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Photo: Emily Khazan

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Trends and seasonality of *Ara ambiguus ambiguus* (Great Green Macaw) and *Ara macao cyanopterus* (Scarlet Macaw) in the Tortuguero Conservation Area, Costa Rica

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Cover Page: A view south from the top of Cerro Tortuguero of the lowland forest and coast characteristic of the study region and of the town of San Francisco. Photo by Emily Khazan on 14 March 2015.

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Abstract

Once widespread throughout the Costa Rican lowlands, *Ara ambiguus ambiguus* (Great Green Macaw) and *Ara macao cyanopterus* (Scarlet Macaw) were considered rare and locally extinct, respectively, in the Tortuguero area of northeastern Costa Rica until 2014. In 2017, Caño Palma Biological Station staff began weekly macaw surveys at five look-out points in the region. Surveys were carried out from January 2017 to June 2021 to identify and count all macaws sighted. After 27,764 sightings across over 1,048 surveys, we documented strong seasonal variation in activity for both species, with increased observations during each of the species' non-breeding seasons. This underscores the importance of landscape connectivity, which enables individuals to access different resources throughout the year. Overall, we observed relatively large numbers of both species of macaw, documenting slight increases in the presence of both *A. ambiguus ambiguus* and *A. macao cyanopterus* over the 4.5-year period examined. Our findings highlight the importance of the Tortuguero Conservation Area for the populations of both macaw species across the region and the utility of long-term monitoring efforts in documenting trends in regional abundance.

Keywords

Ara ambiguus ambiguus, *Ara macao cyanopterus*, endangered species, macaw, monitoring, population trends, Psittacidae

Resumen

Tendencias y estacionalidad de *Ara ambiguus ambiguus* (Guacamayo Verde) y *Ara macao cyanopterus* (Guacamayo Roja) en el Área de Conservación Tortuguero, Costa Rica • *Ara ambiguus ambiguus* (Guacamayo Verde) y *Ara macao cyanopterus* (Guacamayo Rojo) eran consideradas especies raras y localmente extintas, respectivamente, en el área de Tortuguero, en el noreste de Costa Rica, hasta 2014. En 2017, el personal de la Estación Biológica Caño Palma comenzó a realizar censos semanales de guacamayos en cinco miradores de la región. Los muestreos se llevaron a cabo desde enero de 2017 hasta junio de 2021 con el objetivos de identificar y contar todos los individuos avistados. Tras 27.764 avistamientos en más de 1.048 conteos, documentamos una marcada variación estacional en la actividad de ambas especies; con un aumento en los avistamientos durante las temporadas no reproductivas de cada una. Esto resalta la importancia de la conectividad paisajística; la cual permite que los individuos accedan a diferentes recursos a lo largo del año. En general, observamos números relativamente grandes de ambas especies de guacamayos; y registramos ligeros incrementos en la presencia de *A. ambiguus ambiguus* como de *A. macao cyanopterus* durante el período de 4,5 años analizado. Nuestros hallazgos resaltan la importancia del Área de Conservación Tortuguero para las poblaciones de ambas especies de guacamayos en la región; así como la utilidad de los esfuerzos de monitoreo a largo plazo para documentar las tendencias en la abundancia regional.

Palabras clave

Ara ambiguus ambiguus, *Ara macao cyanopterus*, especies amenazadas, Guacamayo, monitoreo, Psittacidae, tendencias poblacionales

