

Research Article

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Author for correspondence:


*Michael A. Patten,

Email: michael.a.patten@nord.no,

*David C. Hille,

Email: dhille@nnu.edu

Parrot population trends in Nicaragua revealed by long-term monitoring

David C. Hille^{1*} , David A. Wiedenfeld², Martín Lezama-López³,
Donald J. Brightsmith⁴ and Michael A. Patten^{5*}

¹Department of Biology, University of Oklahoma, 111 Chesapeake St, Norman, OK, 73019, USA, present address: Department of Biology, Northwest Nazarene University, 623 S. University Boulevard, Nampa, ID, USA; ²Sutton Avian Research Center, Bartlesville, OK, USA, present address: American Bird Conservancy, The Plains, VA, USA; ³Consultant on Wildlife Management and Ecology, Managua, Nicaragua; ⁴Schubot Avian Health Center, Department of Veterinary Pathology, Texas A&M University, College Station, TX, USA and ⁵Ecology Research Group, Nord University, Steinkjer, Norway

Summary

Monitoring parrot populations is of high importance because there is a general lack of quantified population trends for one of the most threatened avian orders. We surveyed parrots in Nicaragua in 1995, 1999, 2004, and 2013 at a minimum of 227 points within 56 sites stratified among the Pacific, Central Highlands, and Caribbean biogeographical regions to assess population trends. From point-count data we calculated encounter rate, flock rate, and flock size metrics and we used presence/absence data to generate species-specific occupancy estimates. Encounter rate, flock rate, and flock size data suggested family-level declines from 1995 to 2004 with some recovery between 2004 and 2013. Patterns of parrot occupancy varied among species with four decreasing, five increasing, and two with no detectable change. Six species of conservation concern are identified, including the Critically Endangered Great Green Macaw and Yellow-naped Parrot, additionally Olive-throated Parakeet, Scarlet Macaw, Brown-hooded Parrot, and White-crowned Parrot, only listed as Least Concern. All six are likely suffering from deforestation and potential unchecked trade activity in the Caribbean. Differing population trends of the regionally disjunct Yellow-naped Parrot subspecies suggest a link to variable deforestation and trade pressure experienced between the Pacific and Caribbean. Our results highlight the importance of actively monitoring changing parrot populations, even when considered Least Concern, so that directed conservation actions can be taken if needed.

Introduction

The detection of population trends from quantitative data is a foundational tool in avian conservation. Successful large-scale and long-term efforts such as the North American Breeding Bird Survey (BBS) and the European Breeding Bird Atlas (EBBA) report changes in abundance and distribution, and provide data for governmental species assessments, determination of priority species, identification of conservation locations, as well as the basis for comprehensive reports (Hudson *et al.* 2017, Keller *et al.* 2020).

Conservation planning in the tropics needs effective biodiversity monitoring such as this to inform conservation action (Marsh and Trenham 2008, Jones *et al.* 2013) in response to a sustained biodiversity crisis which threatens to cause numerous species extinctions and considerable loss of ecosystem services in the tropics (Bradshaw *et al.* 2009).

Order Psittaciformes (macaws, parrots, parakeets, lorries, and cockatoos; hereafter referred to only as parrots) is one of the world's most at-risk avian orders (Collar 1996, Olah *et al.* 2016) and warrants research to quantify population trends to inform successful conservation action for these species (Brawn *et al.* 1998). There remains a lack of population trend data for parrots. A literature review by Marsden and Royle (2015) reported that density estimates are available only for 25% of parrot species and abundance changes are similarly deficient. Population trend data available in the literature for the region of focus in our study are primarily limited to sub-regions of Mexico (Marín-Togo *et al.* 2012, Plasencia-Vásquez and Escalona-Segura 2014) or individual species. McReynolds (2012) completed a Belize-limited abundance estimate of the Scarlet Macaw (*Ara macao*), Vaughan *et al.* (2005) monitored Scarlet Macaw populations in Costa Rica from 1990 to 2003, and there exists a distribution-wide population assessment of the Yellow-naped Parrot (*Amazona auropalliata*) (Wright *et al.* 2018, Dupin *et al.* 2020).

Populations of parrots in the Neotropics face two principal threats: habitat loss because of anthropogenic land use and pressure from the international and domestic pet trade (Berkunsky *et al.*

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2017, IUCN 2021). From 1990 to 1997, the whole of Latin America had an annual 0.33% mean net deforestation rate of humid forest (Lambin *et al.* 2003). Additionally, parrots are commonly reported in the international pet trade (legal and illegal): their incidence is 14 times more likely than if trade was random among all birds (Bush *et al.* 2014). A mix of domestic and international pet trade is common throughout the Neotropics (Beissinger 2001, Daut *et al.* 2015) and is considered a threat to 68% of populations (Berkunsky *et al.* 2017).

Within the design of a national monitoring programme established in 1994 (Wiedenfeld 1995), we surveyed the country of Nicaragua four times in 18 years to estimate parrot population trends and discuss potential correlates. As a conservation objective, we aimed to identify species of conservation concern, within the context of three biogeographical regions in Nicaragua. In addition, our study provides much needed parrot population trend data for the region of Central America.

