minded management and local involvement in urban areas. In addition, many, if not most naturalized parrot populations have few negative environmental impacts (Brightsmith and Kiacz, chap. 9 this vol.). As a result, many naturalized parrot populations can act as ideal flagships to help lead a reconnection with nature and encourage local participation in conservation-minded recreation.

Naturalized parrots may also provide some small-scale economic opportunities to local communities, which in turn build support for the parrots' populations (Seymour, 2013). At a local park in Brownsville, Texas, an average of six birdwatchers per evening are present year-round to watch as flocks of native and naturalized parrots come to roost, making them a local tourist attraction (Kiacz and Brightsmith, unpubl. data). Festivals for birds and birdwatchers are gaining popularity throughout the Americas and Europe, and in some cases, parrots can be a major draw for participation. At the annual Rio Grande Valley Birding Festival in Texas, nearly 120 participants pay to ride through neighborhoods in search of the native and naturalized urban parrots. Similarly, the San Diego Bird Festival fills its Parrot Party Bus with participants hoping to catch a glimpse of some of the 13 naturalized parrot species in southern California. Proceeds from the Rio Grande Valley festival have been used to support parrot research and local conservation initiatives, and the San Diego festival supports local wildlife rehabilitation and educational programs through the San Diego Audubon Society. Events such as these are likely to grow in popularity and should be embraced by local communities as ways to gain benefits from naturalized parrots.

Although negative economic and social impacts from naturalized parrots do exist, these impacts are mostly insignificant and caused by only two species (Monk and Rose-ringed Parakeets), and the general public largely sees the birds as affable and charismatic additions to their daily lives (Crowley, chap. 3 this vol.). The fact that many people rally around “their” parrots to protect them from extirpation is evidence that there is positive value that can balance the negatives in many cases. Events such as those mentioned above suggest that parrots have already started the process of bringing nature to the people and may be helping to reduce nature deficit disorder and increase support for conservation initiatives, including research on parrots in native and naturalized habitats.

5.8. Conclusions

In this chapter, we examined actual and potential benefits of naturalized populations of parrots. Some of these benefits have real-world conservation value—naturalized parrots can be used as cheap, low-impact sources for captive breeding programs and are especially useful if they are one of the six naturalized species in need of *ex situ* conservation. These populations are further useful for translocations, as rewilding them should be less expensive, and they are likely better equipped for problems they will face living in the wild. However, when using naturalized populations, biologists lose their ability to control hybridization and disease, and societal connections with the parrots can hamper capture efforts.

Naturalized parrots may also have value as research systems to help quantify life history parameters of parrots, advance our understanding of invasion biology, and develop new conservation management techniques for use in captive, native, and naturalized populations. Study of these populations is necessary if we want to fully understand the parrots' impacts on ecosystems, so we can rationally define and manage these populations.

The social impacts naturalized parrots make in some urban areas, while hard to quantify, may not be trivial, based on the actions local people take to protect the birds. It remains to be seen, however, if these parrots can get people outdoors and reconnect them with nature in urban environments at a large scale, and if this can translate into more concern for nature and actions that benefit conservation. From an economic perspective, naturalized parrots may generate some tourism revenue, but at a global level, the money generated is certainly less than the damage caused (Brightsmith and Kiacz, chap. 9 this vol.). However, individual populations that do not cause economic damage could have a net positive contribution.

All these impacts, negative, neutral, or positive, deserve to be analyzed and taken into consideration when determining how these populations are to be defined and managed. Most documented negative impacts have been caused by specific populations of Rose-ringed Parakeets and Monk Parakeets. Therefore, analysis of each naturalized population of each parrot species should stand on its own merit and not be lumped with other species or populations, since they are all distinctive. The impacts each population has depend on life history strategies as well as the ecosystems it inhabits, and each arouses a different perspective in the society with which it coinhabits. All these factors make naturalized parrots an interesting and worthy study system for researchers across the globe.

