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RESEARCH ARTICLE

Nest survival of a long-lived psittacid: Scarlet Macaws (*Ara macao cyanoptera*) in the Maya Biosphere Reserve of Guatemala and Chiquibul Forest of Belize

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ABSTRACT

The Scarlet Macaw (*Ara macao*) is a widely distributed parrot that has suffered reduced abundance and increased isolation in Mesoamerican populations. Understanding environmental and temporal factors that influence nest survival may assist efforts to increase annual recruitment for this species, improving population viability. We examined nest survival of Scarlet Macaws in the Maya Biosphere Reserve of Guatemala and Chiquibul Forest of Belize in 2010. Our results suggest that connecting tree canopies have the greatest negative influence on daily nest survival, reducing the probability of a nest surviving the entire nesting period from 0.89 to 0.42. This is likely due to facilitating nest access to predators. Nine of 20 nests in Belize, but no nests in Guatemala, were poached. The majority of poached nests were located in close proximity to a reservoir, which may facilitate access to nests. Based on previous estimates of nest survival required for this population to remain stable, our 2010 data suggest that the population in Guatemala could be growing, but that poaching has reduced nest survival below the threshold for population stability in Belize. Reducing habitat loss in Guatemala and nest poaching in Belize would most benefit this historically connected population.

Keywords: Ara macao, Belize, Guatemala, macaw, nest survival, parrot, poaching

Supervivencia del nido de un psitácido longevo: *Ara macao cyanoptera* en la Reserva de Biosfera Maya de Guatemala y el Bosque Chiquibul de Belice

RESUMEN

Ara macao es una especie de guacamayo ampliamente distribuida que ha experimentado una reducción de su abundancia y un aumento del aislamiento en las poblaciones de Mesoamérica. Entender los factores ambientales y temporales que influencian la supervivencia del nido puede contribuir con los esfuerzos para aumentar el reclutamiento anual de esta especie, mejorando la viabilidad poblacional. Estimamos la supervivencia del nido en la Reserva de Biosfera Maya de Guatemala y el Bosque Chiquibul de Belice en 2010. Los resultados sugieren que la conexión de las copas de los árboles tiene la mayor influencia negativa en la supervivencia diaria del nido, reduciendo la probabilidad del nido de sobrevivir durante todo el período de nidificación de 0.89 a 0.42. Esto se debe probablemente a la facilitación a los depredadores del acceso al nido. Nueve de 20 nidos en Belice, pero ningún nido en Guatemala, sufrieron furtivismo. La mayoría de los nidos afectados por furtivismo estuvieron localizados en las cercanías de una represa, lo que puede facilitar el acceso al nido. En base a estimaciones previas de la supervivencia del nido que se requiere para que esta población permanezca estable, nuestros datos del 2010 sugieren que la población en Guatemala podría estar creciendo, pero que el furtivismo ha reducido la supervivencia del nido por debajo del umbral de estabilidad poblacional en Belice. La reducción de la pérdida de hábitat en Guatemala y del furtivismo de los nidos en Belice beneficiaría enormemente a esta población históricamente conectada.

Palabras clave: Ara macao, Belice, furtivismo, guacamayo, Guatemala, loro, supervivencia del nido

INTRODUCTION

The Scarlet Macaw (*Ara macao*) is a large, secondary cavity-nester, with a distribution ranging from southern Mexico to northern Bolivia (Forshaw 2010). It is listed as a CITES Appendix I species and receives legislative protection in most countries across its distribution (Collar and Juniper 1992, CITES Secretariat 2001). However, internal and illegal trade is persistent across its range (Snyder et al. 2000, Gonzalez 2003, Dear et al. 2005, Guzman et al. 2007). The northern subspecies, *A. m. cyanoptera*, which has declined significantly, has a disjunct range between

