



Evaluating management strategies in the conservation of the critically endangered Blue-throated Macaw (*Ara glaucogularis*)



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ABSTRACT

We model the dynamics of the remaining wild population of the Blue-throated Macaw (*Ara glaucogularis*), a critically endangered and Bolivian endemic species exposed to different management strategies. The model becomes a tool to quantify how effective management actions may be. We construct a birth-pulse, post breeding census, deterministic, stage structured projection matrix model to describe the population dynamics. The model shows that population growth is sensitive to changes in the probability of survival in the adult stage, followed by changes in fertility. We describe the long-term behavior of the population as result of the combination of the maternity function and the nestlings' survival probability. Under the scenarios of increasing population, the number of years that are necessary to double the current wild population varied between 33 and 215 years without reintroduction, and between 7 and 46 years if 50 adult macaws are reintroduced ten years later since the simulation starts. Stakeholders of the Blue-throated Macaw Conservation Project may profit from a simple graphical tool based on this model for management decision making. By knowing the adult population size and the number of hatched eggs at the beginning of each breeding season, the field team could assess the necessary effort on nestlings' management to increase the chances of a positive population growth. Evaluating beforehand the impact of management actions on Blue-throated Macaws could contribute to the improvement and effectiveness of conservation actions on the critically endangered Blue-throated Macaw population.

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1. Introduction

Macaws are the most endangered group of the Psittacidae family, counting one extinct species, three critically endangered ones. Habitat loss, trade and the hunting for indigenous ornamental feathers dresses are the main causes of macaws' population decline (Snyder, 2000; Birdlife International, 2016). More than 50% of macaw species are included in the Red List as Endangered, Vulnerable, or Near Threatened species (Birdlife International, 2016). Rediscovered in the savannahs of Bolivia in 1992, the Blue-throated Macaw *Ara glaucogularis* is the last critically endangered macaw still sustaining a wild population (Birdlife International, 2016; Forshaw, 1989; Hesse and Duffield, 2000).

The wild population of the Blue-throated Macaw is unlikely to count more than 115–125 individuals (Birdlife International, 2016). A number of conservation actions aimed to recover the wild pop-

ulation were conducted during the last 15 years. However, our knowledge of the species' biology is limited to descriptions and estimations of range, habitat use, population size, and some basic reproductive parameters, recently described (Hesse and Duffield, 2000; Yamashita and Barros, 1997; Herrera et al., 2007; Berkunsky et al., 2014).

The conservation initiatives on the Blue-throated Macaw focus on actions aimed at providing long-term solutions (Berkunsky et al., 2014). As it occurs in many small populations, the limited number of individuals is one of the most serious threats, and all the efforts are addressed to boost the reproductive output by managing the wild population, and to reinforce it by reintroductions of captive-bred individuals. How effective these management actions will be, must be related to how precisely current threats and limiting factors, such as nest predation, nest flooding, brood reduction and nest site availability (Berkunsky et al., 2014; Kyle, 2006), can be identified. These actions include the protection of natural nests, the provision and protection of nest boxes, the use of defenses against predators and drainage systems for the boxes, and the hand-feeding of nestlings during first weeks of life (Berkunsky et al.,

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2014). Although the relative effectiveness of management actions is known, yet these were never analyzed in the global context. As part of a management strategy, knowledge of the impact and scope of each action facilitates decision-making and optimizes resources for conservation.

Modeling results in an effective tool for quantifying how effective management actions may be, and can help to better understand how accurately the current threats and limiting factors are being identified (Noon and Sauer, 1992; Simons, 1984). Strem (2008) developed a demographic model of the Blue-throated Macaw population in 2008 conducting a population viability analysis (PVA) using individual-based (VORTEX 9.72) and cohort-based (RAMAS GIS 4.0) programs. The accumulation of new data and plans for reintroduction since 2008 indicate that it is time to reassess the population and conservation projects (Berkunsky et al., 2014). Deterministic models can be a useful and simple tool for the management of endangered species (Caswell, 2001). A small number of input variable still providing good estimates of the effects of anthropogenic perturbations on species near the threshold of extinction. Also it can provide insight into the potential consequences of threatening processes and highlight the urgency with which management authorities need to act (Otway et al., 2004).