Methods

Study species

A total of 16 parrot species are found in Nicaragua (Table 1, nomenclature follows American Ornithological Society 2021), with distributions that generally are characterised by the boundaries of three biogeographical regions: Pacific, Central Highlands, and Caribbean (Figure 1). Based on negative population trends throughout their global distributions, four species have received more explicit conservation attention. The Great Green Macaw *Ara ambiguus* and Yellow-naped Parrot *Amazona*

auropalliata (represented by subspecies *auropalliata* and *parvipes*) (Dickinson and Remsen 2013) have been recently listed as Critically Endangered (IUCN 2021), the Orange-fronted Parakeet *Eupsittula canicularis* has recently been listed as Vulnerable, and the Mealy Parrot *Amazona farinosa* is Near Threatened (IUCN 2021). The Scarlet Macaw *Ara macao* subspecies *cyanoptera* in northern Central America (Wiedenfeld 1994, Dickinson and Remsen 2013) is listed as an Endangered species by the US Fish and Wildlife Service under the Endangered Species Act (Department of Interior 2019). Furthermore, a 2004 report on parrot populations submitted to CITES and the Nicaraguan government showed widespread population declines and prompted the 2004 passing of a ban on all international and domestic parrot commerce (Lezama *et al.* 2005).

Study area

Survey sites were located in 14 of Nicaragua's 16 political departments (Figure 1). Sites ranged in elevation from sea level to 1,589 m. The number of sites varied from 57 to 74 among years and were stratified among the three biogeographical regions of the country (Taylor 1963) (Figure 1): 34–44% in the Pacific (18% of Nicaragua's terrestrial territory), 9–12% in the Central Highlands (22% of Nicaragua's terrestrial territory), and 44–55% in the Caribbean (60% of Nicaragua's terrestrial territory). Fewer sites were established in the Central Highlands, where populations of Green Parakeet (*Psittacara holochlorus*) and Barred Parakeet (*Bolborhynchus lineola*) are mainly restricted (Table 1), because

Table 1. 16 species of Nicaraguan parrots with information on the biogeographical regions within their distributions; primary regions are highlighted. Global conservation information is reported from the IUCN database.

Scientific name	Common name	Biogeographic region			IUCN status
		Pacific	Central Highlands	Caribbean	
<i>Eupsittula nana</i>	Olive-throated Parakeet		x	x	Least Concern
<i>Eupsittula canicularis</i>	Orange-fronted Parakeet	x	x		Vulnerable
<i>Ara ambiguus</i>	Great Green Macaw			x	Critically Endangered
<i>Ara macao</i>	Scarlet Macaw	x		x	Least Concern
<i>Psittacara holochlorus</i>	Green Parakeet		x		Least Concern
<i>Psittacara strenuus</i>	Pacific Parakeet	x			Least Concern
<i>Psittacara finschi</i>	Crimson-fronted Parakeet	x	x	x	Least Concern
<i>Bolborhynchus lineola</i>	Barred Parakeet		x		Least Concern
<i>Brotogeris jugularis</i>	Orange-chinned Parakeet	x	x	x	Least Concern
<i>Pyrilia haematotis</i>	Brown-hooded Parrot		x	x	Least Concern
<i>Pionus menstruus</i>	Blue-headed Parrot			x	Least Concern
<i>Pionus senilis</i>	White-crowned Parrot	x	x	x	Least Concern
<i>Amazona albifrons</i>	White-fronted Parrot	x	x		Least Concern
<i>Amazona autumnalis</i>	Red-lored Parrot	x	x	x	Least Concern
<i>Amazona farinosa</i>	Mealy Parrot			x	Near Threatened
<i>Amazona auropalliata</i>	Yellow-naped Parrot	x		x	Critically Endangered
<i>A. a. auropalliata</i>	Yellow-naped Parrot	x			–
<i>A. a. parvipes</i>	Yellow-naped Parrot			x	–

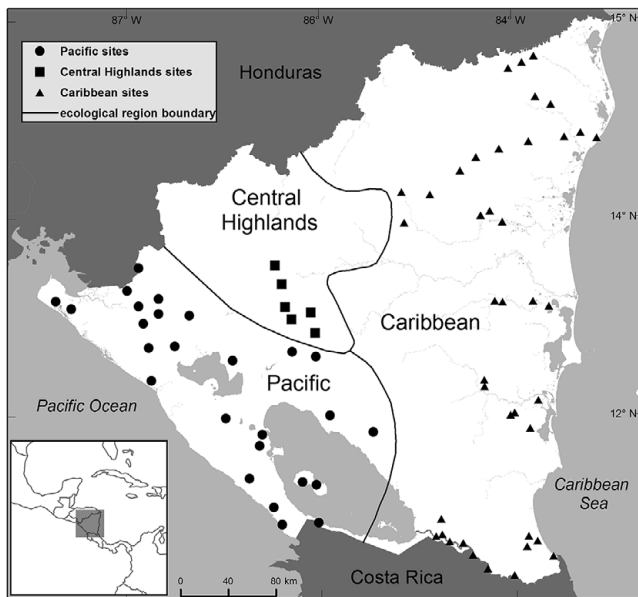


Figure 1. Parrot survey sites stratified within three biogeographical regions were located on accessible rural roads or rivers from sea level to 1,589 m.

of political conflicts present in this region during the 1995 and 1999 surveys.

Parrot surveys

A single site (as defined by occupancy modelling methodology) was formed by several point counts along a transect. Transects were established along rural roads or rivers when 5–25 km reaches of road or river were available and the conditions met point selection criteria. Points on a transect were selected randomly, but adhering to three criteria: 1) ≥ 5 km from the previous point; 2) ≥ 100 m from human dwellings; 3) with open canopy above the point. Sufficient open canopy was necessary because flocks are highly mobile and many observations are made of flocks flying overhead. Points were held consistent between survey years. When criteria were not met in subsequent years in order to hold a point consistent, usually because of human development along a transect, we either moved points along the transect or created a new transect. Points were determined to be the same as in previous surveys if we could complete the survey within 1 km of previously recorded geographical coordinates.