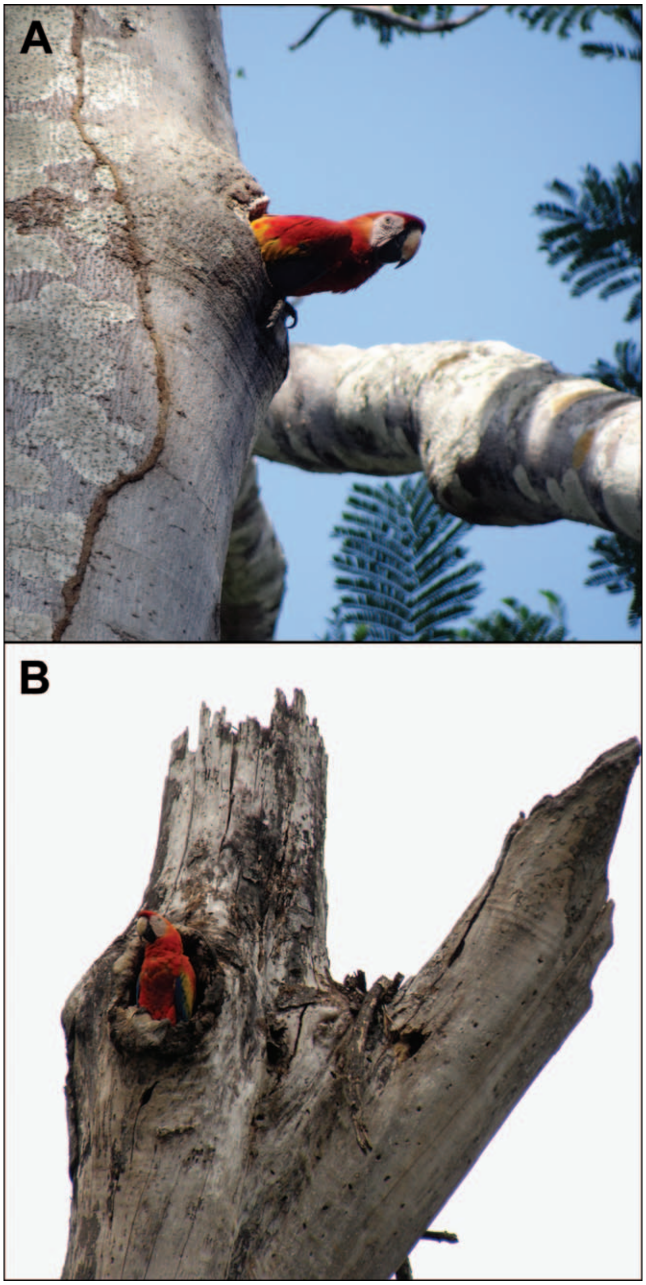

FIGURE 1. Scarlet macaws nesting in (**A**) a live tree and (**B**) a dead tree.

northeastern Nicaragua and southern Mexico. Habitat destruction and the illegal pet trade have resulted in isolated populations and reduced population viability, putting these populations at risk (Ridgely 1982, Sparks and Soper 1990, Wiedenfeld 1994, Snyder et al. 2000). The Scarlet Macaw is listed in Mexico as a species in danger of extinction (CITES Secretariat 2001), with approximately 200 breeding pairs (Iñigo-Elías 1996); it is on Guatemala's Red List of Wild Fauna, with 250–300 individuals (Eisermann and Avendaño 2006); and it is described as 'endangered' in Belize (Meerman 2005), with fewer than 250 individuals (Matola 1999). In Honduras they are reportedly extirpated from the Pacific slope, but remain numerous in the more wild and remote regions of the Caribbean slope (Ridgely 1982, Renton 2000). In Nicaragua, Martínez-Sánchez and Will (2010) report that Scarlet Macaws are rare or extirpated in the Pacific region, rare in the central highlands, and increasingly less abundant in the Caribbean region. More recent work has found them persisting in the broadleaf forests of the large rivers, Saslaya National Park, Bosawas Biosphere Reserve, and the Cosigüina Volcano area (D. Hille personal communication).

Nest failure in Neotropical birds is most commonly attributed to predation, with the addition of nest poaching for parrot species (Ricklefs 1969, Skutch 1985, Wright et al. 2001). Cavity-nesters experience lower predation rates than open-nesting species (Martin and Li 1992, Auer et al. 2007; but see Nilsson 1986). However, because they depend on preexisting cavities, nest sites may be limited (Cockle et al. 2010), and cavity-nesters may face intense inter- and intra-specific competition for nest sites (Renton and Brightsmith 2009). They are selective at multiple scales, with the degree of specificity varying across species and in some cases within species across landscapes (Monterrubio-Rico and Escalante-Pliego 2006, Cornelius 2008, Politi et al. 2009, Díaz and Kitzberger 2012). Scarlet Macaws (Figure 1) have been observed to use a wide range of nest sites in Peru, suggesting flexibility in cavity selection compared with Blue-and-Yellow Macaws (*A. ararauna*) and Red-and-Green Macaws (*A. chloropterus*; Renton and Brightsmith 2009).

Cavity and nest-tree characteristics, including visibility from the nest cavity, connecting canopy, and cavity depth, may be important factors influencing predation risk. Greater visibility from the nest may reduce adult susceptibility to predation through increased predator detection (White et al. 2006, Cockle et al. 2011, D. Brightsmith personal communication), but may increase nest predation. De Santo et al. (2002) found that successful tapaculo (Rhynocrypidae) nests were more concealed with deeper cavities than depredated cavities. Neotropical secondary cavity-nesters, including Scarlet Macaws, may prefer tall trees with little connectivity to surrounding trees (Renton and Brightsmith 2009, Cockle et al. 2010, 2011, L. Gentle personal communication, J. Meerman personal communication). This might reduce nest access of nonvolant predators and cavity competitors such as boa snakes (Boidae), tropical rat snakes (*Spilotes pullatus*), iguanas (*Ctenosaura* spp.), kinkajous (*Potos flavus*), and tayra (*Eira barbara*; Matola and Sho 2002, Vaughan et al. 2003, Koenig et al. 2007, Berkunsky et al. 2011). Cavity depth may also play an important role: Deep nest cavities are believed to reduce the chance of predation and botfly parasitism, improve thermoregulation, and increase nest reoccupation rates for macaws (Silva 1993, Berkunsky and Reboreda 2009, Cockle et al. 2011). Wiley et al. (2004) observed that deeper artificial nests reduced Pearly-eyed Thrasher (*Margarops fuscatus*) predation of Puerto Rican Parrot (*Amazona vittata*) nests. Other cavity-nesters such as Lewis's Woodpecker (*Melanerpes lewis*) also experience lower predation risk with deeper nest cavities (Zhu et al. 2012).

The probability of a nest surviving each day may increase with each additional day, resulting in a higher survival probability later in the nesting period. Nest age has been found to have a greater, positive influence on nest survival than vegetation features around the nest cavity for other cavity-nesting species (Kozma and Kroll 2010). Chalfoun and Martin (2010) suggest that behavioral adjustment, such as reduced nest visitation, occurs in nesting birds that have experienced prior nest predation events. Scarlet Macaw adults spend more time away from nests as the nesting cycle progresses (Iñigo-Elías 1996, Vaughan et al. 2009). Increasing visitation intervals for Scarlet Macaws are facilitated by a larger nestling crop, relative to other parrots and birds, and improved thermoregulation with increasing size and feathering (Silva 1993, Flammer and Clubb 1994, Vaughan et al. 2009). In addition, Scarlet Macaw chicks are better able to defend themselves as they near fledging (García Anleu et al. 2006).

