

Yellow-naped Amazon *Amazona auropalliata* populations are markedly low and rapidly declining in Costa Rica and Nicaragua

TIMOTHY F. WRIGHT, THOMAS C. LEWIS, MARTÍN LEZAMA-LÓPEZ,
GRACE SMITH-VIDAURRE and CHRISTINE R. DAHLIN

Summary

Accurate assessments of population sizes and trends are fundamental for effective species conservation, particularly for social and long-lived species in which low reproductive rates, aging demographic structure and Allee effects could interact to drive rapid population declines. In the parrots (Order Psittaciformes) these life history characteristics have combined with habitat loss and capture for the pet trade to lead to widespread endangerment, with over 40% of species classified under some level of threat. Here we report the results of a population survey of one such species, the Yellow-naped Amazon, *Amazona auropalliata*, that is classified as 'Endangered' on the IUCN Red List. We conducted a comprehensive survey in June and July of 2016 of 44 night roosts of the populations in contiguous Pacific lowlands of northern Costa Rica and southern Nicaragua and compared numbers in Costa Rica to those found in a similar survey conducted in June 2005. In 2016 we counted 990 birds across 25 sites surveyed in Costa Rica and 692 birds across 19 sites surveyed in Nicaragua for a total population estimate of only 1,682 birds. Comparisons of 13 sites surveyed in both 2005 and 2016 in Costa Rica showed a strong and statistically significant decline in population numbers over the 11-year period. Assessment of group sizes approaching or leaving roosts indicated that less than 25% of groups consisted of three or more birds; there was a significantly higher proportion of these putative family groups observed in Nicaragua than Costa Rica. Taken together, these results are cause for substantial concern for the health of this species in a region that has previously been considered its stronghold, and suggest that stronger conservation action should be undertaken to protect remaining populations from capture for the pet trade and loss of key habitat.

Introduction

Effective conservation action depends fundamentally on quantitative assessments of the size, distribution and temporal trends of populations. Assessment of population trends are especially important for long-lived species with low annual reproductive rates, as such species may be less capable of rebounding quickly from reductions in population size caused by natural or anthropogenic factors (Heinsohn *et al.* 2009, Lotze *et al.* 2011). Furthermore, high adult survival in such species may mask the long-term consequences of low reproductive rates such as an ageing demographic structure with an increasing proportion of non-breeders (Lee *et al.* 2017). Such populations run the very real risk of rapid crashes when large proportions of the population reach reproductive senescence. In social species, the propensity for such crashes can be compounded by Allee effects, in which population growth becomes negative when population size drops below a threshold at which social groups no longer function (Courchamp *et al.* 2008, Hutchings 2015).

The parrots and cockatoos (Order Psittaciformes, hereafter 'parrots') are among the longest-lived group of birds and have generally low annual rates of reproduction (Young *et al.* 2012, Toft and Wright 2015). They typically have a complex fission–fusion social organisation in which long-term pair bonds are maintained within feeding flocks that in turn merge at communal night roosts (Toft and Wright 2015, Bradbury and Balsby 2016). The parrots are also the most endangered large order of birds, with 112 of 398 extant species (28%) classified on the 2016 IUCN Red List as 'Vulnerable', 'Endangered' or 'Critically Endangered', and an additional 60 species (15%) listed as 'Near Threatened' (BirdLife International 2016b). Although the causes of endangerment vary among species, two predominate: loss of suitable habitat and capture for the pet trade (Snyder *et al.* 2000, Wright *et al.* 2001, Pain *et al.* 2006, Olah *et al.* 2016, Berkunsky *et al.* 2017). The pet trade may have a particularly pernicious effect on populations as poaching often targets nestlings, leaving a standing adult population that may appear healthy but suffers from low recruitment of young birds. There are many anecdotes of rapid declines of parrot populations that may be caused entirely or in part by ageing population structures driven by the pet trade (Snyder *et al.* 2000, BirdLife International 2016a), but a lack of repeated and quantitative census data for most species makes it difficult to determine how widespread such crashes are.

The Yellow-naped Amazon *Amazona auropalliata* is a widespread parrot species that inhabits the tropical dry forest habitat that extends along the Pacific slope of Mesoamerica from southern Mexico to northern Costa Rica (Forshaw 2006). It is currently classified as 'Endangered' on the IUCN Red List and is thought to be declining across all of its range (BirdLife International 2017), but relatively few systematic surveys of population numbers have been conducted. Costa Rica populations have been the subject of a long-term study of geographic variation in vocalisations that have included surveys of night roosts in 1994, 2005 and 2016 (Wright 1996, Wright *et al.* 2008). Surveys in Nicaragua conducted in 1994, 1999 and 2004 found continuous declines in numbers sighted at point counts over this 10 year span (Lezama-López 2009). Reports from elsewhere in its range note declining populations, loss of key habitat, and large numbers of birds exported for the pet trade (Wiedenfeld 1993, Grijalva 2008, BirdLife International 2016b). Costa Rica is generally held to be a stronghold of the species, but small-scale studies of nesting success have reported high levels of nest poaching (Wright *et al.* 2001, BirdLife International 2017, Dahlin *et al.* 2018) and this species is commonly found as pets in Costa Rican households (Drews 2003). Overall, current estimates of the total population of the Yellow-naped Amazon vary widely from 10,000 to 50,000 individuals, reflecting considerable uncertainty in the status of different populations (BirdLife International 2017).

Costa Rica and Nicaragua in particular represent an interesting contrast in land-use regimes and approaches to conservation that could potentially impact parrot populations. Over the last 40 years, Costa Rica has emphasised protection and regulation of large swathes of its national territory in a system of "Áreas de Conservación" that include national parks, wildlife refuges and biological reserves that encompass many different ecosystems and enjoy some degree of protection from over-exploitation (Janzen and Hallwachs 2016). A much smaller portion of Nicaragua's territory is under protected status, and a large proportion of what is protected is owned by private landowners who agree to dedicate part of their holdings to conservation and restoration of native habitat, a system known as "Reservas Silvestres Privadas" (Anonymous 2013a). Outside of these protected areas, large parcels of Nicaragua's Pacific slope are devoted to high-intensity commercial or small-scale subsistence agriculture. The effects of the differences between these two countries in land-use and conservation regimes on the health of Yellow-naped Amazon populations are currently unknown.

In this study we report the results of a systematic census conducted in June and July 2016 of population numbers and group sizes at night roosts of the Yellow-naped Amazon in Costa Rica and Nicaragua. Our comparison of populations in the contiguous range of this species on the Pacific slope of the two countries allows us to contrast trends between two neighbouring countries with different land-use and conservation regimes, while measurement of groups sizes provides a rough estimate of reproductive success. We also compare these results to those from a 2005 survey in Costa Rica, providing a window on temporal trends within this country between 2005 and 2016.

Methods

Study area

We conducted surveys of roosts in the Pacific lowlands of northwestern Costa Rica and southwestern Nicaragua from 1994 to 2016 (Figure 1). This region lies in the tropical dry forest biome and is characterised by strong seasonality, with a rainy season running from June to December, and a dry season with little rainfall from January to April. It lies at the southern end of the range of the Yellow-naped Amazon, which runs from north-western Costa Rica to south-western Mexico (BirdLife International 2017). Broad scale surveys were conducted in Costa Rica in 2005 (6–23 June) and 2016 (3–29 June) and in Nicaragua in 2016 (24 June–10 July). This period of the year coincides with the post-fledging period when young can be observed in close association with their parents at roosts and feeding sites (T. Wright, C. Dahlin & M. Lezama unpubl. data) as seen in other amazon parrots (Salinas-Melgoza and Renton 2007). Additional smaller-scale surveys were conducted in Costa Rica in April and May 1994 and in Nicaragua in May 2008 and June 2009, 2011 and 2014. Potential roost sites for surveys were identified via previous field studies (Wright 1996, Lezama *et al.* 2004, Wright *et al.* 2008), consultation with local experts and residents, and in 2016, by reports of sightings registered on the Cornell Lab of Ornithology’s eBird website (www.ebird.org).