In this work we model the dynamics of the wild Blue-throated Macaw population under different management strategies. By quantifying the impact of management actions on Blue-throated Macaws we hope to contribute to the improvement and effectiveness of Blue-throated Macaw conservation projects and measures.

2. Materials and methods

2.1. Study site

The Llanos de Moxos is a 160,000 km² expanse of seasonally inundated savannahs in Northern Bolivia, interspersed with a complex mosaic of forest islands and riverine gallery forests, occupying the extremely flat Beni-Mamore-Itenez basin in Southwest Amazonia, located between the Precambrian Shield to the East and the Andes to the West and South (Forshaw, 1989). The landscape is dominated by flat, low-lying areas, which are seasonally inundated and covered by completely open treeless savannah (Langstroth, 1996). Forest islands are scarce and restricted to raised areas (mounds) which are sufficiently elevated to escape annual flooding. Most forest islands are eroded relics of natural levees or terraces of abandoned river channels, and therefore constitute fragments of former gallery forest (Hanagarth and Sarmiento, 1990).

2.2. Blue-throated Macaw's biology and management

The Blue-throated Macaw is a critically endangered parrot, endemic of Llanos de Moxos (Jordan and Munn, 1993), throughout a geographic range of 2508 km² in Beni Department, Bolivia (Hesse and Duffield, 2000). The habitat availability is enough to support a large population of macaws, and there is no evidence of limiting resources for the species, at least at these low numbers (Hesse and Duffield, 2000; Berkunsky et al., 2014; Strem, 2008).

The species has a monogamous mating system (Snyder, 2000; Forshaw, 1989). In captivity, an individual reaches sexual maturity, on average, at the age of five years (Bueno, 2000; Voss, 2005). In the wild, the breeding season of Blue-throated Macaws begins during the dry season (August) and extends over the rainy season, lasting until February (Berkunsky et al., 2014). In the wild, clutch size varies from 1 to 3 eggs, the latter being most common. Eggs are laid at 1–2 day intervals, incubation period is 25–26 days, and nestlings fledge approximately 90 days after hatching (Berkunsky et al., 2014). Data on sex ratio in the wild are scarce; neverthe-

Table 1

Number of counted pairs and individuals per year and median of the monitored population of Blue-throated Macaw for the period 2004–2011 by The World Parrot Trust in Beni, Bolivia.

	2004	2005	2006	2007	2008	2009	2010	2011
Pairs laying eggs	6	6	7	10	2	8	4	3
Successful pairs	3	1	6	6	2	8	4	2
Hatched eggs	3	1	8	13	4	16	10	3
Fledglings	2	1	6	10	0	9	3	2
Juveniles and adults	50	60	60	80	65	70	70	70

less, the sex ratio (males/females) in the Loroparque Fundación, the largest captive population in the world counting some 150 individuals, is close to 1:1 (Bueno, 2000).

Currently, there is no data on the mean lifespan of Blue-throated Macaw in the wild. We took into account the value reported by Strem (2008), who estimated it to be at least 40 years. Because there is no evidence to suggest a post-reproductive stage, age of last reproduction and maximum age were assumed to be the same.

The wild Blue-throated Macaw population is estimated to fall between 115 and 125 individuals. At least 16 breeding pairs were identified and followed over 8 years. During this study period there were no new adult pairs recruited into the breeding population. Table 1 summarizes data collected during eight consecutive breeding seasons from 2004 to 2011 (Berkunsky et al., 2014; Kyle, 2006). The variables measured were: numbers of adults and juveniles, breeding and successful pairs, hatched eggs and fledglings per nest. Each year, between 2 and 10 pairs laid eggs, with a median of 6 pairs. They produced between 0 and 10 fledglings, with a median of 2.5 fledglings.