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Résumé

Tendances et saisonnalité de *Ara ambiguus ambiguus* (Ara de Buffon) et de *Ara macao cyanopterus* (Ara rouge) dans l'aire de conservation de Tortuguero, au Costa Rica • Autrefois répandus dans les basses terres du Costa Rica, *Ara ambiguus ambiguus* (Ara de Buffon) et *Ara macao cyanopterus* (Ara rouge) ont été considérés jusqu'en 2014 comme rares et localement éteints, respectivement, dans la région de Tortuguero, au nord-est du Costa Rica. En 2017, le personnel de la station biologique de Caño Palma a commencé un suivi hebdomadaire des aras sur cinq points d'observation de la région. Le suivi a été réalisé de janvier 2017 à juin 2021 afin d'identifier et de compter tous les aras observés. Après 27.764 observations sur 1.048 relevés, nous avons constaté une forte variation saisonnière de l'activité des deux espèces, avec une augmentation des observations en dehors des saisons de reproduction des espèces. Cela souligne l'importance de la connectivité des paysages, qui permet aux individus d'accéder à différentes ressources tout au long de l'année. Dans l'ensemble, nous avons observé des effectifs relativement importants des deux espèces d'aras, avec de légères augmentations de la présence de *Ara ambiguus ambiguus* et de *Ara macao cyanopterus* au cours de la période de 4,5 ans étudiée. Nos résultats soulignent l'importance de l'aire de conservation de Tortuguero pour les populations des deux espèces d'aras dans la région ainsi que l'utilité des efforts de suivi à long terme pour documenter les tendances de l'abondance régionale.

Mots clés

Ara ambiguus ambiguus, *Ara macao cyanopterus*, aras, espèce menacée, Psittacidae, suivi, tendances démographiques

Psittacid species are threatened globally by habitat loss, habitat fragmentation, and the illegal pet trade (Chan *et al.* 2021, Vergara-Tabares *et al.* 2020). Two species of macaw in Costa Rica, *Ara ambiguus ambiguus*, the Great Green Macaw (hereafter referred to as 'GGM'), and the northern, Central American subspecies of *Ara macao cyanopterus*, the Scarlet Macaw (hereafter referred to as 'SM'), are listed in Appendix 1 of the Convention on International Trade of Endangered Species (CITES 2017) and Article 1 of the Costa Rican National System of Conservation Area's (SINAC) list of species in danger of extinction and with reduced and threatened populations (SINAC 2017). GGM and SM are vulnerable to the effects of habitat loss, leading to decreased availability of nesting sites and to decreased foraging resources across both breeding and non-breeding habitat (Vaughan *et al.* 2005, Chassot and Monge-Arias 2012, McReynolds 2012). Both species rely on almendro trees (*Dipteryx panamensis*: Fabaceae), using naturally occurring cavities in mature trees for breeding and foraging extensively on almendro fruits, thus requiring mature forests to successfully breed and forage (Chun 2008).

Across Costa Rica, nearly 70% of primary forest cover has been lost since the beginning of the 20th century (Chassot *et al.* 2005), resulting in a 90% decrease in the breeding range of GGM (Chassot and Monge-Arias 2012) and a diminished population estimated at only 200 individuals in Costa Rica over two decades ago (Powell *et al.* 1999). Similarly, the once widespread Central American subspecies of SM is now restricted to two isolated populations in Costa Rica on the Pacific Coast (Monge *et al.* 2016). This morphologically and taxonomically distinct subspecies located in Central America (while its sister taxon occurs in the Amazon basin) is threatened by a higher rate of population loss than the subspecies *Ara macao macao* based on genetic analyses (Schmidt *et al.* 2020). In the Tortuguero area of northeastern Costa Rica, GGM were considered rare, and SM were considered locally extinct until late 2014 (Restrepo Machado 2015, IUCN 2016).

To combat the decreasing population trends of both macaw species, particularly in the northeast of Costa Rica and neighboring Nicaragua, the San Juan–La Selva Biological Corridor was created in 2005 (Chassot and Monge-Arias 2012). This corridor connects six protected areas covering a total of 1,204,812 ha and promotes reforestation with macaw-friendly trees, especially almendro trees (Chassot and Monge-Arias 2012). Like other parrots, GGM and SM move seasonally taking advantage of resources across a broad landscape (Stahala 2008). Since the creation of the biological corridor, GGM has been recorded using the corridor to move seasonally between non-breeding habitats along the Caribbean coast and breeding habitats further inland in the foothills of Costa Rica's central mountain range (Chassot *et al.* 2007). However, the GGM population in Costa Rica is still considered to be decreasing (BirdLife International 2022), while the SM population in parts of Costa Rica is thought to be increasing (Vaughan 2019).