We surveyed by means of point-count transects (Cassagrande and Beissinger 1997), with a distance of ≥ 5 km between points; a longer distance to ensure data independence as necessitated by the long-distance daily mobility of parrots. We arrived at all points by 4×4 truck or motorised boat. Each transect included 1–6 point counts ($\bar{x} = 3.9 \pm 1.3$) depending on available time and accessibility, and between all four survey years only four transects were surveyed with a single point. Geographical coordinates of points were recorded using GPS (WGS84). Of 287 points in 2013, 57% were in common with the 1995 surveys ($N = 237$), 73% with the 1999 surveys ($N = 227$), and 79% with the 2004 surveys ($N = 256$).

Surveys were conducted during the dry season, December–March, which corresponds with the early breeding season of parrots in Nicaragua (Wiedenfeld 1993). Surveys began in the Pacific and moved eastward to track the onset of the dry season. Within a

biogeographical region (Pacific, Central Highlands, and Caribbean), surveys were conducted north to south. Following this sequence ensured that site survey dates were approximately consistent across years.

At least two observers completed all surveys, and each point was surveyed only once using the same protocol each survey year. Point counts were completed from the roadside ≤ 10 m from the vehicle or floating on a boat anchored to the riverbank. Surveys were conducted during the hours of greatest parrot activity: morning (~ 5 h30 to ~ 8 h00) and afternoon (~ 16 h00 to ~ 18 h00) (Wiedenfeld 1993, Marsden 1999). Time of day (am or pm) at each transect was held constant among years. At each point 15-minute surveys were conducted to maximise the chance of recording rare species following the suggestion of Wiedenfeld (1993), during which we recorded species presence or absence, number of individuals of each species, number of flocks (flock = two or more parrots associated together), and flock size. Species were identified visually and vocally, but only visually confirmed birds were included in the analysis. Owing to the effect of rain on bird activity (Robbins 1981), counts were not used when there was light rain or fog for more than 10 minutes or heavy rain or fog for more than five minutes during the count.

From the point-count data, with all points across all transects included, we calculated three informative metrics to allow a cursory taxonomic family-level comparison between the four survey years. We calculated: encounter rate, which is the average number of parrots observed at each point; flock rate, the average number of flocks observed at each point; flock size, the average number of parrots in each flock.

Surveys were authorised by the Nicaraguan Ministerio del Ambiente y los Recursos Naturales (MARENA) and took place in 1995, 1999, 2004, and 2013; the 2013 survey was approved by the animal use committee of University of Oklahoma (IACUC permit R12-018) and authorised by MARENA permit id - DGPN/DB-IC-010-2012.

Occupancy modelling

We used occupancy modelling to estimate population parameters among survey years. Presence/absence occupancy can be a good surrogate for density when data limitations prevent the calculation of robust density estimates (Bart and Klosiewski 1989), provided that underestimates are corrected for imperfect detection (MacKenzie 2005). Despite their raucous vocalisations, most Neotropical parrots are cryptically coloured and secretive (Casagrande and Beissinger 1997). Occupancy modelling accounts for imperfect detection to estimate the state variable “occupancy”, the probability a site is occupied (MacKenzie *et al.* 2002).

We completed all modelling using PRESENCE version 6.1 (Hines 2006). Occupancy modelling requires that a spatially variable number of sites (N) be surveyed on multiple sampling occasions (T). In our design, each set of point counts along a transect was treated as a sampling site (N) and the points along each transect were treated as the sample occasions (T) (MacKenzie *et al.* 2002).

The single-season models we ran varied in number of sampling sites ($N = 10$ –56), depending on the species and year, and was determined by the number of sites within a species’ range (range was described by observed presence during the study period). Survey sites had 1–6 sample occasions. Missing sampling occasions because of incomplete or variable sampling were accounted for in the models without causing bias, allowing for survey sites without equal samples. However, an excess of missing sampling occasions

can bias occupancy and variance estimations (MacKenzie *et al.* 2002). To limit bias, we selectively reduced missing sampling occasions by lowering the sampling occasions from six to five if doing so caused: 1) decreased occupancy standard error (SE) by 20%; 2) parameters to be estimated when they previously were not; 3) improved p value of goodness of fit to >0.05 ; or 4) lowered overdispersion (\hat{c}) from $\hat{c} >4.00$ to $\hat{c} <4.00$. In these cases, the sixth data point to be eliminated was chosen randomly.

Determining rates of change of occupancy is the ultimate goal of the multi-season models (MacKenzie *et al.* 2003), but we ran single-season model analyses to accommodate the inclusion of the necessary replacement points. For each species in each survey year, we ran a series of models to provide the most robust estimation of occupancy. We started with both constant detection probability, $\psi(\cdot)p(\cdot)$, and survey-specific detection probability, $\psi(\cdot)p(\text{survey})$, models. We used the most parsimonious base model to create a set of candidate models by individually adding time-of-day (am or pm) and biogeographical region (Pacific, Central Highlands, and Caribbean) covariates as well as the additive combination of the two, for a total of four candidate models. Time-of-day and biogeographical region may influence detection, so inclusion as covariates corrects for these two possible confounding factors. Of the four candidate models, we selected the most parsimonious model based on Akaike information criterion values for small sample sizes (AIC_c) (Burnham and Anderson 1998). We assessed model goodness of fit, and c -hat (\hat{c}) to measure overdispersion, of the most global model by calculating the Pearson's chi-square statistic with a parametric bootstrap procedure ($N = 999$) (MacKenzie and Bailey 2004) in program PRESENCE (version 6.1) (Hines 2006). Poor fit was determined when $\hat{c} >1.15$, in which case selection was based on QAIC_c values, the quasi-likelihood adjustment for overdispersion (Burnham and Anderson 1998) with SE inflated by a factor of $\sqrt{\hat{c}}$ (MacKenzie and Bailey 2004). Models with $\hat{c} >4.00$ or goodness of fit p value <0.05 were considered unacceptable and were not used; these most likely resulted when insufficient occurrences combined with low number of sites and occasions. We calculated 84% confidence intervals (CI) from site occupancy rates SE rather than 95% CI because the former is nearer to the standard of $\alpha = 0.05$ (Payton *et al.* 2003).