Long term conservation management is in place for the Blue-throated Macaw in Beni, Bolivia since 2000 (Hesse and Duffield, 2000). To reduce nesting failure, drainage holes or roofs were installed in all known nests prone to flooding. Other actions aimed at avoiding nest failure included passive and active anti-predator defenses. Passive defenses are metal flashing wrapped around tree trunks and branches pruned back from cavities to abate climbing predators. Active defenses involve a high level of daily monitoring by volunteers. Most of the defenses seem to be effective given that no nests have been flooded since 2008, and that 2010 was the first year since the beginning of Blue-throated Macaw nest monitoring with no recorded predation.

The conservation project also provided nest boxes which have a good drainage and could be placed to safer positions. However, it takes time for Macaws to get used to nest boxes, since until 2014 only five pairs had used nest-boxes in fourteen different attempts.

To avoid brood reduction, the project monitors nests in a daily basis, identifying nestlings that need a boost, and helping them by hand-feeding. Since 2007, thanks to this intervention, no nestlings have died because of brood reduction and the average number of fledglings per nest has increased from one to two.

Another management action has been moving individuals who are in captivity to a Wildlife's Custody Center in Sachojere, Beni, Bolivia. Up to date, six individuals have already been recovered, whose final destination will be their reintroduction in Llanos de Moxos to strengthen existing populations. In a first stage, at least 50 individuals are expected to be reintroduced.

2.3. Matrix model development

We used a birth-pulse, post breeding census, deterministic, stage projection matrix model to describe the dynamics of the total population of the Blue-throated Macaw as proposed by Caswell (2001). The equation describing this model is of the form: $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$, where vector $\mathbf{n}(t)$ gives the population in each stage at time t and \mathbf{A} is a Lefkovich projection matrix.

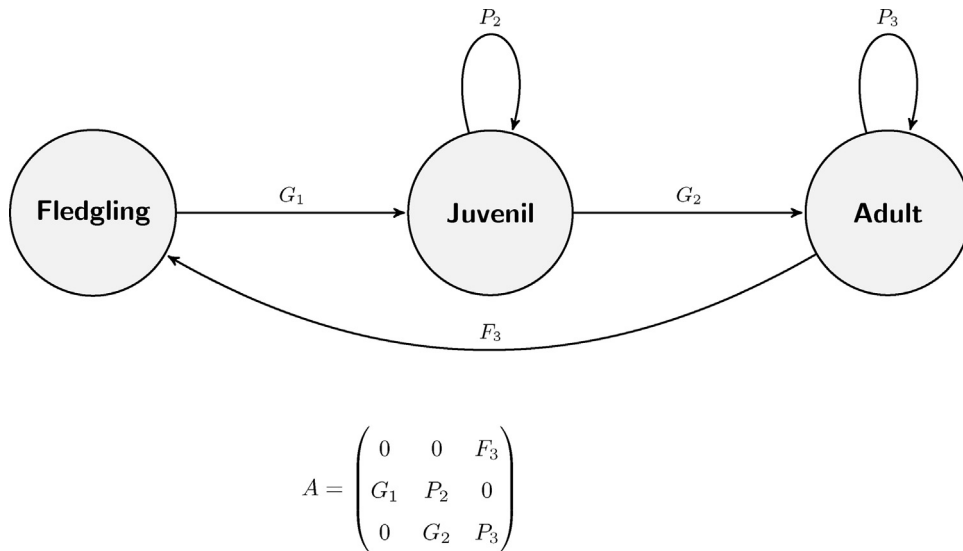


Fig. 1. Life cycle graph and the corresponding Lefkovich population matrix for the Blue-throated Macaw in Beni, Bolivia considering three stages: fledgling, juvenile and adult; and vital rates: permanence (P), growth (G) and fertility (F).