Roost counts and reproductive success

Roost counts were conducted in either the evening, as birds arrived at the roost, or in the early morning when birds departed from the roost, with only one count conducted per roost.

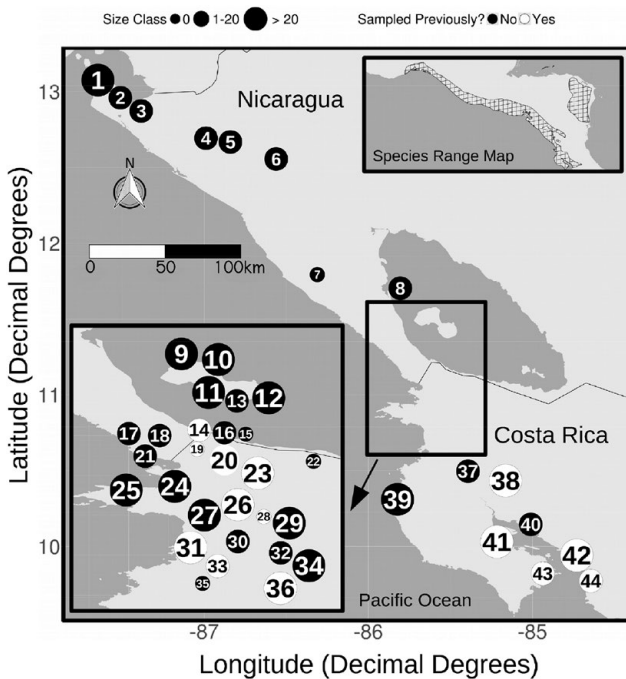


Figure 1. A map of roost sites surveyed in Costa Rica and Nicaragua. Sites are labelled with numbers corresponding to the numbers in Table 1. The size of the site label represents the relative number of birds observed at that roost (small = 0 birds, medium = 1–20 birds, large = > 20 birds). Filled circles were only surveyed in 2016, open circles were also surveyed in earlier years. The species range polygon is provided by BirdLifeInternational and NatureServe (2015).

We counted birds in the evening from 17h00 until nightfall at approximately 18h30 and in the morning from first light at approximately 05h15 until 06h30. Yellow-naped Amazons are diurnal and rarely fly in the dark (T. Wright, C. Dahlin & M. Lezama unpubl. data), so these two time-periods represented the best times to estimate the number of parrots arriving at or departing from night roosts (Cougill and Marsden 2004, Matuzak and Brightsmith 2007). Cougill and Marsden (2004) conducted morning and evening roost counts at a single roost of the Red-tailed Amazon *Amazona brasiliensis* in Brazil and observed no systematic bias in the number of birds observed in the morning versus the evening; for that reason we include data from both types of counts in our study.

Roost counts were conducted by one or two observers. The topography of different roost sites required different positioning of observers as lines of sight varied among sites; generally when the local landscape permitted, two observers were positioned on opposite sides of the roost allowing for maximum arc of sight. At roosts where it was only possible for birds to fly from certain directions (i.e. in mangrove patches bordered by the ocean) one observer was positioned with a full line of sight over the birds' flight path. Birds were counted as they came in to roost based on visual observations, and the direction from which they flew recorded so that any double counting of birds could be corrected when counts from multiple observers were combined. For some sites at which formal counts were not conducted or were not possible due to logistical or geographic constraints, we estimated the size of the population based on the birds seen and heard in the area. Although we believe count data give a more accurate assessment of roost size, the estimate data are still valuable for helping to generate an overall picture of population size across the region surveyed. We differentiate between the two types of data in Table 1.

To estimate reproductive success, we recorded the size of groups of birds as they flew into the roost. Our own observations (T. Wright, C. Dahlin & M. Lezama unpubl. data) and other studies of amazon parrots (Matuzak and Brightsmith 2007, Salinas-Melgoza and Renton 2007) suggest that groups flying in close proximity, particularly in the post-fledging period, often represent mated pairs accompanied by their recently fledged young. In 2016, we recorded the size of groups and used those data to estimate the proportion of groups that consisted of reproductively successful pairs with recently fledged offspring (e.g. groups of > 2 individuals). This approach does depend critically on the assumption that any groups consisting of three or more birds represent a successful reproduction event. Any groups of three or more that consist of multiple adult pairs or of unaffiliated juveniles would inflate this estimate of reproductive success.

Roost site characteristics

In addition to counts, we recorded descriptive data for each roost site. Location (latitude and longitude) and elevation were recorded for most sites with a handheld GPS unit; in a few cases location was calculated *post hoc* using Google Earth (vers. 7.1.7.2602) and elevation with the website Geoplaner (www.geoplaner.com). In 2016, we also classified the predominant type of roost substrate as either mangrove or mixed deciduous forest, and recorded whether the roost was within 100 m of human habitation as a measure of tolerance of anthropogenic disturbance.

Data analysis

Roost counts for roosts surveyed in 2016 were summed over the entire survey area to obtain an estimate for the entire population, and also within Costa Rica and Nicaragua separately to obtain a minimum population size for each country. We tested for a difference in the mean roost sizes between the two countries using a t-test. For roosts surveyed both in 2016 and earlier years we graphed the counts by year and tested for a difference between sites counted in both 2005 and 2016

Table 1. Population counts, estimates and reproductive success at sites in Costa Rica and Nicaragua.

Country	Year	Site Name	Site Number ¹	Latitude (deg, min)	Longitude (deg, min)	Elevation (m)	Human Habitation within 100m	Roost Observed	Date	AM/ PM	Count	Estimate	% Pairs with Young
Costa Rica	1994	Pelón Altura	26	10° 50.108'	85° 33.517'	103	Yes	Yes	4/11/94	PM	64	80–85	
	1994	Murciélago Santa Elena		10° 54.139'	85° 43.559'	31		Yes	5/13/94	PM	20	20–25	
	1994	Santa Rosa		10° 50.289'	85° 37.119'	295	Yes	Yes	5/21/94	PM	27	30–35	
	2005	Pelón Altura	26	10° 50.463'	85° 33.750'	103	Yes	Yes	6/3/05	PM	71	100–120	
	2005	Ahogados	28	10° 45.799'	85° 31.374'	86		Yes	6/4/05	PM	33	30–40	
	2005	Santa Rosa		10° 50.289'	85° 37.119'	295	Yes	Yes	6/3/05	AM	12		
	2005	Los Inocentes	23	11° 01.999'	85° 30.112	286	Yes	Yes	6/7/05	PM		75–100	
	2005	Las Parcelas de Santa Elena	20	11° 06.868'	85° 25.325'	135	Yes	Yes	6/8/05	PM		100–150	
	2005	Peñas Blancas	19	11° 11.537'	85° 37.359'	93		No	6/9/05	AM	0		
	2005	Playa Cabuyal	31	10° 40.456'	85° 38.902'	7	Yes	Yes	6/11/05	PM	144	200	
	2005	Las Trancas	33	10° 34.477'	85° 35.733'	44	Yes	Yes	6/12/05	PM	30	50–100	
	2005	Playa Iguanita		10° 37.555'	85° 37.455'	16		No	6/13/05	PM	0		
	2005	Pelón de la Bajura	36	10° 29.337'	85° 24.741'	27		Yes	6/17/05	PM		200	
	2005	Tárcoles	44	09° 47.547'	85° 38.565'	1		Yes	6/19/05	PM	4		
	2005	Tivives	42	09° 51.930'	84° 41.852'	12		Yes	6/19/05	PM		30–40	
	2005	Taboga-Cortijo	38	10° 20.991'	85° 08.013'	43	Yes	Yes	6/20/05	PM	106	150–200	
	2005	Hacienda Mojica		10° 24.347'	85° 11.804'	21	Yes	No	6/21/05	AM	0		
	2005	Palenque de Liberia		10° 32.888'	85° 25.924'	132	Yes	Yes	6/21/05	PM	5		
	2005	Curú	43	09° 47.095'	84° 56.264'	17		Yes	6/22/05	PM	43		
	2005	Puerto San Pablo	41	10° 02.901'	85° 12.279'	17		No	6/23/05	PM	12		
	2016	Tivives	42	09° 53.161'	84° 41.015'	12	Yes	Yes	6/3/16	PM	87		28
	2016	Tárcoles	44	09° 46.691'	84° 37.573'	1		No	6/4/16	PM	6		
	2016	La Ensenada	40	10° 08.826'	85° 02.455'	78		No	6/5/16	PM	4		
2016	Taboga-Cortijo	38	10° 21.016'	85° 07.945'	43	Yes	Yes	6/6/16	PM	38			

