Current status of the Critically Endangered Black-winged Trumpeter *Psophia obscura* in one of its last strongholds

ELILDO A. R. CARVALHO JR 1,2*, ELOÍSA N. MENDONÇA 3, ALEXANDRE M. C. LOPES 4 and TORBJØRN HAUGAASEN 2

1 Centro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros, Instituto Chico Mendes de Conservação da Biodiversidade, Estrada Municipal Hisaichi Takebayashi 8600, 12952-011, Atibaia/SP, Brasil.
2 Faculty of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, 1432, Ås, Norway.
3 Reserva Biológica do Gurupi, Instituto Chico Mendes de Conservação da Biodiversidade, BR 222 km 12, 65.930-000, Açaílandia/MA, Brasil
4 Projeto Tamanduá, Rua Marocas Bittencourt Lopes 52, 64211-080 Parnaíba/PI, Brasil.

*Author for correspondence; email: elildojr@gmail.com

(Received 21 October 2021; revision accepted 04 March 2022)

**Summary**

The ‘Critically Endangered’ Black-winged Trumpeter *Psophia obscura* is endemic to the Belém Centre of Endemism in extreme eastern Amazonia and has a declining population and range. Here we report on a five-year (2016–2020) systematic camera-trap (*n* = 61) study of the species in Gurupi Biological Reserve, one of its most important conservation areas. We used a multi-season occupancy model to identify factors affecting occupancy rates and to assess occupancy trends in the reserve. Occupancy was negatively related to elevation and site-level tree density, and was positively related to post-logging recovery times. Average annual occupancy rates remained stable throughout the study period (ranging between 0.57 and 0.67) and this stability was largely driven by high between-year survival rates. Results confirm that the Black-winged Trumpeter is an interior-forest specialist that is highly sensitive to forest disturbance, which underlines the importance of the Gurupi Biological Reserve as a core site for the conservation of the species. However, the species is long-lived, so continuous monitoring is needed to further clarify population trends. We also recommended that the status of the species in other forest remnants, most of which remain unprotected, is assessed.

**Keywords:** Amazonia, Belém Centre of Endemism, Black-winged Trumpeter, *Psophia obscura*

**Introduction**

The genus *Psophia* (hereafter, trumpeters) comprises eight species endemic to the Amazon and Guiana regions of northern South America (Ribas *et al.* 2012, Pacheco *et al.* 2021). Trumpeters are large-bodied (> 1 kg), terrestrial, group-living and highly territorial (Sherman 1995b, Sherman...
and Eason 1998). They are predominantly frugivorous (Erard et al. 1991, 2007, Winkler et al. 2020) and play an important role in forest dynamics as they swallow entire fruits and disseminate their intact seeds (Erard et al. 2007).

Trumpeters are forest-interior specialists and thus highly sensitive to disturbance (Parry et al. 2007, Moura et al. 2014, Michalski and Peres 2017, Benchimol and Peres 2021). They tend to be rare or absent from disturbed and secondary forests (Parry et al. 2007), and they often disappear from all but the largest fragments in fragmented forest landscapes (Moura et al. 2014, Michalski and Peres 2017, Benchimol and Peres 2021). Indeed, they share most of the ecological attributes that make a bird species sensitive to forest disturbance, including large body size, slow breeding rate, and a dependency on forest habitat and its fruit and invertebrate food resources (Newbold et al. 2013). In addition, their large body size, conspicuousness and group-living habits makes them vulnerable to hunters (Thiollay 2005). Consequently, three trumpeter species are currently categorized as threatened and two as ‘Near Threatened’ on the IUCN Red List of Threatened Species (IUCN 2021).