Upon selecting the most parsimonious model for a species in each survey period, we arcsin-square root transformed the estimated site occupancy rates (Psi-conditional) because they are proportional data bound between 0 and 1. We tested for change between survey years in each species with an analysis of variance (ANOVA) with the Tukey's honestly significant difference (HSD) *post hoc* test with the four years as the factor levels of the predictor variable of time and occupancy rate as the response variable.

Results

Taxonomic family-level trends

A total of 14 of 16 parrot species known to occur in Nicaragua were recorded during surveys at least once during the study, and 12 were recorded during surveys in all four survey years. All 16 species were observed somewhere in the country by D.C.H. during the 2013 field season, showing that none has been extirpated from Nicaragua. The Blue-headed Parrot *Pionus menstruus* was recorded only in the 2013 surveys, suggesting that this species expanded its distribution northward into Nicaragua after 2004. The Crimson-fronted Parakeet *Psittacara finschi* increased greatly in raw numbers from zero recorded in 1995 and 1999, 39 individuals in 2004, and 1,885 in 2013. Over this period, the

species expanded its distribution from the limited southeastern portion of Nicaragua in the 1990s to the present-day distribution that includes the Pacific and Central Highlands and reaches Honduras (Portillo-Reyes *et al.* 2017).

When all species are considered together, the data show a steady decline from 1995 to 2004 in encounter rate, flock rate, and flock size (Figure 2), with a partial recovery by 2013. However,

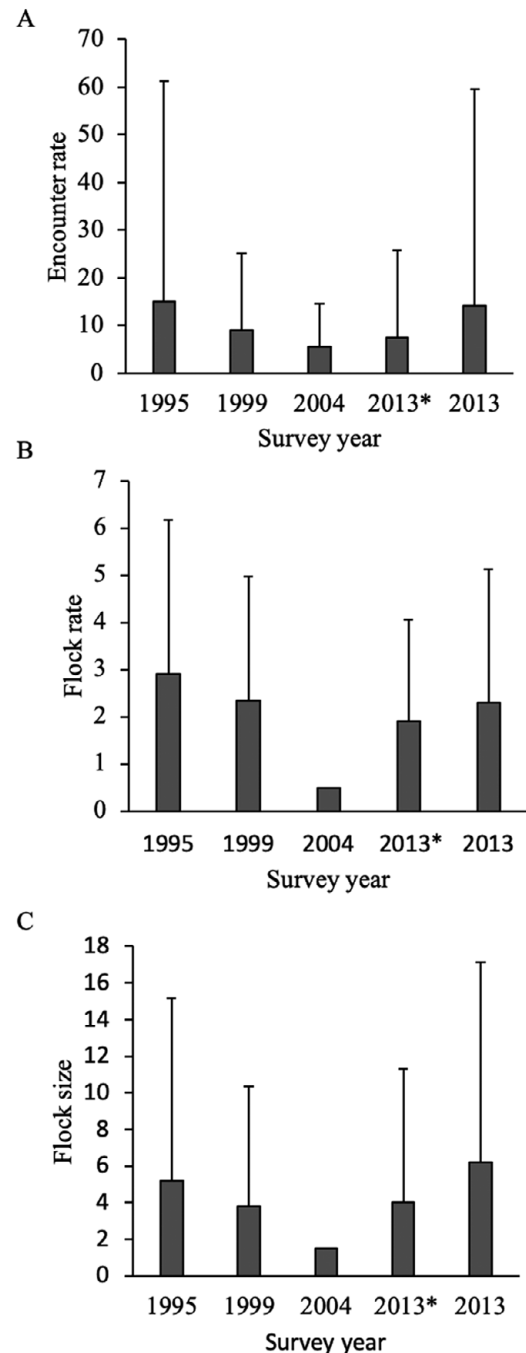


Figure 2. Cursory taxonomic family-level comparison between the four survey years compare: A) encounter rate, which is the average number of parrots observed at each point; B) flock rate, the average number of flocks observed at each point (flock = 2 or more parrots associated together); C) flock size, the average number of parrots in each flock. Error bars show standard deviation (2004 flock rate and flock size standard deviations were not calculated due to missing raw data from 2004). 2013 data denoted with * excludes Crimson-fronted Parakeet data.

if Crimson-fronted Parakeet data are excluded from the 2013 data, numbers remain depressed from 1995 to 2013 (encounter rate = 50% decrease; flock rate = 35% decrease; flock size = 23% decrease), despite some recovery from 2004 to 2013 (encounter rate = 33% increase; flock rate = 276% increase; flock size = 168% increase).