The Blue-throated Macaw population was modeled considering three biologically defined stages with a projection interval (time from t to $t + 1$) of 1 year: (1) fledglings, (2) juveniles and (3) adults. The population projection matrix parameters (i.e. vital rates) are permanence (P), growth (G) and fertility (F). P_i is the probability that an individual in stage i (at time t) will survive and remain in stage i (at time $t + 1$), G_i is the probability that an individual in stage i (at time t) will survive and grow to stage $i + 1$ (at time $t + 1$), and F_i is defined as the number of offspring in time $t + 1$, per individual in stage i at time t . In Fig. 1 it is showed the life cycle graph and the corresponding Lefkovich population matrix for the Blue-throated Macaw in Beni, Bolivia.

The projection matrix A is primitive (i.e. A is nonnegative and there is a k such that A^k is positive) and it satisfies the hypothesis of the Strong Ergodic Theorem since the population is ergodic, meaning that its long-term behavior is independent of its initial state (Caswell, 2001; Cohen, 1979). Considering that λ_1 is the real dominant eigenvalue of A , which existence is guaranteed by the Perron-Frobenius Theorem (Gantmacher, 1959), and \mathbf{w}_1 the associated eigenvector, it is obtained that $\lim_{t \rightarrow \infty} \mathbf{n}(t) = c_1 \lambda_1^t \mathbf{w}_1$. Consequently, the modeled population will grow at a rate given by the dominant eigenvalue (λ_1), and, independently of the initial population vector, the stable stage distribution will be given by the right eigenvector associated (\mathbf{w}_1) to the dominant eigenvalue. When reaching a stable distribution, this eigenvector will give information on the proportion of the population in each of the stages.

2.3.1. Estimation and sensitivity of the vital rates

Parameters P_i and G_i , in a stage structured model, can be estimated from information on stage duration. Caswell (2001) proposed to separate the process of survival and growth by introducing two probabilities:

$$\sigma_i = P(\text{survival of an individual in stage } i)$$

$$\gamma_i = P(\text{growth from } i \text{ to } i + 1 | \text{survival})$$

resulting

$$G_i = \sigma_i \gamma_i$$

$$P_i = \sigma_i (1 - \gamma_i)$$

In each stage σ_i is constant and the age distribution within the stage is stable for a stable age distribution in each stage. The estimation of γ_i is done using:

$$\gamma_i = \frac{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - \left(\frac{\sigma_i}{\lambda}\right)^{T_i-1}}{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - 1},$$

where T_i represents the duration of stage i .

We considered that population lives until the age of forty years, the duration of fledgling stage is four years and that individuals can reproduce until they die.

The value of σ_1 was taken from Strem (2008), where it was estimated to be 0.7. The value of γ_1 is 1, since in one time step all individuals in the first stage, grow to the new stage, juvenile. The inability to distinguish juveniles from adults when censuses were taken for this population in Beni, Bolivia and since the observations of captive populations indicate no significant differences in survival of juveniles and adults, determined to assume: $\sigma_2 = \sigma_3 = \sigma$.

Fertility (F_i) is defined as the number of offspring in time $t + 1$, per adult individual in time t , and it is usually described as $F_i = m_i P_i$ where m_i is the product between the expected number of hatched eggs per individual in adult stage per year, maternity function (m) and the probability of survival of these hatched eggs for the fraction of the time interval p from hatching to fledgling, ($l(p)$).