Table 1. Continued.

Country	Year	Site Name	Site Number [†]	Latitude (deg, min)	Longitude (deg, min)	Elevation (m)	Human Habitation within 100m	Roost Observed	Date	AM/ PM	Count	Estimate	% Pairs with Young
	2016	Puerto San Pablo	41	10° 02.873'	85° 12.243'	18		No	6/7/16	PM	24		
	2016	Curú	43	09° 47.099'	84° 56.266'	17		Yes	6/9/16	PM	6		
	2016	Playa Grande	39	10° 20.408'	85° 49.525'	5	Yes	Yes	6/10/16	PM	35		
	2016	Lakeside	35	10° 32.098'	85° 36.752'	49		No	6/12/16	PM	0		
	2016	San Fidel	32	10° 35.100'	85° 26.536'	141		No	6/14/16	AM	13		
	2016	Las Trancas	33	10° 34.477'	85° 35.733'	44	Yes	No	6/13/16	AM	9		
	2016	Finca Charlie Red	34	10° 34.117'	85° 25.078'	131	Yes	Yes	6/16/16	PM	263		17
	2016	Pelón Bajura	36	10° 28.682'	85° 24.762'	28		Yes	6/19/16	PM	63		0
	2016	Rosa María	27	10° 49.421'	85° 36.898'	274	Yes	Yes	6/20/16	PM	41		16
	2016	Ahogados	28	10° 45.799'	85° 31.374'	86		No	6/20/16	PM	0		
	2016	Horizontes	30	10° 42.777'	85° 35.717'	165		No	6/21/16	AM	16	30–50	
	2016	Playa Cabuyal	31	10° 40.456'	85° 38.902'	7	Yes	Yes	6/22/16	PM	66		3
	2016	Cuajiniquil	24	10° 56.974'	85° 41.993'	4	Yes	Yes	6/23/16	PM	115	200–250	31
	2016	Bahía Santa Elena de Murciélago	25	10° 55.144'	85° 48.829'	3		No	6/24/16	PM	32	50–60	
	2016	La Virgen	22	11° 06.537'	85° 23.157'	214		No	6/25/16	PM	0		
	2016	Las Parcelas de Santa Elena	20	11° 06.868'	85° 25.325'	135	Yes	Yes	6/26/16	PM	37	50–80	19
	2016	Peñas Blancas	19	11° 11.537'	85° 37.359'	93		No	6/26/16	AM	0		
	2016	Los Inocentes	23	11° 01.999'	85° 30.113'	286		No	6/27/16	PM	40	30–50	
	2016	Pelón Altura	26	10° 50.108'	85° 33.517'	103	Yes	Yes	6/28/16	PM	31		8
	2016	Irigiray	29	10° 43.232'	85° 30.703'	76	Yes	Yes	6/28/16	PM	49		25
	2016	Palo Verde	37	10° 24.078'	85° 18.945'	9	Yes	Yes	6/29/16	PM	15		0
Nicaragua	2008	Puente Río Sapoa	14	11° 14.128'	85° 36.870'	30		Yes	4/24/08	PM	10		100
	2009	Puente Río Sapoa	14	11° 14.128'	85° 36.870'	30		Yes	6/19/09	PM	13		100
	2011	Puente Río Sapoa	14	11° 14.128'	85° 36.870'	30		Yes	6/11/11	PM	15		43
	2014	Puente Río Sapoa	14	11° 14.128'	85° 36.870'	30		Yes	6/24/14	PM	15		29

Table 1. Continued.

Country	Year	Site Name	Site Number [†]	Latitude (deg, min)	Longitude (deg, min)	Elevation (m)	Human Habitation within 100m	Roost Observed	Date	AM/ PM	Count	Estimate	% Pairs with Young
	2016	Hacienda Alemania	7	11° 46.217'	86° 21.105'	116		No	6/24/16	PM	0		
	2016	Ostional	21	11° 06.690'	85° 45.523'	6	Yes	Yes	6/25/16	PM	17		11
	2016	Escamequita	17	11° 12.301'	85° 48.245'	25		No	6/27/16	AM	15		90
	2016	Cangrejo	18	11° 11.589'	85° 45.704'	50		No	6/26/16	PM	3		100
	2016	Isla Vista	15	11° 13.751'	85° 32.948'	145		No	6/28/16	PM	0		
	2016	La Conga		11° 13.656'	85° 34.769'	49	Yes	No	6/28/16	PM	4		100
	2016	Puente Río Sapoá	14	11° 14.128'	85° 36.870'	30	Yes	No	6/29/16	AM	10		0
	2016	Tichana	12	11° 24.876'	85° 28.704'	54	Yes	Yes	6/30/16	PM	104	100	35
	2016	San Ramón	13	11° 24.396'	85° 31.717'	43	Yes	Yes	7/1/16	AM	17		45
	2016	Mérida	11	11° 27.251'	85° 33.730'	51	Yes	Yes	7/1/16	PM	182	196	41
	2016	Pul	9	11° 35.234'	85° 36.266'	49	Yes	Yes	7/2/16	PM	62		41
	2016	Peña Inculca	10	11° 31.027'	85° 33.640'	57	Yes	Yes	7/2/16	PM	202	230	42
	2016	Cañas, Zapatera	8	11° 42.886'	85° 49.587'	49		Yes	7/4/16	AM	5	10	75
	2016	El Terrero	6	12° 32.946'	86° 38.062'	139		No	7/6/16	AM	5		50
	2016	Las Banderas	4	12° 42.412'	87° 01.655'	662		No	7/7/16	PM	6	6	50
	2016	Los Placeres	1	13° 01.353'	87° 36.221'	58		Yes	7/9/16	AM	38		25
	2016	La Piscina	3	12° 57.556'	87° 29.324'	10		Yes	7/9/16	PM	9	12	25
	2016	Potosí	2	12° 59.650'	87° 31.589'	166		Yes	7/10/16	AM	7		33
	2016	Argelia	5	12° 41.460'	86° 55.692'	654		No	7/10/16	PM	6	6	0

[†]Site numbers correspond to numbers on the map in Figure 1 and ascend from north to south.

using a paired t-test to estimate broad population trends over the 11-year period. We excluded from this analysis sites at which no birds were counted in either the 2005 or 2016 surveys. We calculated the proportion of pairs with fledglings as an estimate of reproductive success and compared this estimate between Costa Rica and Nicaragua using a t-test. We tested for differences in roost characteristics between Costa Rica and Nicaragua using t-tests or Fisher's exact tests as appropriate. We tested for associations between roost size and roost characteristics using t-tests or linear regressions. All proportions were calculated in Excel (vers 14.6.8) and graphs made and statistical tests conducted in JMP (vers 10.0.2). The alpha level for significance for all tests is $P < 0.05$, and all means are reported \pm SD.