The Black-winged Trumpeter (Psophia obscura; Fig. S3 in the online supplementary material) is endemic to the Belém Centre of Endemism in extreme eastern Amazonia (Oppenheimer and Silveira 2009, Ribas et al. 2012). The Belém Centre of Endemism coincides with the oldest and most deforested human occupation frontier of the biome and its most threatened region (Moura et al. 2014, Vedovato et al. 2016, Celentano et al. 2017, Silva Junior et al. 2020). Due to continued habitat loss and its vulnerability to hunting, the Black-winged Trumpeter is suspected to be declining with possibly <250 individuals left in the wild. It is therefore categorized as ‘Critically Endangered’ by both IUCN (IUCN criteria A and C; BirdLife International 2018) and the Brazilian Red List of threatened species (IUCN criterion A; Ministério do Meio Ambiente - MMA 2014, Silveira 2018). However, there are no population size estimates for the species, so its categorization, based on the suspected number of mature individuals (criterion C) is questionable.

Despite its threatened status, little is known about the species apart from occasional records in bird inventories throughout its range (Portes et al. 2011, Lees et al. 2012, Lima and Raices 2012, Moura et al. 2014). Current distribution is limited to some of the largest and most undisturbed fragments of the Belém Centre of Endemism (Portes et al. 2011, Moura et al. 2014) and most of the remaining individuals belong to one of two disjunct populations: a western population at unprotected forest remnants in the municipality of Paragominas and an eastern population at Gurupi Biological Reserve and contiguous Indigenous Lands (Lees et al. 2012, Lima and Raices 2012, BirdLife International 2018).

In this study, we investigate site occupancy dynamics of a Black-winged Trumpeter population at Gurupi Biological Reserve, a key stronghold for conservation of the species. More specifically, we use data from five years of camera trap monitoring and a dynamic occupancy modelling approach to investigate potential factors affecting occupancy rates and trends in the reserve as a function of apparent survival and colonization rates.

Methods

Study area

Gurupi Biological Reserve is a 270,000-ha protected area located in extreme eastern Amazonia (Fig. 1). Together with contiguous Indigenous Lands, the reserve comprises the last remaining block of continuous Amazonian forests in the Belém Centre of Endemism (Silva Junior et al. 2020), and it is one of the two most important strongholds for the Black-winged Trumpeter (Lima et al. 2014, BirdLife International 2018). The reserve has a tropical monsoonal climate with mean annual temperatures >26 C° and mean annual rainfall of 1,800 mm (Alvares et al. 2013). The terrain is flat to undulating with elevation ranging from 50 to 340 m above sea level. The reserve was entirely covered by evergreen tropical forest, but has lost about 30% of its forest cover to illegal deforestation in the last decades (Celentano et al. 2017). Much of its remaining forests is degraded by illegal
selective logging and fires (Celentano et al. 2017, Paiva et al. 2020). Still, it safeguards a significant portion of the regional biodiversity, including the full complement of medium- to large-sized terrestrial vertebrates (Lopes and Ferrari 2000, Lima et al. 2014, Carvalho et al. 2020).

**Camera trapping**

Camera trap surveys were conducted between 2016 and 2020 as part of the Brazilian *in situ* monitoring program of Federal Protected Areas (Programa Monitora). Sampling followed the
Tropical Ecology Assessment and Monitoring (TEAM) protocol for vertebrates (Rovero and Ahumada 2017): during every dry season (August to November), we deployed camera-traps (model Bushnell Trophy Cam) at 61 permanent sampling sites distributed in two regular arrays with a density of one sampling site per 2 km² (Fig. 1). Cameras were attached to trees at knee height, perpendicular to the ground and facing either north or south to avoid direct sunlight at sunrise and sunset, and the vegetation directly in front of cameras was cleared. Cameras were set to operate continuously for at least 30 days per year. Images were processed in the wild.ID software (Fegraus and MacCarthy 2016). We assumed a 60 min interval for independence between detection events at the same sampling site. Although the same sites were sampled in all years, the number of operational cameras varied between years due to occasional camera malfunctions (Table. S1).