Scarlet Macaws exhibit low fecundity, so even low rates of poaching and other causes of nest failure may significantly affect population viability (Boyd and McNab 2008). The Wildlife Conservation Society in Guatemala has reduced the threat of poaching to breeding Scarlet Macaws in parts of the Maya Biosphere Reserve through nest guarding. However, poaching is a substantial cause of nest failure in the Chiquibul Forest of Belize (Arevalo 2011). Parrot poaching is generally an opportunistic source of income (Pires and Clarke 2012). This is thought to be the case in Belize, where Guatemalans poach nests in addition to illegally extracting other natural resources such as xaté, the leaves of *Chamaedorea* spp. palms (Bridgewater et al. 2006). Experienced poachers have knowledge of the breeding ecology of Scarlet Macaws in the region (Arevalo 2013). A reservoir in Belize facilitates *xatero* and nest-poaching activity, especially from March to June when water levels are low enough to allow passage across exposed flats (FCD personal observation).

We hypothesized that daily nest survival rates in Guatemala and Belize would be positively related to nest attributes that reduced predation exposure of eggs and chicks, but not necessarily exposure of adults. We predicted that reduced visibility from the cavity entrance, no canopy connectivity, and deeper nest cavities would positively influence daily nest survival rates. We predicted that nest failure would be concentrated early in the nesting cycle, within 50 days after egg-laying, when adults are most active around the nest. We hypothesized that the Chalillo Dam reservoir would impose a greater risk of poaching by facilitating access to, and detection of, nesting locations. We predicted that poached nests in Belize would be closer to the reservoir than unpoached nests, and that poaching would increase as the nesting season advanced and *xateros* became more active (Adele 2010).

METHODS

Study Areas

We worked in the lowland forests of the western-central Maya Biosphere Reserve in Guatemala (17.335°N, 90.308°W) and the riparian forests of the Chiquibul Forest in Belize (16.791°N, 88.947°W; Figure 2). The Maya Biosphere Reserve is a 2.11 million ha protected area managed by Consejo Nacional de Areas Protegidas (CONAP), and is divided into three management classifications: core, multiple-use, and buffer zones (McNab and Ramos 2007). Nests in this study area were located in core and multiuse areas. Core areas are equivalent to IUCN Category Ib Protected Areas (IUCN 2012), and contain 16 human communities that have obtained temporary residence status and use of natural resources (McNab and Ramos 2007). Multiple-use areas are equivalent to IUCN Category VI Protected Areas (IUCN 2012), and are largely timber and nontimber concessions (McNab and Ramos 2007). Our study area was in tropical evergreen seasonal broad-leaved lowland forest reaching 200 m in elevation (Vreugdenhil et al. 2002). Intensive nest-monitoring and protection efforts have been conducted by the Wildlife Conservation Society, Guatemala Program, since 2003. The mean minimum and maximum temperatures are 20°C and 32°C, respectively, and the area receives 1,600 mm of precipitation annually, with a pronounced wet season from June to October (Instituto Nacional de Sismologia, Vulcanologia, Meteorologia e Hidrologia 2010).

The Chiquibul Forest comprises 167,000 ha in west-central Belize and includes the Chiquibul Forest Reserve and Chiquibul National Park, both managed by the Belize Forest Department (BFD). It is between the western slopes of the Maya Mountains, reaching a maximum elevation of 1,124 m, and the western border with Guatemala. The Chiquibul Forest Reserve was created for the management of extractive resources as well as biodiversity protection (Meerman and Wilson 2005). The Chiquibul National Park is comanaged by Friends for Conservation and Development, and was created primarily for biodiversity protection. The primary riparian watercourses of the study area drop to 300 m elevation, and have a variety of tropical evergreen seasonal broad-leaved forest, evergreen seasonal mixed submontane forest, and deciduous broad-leaved