Results

Roost counts: Regional trends

We conducted roost counts at 44 sites in Costa Rica and Nicaragua over 37 days in 2016 and observed birds roosting at 23 of these sites (Table 1, Figure 1). The total number of individuals counted in 2016 was 1682 birds, the maximum roost count was 263 birds and the mean per site was 38.2 ± 56.7 birds. The distribution of roost sizes was highly skewed, however, as the median roost size was 15.5 birds, 25 roosts (57%) had 20 birds or less, and only 9 roosts (20%) had 50 or more birds counted (Figure 2).

Roost counts: Trends by country

In Costa Rica we conducted roost counts at 25 sites in 2016, and observed birds roosting at 13 of these sites. At 8 of the other 12 sites birds were counted but roosting was not confirmed (i.e. the birds departed the area before nightfall), while at the remaining four sites no birds were observed during the count. The mean number counted at all sites was 40.0 ± 54.8 birds, while the mean counted at confirmed night roosts was 60.4 ± 65.9 birds. Only five roosts had roost counts of more than 50 birds; these roosts were dispersed across the range of this species in Costa Rica, with three located in or near coastal mangrove forests and two in mixed-deciduous forest in agricultural areas (Figure 1). The maximum roost count was 263 birds and the total number of birds counted across all sites in Costa Rica was 990 birds.

We conducted counts at three sites in 1994 and counts or estimates at 17 sites in 2005 in Costa Rica (Table 1, Figure 1). The mean roost size at all sites in 1994 was 37 ± 24.6 birds, while the mean of all sites counted in 2005 was 38 ± 46.3 . We conducted counts or estimates at 12 sites in 2005 that were also included in the 2016 survey. Nine of the 12 roosts showed reductions in population numbers from 2005 to 2016 (Figure 3), and the mean roost size decreased from a mean of 74 ± 59.9 birds in 2005 to 33.9 ± 27.3 in 2016, a mean decline of 54% in the 11 years separating

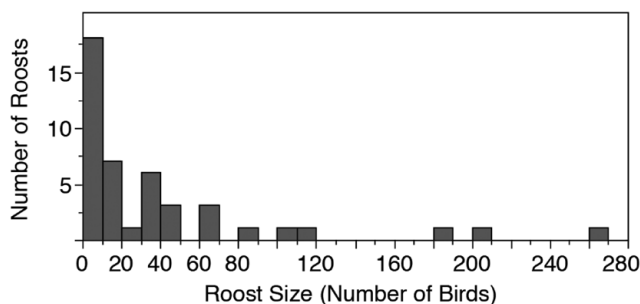


Figure 2. A histogram representing the relative distribution of roost counts in Costa Rica and Nicaragua in 2016. 80% of 44 roost sites observed had 50 or fewer birds.

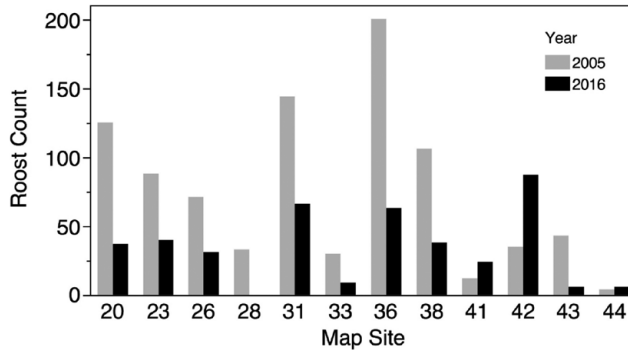


Figure 3. A comparison of roost sizes in 2005 and 2016 for 12 roosts in Costa Rica. Nine of 12 roosts had smaller populations in 2016 than in 2005. Site numbers correspond to those in Table 1 and Figure 1.

the two counts. This decline was statistically significant (paired *t*-test, *df* = 11, *t*-ratio = -2.8, *P* < 0.02) and remained significant when only the 6 roosts that had actual counts in both surveys were considered (paired *t*-test, *df* = 5, *t*-ratio = -5.1, *P* < 0.004).

In Nicaragua we conducted roost counts at 19 sites in 2016, and observed birds roosting at 10 of these sites (Table 1, Figure 1). At seven of the other nine sites birds were counted but roosting was not confirmed, and at the remaining two sites no birds were observed during the count. The mean count at confirmed night roosts was 64.3 ± 74.1 birds, the maximum roost count was 202 birds and the total number of birds counted across all sites in Nicaragua was 692 birds. Only four roosts in Nicaragua had 50 or more birds; all of these were located on the island of Ometepe in Lake Nicaragua (Figure 1). There was no difference between Costa Rica and Nicaragua in mean roost size counted in 2016 (*t* = 0.2, *df* = 36, *P* < 0.86). We conducted counts in 2008, 2009, 2011 and 2014 at one of the Nicaraguan roosts included in our 2016 survey, Río Sapoá (Table 1). These counts ranged from 10 to 15 birds; in 2016 we counted 10 birds, which is at the lower end of the historic range of counts.

Estimated reproductive success

We collected data on group size at 27 sites in 2016 to assess the proportion of pairs that successfully fledged young that year. Group sizes ranged from one to five birds. The percentage of groups in Costa Rica containing more than two birds, which possibly represent pairs with one or more recently fledged young, ranged from 0 to 31% across 10 sites, with a mean per site of $15 \pm 11.4\%$ of pairs. The proportion of groups containing young in Nicaragua ranged from 0 to 100% across 17 sites with a mean of $45 \pm 31\%$ of pairs. The difference between the two countries in mean proportion of groups containing young was statistically significant (*t* = 3.4, *df* = 22, *P* < 0.005). Across both neighbouring countries, however, only 120 groups consisted of more than two individuals while 498 groups consisted of pairs only, suggesting that only 24% of groups consisted of pairs accompanied by recently fledged young. Forty-nine of these 120 putative family groups (41%) were observed at the five roosts located on the island of Ometepe in Nicaragua. There was no relationship between the size of the roost and the percentage of pairs observed with young (linear regression, $r^2 = 0.04$, *df* = 24, *F* = 0.9, *P* = 0.34).

Roost characteristics

We recorded the elevation, roost substrate and proximity to human habitation of each surveyed roost. The elevation of confirmed roosts in Costa Rica ranged from sea level to 286 m

with a mean of 80.8 ± 83.7 m. The elevation of confirmed roosts in Nicaragua ranged from sea level to 682 m, with a mean of 127 ± 192.4 m. The difference in mean roost elevation between the two countries was not significant ($t = 1.0$, $df = 23$, $P < 0.4$), and all but one roost was located below 300 m. Roosts were most likely to be located in mixed-deciduous forest. In Costa Rica, four of 13 (30%) confirmed roosts counted in 2016 were located in mangroves; the remaining 70% were located in mixed deciduous forest. In Nicaragua, only one of 10 (10%) confirmed roosts was located in mangroves and the remaining 90% were in mixed deciduous forest. The proportional use of these two classes of roost substrate did not differ between the two countries (Fisher's exact test, $P = 0.33$). In Costa Rica, 11 of the 13 (85%) of the confirmed roosts in 2016 were located within 100 m of human habitation, while in Nicaragua six of 10 (60%) of the confirmed roosts were within 100 m of human habitation. The difference between the two countries was not significant (Fisher's exact test, $P = 0.34$).