Occupancy predictors

We quantified seven site-level variables to represent environmental and anthropogenic factors that may plausibly affect Black-winged Trumpeter occupancy and detection rates: (1) Site elevation (mean = 141.7 m, range: 77–270 m) was extracted from the ALOS global digital surface model provided by the Japan Aerospace Exploration Agency (JAXA) (Tadono et al. 2014). (2) Distance to water (mean = 1.2 km, range: 0.1–3.8) is the shortest distance between sampling sites and their nearest stream. (3) Distance to edge (mean = 2 km, range: 0.2–5) is the shortest distance between sampling locations and the nearest forest edge, estimated using the 30 m resolution land cover classification of the MapBiomas monitoring system for 2016 (Souza et al. 2020). (4) Site-level tree density (mean = 798 trees/ha, range: 523–1569) and (5) basal area (mean = 27.4 m²/ha, range: 8.2–45) were estimated using the point-centred quarter method (Cottam and Curtis 1956). Starting from each camera location, we ran three 50-m transects in the direction of 0, 120 and 240 magnetic degrees. Along each transect, we established five sampling points at 10-m intervals. The area around each point was divided into four quarters and the diameter at breast height (dbh) of the nearest tree with dbh ≥ 10 cm at each quarter was recorded. Tree density was estimated using the equation: \( D = \frac{\pi}{4} \cdot \meanBA \cdot D \), where \( \meanBA \) is the mean basal area of sampled trees across all quarters (Cottam and Curtis 1956). Basal area was estimated using the equation \( \text{BA} = \pi \cdot \left( \frac{\text{dbh}}{2} \right)^2 \). To minimize the weight of a few exceptionally large trees, basal area of trees in the top 2.5% quantile \( (n = 9 \text{ trees}) \) were replaced by the quantile threshold value. Finally, we quantified two variables representing site-level impacts of past illegal logging: (6) recovery time (mean = 13, range: 6–21) as the number of years elapsed since any portion of a buffer of 500 m around each sampling site was logged for the last time, and (7) logging bouts (mean = 2, range: 1–5) as the number of different years in which each 500 m buffer zone was logged. To recover the history of illegal logging, we used visual interpretation of 1984–2016 Landsat time series data (Carvalho et al. 2020). Evidence of logging, such as roads, log decks and large canopy gaps are detectable in Landsat imagery for one to several years after logging (Stone and Lefebvre 1998, Matricardi et al. 2007, Asner et al. 2009). We used the USGS Earth Explorer interface (http://earthexplorer.usgs.gov) to download Landsat images from every year of the series and selected, whenever possible, cloudless images from dry season months. We then recorded the presence or absence of logging signs within 500-m buffers centred on each camera trap site and for each year in the series. By this procedure we estimated both recovery time and the number of logging bouts. For unlogged sites, we set maximum recovery time as 33 years, corresponding to the start of the time series. More details are provided in Carvalho et al. (2020).

All variables were standardized before the analysis. Distance to edges was log-transformed before the analysis. We used Pearson coefficients \( (r) \) to test for collinearity among predictors, retaining for analysis only one variable from any pair with high \( |r| > 0.60 \) correlation. Thus, distance to water and logging bouts were removed from analysis as they were correlated with elevation and recovery time respectively.
Data analyses

We used multi-season occupancy modelling (MacKenzie et al. 2003) to investigate Black-winged Trumpeter occupancy trends. This approach uses detection/non-detection data to estimate occupancy rates (the proportion of sites occupied by the species) and to model temporal changes in occupancy as a function of local survival and colonization processes, while accounting for imperfect detection (Royle and Dorazio 2008, Kéry and Schaub 2012, MacKenzie et al. 2017). The model requires sampling at two temporal scales, namely primary and secondary periods. Occupancy at any given sampling site may change between primary periods, but not between secondary periods that are nested within primary periods (MacKenzie et al. 2003). In our analysis, primary periods corresponded to years and secondary periods to six-day sampling occasions. To meet the assumption of population closure within primary periods, we only use data from the first 30 days of sampling for any site and year. To increase detection probabilities and facilitate model convergence in data analysis, we collapsed data into six-day sampling occasions.