The seasonal movements facilitated by this corridor are critical to the ecology of this genus. Renton (2002) found three-fold increases in occurrence metrics of SM during the rainy season and similarly, Rivera-Ortiz *et al.* (2008) found that the number of *Ara militaris* declined from 40 to 2 during the dry, non-breeding season. In contrast, Karubian *et al.* (2005) found an increase in macaw activity during the dry, non-breeding season, which they attributed to sampling in a "terra firme" forest rather than a seasonally inundated forest. These studies show the regular, long-range movements of these species from breeding to non-breeding ranges and are consistent with our understanding of seasonal altitudinal migrations of the Nicaragua/Costa Rica population of GGM (Monge *et al.* 2016).

These movements are assumed to be driven by geographic variation in food availability. This is supported by Berg *et al.* (2007) and Bonadie and Bacon (2000) who found seasonal movements to be associated with patterns of food scarcity and fecundity of the primary large seed-producing trees in each area. Given that the perilous decline of GGM in Ecuador is believed to be driven in large part by food scarcity, restricted access to supplemental food sources likely limits the population recovery of GGM in Costa Rica. Both species of macaws are known to forage extensively on the non-native beach almond (*Terminalia catappa*) which is prevalent in the Tortuguero area and has a distinct phenology from native species (Henn *et al.* 2014, Villegas-Retana and Araya-H. 2017, Caño Palma Biological Station [CPBS] unpublished data). This may provide an essential supplementary food source during periods of low seed production by native species such as almendro.

Here, we used a 4.5-year dataset of a continuing long-term

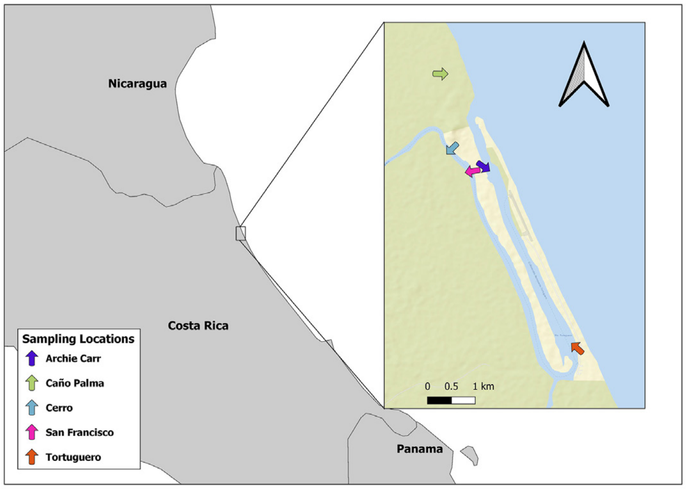

Fig. 1. Map of study area on the Caribbean coast of Costa Rica, including each survey site indicated by an arrow. The direction of the arrow indicates the viewing area. While some sites are close together geographically, the angle at which researchers collected data ensured a unique vista from each site which maximizes detection across a broad area and minimizes double counting of the same birds at two sites. Lighter green indicates human-modified areas like settlements or small-scale agricultural areas while the darker green indicates forest cover. Map by Emily Khazan and Sebastián Durán, based on Open Street Maps.

study to examine trends in the presence and frequency of both macaw species in the Tortuguero Conservation Area. Given the migratory nature of macaws described above, we expect high influence of seasonality in macaw abundance in the Tortuguero area. Given the lack of suitable nesting trees, we expected increases in macaw activity outside of the breeding season from February to April. The amount of fluctuation within this non-breeding period is unclear as this region experiences two distinct rainy seasons unlike the regions described in the literature. Similarly, the seasonality of almendro fruiting is less distinct in this region than in Panama, where it peaks at the start of the dry season (Bonaccorso *et al.* 1980, CPBS unpublished data). Finally, we expect consistent, yet large flock sizes as predicted by the higher gregariousness during the non-breeding season observed by Gilardi and Munn (1998) and Karubian *et al.* (2005). We also aim to demonstrate the seasonal patterns in frequency of records of both macaw species and the clear role that the region plays in maintaining regional macaw populations. Overall, this study examines the relative abundance and seasonal patterns of two charismatic and endangered bird species and provides invaluable information on the importance of a region overlooked for its conservation potential.