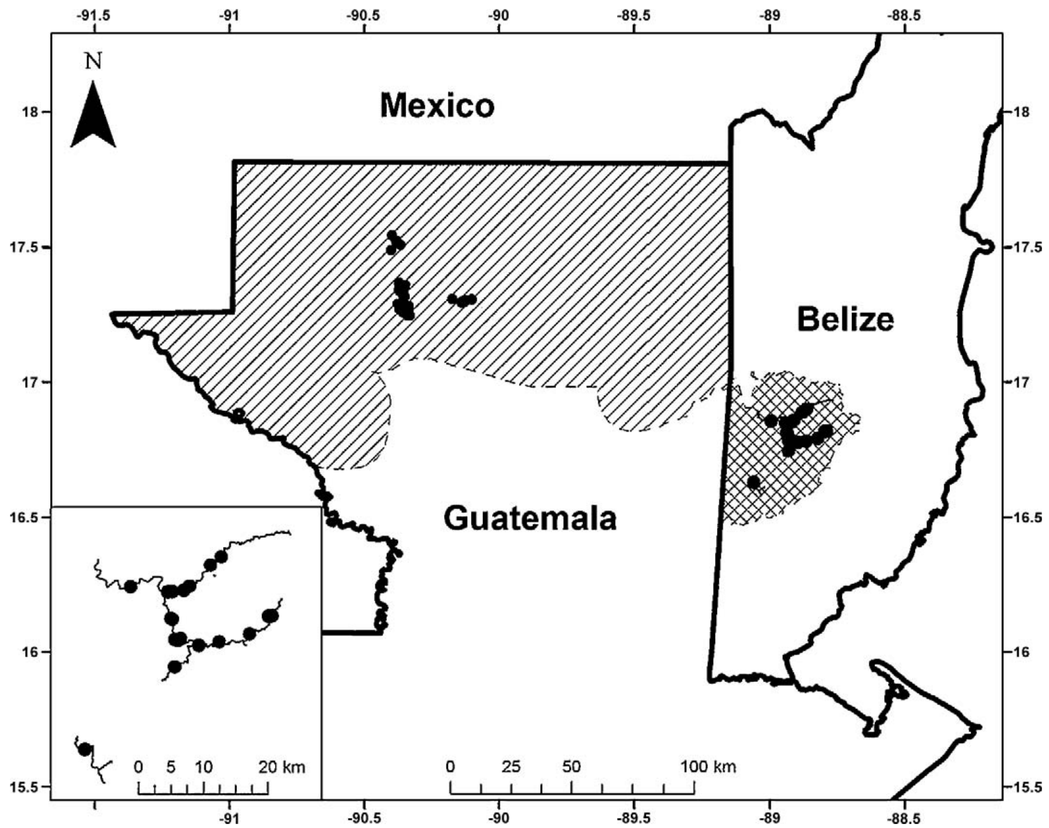

FIGURE 2. Scarlet Macaw nest sites in the two study areas: western-central Maya Biosphere Reserve in the Department of Petén, Guatemala, and the Chiquibul Forest in the Cayo District, Belize. Inset (lower left) details search areas and nests in Belize.

lowland riparian shrubland community types that vary with soil and landscape position (Meerman and Sabido 2001). Riparian areas in the Chiquibul Forest receive 2,000–3,000 mm of rainfall per year and undergo frequent flood events during the rainy season in June–December (Dubbin et al. 2006). Average minimum and maximum temperatures are 20.5°C and 31.3°C inland, and 17.7°C and 25.3°C in the mountains (Belize National Meteorological Service 2011).

Nest Searching and Monitoring

Nest searching and monitoring efforts were initiated on January 7, 2010, and terminated on August 24, 2010. In Guatemala, nest locations were known from previous monitoring efforts conducted by the Wildlife Conservation Society; nests were located using searches on foot guided by observations made from atop trees, observation towers, and overflights. Nest monitoring visits were more frequent in Guatemala; generally weekly, due to nest protection efforts, compared to every 3–4 weeks in Belize. In Belize, prior studies noted that all known successful nesting attempts occurred in floodplain habitat located along the upper Macal River and a tributary, Raspaculo Branch in the Chiquibul Forest (Barlow and Caddick 1989, Mallory 1994, Renton 1998, Renton 2006). A constant search effort was utilized in the primary riparian areas of the Chiquibul Forest that were accessible by kayak. Weekly 5-day searching and monitoring efforts rotated among four riparian areas: upper Macal River, Raspaculo Branch, Monkeytail Branch, and Chiquibul Branch. Parts of the Macal River and Raspaculo Branch are flooded as part of a hydroelectric dam reservoir. The rotating search schedule may have resulted in missed nesting attempts, especially in Belize, that failed early in the nesting cycle. Individuals or pairs of Scarlet Macaws that were encountered were observed until they flew out of sight or revealed a nest cavity. When visiting occupied nests, surrounding areas were scanned from the nest trees for additional nests, a type of adaptive sampling (Thompson and Seber 1996), based on the assumption that nest clustering could occur due to patchy floodplain habitat (Meerman and Sabido 2001).

Nest visits took place during each of the rotating searching and monitoring intervals until the nesting cycle completed or failed. The single-rope climbing technique was used to access nests (Houle et al. 2004), and the number of eggs and/or chicks was recorded at each visit. In Guatemala the number of visits per nest ranged from 2 to 14, and in Belize from 2 to 6. Nestling age was estimated by measuring the length of the unflattened wing chord and interpreting the growth curve data from Iñigo-Elías (1996) and Renton (1998), or by using photographs documenting the development stage of nestlings when retrieving chicks was not possible. Since incubation ranges from 22 to 28 days (Silva 1993, Vaughan 2002), we used 25 days prior to the estimated date of hatching to estimate the date of egg-laying. Nestlings require about 65–75 days following hatching to reach the fledging stage (Iñigo-Elías 1996, Vaughan 2002). Fledging dates were assigned ahead of time based on hatching dates, and we attempted to revisit the nest close to the approximated fledging date to count the number of young. Number of fledged chicks and fledging date were recorded. For nests of unknown age that failed prior to eggs hatching ($n = 7$) a mean egg-laying date was assigned, using half of the mean days required prior to hatching. An age threshold was used to estimate fledging success, due to the variability in the time required to fledge and the long interval lengths between nest visits in Belize (C. Vaughan personal communication, D. Brightsmith personal communication). Nests where chicks were not seen after 60 days following hatching that lacked signs of poaching or predation were presumed to have survived. By this age, chicks are sufficiently large enough to defend themselves against avian predators (García Anleu et al. 2006). For nests that failed, date and cause were documented if possible. Evidence of predation can include broken eggshells with the contents consumed, partial remains of chicks, and feathers or hair from a potential predator. Poaching is evident from fresh scars on a nest tree trunk made by climbing spurs, or the cutting down or burning of a nest tree. In cases in which the cause of failure was not obvious, it was recorded as unknown.

Nest Habitat Data Collection

We collected nest habitat data at each nest either prior to or at the end of the breeding season in Guatemala and at the end of the breeding season in Belize. Habitat characteristics measured included: presence of adjacent tree canopy touching nest tree canopy (yes or no), cavity entrance width (cm), cavity depth below entrance (cm), interior basal cavity area (cm^2), and depth of the tree cortex (cavity wall) at the entrance (cm). Front visibility (m^2) from the nest cavity entrance was measured using methods described by White et al. (2006). This is an aerial calculation based on distance to the nearest obstruction for five 45° equiangular compass bearings, beginning with the compass azimuth facing away from the nest cavity entrance, and followed by two compass bearings rotating in a clockwise direction and two rotating counterclockwise from the cavity entrance. The area was then calculated for the four triangles. For nests located in Belize, the distance to the Chalillo Dam reservoir shoreline at maximum capacity was calculated using ArcGIS 9.3 (ESRI, Redlands, CA, USA).