Species-specific occupancy modelling results

Robust occupancy rates were obtained for 12 of the 16 species, and 11 species had estimates for at least two years (Table S1), which allowed for occupancy trend analysis (Table 2); Great Green Macaw only had one year of estimates generated (1995) due to lack of detections. We could not estimate occupancy for Scarlet Macaw because we did not detect it in any of the four survey years or for Blue-headed Parrot due to its rarity, and survey sites did not sufficiently cover the distributions of two additional species (Green Parakeet and Barred Parakeet).

Overall, four species decreased in mean occupancy rates (Table 2 and Figure 3). Olive-throated Parakeet *Eupsittula nana* decreased 26% from 1999 to 2004 ($F_{2,95} = 3.35$, $p = 0.039$, $\eta^2 = 0.07$), Brown-hooded Parrot *Pyrilia haematotis* 70% from 1999 to 2013 ($F_{1,48} = 13.43$, $p = 0.001$, $\eta^2 = 0.22$), White-crowned Parrot *Pionus senilis* 36% from 1995 to 2004 ($F_{3,146} = 19.74$, $p < 0.001$, $\eta^2 = 0.29$), and Yellow-naped Parrot 42% from 1995 to 2004 ($F_{3,167} = 4.73$, $p = 0.003$, $\eta^2 = 0.08$). Five species increased in mean occupancy rates (Table 2). Orange-fronted Parakeet increased 26% from 1995 to 2013 ($F_{3,122} = 4.79$, $p = 0.003$, $\eta^2 = 0.11$), Pacific Parakeet *Psittacara strenuus* 225% from 1999 to 2013 ($F_{2,29} = 4.21$, $p = 0.025$, $\eta^2 = 0.23$), Crimson-fronted Parakeet 230% from 1995 to 2013 ($F_{2,83} = 40.48$, $p < 0.001$, $\eta^2 = 0.49$), Orange-chinned Parakeet *Brotogeris jugularis* 39% from 1995 to 2013 ($F_{3,217} = 4.33$, $p = 0.05$, $\eta^2 = 0.06$), and White-fronted Parrot *Amazona albifrons* 64% from 1995 to 2013 ($F_{3,123} = 4.65$, $p = 0.004$, $\eta^2 = 0.10$). Two species had no detectable

change (Table 2): Red-lored Parrot *Amazona autumnalis*, $F_{3,144} = 0.96$, $p = 0.415$, $\eta^2 = 0.02$ and Mealy Parrot, $F_{2,65} = 0.91$, $p = 0.407$, $\eta^2 = 0.03$.

Distributions of the declining species are primarily in the Caribbean. No species distributed solely in the Pacific and Central Highlands declined. Furthermore, three species (Orange-fronted Parakeet, Pacific Parakeet, and White-fronted Parrot) that occur chiefly in the Pacific biogeographical region increased significantly (Tables 1 and 2).

Patterns of species-specific occupancy shifted across years. Although there is no change from 1995 to 1999 ($N = 8$ spp. analysed), two of eight species analysed decreased from 1999 to 2004, and one species increased from 2004 to 2013 ($N = 7$ spp. analysed) (Figure 4). Four species increased in all three time periods analysed (1995–1999, 1999–2004, and 2004–2013; Orange-fronted Parakeet, Crimson-fronted Parakeet, Orange-chinned Parakeet, and White-fronted Parrot ($N = 7$ spp. analysed) (Table 2). Without taking subspecies into consideration, no species showed both significant decrease and significant increase across the three time periods analysed.

When analysed separately, trends for the two Yellow-naped Parrot subspecies differed: the Pacific subspecies (*auropalliata*) decreased by 25% from 1995 to 2004 and increased by 119% from 2004 to 2013 (Table 2 and Figure 5); $F_{2,59} = 7.91$, $p = 0.001$, $\eta^2 = 0.21$, but the Caribbean subspecies (*parvipes*) decreased by 56% from 1995 to 2013 (Table 2 and Figure 5); $F_{2,63} = 14.25$, $p < 0.001$, $\eta^2 = 0.31$.

Discussion

Nicaraguan parrot populations changed considerably from 1995 to 2013, which demonstrates that population trends are dynamic. There appears to be taxonomic family-level declines from 1995 to 2004, followed by a rebound leading up to 2013. However, species-specific occupancy rate assessments showed variable

Table 2. Estimated occupancy rates (with standard errors) for 12 species (dash denotes reliable estimates were not achieved) and individually for the two subspecies of Yellow-naped Parrot.

Species	1995	1999	2004	2013
Olive-throated Parakeet	0.71 ± 0.12	0.89 ± 0.21	0.66 ± 0.13	–
Orange-fronted Parakeet	0.77 ± 0.11	0.80 ± 0.10	0.95 ± 0.12	0.97 ± 0.07
Great Green Macaw	0.20 ± 0.25	–	–	–
Pacific Parakeet	0.25 ± 0.24	0.20 ± 0.14	–	0.65 ± 0.24
Crimson-fronted Parakeet	0.27 ± 0.24	–	0.38 ± 0.33	0.89 ± 0.14
Orange-chinned Parakeet	0.57 ± 0.11	0.74 ± 0.15	0.66 ± 0.11	0.79 ± 0.09
Brown-hooded Parrot	–	0.55 ± 0.31	–	0.13 ± 0.06
White-crowned Parrot	0.92 ± 0.92	0.75 ± 0.17	0.59 ± 0.25	–
White-fronted Parrot	0.49 ± 0.10	0.70 ± 0.11	0.62 ± 0.13	0.84 ± 0.12
Red-lored Parrot	0.92 ± 0.09	0.90 ± 0.09	0.81 ± 0.16	0.94 ± 0.45
Mealy Parrot	0.27 ± 0.14	0.14 ± 0.11	0.19 ± 0.13	–
Yellow-naped Parrot (combined)	0.80 ± 0.12	0.76 ± 0.17	0.57 ± 0.13	0.74 ± 0.24
Yellow-naped Parrot (ssp. <i>auropalliata</i>)	0.56 ± 0.14	–	0.42 ± 0.17	0.92 ± 0.26
Yellow-naped Parrot (ssp. <i>parvipes</i>)	0.86 ± 0.16	0.81 ± 0.20	–	0.38 ± 0.20