There was a significant difference in mean roost size between roosts located within 100 m of human habitation versus farther away, with roosts within 100 m of human habitation having larger mean roost sizes (77 ± 74 vs. 30 ± 27 birds; $t = 2.2$, $df = 20.8$, $P < 0.04$). There was no association between roost elevation and roost size (linear regression, $r^2 = 0.006$, $df = 22$, $F = 0.1$, $P = 0.72$), nor did mean roost size differ between roosts located in mangroves versus mixed-deciduous forest ($t = 0.7$, $df = 9.7$, $P < 0.52$).

Discussion

Our surveys provide a robust assessment of current population sizes of the Yellow-naped Amazon on the Pacific slope of Costa Rica and Nicaragua and an estimate of temporal trends of populations in Costa Rica. Both assessments are cause for substantial concern regarding the health of populations of this endangered species. By every metric we measured, populations in Costa Rica and Nicaragua are small, have declined in the last decade, and are likely to continue to do so given our estimate of reproductive success. Below we summarise these trends, compare them to those seen in other Neotropical parrot species, and discuss likely factors contributing to a rapid population decline of this species in Costa Rica and Nicaragua. We conclude with a list of recommendations for conservation action.

Population trends

In 2016, we observed 990 birds distributed across 21 sites in Costa Rica, and 692 birds distributed across 17 sites in Nicaragua, for a total of only 1,682 birds. The majority of roosts observed in 2016 had fewer than 50 birds, and a direct comparison of 12 roosts counted in 2004 and 2016 showed a 54% decline in mean roost size over the 11-year period. Matuzak and Brightsmith (2007) estimated that during their study the Curú roost consisted of around 300 birds; in our survey 12 years later we counted only 17 birds, representing a 95% decline in numbers at this roost. The rapid decline at many roosts, low overall population numbers and the small average size of most local populations are all cause for significant concern about the long-term viability of this species at the southern portion of its Central American range. There are a few exceptions to these trends. The most notable are the roosts observed on the island of Ometepe in Lake Nicaragua, where the average roost size was 113 birds, three of the five roosts with more than 100 birds in our survey were located, and 41% of all pairs with young were observed. As discussed below though, this location is vulnerable to the same factors that are driving declines elsewhere in Nicaragua and Costa Rica. The other possible exceptions are two mangrove areas deep within the large and well-protected Área de Conservación Guanacaste, which we were not able to access during our survey but are reported by park officials to each contain a large roost of 200–300 birds (T. Lewis pers. obs). These exceptional areas notwithstanding, our results should serve as a clear warning that this species is increasingly vulnerable to extinction in the southern portion of its range, an area typically thought

of as its stronghold (BirdLife International 2016b; 2017). It now appears that populations here are following the path towards decline and local extirpation already seen in more northern parts of its range, including El Salvador, Guatemala, Honduras and Mexico (Eisermann 2003, Marin-Togo *et al.* 2012, BirdLife International 2017).

It is important to note some limitations to our survey approach. First, we counted each roost once, thus our estimates are subject to any day-to-day variability in the numbers of individuals attending a given roost. Cougill and Marsden (2004) found considerable day-to-day variability in the size of a single roost of Red-Tailed Amazons, but noted that the greatest variability in size was between seasons, with the peak numbers observed in the post-breeding season when both adults and recently fledged young attend roosts. Our surveys were conducted over 37 days within the immediate post-breeding season, suggesting our estimates are not subject to seasonal variation and should approximate the actual number of birds in the region. Second, we generally surveyed neighbouring roosts on consecutive days, thus some error could be introduced if birds frequently move between these roosts, but radiotracking data from this population suggests that such roost switching is relatively infrequent (Salinas-Melgoza *et al.* 2013). Third, we may not have counted all roosts within the survey area. We relied on a variety of approaches, including over 20 years of personal experience working with this species in this region, to locate roosts. We are aware of two roosts in the mangrove areas deep within the Área de Conservación Guanacaste in Costa Rica and an island population on the Islas Solentiname in Nicaragua that are difficult to access and thus were not included in the survey, but aside from these we are confident that we have counted most major roosts within the surveyed region.

Our estimates of reproductive success should be interpreted with caution. We found that on average 24% of groups flying to or from roosts consisted of three or more birds, suggesting that, at most, one quarter of the population of adult pairs is successfully reproducing. This proportion is roughly similar to those seen in other studies using similar methodology. A study conducted at the Curú site in Costa Rica in the post-breeding seasons found that 17–18% of groups flying to or from the roost consisted of pairs with young (Matuzak and Brightsmith 2007), while counts of Red-tailed Amazons at a single roost over an entire year throughout found 18% of groups flying to roosts and 24% of groups flying from roosts consisted of three or more individuals (Cougill and Marsden 2004). It is important to evaluate, however, the critical assumption that groups of three or more birds consist of mated pairs and their recently fledged young. While our observations suggest this is often the case, this estimate is best viewed as a theoretical best estimate of reproductive success. Our own data on nesting success from nest monitoring conducted from 1999 to 2008 in some of the same Costa Rican populations surveyed here found that only 11% of nests successfully fledged young, with most of the mortality arising from nest poaching (Dahlin *et al.* 2018). Nesting success is higher in populations of the sister species the Yellow-headed Amazon, *Amazona oratrix*, where 49 of 155 (31%) of nests monitored within or adjacent to protected areas over two nesting seasons from 2016–2017 successfully fledged young, but only limited roost surveys have been conducted in these populations due to an absence of stable roosting sites (C. Britt unpubl. data, F. Tarazona and C. Britt unpubl. data). Direct comparisons between data from nest monitoring and roost surveys are needed to fully evaluate whether the more expedient method of estimating reproductive success from group sizes at roost counts provides an accurate measure of this critical demographic variable.

Factors contributing to decline

Although our study was not designed to directly measure the impact of various factors on Yellow-naped Amazon populations, there is substantial evidence from this and other studies that two factors are primarily responsible for the decline: capture for the pet trade and conversion of habitat for intensive agriculture. The tropical dry forest ecosystem that is the

predominant habitat of the Yellow-naped Amazon has long been heavily impacted by anthropogenic disturbance (Janzen and Hallwachs 2016). For the past 200 years this disturbance was primarily in the form of low-intensity cattle grazing and subsistence farming. Yellow-naped Amazons appear quite tolerant of low-level disturbance; in our surveys most roosts were found in secondary deciduous forest, and many were in close proximity to human habitation; we actually found that mean roost size was larger for roosts located within 100 m of human habitation than for those located farther away. Furthermore, our observations suggest that Yellow-naped Amazons are capable of, and may actually prefer, to nest in more open landscapes such as those maintained by cattle ranching or controlled burns (Dahlin *et al.* 2018). Thus it is not human activity in general, but rather specific forms of human activity that are driving the observed declines in the Yellow-naped Amazon.