Then, the characteristic polynomial of A is

$$\chi_A(\lambda) = \begin{vmatrix} \lambda & 0 & -m l(0.25) \sigma \left(1 - \frac{\left(\frac{\sigma}{\lambda}\right)^{35} - \left(\frac{\sigma}{\lambda}\right)^{34}}{\left(\frac{\sigma}{\lambda}\right)^{35} - 1}\right) \\ -0.7 & \lambda - \sigma \left(1 - \frac{\left(\frac{\sigma}{\lambda}\right)^4 - \left(\frac{\sigma}{\lambda}\right)^3}{\left(\frac{\sigma}{\lambda}\right)^4 - 1}\right) & 0 \\ 0 & -\sigma \left(\frac{\left(\frac{\sigma}{\lambda}\right)^4 - \left(\frac{\sigma}{\lambda}\right)^3}{\left(\frac{\sigma}{\lambda}\right)^4 - 1}\right) & \lambda - \sigma \left(1 - \frac{\left(\frac{\sigma}{\lambda}\right)^{35} - \left(\frac{\sigma}{\lambda}\right)^{34}}{\left(\frac{\sigma}{\lambda}\right)^{35} - 1}\right) \end{vmatrix} \quad (1)$$

Sensitivity predicts the impact of hypothetical alterations in parameters on population growth rate (de Kroon et al., 1986). The sensitivity of λ to small changes in a model parameter a_{ij} is, as Caswell (Caswell, 2001) defined, is the partial derivative of λ with respect to a_{ij} . The sensitivity of λ to all of the a_{ij} can be calculated in a sensitivity matrix $S = \left(\frac{\partial \lambda}{\partial a_{ij}}\right)$.

Table 2

Estimation of the number of adults and the values of maternity (*m*) and nestling survival (*l*) of the monitored population of Blue-throated Macaw for the period 2004–2011 by The World Parrot Trust in Beni, Bolivia.

Year	Adults	<i>l</i>	<i>m</i>
2004	43	0.6667	0.0698
2005	49	1.0000	0.0204
2006	55	0.7500	0.1455
2007	75	0.7692	0.1733
2008	56	0.0000	0.0714
2009	70	0.5625	0.2286
2010	65	0.3000	0.1538
2011	59	0.6667	0.0508
Median	57.5	0.6667	0.1084

2.4. How management actions affect parameters

The management actions can affect fertility (*F*) in different ways. For example, the protection of cavities results in a higher number of eggs hatched, and consequently the maternity function (*m*) increases its value. On the other hand, protection and hand-feeding of nestlings increase their probability of survival (*l*). Hence, we combined the quartiles of the maternity function (*m*) and the survival of nestlings for identifying which combination of their values allows population growth. We estimated the number of years needed to double the current wild population of macaws, under three reintroduction scenarios: (a) no reintroduction; (b) reintroduction of 50 adult macaws in groups of ten individuals per year during five consecutive years; and (c) reintroduction of 50 adult macaws in one single group.

3. Results

From the values in Table 1, we compute the number of hatched eggs per individual in adult stage per year (*m*) and the probability of survival of these hatched eggs for the fraction of the time interval *p* from hatching to fledgling (3 months, *p* = 0.25), calculated as the number of fledglings over the number of hatched eggs. The results obtained are shown in Table 2.

We used median and quartiles to estimate the parameters of the model. From the characteristic polynomial $\chi_A(1) = 0$, and suppose that the population is stable, we have $\sigma_2 = \sigma_3 = 0.9735$ and, consequently:

$$\gamma_2 = \frac{\sigma_2^4 - \sigma_2^3}{\sigma_2^4 - 1} \approx 0.2400$$

$$\gamma_3 = \frac{\sigma_3^{35} - \sigma_3^{34}}{\sigma_3^{35} - 1} \approx 0.01745$$

Table 5

The long-term behavior of the wild Blue-throated Macaw population determined from each dominant eigenvalue (value in parenthesis) as result of the combination of quartiles of the number of hatched eggs per adult per year [*m*] and survival of nestlings from hatching to fledging [*l*]. A dominant eigenvalue higher than 1 implies the population will increase.

		Survival of nestlings from hatching to fledging <i>l</i>		
		Low [0.4969]	Medium [0.6667]	High [0.7548]
Number of hatched eggs per adult per year [<i>m</i>]	Low [0.0650]	Decreasing (0.9782)	Decreasing (0.9905)	Decreasing (0.9877)
	Medium [0.1084]	Decreasing (0.9905)	Stable (1.0000)	Increasing (1.0046)
	High [0.1587]	Increasing (1.0032)	Increasing (1.0156)	Increasing (1.0216)

Table 6

Time (in years) necessary to double the current wild population for each scenario of increasing population for the Blue-throated Macaw in Beni, Bolivia.