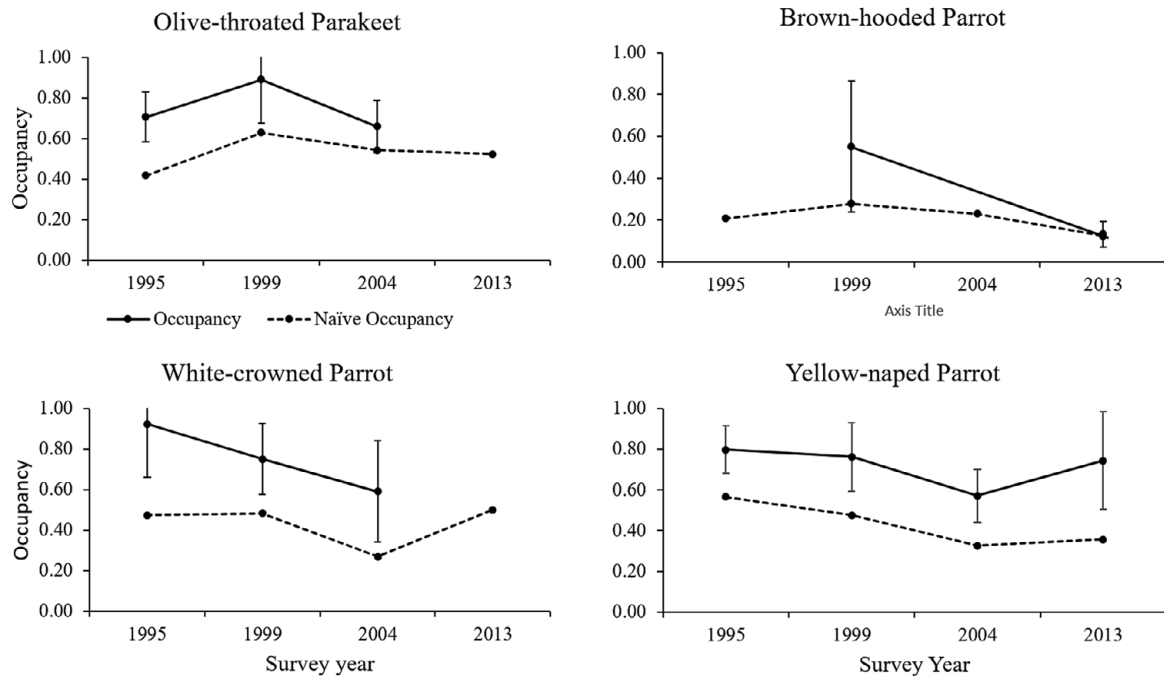


Figure 3. Mean occupancy rates (84% CI) for four species tested significant for decreases during segments of the study period: Olive-throated Parakeet (1995–2004), Brown-hooded Parrot (1999–2013), White-crowned Parrot (1995–2013), and Yellow-naped Parrot (1995–2004 and 1999–2004). Mean occupancy rates are not presented when models could not support robust estimates. Naïve occupancy is shown, which is the ratio of number of sites in which a species is present to the total number of sites, before correcting for imperfect detection.

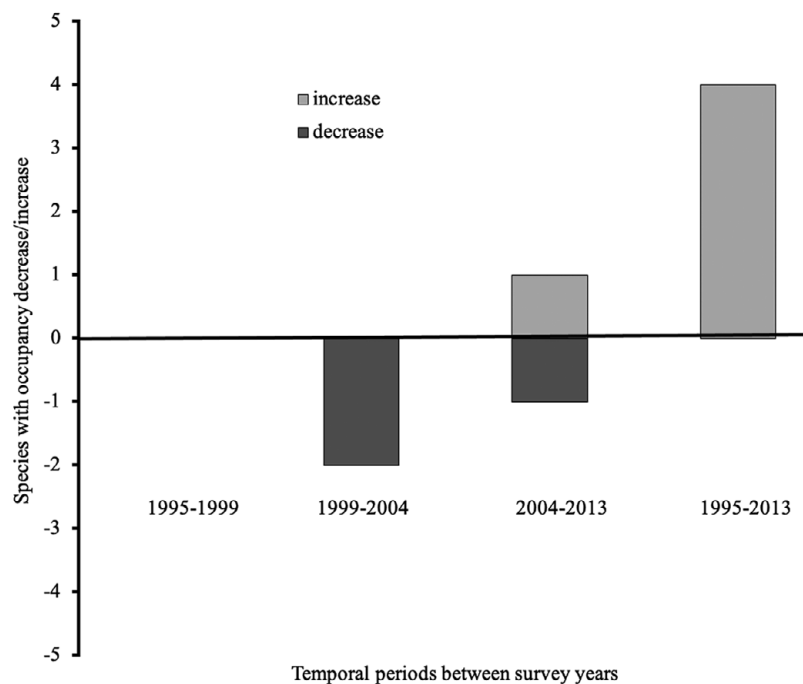


Figure 4. Species-specific patterns of decrease or increase in the temporal periods between survey years (1995 – 1999, 1999 – 2004, 2004 – 2013), and over the entire study period (1995 – 2013) demonstrate varied patterns within the study period.

trends which are potentially related to habitat loss and the pet trade, and the contrasting trends of the Yellow-naped Parrot subspecies may provide insight on some benefits of the 2004 trade ban.