The massive scale of the global pet trade in Neotropical parrots has been recognised for some time (Wright *et al.* 2001) and is implicated in declines of a great number of species (Cockle *et al.* 2007, Marin-Togo *et al.* 2012, Clarke and de By 2013). In the case of the Yellow-naped Amazon, both their tolerance for close proximity to humans and their well-developed vocal mimicry abilities have rendered them especially vulnerable to the parrot trade. In the past, much of this trade was driven by demand in developed countries (Wright *et al.* 2001, Vall-Iloera and Cassey 2017), but now there is increasing evidence that demand from internal markets within Latin America is driving the poaching of this species and others (Drews 2003, Daut *et al.* 2015, Pires 2015, Pires *et al.* 2016, Berkunsky *et al.* 2017). Our anecdotal but frequent observation of pet Yellow-naped Amazons in both Costa Rica and Nicaragua suggest this trade is an ongoing threat in these countries (C. Dahlin, M. Lezama López, and T. Wright pers. obs.).

Habitat loss is commonly reported as contributing to the decline of many Neotropical parrots (Snyder *et al.* 2000, Clarke and de By 2013, BirdLife International 2016a). In the case of the Yellow-naped Amazon, recent changes in land-use and conservation practices in both Costa Rica and Nicaragua are likely contributors to population declines. Over the last 40 years, Costa Rica has placed large portions of its territory into regional Áreas de Conservación that are managed for biodiversity protection and ecosystem services. Over the last 25 years we have commonly seen birds moving between these protected areas and the low-intensity agrolandscape surrounding it (T. Wright and C. Dahlin, pers. obs.) and another study documented extensive feeding by Yellow-naped Amazons in human-modified areas at the Curú site in Costa Rica (Matuzak *et al.* 2008). In the last decade, however, these agro-landscapes have been increasingly converted from ranching to higher-intensity uses such as rice and sugar cane farming; Yellow-naped Amazons are now rarely seen in these high-intensity agricultural areas which lack suitable trees for nesting and feeding (C. Dahlin and T. Wright pers. obs.). Nicaragua has also suffered widespread loss of tropical dry forest habitat to high-intensity agriculture, and of mangrove habitat to shrimp farming and salt production (Tarrason *et al.* 2010, Aide *et al.* 2013, Benessaiah and Sengupta 2014). As a result, on the Pacific slope of Nicaragua, Yellow-naped Amazons are virtually absent from the lowlands and are now found mostly on the upper slopes of volcanoes where some forest has been preserved as national parks and reserves, and on islands within Lake Nicaragua where there is less intensive agriculture. One bright spot in Nicaragua is the recent strengthening of a system of private reserves that are incentivised by the national government to protect and restore native habitat. If this trend can be maintained it could eventually result in an increase in the availability of suitable habitat for this species on the Pacific slope of Nicaragua (D. Hille, D. Wiedenfeld, M. Lezama López, D. Brightsmith & M. Patten unpubl. data).

Other factors may also be contributing to the decline of the Yellow-naped Amazon. Global climate change has resulted in gradual increases in temperature and declines in rainfall in the Pacific slope for Costa Rica and Nicaragua (Hidalgo *et al.* 2013); these changes may affect the timing and amount of the fruits and seeds available for Yellow-naped Amazons. Perhaps more immediate, though, are Allee effects, which can cause a population's growth rate to become

negative when population size falls beneath a certain threshold (Courchamp *et al.* 2008). In social species, these can occur when groups are too small to offer protection from predators, when suitable mates become scarce, or when opportunities for cooperative interactions such as sharing public information about food are rare (Courchamp *et al.* 2008). Rapid declines have been reported in a wide range of parrot species, including such iconic species as the Kakapo *Strigops habroptilus* (Bergner *et al.* 2016), African Grey Parrot *Psittacus erithacus* (Annorbah *et al.* 2016), Swift Parrot *Lathamus discolor* (Heinsohn *et al.* 2015), and the Carolina Parakeet *Conuropsis carolinensis* (Snyder 2004). While in most cases factors such as capture for the pet trade, habitat loss, or introduced predators are implicated in the initial population decline, Allee effects are suspected to have accelerated the pace of population collapse in many of these species (Snyder 2004). Certainly, the possibility of Allee effects should be considered very seriously in a social species like the Yellow-naped Amazon. While we did not find a relationship between roost size and the proportion of groups that likely represented pairs and recently fledged young, we only found 120 putative family groups in our survey and 49 of these were from the roosts on Ometepe. Rapid declines and population crashes have already been reported for this species in several parts of its range (BirdLife International 2017). In this context, the recent population decline we document at the Curú site and the fact that over 50% of the roosts we surveyed in Costa Rica and Nicaragua had 20 or fewer birds is further cause for serious alarm. Our data will provide a critical baseline for future work addressing the important question of whether small populations of this species are especially vulnerable to rapid declines due to Allee effects or global climate change.

Conservation action recommendations

In December 2017, IUCN upgraded the status of this species from 'Vulnerable' to 'Endangered'. The data presented here, which show a > 50% decline in population at many roosts over the last 11 years, strongly support this change in conservation status and emphasise the need for rapid action before this species experiences further declines. The possession of wild animals, including parrots, is now illegal and subject to hefty fines in Costa Rica (Anonymous 2013b). Continued efforts at enforcing these regulations, coupled with substantive education programs to raise public awareness of the importance of parrot conservation, are recommended to reduce endemic poaching in Costa Rica. Similar regulations and education efforts are recommended for Nicaragua, where Yellow-naped Amazon populations are generally smaller, with the notable exception of Ometepe, which still hosts sizeable populations that merit special protection. Captive breeding and reintroduction programmes could also be valuable, particularly if they target areas with adequate habitat and protection of nests. In the longer term, conservation and restoration of dry forest habitat with preservation of large native trees required for nesting cavities will be important, particularly in Nicaragua, which has had more extensive deforestation and more limited restoration efforts. Further development of collaborations between conservationists, landowners and reserve managers will be critical for preserving this iconic parrot species in the southern portion of its range. On a larger scale, there is a dearth of reliable data on current populations of this species in the remainder of its range (BirdLife International 2016b). Standardised surveys conducted with similar methodology in the remainder of the Yellow-naped Amazon's range in north-eastern Nicaragua, El Salvador, Honduras, Guatemala and southern Mexico would provide an improved picture of the overall status of this species and help target both studies of the factors impacting populations, and conservation strategies to improve their health.

Acknowledgements

We thank Sophie Nazeri, Molly Dupin, Alesa Trimeloni, Dominique Hellmich, Norland Zambrano, José Martín Vallecillo, and Orlando Jarquín for assistance with 2016 roost counts, Hugo

Guadamuz Rojas and Sarah Garcia for assistance with 2005 roost counts, Hugo Guadamuz Rojas for assistance with the original roost survey in 1994, and Sophie Nazeri for extracting data on 2005 and 1994 roost counts from field notebooks. We gratefully acknowledge Roger Blanco of the Área de Conservación Guanacaste in Costa Rica, Roberto Zuñiga of the Área de Conservación Tempisque in Costa Rica, Myrna Moncada of the Red de Reservas Silvestres Privadas in Nicaragua, Carlos R. Mejía of the Ministerio del Ambiente y Recursos Naturales in Nicaragua and their staff for facilitating this research, and the many landowners in Costa Rica and Nicaragua for their support of our work and dedication to the protection of biodiversity. Funding was provided by the University of Pittsburgh Central Research Development Fund (C. R. D., grant number 9009626), New Mexico State University Manassee Scholar Award (T. F. W.), the Ara Project (T. L.) and the World Parrot Trust (T. L.).