We modelled occurrence of the species at site \( i \) in year \( k \) \((z_{i,k})\) as a Bernoulli outcome governed by occupancy probability at site \( i \) in year \( k \) \((\psi_{i,k})\):

\[
z_{i,k} \sim \text{Bern}(\psi_{i,k})
\]

We modelled observations, consisting of detection/non-detection of the species at site \( i \), sampling occasion \( j \) and year \( k \) \((y_{i,j,k})\) as Bernoulli outcomes governed by the product of \( z_{i,k} \) and detection probability at site \( i \), sampling occasion \( j \) and year \( k \) \((p_{i,j,k})\):

\[
y_{i,j,k} \sim \text{Bern}(z_{i,k} \cdot p_{i,j,k})
\]

We used a logit link function to model detection probability as a function of random site and year effects, while assuming constant detection within the same site and year:

\[
\text{logit}(p_{i,j,k}) = a_i + \epsilon_k
\]

We used a logit link function to model initial occupancy (year \( k=1 \)) as a function of random site effects, elevation, distance to edge, basal area, tree density, and recovery time:

\[
\text{logit}(\psi_{i,1}) = a_i + b_1 \cdot \text{elevation}_i + b_2 \cdot \text{distEdge}_i + b_3 \cdot \text{basalArea}_i + b_4 \cdot \text{treeDensity}_i + b_5 \cdot \text{recovery}_i
\]

We modelled occupancy in subsequent years as a function of year-specific survival (\( \phi \)) and colonization (\( \gamma \)) rates, estimated from the data:

\[
\psi_{i,k+1} = \psi_{i,k} \cdot \phi_k + (1 - \psi_{i,k}) \cdot \gamma_k
\]

To assess whether year-to-year changes in occupancy were significant, we estimated the derived parameter growth rate (\( \lambda \)) as follows (Royle and Dorazio 2008):

\[
\lambda = \frac{\psi_{k+1}}{\psi_k}
\]

We fitted the model in a Bayesian framework, adapting the specifications provided by (Kéry and Schaub 2012). We implemented the model in JAGS (Plummer 2015) using the R2jags package (Su and Yajima 2012). We used non-informative priors for all parameters and ran three chains with
250,000 Markov Chain Monte Carlo (MCMC) iterations, with a burn-in of 100,000 and a thinning rate of 150. We evaluated parameter convergence using the Gelman-Rubin diagnostic (Gelman and Shirley 2011). We considered that there was support for a covariate effect when the 95% posterior credible interval (CI) for the parameter did not include zero. We considered that there was evidence for significant change in occupancy between a given year $k$ and $k+1$ if the posterior credible interval of $\lambda$ did not overlap 1 (Ahumada et al. 2013). Data and R codes for analysis are available at https://github.com/ICMBio-CENAP/Psophia-obscura.

Results

A total effort of 8,674 camera-trap days across five years of sampling yielded 2,876 photos of Black-winged Trumpeter, corresponding to 181 independent detection events (figures refer to data not yet collapsed into six-day occasions; Table S1). In any given year, the species was recorded at 14–22 sites, corresponding to naïve (i.e., uncorrected for imperfect detection) occupancy rates of 0.24–0.39. Table 1 presents posterior summaries for selected model parameters.

Average initial (i.e. for 2016) occupancy probability was 0.57 and average initial detection was 0.14. Initial occupancy probability was negatively related to elevation and tree density, and positively related to recovery time (Table 2, Fig. 2, Fig. S1). Basal area was positively but not significantly related to occupancy, while distance to edges had no relationship with occupancy (Table 2, Fig. S1).