Species of conservation concern

Declining occupancy rates or complete absence from surveys indicate six parrot species that need conservation attention in Nicaragua: the Olive-throated Parakeet, Great Green Macaw, Scarlet

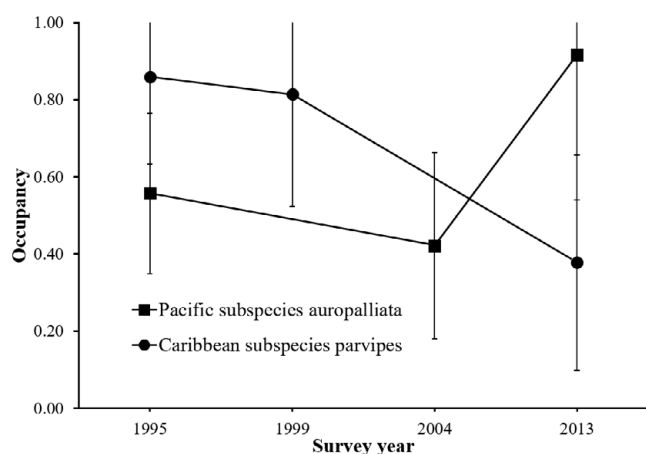


Figure 5. Mean occupancy rates (84% CI) for Yellow-naped Parrot subspecies tested significant for change during segments of the study period: *A. a. auroballiata* decreased (1995–2004) and increased (2004–2013); *A. a. parvipes* decreased (1995–2013).

Macaw, Brown-hooded Parrot, White-crowned Parrot, and Yellow-naped Parrot need to be considered species of conservation concern. The Great Green Macaw is already listed as Critically Endangered and the Yellow-naped Parrot as Endangered, but the remaining four are listed as Least Concern (IUCN 2021). Data from Mexico corroborate a regional concern, as the four species that also occur there have experienced considerable habitat loss within their historical distributions: Olive-throated Parakeet at 48%, Scarlet Macaw at 86%, Brown-hooded Parrot at 48%, and White-crowned Parrot at 49% (Ríos-Muñoz and Navarro-Sigüenza 2009).

The Great Green Macaw and Scarlet Macaw warrant the highest levels of concern. Their absence from many areas in the study likely resulted from habitat loss compounded by illegal capture. The historical range of the Scarlet Macaw broadly spanned Nicaragua, ranging from sea level to 1,100 m in elevation and a variety of forests, including dry, highland pine and pine-oak, cloud, humid lowland, and gallery, as well as pine savannahs (Wiedenfeld 1994). The present distribution is limited to a small, isolated Pacific population in the Cosigüina Natural Reserve and two disjunct and diffuse populations in the Caribbean in the Bosawas Biosphere Reserve and the Indio Maíz Biological Reserve (D.C.H. personal observation). Not being detected within surveys during the entire study period either in its historical or present distribution is an alarming reality of its current status within Nicaragua. The Great Green Macaw was detected enough to estimate occupancy in 1995, although it was not detected again until 2013 in only a very small portion of its historical range. Perhaps population size has increased in the extreme southernmost extent of its Nicaraguan range after the international San Juan–La Selva Biological Corridor was established in 2001 to facilitate conservation of this species (Chasot and Arias 2012).

Species-specific occupancy trends, deforestation, and trade

Parrots in Nicaragua face the same threats as most of the parrots throughout the Neotropics: habitat loss and pet trade. Nicaragua lost 49.5% of forest cover from 1950 to 2008 to deforestation (INAFOR 2009). Whereas there has been a regional net gain of woody vegetation from 2001 to 2010 in Mexico and Central America, Nicaragua is one of two countries in that region with a net loss (Aide 2013), and Global Forest Watch (2021) reported

860 kha of tree cover loss from 2001 to 2013, 6.7% of the total land area. As for the pet trade, the Nicaraguan government documented annual averages of 4,730 legal international parrot exports from 1989 to 1998 (Wiedenfeld *et al.* 1999), and 4,720 from 1999 to 2003 (Lezama *et al.* 2005). In addition, domestic commerce in Nicaragua is sizeable; national studies estimated 18,000–24,000 individuals per year supply domestic demand (Gutiérrez and Gómez 1996, Zegarra-Adrianzen 2004). One marketplace count tallied 13,622 parrots during four visits in a single year (Perez 1997). An unknown number of birds are also captured each year but not marketed, kept in the homes of their captors. Although now illegal, parrots are commonly seen in Nicaragua in both rural and urban homes and sold in public markets (D.C.H. personal observation). It stands to reason that the combination of habitat loss and trade pressure in Nicaragua will affect the national parrot populations and should be considered while interpreting the population trends.

All species that increased either rely primarily on habitat in the Pacific, or adapt successfully to anthropogenically disturbed habitat (IUCN 2021), or both. Distributions of the declining species are primarily in the Caribbean, which has experienced the most deforestation in Nicaragua during the study period. Nicaragua's borders with Honduras and Costa Rica within the Caribbean have been identified as deforestation hotspots (Lambin *et al.* 2003), and an analysis by Aide *et al.* (2013) demonstrated the Caribbean coast of Nicaragua was a hotspot for deforestation in Latin America and the Caribbean from 2001 to 2010. Global Forest Watch (2021) reported 662 kha of tree cover loss from 2001 to 2013 in the political departments comprising the Caribbean, representing 77% of Nicaragua's total tree cover loss for this time period. In addition, species that increased within the Caribbean adapt successfully to anthropogenically disturbed habitat (Crimson-fronted Parakeet and Orange-chinned Parakeet) (IUCN 2021). Deforestation appears to be a likely factor in species-specific trends.