References

- Aide, T. M., Clark, M. L., Grau, H. R., López-Carr, D., Levy, M. A., Redo, D., Bonilla-Moheno, M., Riner, G., Andrade-Núñez, M. J. and Muñiz, M. (2013) Deforestation and reforestation of Latin America and the Caribbean (2001–2010). *Biotropica* 45: 262–271.
- Annorbah, N. N. D., Collar, N. J., and Marsden, S. J. (2016) Trade and habitat change virtually eliminate the grey parrot *Psittacus erithacus* from Ghana. *Ibis* 158: 82–91.
- Anonymous (2013a) Establecer los Criterios, Requisitos y el Procedimiento Administrativo para la Declaración, Priorización y Promoción de las Reservas Silvestres Privadas en Nicaragua. (Ministerio del Ambiente y de los Recursos Naturales, Normas Jurídicas de Nicaragua: Managua, Nicaragua).
- Anonymous (2013b) Modificación de la Ley de Conservación de la Vida Silvestre, Ley N° 7317. (La Asamblea Legislativa de la Republica de Costa Rica: San Jose, CR).
- Benessaiah, K. and Sengupta, R. (2014) How is shrimp aquaculture transforming coastal livelihoods and lagoons in Estero Real, Nicaragua?: The need to integrate social-ecological research and ecosystem-based approaches. *Environ. Manage.* 54: 162–179.
- Bergner, L. M., Dussex, N., Jamieson, I. G., and Robertson, B. C. (2016) European colonization, not Polynesian arrival, impacted population size and genetic diversity in the critically endangered New Zealand kakapo. *J. Heredity* 107: 593–602.
- Berkunsky, I., Quillfeldt, P., Brightsmith, D. J., Abbud, M. C., Aguilar, J., Aleman-Zelaya, U., Aramburu, R. M., Ariash, A. A., McNab, R. B., Balsby, T. J. S., Barberena, J. M. B., Beissinger, S. R., Rosales, M., Berg, K. S., Bianchi, C. A., Blanco, E., Bodrati, A., Bonilla-Ruz, C., Botero-Delgadillo, E., Canavelli, S. B., Caparroz, R., Cepeda, R. E., Chassot, O., Cinta-Magallon, C., Cockle, K. L., Daniele, G., de Araujo, C. B., de Barbosa, A. E., de Moura, L. N., Del Castillo, H., Diaz, S., Diaz-Luque, J. A., Douglas, L., Rodriguez, A. F., Garcia-Anleu, R. A., Gilardi, J. D., Grilli, P. G., Guix, J. C., Hernandez, M., Hernandez-Munoz, A., Hiraldo, F., Horstman, E., Portillo, R. I., Isacch, J. P., Jimenez, J. E., Joynerak, L., Juarez, M., Kacoliris, F. P., Kanaan, V. T., Klemann, L., Latta, S. C., Lee, A. T. K., Lesterhuis, A., Lezama-Lopez, M., Lugarini, C., Marateo, G., Marinelli, C. B., Martinez, J., McReynolds, M. S., Urbinaat, C. R. M., Monge-Arias, G., Monterrubio-Rico, T. C., Nunes, A. P., Nunes, F. D. P., Olaciregui, C., Ortega-Arguelles, J., Pacifico, E., Pagano, L., Politi, N., Ponce-Santizo, G., Reyes, H. O. P., Prestes, N. P., Presti, F., Renton, K., Reyes-Macedo, G., Ringler, E., Rivera, L., Rodriguez-Ferraro, A., Rojas-Valverde, A. M., Rojas-Llanos, R. E., Rubio-Rocha, Y. G., Saidenberg, A. B. S., Salinas-Melgoza, A., Sanz, V., Schaefer, H. M., Scherer-Neto, P., Seixas, G. H. F., Serafini, P., Silveira, L. F., Sipinski, E. A. B., Somenzari, M., Susanibar, D., Tella, J. L., Torres-Sovero, C., Trofino-Falasco, C., Vargas-Rodriguez, R., Vazquez-Reyes, L. D., White, T. H., Williams, S., Zarza, R. and Masello, J. F. (2017) Current threats faced by Neotropical parrot populations. *Biol. Conserv.* 214: 278–287.

- BirdLife International (2016a) The IUCN Red List of Threatened Species. Version 2016.3: <<http://www.iucnredlist.org>>.
- BirdLife International (2016b) *Amazona auro-palliata*. The IUCN Red List of Threatened Species 2016: e.T22686342A93107875.
- BirdLife International (2017) *Amazona auro-palliata*. The IUCN Red List of Threatened Species 2017: e.T22686342A118961453.
- BirdLife International and NatureServe (2015) Bird species distribution maps of the world, version 5.0. <http://www.biodiversityinfo.org/spcdownload/r5h8a1/>
- Bradbury, J. W. and Balsby, T. J. S. (2016) The functions of vocal learning in parrots. *Behav. Ecol. Sociobiol.* 70: 293–312.
- Clarke, R. V. and de By, R. A. (2013) Poaching, habitat loss and the decline of Neotropical parrots: a comparative spatial analysis. *J. Experimental Criminol.* 9: 333–353.
- Cockle, K., Capuzzi, G., Bodrati, A., Clay, R., del Castillo, H., Velázquez, M., Areta, J. I., Farina, N. and Farina, R. (2007) Distribution, abundance, and conservation of Vinaceous Amazons (*Amazona vinacea*) in Argentina and Paraguay. *J. Field Ornithol.* 78: 21–39.
- Cougill, S. and Marsden, S. J. (2004) Variability in roost size in an *Amazona* parrot: implications for roost monitoring. *J. Field Ornithol.* 75: 67–73.
- Courchamp, F., Berec, L. and Gascoigne, J. (2008) *Allee effects in ecology and conservation*. Oxford, UK: Oxford University Press.
- Dahlin, C. R., Chelsea, B., Rising, J. and Wright, T. F. (2018) Long-term monitoring of nesting Yellow-naped Amazons, *Amazona auro-palliata* in Costa Rica: breeding biology, vocal behavior and the negative impact of poaching. *J. Field Ornithol.* 89: 1–10.
- Daut, E. F., Brightsmith, D. J., Mendoza, A. P., Puhakka, L. and Peterson, M. J. (2015) Illegal domestic bird trade and the role of export quotas in Peru. *J. Nat. Conserv.* 27: 44–53.
- Draws, C. (2003) The state of wild animals in the minds and households of a Neotropics society: The Costa Rican case study. Pp. 193–205 in D. J. Salem and A. N. Rowan, eds. *The state of the animals II: 2003*. Washington DC: Humane Society Press.
- Eisermann, K. (2003) Status and conservation of Yellow-headed Parrot *Amazona oratrix* “guatemalensis” on the Atlantic coast of Guatemala. *Bird Conserv. Internatn.* 13: 361–366.
- Forshaw, J. M. (2006) *Parrots of the World: an Identification Guide*. Princeton: Princeton University Press.
- Grijalva, A. E. A. (2008) *Monitoreo de la “loro nuca amarilla” (Amazona auro-palliata) como especie clave y establecimiento de sitios importantes para su conservación en el área de conservación Bahía de Jiquilisco, Usulután*. San Salvador: Ministerio de Medio Ambiente y Recursos Naturales.
- Heinsohn, R., Webb, M., Lacy, R., Terauds, A., Alderman, R. and Stojanovic, D. (2015) A severe predator-induced population decline predicted for endangered, migratory Swift Parrots (*Lathamus discolor*). *Biol. Conserv.* 186: 75–82.
- Heinsohn, R., Zeriga, T., Murphy, S., Igag, P., Legge, S. and Mack, A. L. (2009) Do Palm Cockatoos (*Probosciger aterrimus*) have long enough lifespans to support their low reproductive success? *Emu* 109: 183–191.
- Hidalgo, H. G., Amador, J. A., Alfaro, E. J. and Quesada, B. (2013) Hydrological climate change projections for Central America. *J. Hydrol.* 495: 94–112.
- Hutchings, J. A. (2015) Thresholds for impaired species recovery. *Proc. Roy. Soc. B-Biol. Sci.* 282(1809): 11.
- Janzen, D. H. and Hallwachs, W. (2016) Biodiversity conservation history and future in Costa Rica: the case of Área de Conservación Guanacaste (ACG). Pp. 290–341 in M. Kappelle, ed. *Costa Rican ecosystems*. Chicago: University of Chicago Press.
- Lee, A. M., Reid, J. M. and Beissinger, S. R. (2017) Modelling effects of nonbreeders on population growth estimates. *J. Anim. Ecol.* 86: 75–87.
- Lezama, M. S., Vilchez, M., Mayorga, R. and Castellón, R. (2004) *Monitoreo de Psitácidos 2004, Estado Actual y Conservación*. Managua, Nicaragua: Secretaria de la CITES, Nicaragua y Corredor Biológico del Atlántico.
- Lezama-López, M. (2009) Estado de conservación de loro nuca amarilla (*Amazona*