Statistical Analyses

We estimated daily nest survival rate for 28 nests that were successful or failed due to natural mortality. Of the 43 nests that were monitored in 2010, 9 were excluded due to poaching in Belize, and 6 were excluded due to a lack of habitat data collected: 4 in Guatemala due to unsafe access to the nest trees following the breeding season and 2 in Belize due to tree instability. We were unable to climb 1 of the 9 poached nests. We developed 10 a priori models, including global and null models, and used the logistic-exposure method (Rotella et al. 2004, Shaffer 2004) to examine the effects of canopy connectivity, cavity depth, amount of front visibility, and nest age on daily nest survival. Logistic exposure is a likelihood-based method that allows visitation intervals to vary among observations and makes no assumptions about when nest failure occurs between observations. Estimators are more realistic, more precise, and less biased than estimators from the Mayfield method (Shaffer and Thompson 2007). The simplest model, the intercept-only null model, assumed constant daily survival across all nests. An information-theoretic approach using Akaike's Information Criterion corrected for small sample size ($\mathrm{AIC_c}$) was employed to rank models (Burnham and Anderson 2002). The effective sample size was calculated using the method described by Rotella et al. (2004), in which each day survived by each nest is added to the effective sample size and each interval that ends in failure adds one to the effective sample size. The probability of surviving the entire nesting cycle is estimated by exponentiating the daily survival rate (DSR) by the number of days required from incubation to fledging; DSR^{100} for Scarlet Macaws. This assumes a constant DSR throughout the nesting cycle.

A goodness-of-fit test was utilized to examine how well the global model for daily nest survival fit the data (Shaffer 2004). A Pearson correlation test was performed to examine correlations among all model variables. Models with $\Delta\mathrm{AIC_c}$ values ≤ 2 were considered to have substantial empirical support (Burnham and Anderson 2002). Akaike's weights (w_i) were used to evaluate the relative weight of evidence in favor of each model. Odds ratios are often more intuitive than coefficients and were used to approximate the factor of increase or decrease in the daily survival rate by the units of each variable (Hosmer and Lemeshow 2000).

We used an independent, one-tailed t-test for the Belize dataset to examine whether poached nests were closer to the Chalillo Dam reservoir than unpoached nests.

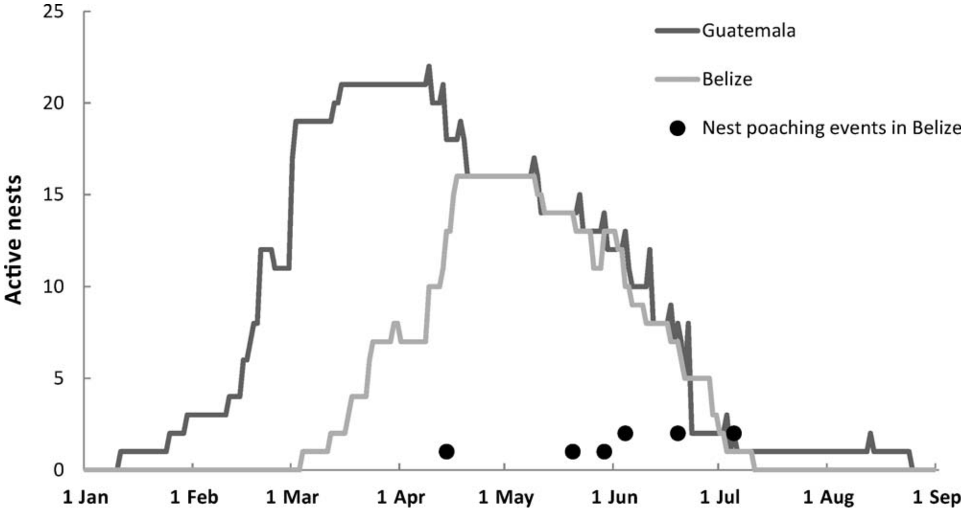

FIGURE 3. Number of active Scarlet Macaw nests throughout the nesting season in 2010 in the Maya Biosphere Reserve of Guatemala and Chiquibul Forest of Belize, and poaching events in Belize.

A post-hoc analysis was performed to examine the effect of nest age on daily survival rate. All 43 nests that were monitored in 2010 were included in the dataset. This is different than the a priori daily survival rate analysis as many of those nests ($n = 15$) were excluded due to a lack of nest characteristic data or poaching. For the three nests in Belize that could not be climbed (this includes one of the poached nests), nesting behavior (i.e. the reluctance of females to leave the nest) led us to assume that incubation was under way. This may have resulted in underestimating the age of these nests. Constant daily survival rates were calculated for Guatemala, Belize, and across both countries using an intercept-only model across all 43 monitored nests. All models were run using the PROC GENMOD procedure in SAS version 9.2 (SAS Institute 2008).

There were a few aspects of our study that might have introduced bias into the analyses, including differences in visitation intervals between countries, probability of nest detection, and elimination of nests due to accessibility. Nests in Guatemala were visited 3–4 times more frequently than nests in Belize. Longer visitation intervals in Belize may have resulted in: 1) a higher percentage of nests that failed early in the nesting cycle before they were found; and 2) undetected occurrences of nest failure late in the nesting cycle, possibly introducing bias through increased daily nest survival rates. In addition, long visitation intervals may have resulted in truncation of the actual values of eggs laid and chicks present, especially in Belize. This would also affect time-related variables such as nest age. The elimination of nests from the dataset due to nest-tree instability may have introduced some bias into the analysis by reducing an already small dataset and removing a particular nest type (nests in dead trees).