Methods

Study Locations

We collected data at five look-out locations throughout the Tortuguero Conservation Area, including the Barra del Colorado National Wildlife Refuge, San Francisco municipal area, and Tortuguero municipal area (Fig. 1). These protected areas are not currently identified as critical macaw habitat and fall to the east of the geographic limit of the San Juan–La Selva Biological Corridor (Chassot *et al.* 2005). The region encompasses the 102,165 ha Barra del Colorado National Wildlife Refuge and the 29,068 ha Tortuguero National Park. Classified as tropical wet rainforest (Holdridge 1967), it receives an average annual rainfall of 5,000 mm concentrated in two rainy seasons typically peaking in July and December (Myers 1981, Khazan *et al.* 2020). The seasonally flooded forests in the area are dominated by *Raphia taedigera* and *Manicaria saccifera* palms with higher-elevation, transitional zones harboring a diverse array of emergent hardwood trees (Lewis *et al.* 2010).

Survey sites were look-out points that were accessible from Caño Palma Biological Station and provided non-overlapping vistas overlooking a water body and surrounding vegetation. Site selection was also based on prior knowledge of frequent macaw sightings. Survey sites were situated at Caño Palma (10°35'37.1"N, 83°31'38.1"W), Cerro Tortuguero (10°34'52.5"N, 83°31'40.7"W), which at 84 m above sea level (asl) is the highest elevation point in the area, Archie Carr (10°34'40.3"N, 83°31'19.0"W), the village of San Francisco (10°34'37.2"N, 83°31'26.5"W), and the village of Tortuguero, adjacent to Tortuguero National Park (10°32'37.3"N, 83°30'14.3"W). Survey sites had a mean separation of 1.6 ± 1.8 km distance from their nearest neighboring point, with the closest sites being Archie Carr and San Francisco (0.247 km), while the furthest site was Tortuguero at 4.227 km from Archie Carr (see Appendix A for pairwise distances between survey sites). Vegetation around survey sites contained almendro trees and/or beach almond trees that provide food and potential nest site resources for macaws (Powell and Bjork 1995, Madriz 2004).

Study Methods

From January 2017 to June 2021, we conducted 1,048 surveys (between 112–323 surveys per year), attempting to sample each site equally (see Appendix B for a breakdown of surveys per site). Surveys took place weekly except when they were precluded by heavy rain or personnel shortages. Due to logistical limitations, not all locations received equal sampling effort across years, however, all sites were sampled in all years. In particular, researchers had limited access to Tortuguero or the national park in 2020–2021 due to the COVID-19 pandemic, which resulted in significantly fewer surveys conducted at that site.

Unless interrupted by extreme weather, we conducted a four-hour morning (0530–0930) and afternoon (1330–1730) survey for a total of eight observation hours on the same day at a single site to avoid counting a single bird at two separate locations (Ralph *et al.* 1993). During each observation period, two observers continuously scanned the sky and tree crowns for macaw activity. Those two observers were used to facilitate continuous monitoring and tracking of birds and were not following the principles of the double-observer method (Forsyth and Hickling 1997). Both observers were at the same location and maintained communication. Macaw activity was measured by the total number of macaws observed that entered the viewing range of the observers during the complete sampling period of eight hours. Upon observation of macaws, we determined species, number of individuals, behavior, and movement, if applicable. Observations of unidentified bird species (i.e., *Ara* sp.), due to poor lighting conditions, were not included in analyses. When individual macaws remained within the area, we tracked their direction of flight so that observers did not count a single bird moving around the viewable area as more than one observation, thereby reducing the possibility of double-counting. However, we recognize that it is inevitable that individuals who left and returned to our field of view during a survey were recounted; we therefore have not attempted to estimate the local population sizes and provide only comparisons of activity levels.