- auropaliata*) en al corredor biológico paso del istmo, Rivas, Nicaragua. Pp. 252–257 in T. D. Rich, C. Arizmendi, D. W. Demarest and C. Thompson, eds. *Fourth International Partners in Flight Conference: Tundra to Tropics*.
- Lotze, H. K., Coll, M., Magera, A. M., Ward-Paige, C. and Airoidi, L. (2011) Recovery of marine animal populations and ecosystems. *Trends Ecol. Evol.* 26: 595–605.
- Marin-Togo, M. C., Monterrubio-Rico, T. C., Renton, K., Rubio-Rocha, Y., Macias-Caballero, C., Ortega-Rodriguez, J. M. and Cancino-Murillo, R. (2012) Reduced current distribution of Psittacidae on the Mexican Pacific coast: potential impacts of habitat loss and capture for trade. *Biodivers. Conserv.* 21: 451–473.
- Matuzak, G. D., Bezy, M. B. and Brightsmith, D. J. (2008) Foraging ecology of parrots in a modified landscape: seasonal trends and introduced species. *Wilson J. Ornithol.* 120: 353–365.
- Matuzak, G. D. and Brightsmith, D. J. (2007) Roosting of Yellow-naped Parrots in Costa Rica: estimating the size and recruitment of threatened populations. *J. Field Ornithol.* 78: 159–169.
- Olah, G., Butchart, S. H. M., Symes, A., Guzman, I. M., Cunningham, R., Brightsmith, D. J. and Heinsohn, R. (2016) Ecological and socio-economic factors affecting extinction risk in parrots. *Biodivers. Conserv.* 25: 205–223.
- Pain, D. J., Martins, T. L. F., Boussekey, M., Diaz, S. H., Downs, C. T., Ekstrom, J. M. M., Garnett, S., Gilardi, J. D., McNiven, D., Primot, P., Rouys, S., Saoumoe, M., Symes, C. T., Tamungang, S. A., Theuerkauf, J., Villafuerte, D., Verfailles, L., Widmann, P. and Widmann, I. D. (2006) Impact of protection on nest take and nesting success of parrots in Africa, Asia and Australasia. *Anim. Conserv.* 9: 322–330.
- Pires, S. F. (2015) The heterogeneity of illicit parrot markets: an analysis of seven neotropical open-air markets. *Eur. J. Criminal Pol. Res.* 21: 151–166.
- Pires, S. F., Schneider, J. L., Herrera, M. and Tella, J. L. (2016) Spatial, temporal and age sources of variation in parrot poaching in Bolivia. *Bird Conserv. Internatn.* 26: 293–306.
- Salinas-Melgoza, A. and Renton, K. (2007) Postfledging survival and development of juvenile Lilac-crowned Parrots. *J. Wildl. Manage.* 71: 43–50.
- Salinas-Melgoza, A., Salinas-Melgoza, V. and Wright, T. F. (2013) Behavioral plasticity of a threatened parrot in human-modified landscapes. *Biol. Conserv.* 159: 303–312.
- Snyder, N. F. R. (2004) *The Carolina Parakeet: Glimpses of a Vanished Bird*. Princeton, NJ: Princeton University Press.
- Snyder, N. F. R., McGowan, P., Gilardi, J. and Grajal, A. (2000) *Parrots: Status Survey and Conservation Action Plan 2000–2004*. Gland, Switzerland and Cambridge, UK: IUCN.
- Tarrason, D., Urrutia, J. T., Ravera, F., Herrera, E., Andres, P. and Espelta, J. M. (2010) Conservation status of tropical dry forest remnants in Nicaragua: Do ecological indicators and social perception tally? *Biodivers. Conserv.* 19: 813–827.
- Toft, C. A. and Wright, T. F. (2015) *Parrots of the Wild: A Natural History of the World's Most Captivating Birds*. Berkeley, CA: University of California Press.
- Vall-Ilosera, M. and Cassey, P. (2017) 'Do you come from a land down under?' Characteristics of the international trade in Australian endemic parrots. *Biol. Conserv.* 207: 38–46.
- Wiedenfeld, D. A. (1993) *Status and management of Psittacines in northeastern Honduras*. CITES Secretariat, COHDEFOR and TRAFFIC, USA.
- Wright, T. F. (1996) Regional dialects in the contact call of a parrot. *Proc. R. Soc. London B* 263: 867–872.
- Wright, T. F., Dahlin, C. R. and Salinas-Melgoza, A. (2008) Stability and change in vocal dialects of the Yellow-naped Amazon. *Anim. Behav.* 76: 1017–1027.
- Wright, T. F., Toft, C. A., Enkerlin-Hoeflich, E., Gonzalez-Elizondo, J., Albornoz, M., Rodríguez-Ferraro, A., Rojas-Suárez, F., Sanz, V., Trujillo, A., Beissinger, S. R., Berovides, A. V., Gálvez, A. X., Brice, A. T., Joyner, K., Eberhard, J. R., Gilardi, J., Koenig, S. E., Stoleson, S., Martuscelli, P.,

Meyers, J. M., Renton, K., Rodríguez, A. M., Sosa-Asanza, A. C., Vilella, F. J. and Wiley, J. W. (2001) Nest poaching in Neotropical parrots. *Conserv. Biol.* 15: 710–720.

Young, A. M., Hobson, E. A., Lackey, L. B. and Wright, T. F. (2012) Survival on the ark: life history trends in captive parrots. *Anim. Conserv.* 15: 28–53.

TIMOTHY F. WRIGHT*, GRACE SMITH-VIDAURRE

Department of Biology, New Mexico State University, Las Cruces, NM, USA.

THOMAS C. LEWIS

The Ara Project, Punta Islita, Guanacaste, Costa Rica and The World Parrot Trust, Glanmor House, Hayle, Cornwall, UK.

MARTÍN LEZAMA-LÓPEZ

Consultant on Wildlife Management and Ecology, Managua, Nicaragua.

CHRISTINE R. DAHLIN

Department of Biology, University of Pittsburgh at Johnstown, Johnstown, PA, USA.

*Author for correspondence; e-mail: wright@nmsu.edu

Received 11 July 2017; revision accepted 27 February 2018;
Published online 9 July 2018