RESULTS

We monitored 43 active nests in 2010, 23 in Guatemala and 20 in Belize. All but 3 nests, 1 in Guatemala and 2 in Belize, were found during the incubation period. The 3 nests not found during incubation were located within 3 weeks following hatching. We found the majority of nests in live trees; 7 of the 43 were in dead trees. Scarlet Macaws in Guatemala almost always used *Acacia glomerosa* ($n = 22$) trees for nesting. In Belize they generally used *Schizolobium parahyba* ($n = 15$). These species are both tall, emergent Fabaceae softwoods. Vaughan (2002) notes that the branches of softwood trees frequently break off, creating potential nest sites. We found this to be true, as most nest cavities apparently formed after branches broke off and then holes rotted in either the tree trunk or in a large branch. Nests in both countries occurred within narrow elevation gradients; 60–160 m in Guatemala, and 415–543 m in Belize.

The nesting season in Guatemala began earlier and was longer than that in Belize. Egg-laying was initiated on January 11 in Guatemala, the number of active nests peaked on April 9, and the nesting season ended on August 24 (Figure 3). In Belize, egg-laying was initiated on March 4, the number of active nests peaked between April 17 and May 9, and the nesting season ended on July 10. Overall, 44% of monitored nests survived, 61% in Guatemala and 25% in Belize (Table 1). In Guatemala, 45% of chicks ($n = 49$) survived to fledging, compared with 33% ($n = 24$) in Belize (Table 1).

The daily nest survival rate from an intercept-only model across all nests, based on an effective sample size of 2541 exposure days, was estimated to be 0.990 ± 0.003 (SE), resulting in a 0.37 (95% CL = 0.23–0.52) probability

TABLE 1. Reproductive effort at Scarlet Macaw nests that were climbed and all nests that were monitored in the Maya Biosphere Reserve in Guatemala and Chiquibul Forest of Belize in 2010.

Nest parameter	Guatemala	Belize	Total
Nests climbed	23	17	40
Mean (SE) clutch size	3.25 (0.05)	2.41 (0.04)	2.83 (0.02)
Hatching success	0.63	0.59	0.61
Mean (SE) brood size	2.13 (0.04)	1.41 (0.05)	1.78 (0.02)
Chick survival (%)	45	33	41
Mean (SE) fledglings per nest	0.96 (0.04)	0.40 (0.04)	0.70 (0.02)
Mean (SE) fledglings per successful nest	1.57 (0.03)	1.60 (0.11)	1.58 (0.03)
All nests	23	20	43
Successful nests	14	5	19
Nest success (%)	61	25	44

of surviving the roughly 100-day nesting cycle. Poaching was the greatest cause of nest failure in Belize (Table 2). Predation was the next-greatest cause of failure, followed by structural failure and adult mortality; the latter was likely an underestimate as determined by adult carcasses found at one nest site. More confirmed predation events occurred in Belize than in Guatemala. However, there was uncertainty about the cause of failure of six nests in Guatemala. For daily nest survival model analysis, the global model exhibited adequate fit ($\chi^2_8 = 7.36$, $P = 0.50$). No variables in our models were found to be correlated ($r \geq 0.70$). The top model included connecting canopy (CC), front visibility (FV), and cavity depth (CaD; Table 3). There was a moderate amount of model uncertainty given that the top five models all had $\Delta \text{AIC}_c \leq 2$. All top competing models included connecting canopy, and 3 of the top 5 models included cavity depth and front visibility. After model-averaging across all models and calculating unconditional standard errors, only the connecting canopy parameter was significant, and daily survival rate increased when nest trees lacked a connecting canopy (Table 4). Arnold (2010) suggests eliminating variables with uninformative parameters when using a limited model set. Using the model with only connecting canopy, daily survival rate decreased from 0.999 to 0.991 when a connecting canopy was present. If the daily survival rate was exponentiated for the full nesting cycle, then the probability estimate for surviving the entire nesting period was 0.423 with a connecting canopy and 0.890 without a connecting canopy.

TABLE 2. Causes of Scarlet Macaw nest failure in the Maya Biosphere Reserve of Guatemala (n = 23) and the Chiquibul Forest of Belize (n = 20).

Cause of failure	Guatemala	Belize	Total
Poaching	0	9	9
Predation	2	3	5
Adult mortality	1	0	1
Structural failure	0	2	2
Unknown, chick missing	4	1	5
Unknown, chick dead in nest	2	0	2

TABLE 3. Daily nest survival models for 28 Scarlet Macaw nests monitored in the Maya Biosphere Reserve of Guatemala and Chiquibul Forest of Belize in 2010 (effective sample size = 2541). CC = connecting canopy, CaD = cavity depth, FV = front visibility, age = nest age. Models were ranked based on the difference in Akaike's Information Criterion adjusted for small sample size (ΔAIC_c) and model weight (w_i). K is the number of model parameters and Dev is the deviance.

Model	K	Dev	ΔAIC_c	w_i
5.590 + 2.552(CC) − 0.010(CaD) − 0.006(FV)[a]	5	62.790	0.000	0.28
5.125 + 2.600(CC) − 0.000(FV)	4	65.331	0.533	0.21
5.193 + 2.053(CC) − 0.010(CaD)	4	65.532	0.734	0.19
5.909 + 2.546(CC) − 0.010(CaD) − 0.000(FV) − 0.006(Age)[b]	6	62.161	1.381	0.14
4.752 + 2.002(CC)	3	68.207	1.403	0.14
5.578[c]	1	76.635	7.831	0.01
5.959 − 0.010(Age)	2	74.712	7.911	0.01
FV CaD	3	74.066	9.270	0.00
5.712 − 0.000(FV)	2	76.413	9.612	0.00
6.132 − 0.000(FV) − 0.010(Age)	3	74.422	9.626	0.00

[a] AIC_c value of the best model = 63.097.
[b] Global model.
[c] Null model.