	Medium hatching, high survival	High hatching, low survival	High hatching, medium survival	High hatching, high survival
Without reintroduction	149	215	45	33
10 individuals per year over 5 years	32	46	10	8
50 individuals at once	31	44	9	7

Table 3

Values of probabilities of survival (σ_i and *l*), growth (γ_i), and the expected number of hatched eggs per adult per year (*m*) for the Blue-throated Macaw in Beni, Bolivia.

Vital rate	Description	Value
σ_1	Annual probability of survival in fledgling stage	0.7000
σ_2	Annual probability of survival in juvenile stage	0.9735
σ_3	Annual probability of survival in adult stage	0.9735
γ_1	Probability of growth from fledgling to juvenile since survived	1.0000
γ_2	Annual probability of growth from juvenile to adult since survived	0.2400
<i>l</i> (0.25)	Probability of survival from hatching to fledging	0.6667
<i>m</i>	Annual median of hatchlings per adult	0.1084

Table 4

Sensitivity analysis ($\lambda = 1$) for vital rates of the projection matrix of the stage structured population model for the Blue-throated Macaw in the Beni, Bolivia.

Vital rate	Value	Description	Sensitivity
P_3	0.9565	Permanency in adult stage	0.8260
F_3	0.0692	Fertility of adults	0.5193
G_2	0.2337	Growth from juvenile to adult	0.1537
P_2	0.7398	Permanency in juvenile stage	0.1380
G_1	0.7000	Growth from fledgling to juvenile	0.0513

From the probabilities of survival, growth, and the expected number of hatched eggs per adult per year (Table 3), and considering that sex ratio (1:1), density-independent growth, and population closed to migration, we estimated permanence (*P*), growth (*G*) and fertility (*F*) of the population projection matrix for Blue-throated Macaw population in Beni, Bolivia.

The sensitivity analysis performed on the vital rates of this projection matrix showed that population growth is more sensitive to changes in the probability of surviving and remaining in the adult stage (P_3), followed by changes in fertility (F_3). Table 4 shows the sensitivity values for $\lambda = 1$.

Table 5 shows the long-term behavior of the population (decreasing, stable or increasing) as result of the combination of quartiles of the maternity function (*m*) and survival probability of nestlings (*l*). Under the four scenarios of increasing population, the number of years that are necessary to double the current wild population varied between 33 and 215 years without reintroduction and between 7 and 46 years if 50 adult macaws are reintroduced (Table 6). In terms of the dominant eigenvalue, the stable population distribution is reached within a period of 12–15 years.