The dynamic occupancy model reveals fluctuating but stable occupancy rates across years, with average annual $\psi$ fluctuating between 0.57 and 0.67 (Table 1, Fig. 3) and always consistently higher than naïve occupancy rates. Detection rates were low and varied little across years, ranging between 0.09 and 0.15 (Table 1). Between-year growth rates ($\lambda$) ranged between 0.92 and 1.2 over years and

| Parameter | Mean | SD | 95% CI |
|-----------|------|----|--------|
| $\psi_{2016}$ | 0.57 | 0.06 | 0.47–0.7 |
| $\psi_{2017}$ | 0.59 | 0.14 | 0.33–0.87 |
| $\psi_{2018}$ | 0.67 | 0.12 | 0.45–0.89 |
| $\psi_{2019}$ | 0.6 | 0.12 | 0.36–0.86 |
| $\psi_{2020}$ | 0.62 | 0.13 | 0.38–0.89 |
| $p_{2016}$ | 0.14 | 0.02 | 0.09–0.19 |
| $p_{2017}$ | 0.09 | 0.03 | 0.05–0.15 |
| $p_{2018}$ | 0.15 | 0.03 | 0.1–0.23 |
| $p_{2019}$ | 0.12 | 0.03 | 0.07–0.18 |
| $p_{2020}$ | 0.1 | 0.02 | 0.06–0.15 |
| $\theta_{2016-2017}$ | 0.72 | 0.15 | 0.42–0.98 |
| $\theta_{2017-2018}$ | 0.81 | 0.13 | 0.52–0.99 |
| $\theta_{2018-2019}$ | 0.72 | 0.15 | 0.4–0.97 |
| $\theta_{2019-2020}$ | 0.81 | 0.13 | 0.52–0.99 |
| $\gamma_{2016-2017}$ | 0.4 | 0.23 | 0.05–0.9 |
| $\gamma_{2017-2018}$ | 0.47 | 0.23 | 0.06–0.94 |
| $\gamma_{2018-2019}$ | 0.37 | 0.23 | 0.03–0.89 |
| $\gamma_{2019-2020}$ | 0.36 | 0.23 | 0.03–0.88 |
| $\mu_{2016-2017}$ | 1.03 | 0.26 | 0.57–1.58 |
| $\mu_{2017-2018}$ | 1.2 | 0.33 | 0.71–1.97 |
| $\mu_{2018-2019}$ | 0.92 | 0.22 | 0.53–1.41 |
| $\mu_{2019-2020}$ | 1.07 | 0.26 | 0.68–1.7 |
were never significantly different from unity (Table 1, Fig. S2), which is consistent with the observed stability in occupancy rates. Occupancy dynamics was characterized by high between-year survival probabilities, with $\phi$ ranging between 0.72 and 0.81 across years, while between-year colonization probabilities were considerably lower, with $\gamma$ ranging between 0.36 and 0.47 (Table 1).

**Discussion**

This study provides the first assessment of factors affecting the distribution and trends of the Black-winged Trumpeter in one of its key conservation areas. Black-winged Trumpeter initial occupancy rate was affected by elevation, tree density and recovery time, a set of variables that represent natural or anthropogenic factors, or a combination of both, while occupancy rates remained stable throughout the study.

The effect of elevation was negative. This is a key determinant of biodiversity distribution in tropical forests as it is correlated to a range of biotic and abiotic variables including water availability, soil and vegetation characteristics, and microclimate (de Castilho et al. 2006, de Toledo et al. 2011, Norris et al. 2014). The negative effect of elevation on trumpeter occupancy may relate to higher humidity and productivity in lower-lying areas; trumpeters prefer the moistest parts of the forest for foraging (Erard et al. 2007) and tend to be more abundant at sites closer to water (Michalski et al. 2015, Paredes et al. 2017, Mere Roncal et al. 2019, del Hoyo et al. 2020). Such habitat specificity probably increases the species’ vulnerability to climate change. Habitat suitability models predict that it might lose more than 70% of suitable areas due to climate change by 2050 (de Moraes et al. 2020).

The results confirm that the species is an undisturbed primary forest specialist (Portes et al. 2011, Moura et al. 2013, Lima et al. 2014, del Hoyo et al. 2020), even though it can tolerate low levels of disturbance (Lima and Raices 2012). The two variables representing forest structure were strongly related to Black-winged Trumpeter occupancy probability, with tree density having a significantly negative effect and basal area having a positive, albeit non-significant, effect. Both variables are indicators of forest successional stage, with basal area increasing (Lu et al. 2003, Myster 2016, Caron et al. 2021) and tree density decreasing (Wright 2005) as forests mature. Such a preference for undisturbed forests seems to be universal for the genus (Parry et al. 2007, Michalski et al. 2015, Michalski and Peres 2017).