Nine of the 20 nests (45%) in Belize were poached between April 14, 2010, and July 10, 2010. The majority of these poaching events (77%) occurred in the final third of the nesting season (May 28 to July 10). The mean age of poached chicks was 19.6 ± 8.6 days ($n = 8$); one poaching event occurred prior to hatching. Nests that were poached were closer (772 ± 567 m, $n = 9$) to the reservoir than unpoached nests (6,734 ± 2,117 m, $n = 11$; $P < 0.01$).

Our exploratory analysis examining the effect of nest age on nest survival using the entire dataset of 43 nests

TABLE 4. Model-averaged parameter estimates for models of Scarlet Macaw nest survival in Belize and Guatemala in 2010. The connecting canopy parameter estimate does not bound zero, indicating strong support for this variable. Nests in trees having a canopy touching the canopy(ies) of adjacent tree(s) have a higher probability of failure. The model intercept is 5.360 ± 0.629.

Parameter	Estimate	Unconditional standard error	95% confidence interval	Odds ratio
Connecting canopy	2.398	0.903	0.628 to 4.168	11.003
Cavity depth	−0.010	0.006	−0.021 to 0.001	0.990
Front visibility	−0.003	0.003	−0.008 to 0.003	0.997
Nest age	−0.007	0.008	−0.022 to 0.008	0.993

revealed that nest age had a positive effect on daily survival rate across both countries ($\text{logit}(\hat{S}) = 2.25 + 0.04[\text{Nest Age}]$), with the age parameter estimate not bounding zero (95% CL = 0.02–0.05). The daily survival rate increased from 0.908 on day 1 to 0.997 on day 100.

DISCUSSION

Cavity and Tree Characteristics

The Scarlet Macaw is a long-lived psittacine that is found increasingly in small, isolated populations across the northern extent of its range. Most studies examining the effects of habitat characteristics on nesting psittacines have focused on nest-site selection and not nest survival or reproductive success. Few studies on Neotropical cavity-adopters or parrots have directly addressed the effects of connecting canopy or visibility on nest-site selection or nest survival. Understanding the factors that influence nest survival may assist efforts to increase annual recruitment. The results of our study suggest that Scarlet Macaw nest survival in Guatemala and Belize is most strongly and negatively influenced by the presence of connecting canopies. Nests in trees lacking a connecting canopy experienced a two-fold higher probability of surviving the entire nesting cycle. Lack of a connecting canopy should promote nest survival, as it reduces access to the cavity by nonvolant predators. Similarly, Black-billed Parrot (*Amazona agilis*) nest survival increased with decreasing canopy connectivity (Koenig et al. 2007).

Nest trees in Guatemala were emergent, whereas trees utilized for nesting in Belize were a combination of isolated trees in floodplains as well as emergent trees on the riparian forest edge (C. Britt personal observation). Other studies have noted the emergent nature or isolation of nest trees in relation to the surrounding vegetation, but have not linked this to nest survival or nest-site selection. Chestnut-fronted Macaws (*Ara severa*), Scarlet Macaws, and Red-and-Green Macaws in Peru were observed to use nest cavities in emergent trees isolated from surrounding vegetation (Brightsmith 2005). Blue-and-Yellow Macaws in Peru used palms that rose above and away from surrounding and overhanging vegetation (Brightsmith 2005, Brightsmith and Bravo 2006), and Blue-fronted Parrots (*Amazona aestiva*) nesting in the Pantanal of Mato Grosso do Sul, Brazil, utilized nests in open areas (Seixas and Mourão 2002).

Emergent or isolated canopies associated with decreased canopy connectivity may be associated with increased front visibility. Greater visibility may facilitate evasion by parents, allowing them to escape predation, but may also lead to conspecific cavity competition which can lead to nest failure (Renton and Brightsmith 2009). Interspecific cavity competitors such as Barred Forest-Falcons (*Micrastur ruficollis*), Bat Falcons (*Falco rufigularis*), and Keel-billed Toucans (*Ramphastos sulfuratus*) were observed near failed nests in Belize (Iñigo-Elías 1996, Vaughan et al. 2003). There were several nests in our study with unknown causes of failure that resulted in chicks found missing ($n = 5$) or dead in the nest ($n = 2$), which may have been due to predation for the former, and cavity competition or starvation resulting from abandonment in the latter, cases. The model-averaged front-visibility estimate suggested a negative effect on daily nest survival; however, the confidence interval bounded zero and a larger sample size may be required to increase precision.

In other cavity-nesting species, factors influencing nest-site selection were not necessarily the same as those affecting nest survival (Zhu et al. 2012). Díaz and Kitzberger (2012) note that factors other than nest characteristics may be important to the reproductive success of Austral Parakeets (*Enicognathus ferrugineus*). Improved foraging habitat (Wightman and Germaine 2006) and maximum daily temperature (Hollenbeck et al. 2011, Newlon and Saab 2011) may be more important to predicting reproductive success than nest-cavity characteristics.

Cavities maintain a stable microclimate (Wiebe 2001, C. Britt personal observation) and, depending on structure, protect eggs and chicks from inclement weather (Radford and du Plessis 2003) as well as predation. Prior studies suggest that increased cavity depth should result in increased reproductive success. Our results suggest that increasing cavity depth may have a small, but surprisingly, negative, impact on nest survival. However, our parameter estimate for cavity depth exhibits too much uncertainty to be conclusive. The result of our exploratory analysis with all nests included suggests that the risk of nest failure decreases over the nesting cycle. The apparent lack of significance of this variable in our main analysis of daily survival rate with all variables included may be the result of a lower sample size (15 nests were excluded due to nest poaching and inaccessibility) and differing visitation intervals between countries.