Data Analyses

For each day (i.e., a total of eight observation hours), we totaled the number of macaws observed per species. Data on frequency of macaw observations did not have a normal distribution, therefore we conducted a non-parametric Kruskal–Wallis rank sum test to compare macaw activity across survey sites. Where a significant difference was found, we performed a pairwise Wilcoxon rank sum test with a Bonferroni correction to determine which sites differed significantly in frequency of macaw observations (Papadakis *et al.* 2020). We employed non-parametric statistical tests due to the non-normal nature of our data.

To better understand trends in frequency of observations of GGM and SM in the Tortuguero area over time, we examined variation in macaw observations within years and across our 4.5-year study period. First, to test for temporal variation within a given year, we calculated the Julian date of all observations and used a generalized additive model ("gam" function in the mgcv package in R) with survey site as a random factor, to create a smoothing function which predicted macaw observations for each Julian date using a penalized regression spline (Grolemund and Wickham 2011). These models are effective to describe and test the significance of non-linear changes such as seasonal variation, and to test for differences in frequency of observations between peak and low periods of activity (Hastie 2017).

Once we determined significant temporal variation in macaw observations within a given year, we used classification and regression trees with the "rpart" function in the rpart package (Therneau and Atkinson 2019) to identify dates associated with "high" and "low" periods. Consistent with the breeding ecology and bimodal peaks in activity observed in the data, we limited tree depth for GGM to two rows, which produced a maximum of four groups, consistent with two "high" periods and two "low" periods per calendar year. For SM, we limited tree complexity, using 25 macaw observations as a cutoff. All survey dates with ≥ 25 SM observations were considered "high", and dates with fewer than 25 SM observations were considered "low".

Using the "high" and "low" temporal periods determined for GGM by the classification and regression tree, we separated observations into four periods of observation including "high 1", "low 1", "high 2", and "low 2". For each species, we then performed a pairwise Wilcoxon rank sum test to determine if there were significant differences in observed activity between the high and low temporal periods identified by the classification and regression tree.

To test for trends in frequency of macaw observations over the 4.5-year study period, we created a generalized linear mixed model ("glmmTMB" function in R package glmmTMB) with a negative binomial distribution due to the zero-inflated nature of the data. The model was created separately per species with number of observations as the dependent variable, date as a fixed factor and site as a random factor (GGM or SM observations ~ Date + (1|Site)). Due to the inconsistent sampling effort at some sites and the potential differences in observations for both species among survey sites, we removed sites with fewer than five surveys per year from the analyses. These omissions include the sites Cerro Tortuguero and the village of Tortuguero in 2021 ($n < 5$ surveys). In addition, given the known association between macaw activity and season, we included the temporal variation of sampling ("high" or "low") as an interactive factor. Finally, to explore patterns in the frequency of macaw observations over time within each survey location, we created separate generalized linear mixed models for each site, using date as a fixed factor.

Results

We recorded a total of 25,641 *Ara ambiguus ambiguus* observations and 2,123 *Ara macao cyanoptera* observations. Frequency of macaw observations was not equal across survey locations for either GGM (Kruskal–Wallis test: H = 128, df = 4, $p < 0.001$) nor SM (Kruskal–Wallis test: H = 46.005, df = 4, $p < 0.001$). We had the lowest number of observed GGM at Caño Palma compared to all other sites (10.1 ± 17.6), while we observed higher numbers at Tortuguero compared to all other sites (Table 1).

Table 1. Results from the pairwise Wilcoxon rank sum test for *Ara ambiguus ambiguus* (GGM) and *Ara macaoc cyanoptera* (SM) observations. *p*-values in the top right of the table reflect results from GGM; those in the lower left section of the table represent SM results. *p*-values for each pair are shown on the left five columns while the mean and standard deviation of observations per sampling period are shown for each species and site in the rightmost two columns. Bolded results are significant at the $p = 0.05$ level.