6. CONCLUSIONS

Highly modified habitats are becoming more common across the globe, extending out from urban areas into suburban neighborhoods housing millions of people. As more land is modified to be more hospitable for humans, wildlife is forced to disperse, adapt, or perish. Attention by researchers and conservationists is often focused on preserving natural habitats in the face of urbanization, and much of the wildlife that has adapted to urban regions are considered a nuisance. But in certain situations, threatened wildlife has found a way to not only survive, but to thrive in highly modified and human dominated landscapes. This unique scenario provides opportunities for researchers and conservationists to better understand wildlife and how they survive in urban regions, and to also better understand why some species cannot. In addition, these urban populations become important bastions that could represent the difference between persistence or extinction. While still a relatively uncommon occurrence, this avenue of study combines urban ecology and the study and management of threatened and endangered wildlife. This allows the public to become more involved in habitat management and species conservation which isn't possible in most scenarios, and a better understanding of this dynamic could provide us with a template of how urbanization could benefit wildlife as we move towards a more urbanized world. In this dissertation, I studied populations of urban and endangered parrots to better understand the drivers of these populations so we as both conservationists and the public can move into the future in a way that benefits both wildlife and people.

Red-crowned Parrots have been known to inhabit south Texas for decades, but their unique situation, including their arrival and ability to persist in this highly modified region, were never documented in detail. Their status as a candidate for listing under the Endangered Species Act and native status in the state of Texas meant that more detailed explanations of the species arrival, current trends, and breeding status, as well as habitat use, were needed. The Texas Parks and Wildlife Department granted funding for research on this population of parrots starting in 2016. My work found a population of 675 Red-crowned Parrots throughout Cameron and Hidalgo counties in Texas; since publication of the second chapter of this dissertation in 2021, the population has increased to roughly 950 birds as of 2023. Overall, the population appears to be healthy and increasing and productivity has averaged 19% over seven seasons of parrot counts (2016-2023; no counts in 2020 due to pandemic) with a high of 25% in 2016 and low of 14% in 2021. Matching productivity data with population trends provides an important baseline for researchers studying not only Red-crowned Parrots but also species where productivity data may be easier to obtain than total population numbers. Although this population of Red-crowned Parrots has increased throughout our 7-year study, all population growth seemed to occur during the 2022 breeding season. During 2022, we also documented productivity at 20%, which is near our average of 19%. This is an almost 40% population growth in one year with a documented 20% productivity rate. In the coming years, it will be important to better understand how this has occurred while questioning our basic assumptions of this population - namely our assumptions that we know and monitor all current roost locations and that there is no or limited connectivity between this south Texas population and populations within Mexico.

I recommend a continuation of the Texas Parks and Wildlife Departments quarterly parrot counts with this population utilizing citizen volunteers from the local communities. Additionally, I would advise the continuation of yearly productivity counts – these counts are slightly more involved and temporally specific – they must be done during fledging season (August – September), and counters must be able to not only count all individuals attending a roost but also record the age (adult or juvenile) of as many parrots as possible. The goal is to create a long-term dataset for this easy to access parrot population and allow researchers the ability to correlate productivity with overall population trends and other variables, including weather or threats such as poaching. Furthermore, productivity counts are a rapid population assessment tool that offers immediate insight to yearly reproductive efforts and could quickly inform management of breeding failure so immediate actions could be taken to remedy the causes.

Species distribution models predicted 39,429 km^2 of suitable habitat is available throughout the southern portions of California, Texas, and Florida, of which roughly 18,965 km^2 is currently occupied by Red-crowned Parrots. Furthermore, 21,200 km^2 of suitable habitat is currently unoccupied – this is a substantial area and if even a portion becomes occupied over the coming decades it could represent a substantial increase in population numbers throughout the United States. This habitat helps offset the previous losses in Mexico, where researchers predicted a loss of 127,278 km^2 of suitable habitat over the previous few decades. High- and medium-quality habitat predicted by the models closely followed urban boundaries. Lower limits of human population density were around 500-1000 people/km^2 while upper limits were extremely variable from 2500-15,000 people/km^2. About 30% of the suitable habitat in North America is within the United States where almost all high-quality habitat was predicted to be in urban areas. These urban areas where parrots are naturalized are expected to grow, and if urbanization maintains similar rates of planting food, roosting, and nesting resources I expect populations of Red-crowned Parrots and similar species to continue to grow as well. Furthermore, most nesting is occurring in nonnative palm trees and although these parrots can use many resources for nesting including native trees, artificial nest boxes, and even buildings, continuing to provide *Washingtonia* spp. palms or similar may play an important role in the parrots continued success. These results emphasize the importance of urbanizing “the right way”, which in these regions over the previous decades has serendipitously coincided with creating habitat suitable for *Amazona* parrot populations. Understanding specific habitat needs for these parrots can help educate the public on how to provide ideal habitat for these endangered populations and can also help our understanding of how the public can be a powerful conservation force if even a small percentage of landowners are managing their properties with wildlife in mind.