Nest Poaching

Nest poaching was the primary cause of nest failure in the Chiquibul Forest of Belize, where nests are afforded little to no management protection. Distance of the nest to the Chalillo Dam reservoir appeared to have an effect, as 7 of the 9 poached nests were located in the immediate vicinity of the reservoir. The riparian vegetation along the Chalillo Dam reservoir is submerged for a portion of the year. Inundation has killed many of the trees and other vegetation, leaving large stands of snags and increasing the openness and visibility in many areas adjacent to the reservoir (C. Britt personal observation). Semiopen habitats have been shown to be more conducive to parrot poaching (Pires and Clarke 2011).

Nest poachers are generally opportunistic and, in Belize, are xateros operating illegally in the Chiquibul Forest and reportedly selling chicks in Guatemala for 2,400 quetzales, or about $185 USD (Guzman et al. 2007, Adele 2010, Pires and Clarke 2012, D. Chan personal communication). This is a significant amount of money relative to the average gross income in Guatemala of $2,650 USD (World Bank 2010). Poachers utilize an extensive trail system moving west–east from the Guatemalan border deep into the Chiquibul Forest (D. Chan personal communication, C. Britt personal observation). Many of these trails cross the Chalillo Dam reservoir and large camps are located near the reservoir as well (C. Britt personal observation). The thick riparian vegetation formerly found around the reservoir has diminished due to repeated flooding, leaving bare or grassy flats during periods of low water in the dry season (L. Gentle personal communication, C. Britt personal observation).

Conservation Concerns

The northern populations of the Scarlet Macaw are threatened with extinction. Recent genetic analysis of individuals in Mexico, Guatemala, and Belize suggests that they originated historically from a single genetic population (K. Schmidt personal communication). However, Scarlet Macaws in Belize are now considered isolated from individuals found in Guatemala and southern Mexico (Rodas 2002, reviewed by McReynolds 2005) and gene flow is now restricted between these two areas (K. Schmidt personal communication). Poaching has reduced recruitment and has likely resulted in unstable populations, weighted toward older individuals, in all three countries (Boyd and McNab 2008, Arevalo 2011). Long-lived cavity-nesters are able to persist despite nest failure, masking the effects of habitat alteration and declining productivity (Marsden and Pilgrim 2003). An estimated low population size, obligate secondary-cavity-nesting strategy, and slow life history increase susceptibility to anthropogenic threats, which makes increasing current recruitment an important component of maintaining population viability (Eisermann and Avendaño 2006, Monterrubio-Rico and Escalante-Pliego 2006, Boyd and McNab 2008).

The two greatest threats to Scarlet Macaws in Guatemala and Belize are habitat loss and poaching. The nests in the western part of the Maya Biosphere Reserve are directly and indirectly threatened by high levels of deforestation and wildfires (Boyd and McNab 2008, Hughell and Butterfield 2008). Communities in and around the Maya Biosphere Reserve utilize a large number of forest products (Mutchnick and McCarthy 1997). Selective logging can lead to a reduction of nest-site availability (Marsden and Pilgrim 2003). Fragmentation caused by human encroachment may lead to increased nest predation (Chalfoun et al. 2002, Tewksbury et al. 2006). Deforestation in Belize is less of a threat; protected areas have largely been shielded from deforestation in the past 30 years (Cherrington et al. 2010). The greatest habitat threat in Belize resulted from the creation of a reservoir in 2005, which impacted the quality of a portion of the known breeding habitat as well as increased poaching susceptibility.

A population viability analysis for Scarlet Macaws, based on available data and expert input, was conducted in 2008 for the subpopulations found in Guatemala, Belize, and Mexico (Boyd and McNab 2008). This analysis determined that an estimated nest survival rate of 0.32 would result in a stable population. However, there was acknowledged uncertainty regarding size, age structure, distribution, and connectivity of the subpopulations. Our nest survival data from 2010 suggest that the Scarlet Macaw subpopulation in Guatemala has a higher nest survival rate than the estimated critical nest survival rate, but that the subpopulation in Belize does not. Without poaching, the nest survival rate for the subpopulation in Belize in 2010 could have been as high as 0.55. It is likely that nesting sites exist in more isolated areas away from the major riparian areas in the Chiquibul Forest. Missing these areas could bias the nest survival rates, making them artificially low. In addition, other aspects of the Scarlet Macaw annual cycle may differ between the Guatemala and Belize populations, also influencing population viability. What is clear is that without intensive enforcement capacity in the protected areas of Guatemala and Belize, long-term conservation of the Scarlet Macaw will continue to be a concern.

Despite the limitations of our study, there are several worthwhile recommendations for stakeholders involved in Scarlet Macaw conservation in these areas. In an intensive management program, reduction of connecting canopy would likely reduce nest accessibility to nonvolant nest predators and some cavity competitors. Amount of front visibility from the nest and cavity depth may also play a role in nest survival, but the level of impact is uncertain. Future studies should look more carefully at the effects of these two characteristics on nest survival to identify potential thresholds before making nest-site modifications. Nest protection has been shown to have a positive effect on parrot nest success, and such measures need to be deployed in Belize (Pain et al. 2006). These measures should concentrate on maintaining a continuous protection presence along the Chalillo Dam reservoir. At a minimum, protection efforts should occur from the peak of the Belize breeding season in early May and continue through to the end of the nesting period.

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