	Archie Carr	*Caño Palma*	San Francisco	Cerro	Tortuguero	GGM observed	SM observed
Archie Carr		***p* < 0.001**	*p* = 0.690	*p* = 1.000	***p* = 0.040**	29.8 ± 41.8	1.07 ± 5.0
Caño Palma	*p* = 0.102		***p* < 0.001**	***p* < 0.001**	***p* < 0.001**	10.1 ± 17.6	1.61 ± 4.8
San Francisco	*p* = 0.690	*p* = 1.000		***p* = 0.015**	*p* = 1.000	31.5 ± 38.4	2.10 ± 7.2
Cerro	***p* = 0.003**	*p* = 1.000	*p* = 0.620		***p* < 0.001**	19.6 ± 23.6	3.40 ± 9.5
Tortuguero	***p* = 0.003**	***p* < 0.001**	***p* < 0.001**	***p* < 0.001**		41.1 ± 53.3	0.10 ± 0.8

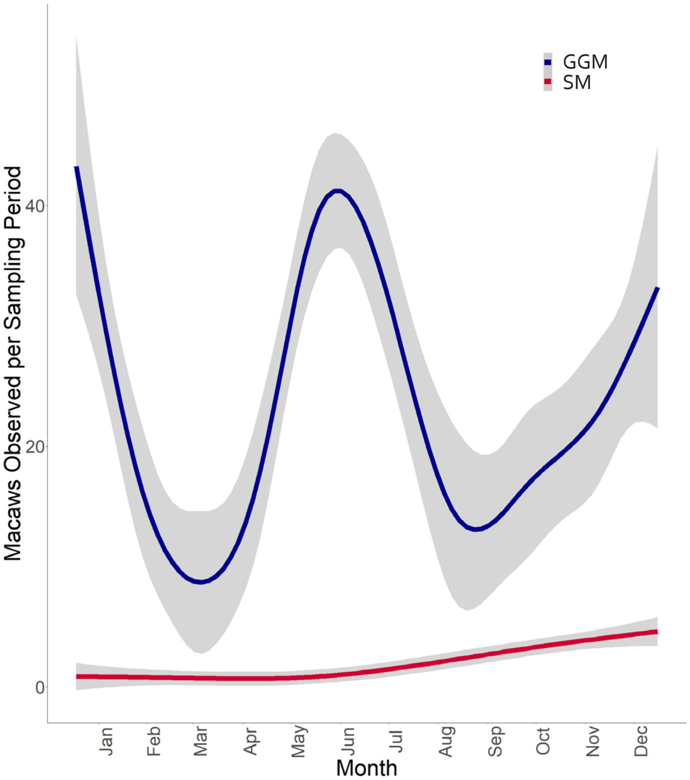

Fig. 2. Overall inter-annual variation in activity of *Ara ambiguus ambiguus* (Great Green Macaw, GGM, blue line) and *Ara macao cyanopterus* (Scarlet Macaw, SM, red line), including data from the complete study period (January 2017–June 2021) and all sample sites with consistent-sampling effort ($n > 5$). Shading represents the confidence interval around each point as determined by a generalized additive model.

We observed lower SM numbers at the Archie Carr and Tortuguero sites compared with the remaining three sites (Table 1). The remaining three sites did not differ significantly among themselves in frequency of macaws detected. The highest number of GGM individuals observed in a single instance was 75, recorded at the Tortuguero site in 2018. For SM the highest number of individuals observed in a single instance was 21, recorded at the Cerro site in 2018.

Generalized additive models demonstrated significant temporal variation within years for both GGM (t = 22.6, $p < 0.001$) and SM (t = 9.144, $p < 0.001$). SM showed a single increasing pattern of frequency towards the end of the year while GGM showed bimodal patterns of high and low frequency of observations (Fig. 2). Classification and regression trees for GGM estimated that the highest number of observations were between 1 to 18 January and from 2 May to 11 July, whereas observation frequency was lowest from 19 January to 1 May and from 12 July to 31 December. SM showed the highest frequency of observations were from mid-August to the end of the calendar year, with low frequency of observations and overall presence in the area for the rest of the year. Wilcoxon rank sum test confirmed that these differences in activity across time periods were statistically significant for both GGM (U = 38,2375, $p < 0.001$) and SM (U = 21,528, $p < 0.001$).