Two species (Olive-throated Parakeet and White-crowned Parrot) in the Caribbean declined despite a reported moderate ability to adapt to anthropogenically disturbed habitat (IUCN 2021). The White-crowned Parrot may be more sensitive to deforestation than thought. For example, on the Yucatan Peninsula, it is rarer in fragmented forests than unbroken forest (Plasencia-Vázquez *et al.* 2014). By contrast, long-term data from the Palenque National Park, Mexico indicated a positive trend (Patten *et al.* 2010), perhaps because this forested area acts as a refuge. That Olive-throated Parakeet decline, despite its ability to adapt to anthropogenically fragmented habitat (Plasencia-Vázquez and Escalona-Segura 2014), may indicate continued illegal domestic trade. This species is commonly sold with the head painted yellow and claimed to be the highly sought Yellow-headed Parrot *Amazona oratrix* in Mexico or Yellow-naped Parrot in Nicaragua (D.C.H. and M.A.P. personal observation). Similarly, illegal trade was implicated in the range reduction in Mexico of Yellow-headed Parrot, Lilac-crowned Parrot *Amazona finschi*, and Mexican Parrotlet *Forpus cyanopygius* despite plentiful habitat for these species (Marín-Togo *et al.* 2012).

Large-scale deforestation did not occur in the Pacific during the study period, and coniferous forests of Mexico and Central America found in the Central Highlands are regional reforestation hotspots (Aide *et al.* 2013), providing both open and edge habitat and secondary forests. Populations of Orange-fronted Parakeet, Pacific Parakeet, White-fronted Parrot, and others may be positively affected by the 2004 trade ban during the period of this study. If the ban did indeed reduce trade pressure post 2004, this could

suggest that populations increase when deforestation rates are low and trade pressure is reduced.

The divergent trajectories of the Yellow-naped Parrot subspecies appear to most clearly highlight variable deforestation and trade pressure experienced between the Pacific and Caribbean. Pacific subspecies *auripalliata* faced low deforestation pressure and the Caribbean subspecies *parvipes* faced high deforestation pressure. As deforestation pressure was low for subspecies *auripalliata*, its significant decline from 1995 to 2004 most likely is attributed to high trade pressure. Wiedenfeld *et al.* (1999) reported that the Yellow-naped Parrot was then the second highest exported parrot and had the highest domestic and international sale price in legal markets. The seemingly unexpected reversal of this trend from 2004 to 2013 suggests that trade pressure lessened, at least locally, perhaps where conservation programmes focused on the subspecies (e.g. work of the NGO *Paso Pacifico*) or where a portion of the population is isolated on the island of Ometepe (Wright *et al.* 2018). In partial contrast to our results, Wright *et al.* (2018) asserted that the regional population between Nicaragua and Costa Rica is rapidly declining. Their roost count data in Costa Rica demonstrate a 54% decline from 2005 to 2016, and because they detected no difference in mean roost size between Costa Rica and Nicaragua from 2016 counts, it could imply the Nicaragua population is as depressed as the Costa Rica population. Nevertheless, our occupancy data show that although the Nicaraguan population was in decline from 1995 to 2004, at least a portion of the population was increasing between 2004 and 2013, and this increase was possibly connected to a presumed decreased trade pressure. Furthermore, even if the populations of both countries were equally depressed in 2016, the Wright *et al.* (2018) estimation of reproductive success reports a significant higher proportion of reproductive success at Nicaraguan roost sites, which suggests an increasing population there.

Meanwhile, Caribbean subspecies *parvipes* experienced a 56% drop in occupancy from 1995 to 2013. Its range has high deforestation pressure, and enforcement of the trade ban is likely lower in this extreme rural region, with no NGOs working towards its conservation.

Conclusions

Long-term monitoring of Nicaraguan parrots provided insight on taxonomic family-level trends, species-specific population trends, and identification of species of conservation concern. All six species of conservation concern are distributed throughout the Caribbean, where deforestation was highest and trade may not be alleviated by the trade ban, so attention ought to be given to management of protected areas and private lands in that region. Protection is crucial in light of continued deforestation at increasing rates; 624 kha of tree cover in the Caribbean was lost from 2014 to 2018, a 75% increase in annual deforestation rate in comparison to the 2001–2013 period (Global Forest Watch 2021). Additionally, the proposed transoceanic canal is forecasted to alter 18,800 ha of habitat directly and affect 62,780 ha indirectly in the Caribbean, including three protected areas (Huete-Pérez *et al.* 2015). Increased access from new roads could facilitate illegal logging and parrot trapping in areas that once were largely inaccessible. Hence, conservation efforts ought to focus on the Caribbean, a conclusion Gillespie (2001) supports in an analysis of threatened forest birds in Nicaragua.

Whereas populations of the parrot family in Nicaragua decreased and subsequently increased over the study period, individual species trends varied, potentially because of varying responses to deforestation. Additionally, there is evidence to suggest that the 2004 national trade ban positively affected parrot populations in the Pacific and Central Highlands during the years of this study. As there remains documented illegal domestic parrot trade throughout the country, we recommend a strong enforcement of the ban. Finally, indications of species-specific responses to habitat loss and trade pressure highlights the need to explicitly test the relative influence of these two factors in order to better manage diverse parrot populations.

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