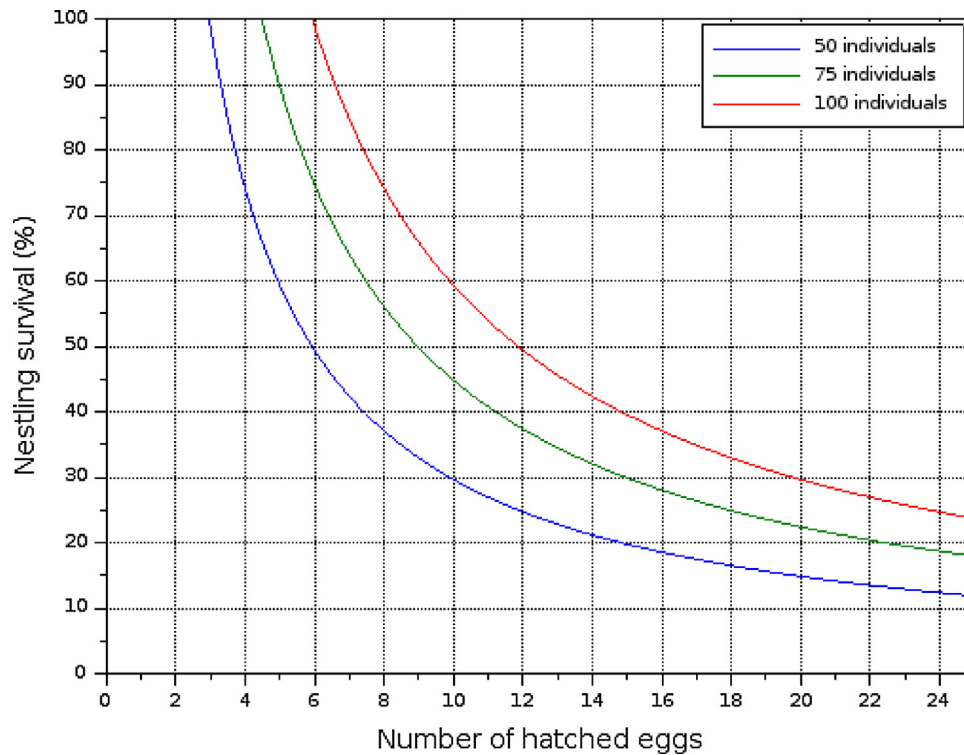


Fig. 2. Relationship between the total number of hatched eggs per year and the percentage of successful fledglings for three stable populations of 50, 75 and 100 adult Blue-throated Macaws (i.e. $\lambda = 1$). Values above the curves imply the population will increase.

4. Discussion

Here we have built a structured stage, discrete-time population model which allowed us to analyze the dynamics of the remaining wild population of Blue-throated Macaw. Our results were supported by the information gathered by monitoring this wild population during eight consecutive breeding seasons (Berkunsky et al., 2014).

The sensitivity analysis showed population growth is sensitive to the survival of adults, followed by their fertility. The priorities of management of the wild population should aim at enhancing these two parameters. Our deterministic approach reached the same conclusion as a previous stochastic approach (i.e. the Population Viability Analysis conducted by Strem (2008)) where adult mortality had a greater impact on the probability of extinction. Successful actions aimed at avoiding the hunting of adults would increase the chances of viability of the population. Meanwhile, increasing the number of fledglings will also have a positive impact on the population size.

The combination of quartiles of the maternity function and the survival probability of nestlings allowed us to identify which combination of values result in population growth. In current wild adult populations, when maternity is close to the median value (i.e. six hatched eggs per year, Table 1), a survival of at least 67% of nestlings (i.e. 4 fledglings) is necessary for a positive population growth; which implies large efforts in feeding and protection of nestlings coinciding with the conclusions of Strem (2008). On the other hand, nine hatched eggs increase the chances of a positive population growth in all three scenarios of nestling survival. The number of hatched eggs could be raised by increasing the availability and protection of cavities, and/or by introducing adult macaws into the wild population.

The model allowed us to simulate different options of reintroduction. The reintroduction of 50 adult macaws would reduce between 4 and 5 times the number of years that are necessary to

double the wild population under current management conditions. The 50-adult macaw reintroduction in the best management scenario would double the wild population in less than 10 years. On the other hand, without reintroduction and keeping current management actions, between 33 and 215 years would be necessary to double the wild population. Both reintroduction strategies, all individual in a single group or five groups of ten individuals each introduced in consecutive years, showed similar times needed to double the current wild population.

We believe that this model can be an effective tool to quantify the effect of management actions as these actions can be translated into changes in the vital parameters. Stakeholders of the Blue-throated Macaw Conservation Project may have a simple graphical tool for management decision making (Fig. 2). By knowing the adult population size and the number of hatched eggs at the beginning of each breeding season, the field team may be able to assess the necessary effort on nestlings' management to increase the chances of a positive population growth. By quantifying the impact of management actions on Blue-throated Macaws, we hope contribute to the improvement and effectiveness of conservation actions in the critically endangered species.

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