My models also found that Red-crowned Parrots have a low tolerance for low temperatures and a high tolerance for high temperatures. Minimum temperatures in suitable habitat were predicted to be a relatively constant 5°C, and all models indicated that high temperatures were not limiting populations in the United States. Ideal precipitation was at least 400 mm, which does indicate that drier regions are not suitable for Red-crowned Parrot persistence, although irrigation in urban settings can likely offset this to a certain extent. While exact changes in climate are difficult to predict, current projections suggest a warming climate in many regions of the southern United States. While far from certain, a slight increase in temperature may result in more suitable habitat available for not only Red-crowned Parrots but for some populations of parrots more generally.

Population modeling showed a rather robust Red-crowned Parrot population in south Texas that can tolerate 30% declines in most key demographic parameters. Percent breeding, fledgling survival, and brood size were three of the most sensitive parameters in these population models. Increases in fledgling survival would provide the largest increases in population growth while decreasing adult mortality would also significantly improve population growth rates. While these are difficult parameters to significantly impact without large investments of time and money, antipoaching education is one cost effective measure that could help increase numbers of fledglings. Our work has shown low levels of poaching still occurring in highly visible locations throughout this urban region – in parks, on college campuses, and on the side of busy roads to name a few examples. Poaching not only removes individuals from the population, but almost always destroys valuable nesting substrate by enlarging cavities or cutting down trees. Therefore, encouraging the planting of previously mentioned nest resources including palm and ash trees, in addition to food and roosting sites, will be important if this population is to be maintained.

Population models also showed that hybridization may play an important role in the future of *Amazona* populations in south Texas. Even at low levels of hybridization (e.g. 0.1%), our models predicted hybrid dominance would eventually occur absent depressive outbreeding effects. While hybrid dominance is not likely to be seen in our lifetimes, I suggest research to determine current rates of hybridization and introgression to help management make the most effective and timely decisions regarding the future of these endangered parrot populations. Besides the possible effects of hybridization, these models show a robust parrot population in south Texas that will likely persist or grow if urbanization continues its current trends in the region, especially if the public becomes more aware of specific habitat they can provide for these populations and other wildlife.

My final chapter outlines the real and possible benefits of naturalized parrots, from conservation and research to economic and social value. While this chapter was published with parrots as the main topic, the ideas presented could apply to any number of wildlife populations which have become or are becoming naturalized across the globe. Naturalized populations of threatened species represent a reservoir of individuals and genetics that can persist while resolving issues affecting populations within their native ranges. Actions like habitat remediation or poaching reduction through educational campaigns or passing laws often take time, and naturalized populations may reduce the urgency at which these need to take place. Nonnative populations could also be used as sources for the pet trade using sustainable harvest techniques, reducing the need and appeal of poaching within the species native range. Naturalized populations also represent an alternative option to expensive and time-consuming captive breeding operations. Populations that are free from selective forces which favor captivity may make individuals better suited for life in the wild and would likely require little to no rewilding; naturalized populations know how to forage and actively avoid predators - including humans. Additionally, urban populations may be free from other selective forces such as extreme weather (drought, hurricanes) and may have reduced potential of spreading diseases that can make captive breeding operations difficult and expensive to maintain. And while many parrot populations are in difficult or dangerous regions to access, urban populations are comparatively accessible, allowing researchers, citizen scientists, and enthusiasts more opportunities to study the birds which can help management make better decisions in the future. But, as my previous population modeling shows, naturalized populations may face threats not present within the species native range, namely hybridization which could harm genetic integrity and the value of individuals as potential stock for translocations.

Urban areas in south Texas, and throughout California and Florida as well, are expected to continue expanding. My body of work shows the ability of Red-crowned Parrots as well as other Psittaciformes to be capable urbanites. As previous research has also shown, many species of parrot are capable at establishing populations and maintaining them in modified and fragmented habitats if certain aspects of the landscape are maintained including adequate nesting, roosting, and foraging sites. Protecting these birds by maintaining large trees, planting palms and forage plants for the future, and education and pride campaigns will not only help conserve populations of threatened parrots but will also provide services for other wildlife and humans. An ecosystem, urban or otherwise, which provides the necessary resources for wildlife to thrive will also provide ample opportunity for people to appreciate and understand our natural world better and would serve both conservation and society greatly.

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