Over the 4.5-year period analyzed herein, our generalized linear mixed models demonstrated a slight but significant increase in frequency of observations of GGM (z = 2.226, df = 1,043, $p = 0.026$) across all survey locations with consistent sampling effort (> 5 surveys per year, with no data from Cerro or Tortuguero in 2021; Fig. 3). There was also a significant increase in frequency of observations of SM (z = 3.598, $p < 0.001$) over the 4.5-year period. Considering each site, GGM observations increased significantly over the study period at Caño Palma (z = 3.315, $p < 0.001$) and San Francisco (z = 2.494, $p = 0.013$), whereas there was a negative and non-significant tendency at Archie Carr (z = -1.411, $p = 0.128$), and no significant changes at Tortuguero (z = 0.943, $p = 0.346$) or the Cerro (z = -1.386, $p = 0.166$). SM observations also increased significantly at the San Francisco site (z = 2.718, $p = 0.007$), but showed no significant changes in Tortuguero (z = 1.518, $p = 0.129$), Caño Palma (z = 0.750, $p = 0.453$), Archie Carr (z = 1.267, $p = 0.205$), and the Cerro (z = 1.861, $p = 0.063$).

Discussion

Over the course of this study, we consistently documented the Endangered *Ara ambiguus ambiguus* (GGM) and *Ara macao cyanopterus* (SM) in the Barra del Colorado Wildlife Refuge and Tortuguero National Park. We documented GGM regularly during its non-breeding period, representing a distinct

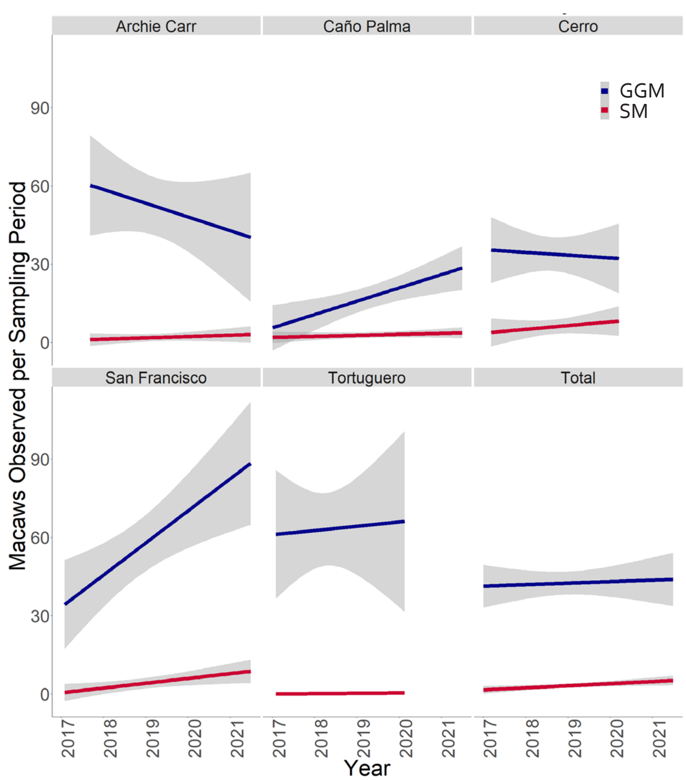

Fig. 3. Temporal trends in macaw activity of *Ara ambiguus ambiguus* (Great Green Macaw, GGM, blue lines) and *Ara macao cyanopterus* (Scarlet Macaw, SM, red lines) at each of the five sampling locations for the years in which we conducted at least five surveys. The shading represents the confidence interval around each point as determined by a generalized linear model.

change from their extremely rare status before 2014. The regularity with which we found GGM foraging in beach almond trees (personal observation of all authors; Chow *et al.* 2021) demonstrates that this region provides important resources for this imperiled species as well as hope for its local recovery. SM now occurs in the Tortuguero area with much greater regularity than it has in the last several decades, and this study demonstrates that its activity and presence in the area have increased over the study period. The trends revealed in our study should be interpreted with caution as they are based on the frequency of macaw observations, which functions as a combination of activity and relative abundance, not population nor abundance per se. Due to the sampling protocol, it is possible that we recounted individuals who left and returned to our field of view during a survey; we therefore have not attempted to estimate the local population sizes.

We observed variable levels of macaw activity among our sampling sites and within each year. This corresponds with the ecology of the species, which depend on diverse resources widely dispersed across the landscape in accordance with their breeding and non-breeding seasons (Powell *et al.* 1999). Consistent with expectations, we observed strong bimodal peaks in activity for GGM which were associated with its non-breeding season (i.e., outside of December–June), during which they seek out feeding grounds distinct from breeding areas (Collar *et al.* 2020a, 2020b). Time periods in which we documented lowest macaw activity coincide with the breeding season for both species, suggesting that few pairs remain in the area to breed, perhaps due to a lack of suitable nesting habitat; ongoing research seeks to determine the suitability of the Tortuguero region for macaw breeding. Neither species displayed activity patterns associated with the beach almond tree fruiting season, despite frequent observations of macaws feeding on these fruits (CPBS unpublished data). While both species of macaw forage extensively on beach almond (Henn *et al.* 2014, Villegas-Retana and Araya-H. 2017), given that the tree is not native to the western hemisphere it is possible that the beach almond serves as a supplementary, rather than primary, food source and that its phenology does not influence the movement patterns of the macaws. Alternatively, it is possible that the beach almond is serving as an essential food resource during periods of low seed production by almendro in the breeding areas. This is consistent with findings by Berg *et al.* (2007) who documented that periods of food scarcity were more highly associated with macaw abundance than periods of peak production.

Overall, our seasonal and frequent observations of GGM and the sustained presence of SM in Tortuguero National Park and the Barra del Colorado Wildlife Refuge demonstrate the integral role of the area during seasonal movements of these charismatic birds. More research, however, is necessary to document the regularity, timing, and context of the movement of these species with respect to their breeding seasons and forage availability. While many conservation actions, such as the creation and maintenance of biological corridors, seem to be positively impacting the resiliency and representation of GGM and SM across Costa Rica, more research and action are needed. For example, the installation of nest boxes could promote broader geographic and higher-density nesting of macaws (Brightsmith 2001) and continued outreach efforts could continue to curb harvesting of birds for the pet trade (Sanz and Grajal 2008). Future research should aim to determine the population size, identify routes for seasonal movements, and find key nesting areas of macaws to better inform landscape-level conservation (Dénes *et al.* 2018). Moving forward, conservation and natural resource managers should look to the Tortuguero region as an important area for supporting the recovery of *Ara ambiguus ambiguus* and *Ara macao cyanopterus*.

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Author Contributions

ESK and MH conceptualized the study. CF collected, LCW and MH curated, and LCW analysed and visualized the data. ESK and MH prepared the initial manuscript draft, and ESK and LCW contributed to reviewing and editing. ESK and CF supervised the study. All authors approved the submitted version of the manuscript.

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Appendix A. Separation distance between sites in kilometers.

	Caño Palma	Cerro	Archie Carr	San Francisco	Tortuguero
Caño Palma					
Cerro	1.380				
Archie Carr	1.848	0.759			
San Francisco	1.883	0.640	0.247		
Tortuguero	6.109	4.932	4.277	4.304	

Appendix B. The number of surveys completed at each of the five sampling sites for each year of monitoring. We considered morning and afternoon point count data as separate sampling periods for the purposes of data analysis.

	2017	2018	2019	2020	2021	Total
Caño Palma	42	82	64	68	39	295
Cerro	51	69	68	13	3	204
Archie Carr	21	65	58	9	37	190
San Francisco	62	82	12	16	35	207