The precise mechanism by which forest structure affects the species is unclear and we can only speculate. Perhaps early successional or disturbed forests lack essential resources. For example, disturbed areas have fewer large trees, which provide the bulk of fruit consumed by trumpeters (Erard et al. 2007), and may lack trees with appropriate cavities for nesting (Sherman 1995a, Cornelius et al. 2008). Dense understory in disturbed areas may also hinder communication and vigilance. This is detrimental to trumpeters, as they require constant acoustic and visual contact between group members to coordinate their movements and watch for predators (Seddon et al. 2002). Whatever the mechanism, the species prefers areas with a structure like mature forests.

Since most logging in the area took place over a decade ago, the positive effect of recovery time implies that logging effects are persistent. The removal of large trees and the increase in understory density due to logging gaps have similar effects to those discussed above. Even though some
parameters such as canopy cover and microclimate recover relatively quickly after logging (Senior et al. 2018, Mollinari et al. 2019), recovery of forest biomass (Gatti et al. 2014), floristic composition (Gaui et al. 2019) and availability of large trees (Pinho et al. 2020) may take much longer. This is particularly prominent in illegally logged areas, which undergo more severe damage in their

Figure 2. Predicted effect of model covariates on Black-winged Trumpeter initial occupancy probabilities at Gurupi Biological Reserve: (A) elevation (masl); (B) tree density (stems/ha); (C) post-logging recovery time (years). Solid black line represent posterior mean and light grey lines the uncertainty in estimates, based on a random posterior sample of 200 iterations.
structure and composition (Pacheco et al. 2016). Overall, trumpeter responses to logging seem to depend on the amount of damage to the residual forests. Previous studies found variable responses from trumpeters, from negative responses to conventional logging that persist for over a decade (Thiollay 1997) to slightly positive responses to reduced-impact logging in the short-term (Bicknell and Peres 2010). A previous study using a subset of the same data used here did not find a significant response to logging by the Black-winged Trumpeter, although the direction of the response was consistent with what is reported here (Carvalho et al. 2020).

The dynamic model revealed fluctuating but stable occupancy rates across years. Given that trumpeters are highly territorial with relatively inflexible home range boundaries (Sherman and Eason 1998) and that camera spacing was large enough to ensure there was no more than one camera per territory (assuming territories of approximately 70 ha; Sherman and Eason 1998), this suggests that the number of occupied territories, and possibly the population, has remained constant throughout the study. This finding underlines the importance of the Gurupi Biological Reserve as a core site for the conservation of the species, whose decline is inferred mostly from the continued loss of habitat (BirdLife International 2018, Silveira 2018), as there are no monitoring data available.

Stable occupancy rates can be interpreted as evidence of territorial saturation, where all suitable sites are occupied, and no vacant territories are available for expansion. Territorial saturation is probably the rule among trumpeters, and has been suggested as a candidate driver for the evolution of cooperative breeding in the genus (Sherman 1995b). This is because trumpeter territory sizes are largely defined by food availability during the lean period (Sherman 1995b, Sherman and Eason 1998), and this limits the number of territories that can fit within a given area. Consistent with this view is the fact that population dynamics was shaped primarily by high survival rates and not colonization, as revealed by the consistently higher estimates for $\phi$ compared to $\gamma$. In fact, this was expected as adult trumpeters have high survival rates (Sherman 1995b) and groups can persist even longer than individuals, leading to continuous occupation of territories by the same group on a multi-year basis.

Figure 3. Temporal dynamics in Black-winged Trumpeter occupancy probabilities at Gurupi Biological Reserve, 2016-2020. The solid black line represents the posterior mean, and light grey lines the uncertainty in the estimate, based on a random posterior sample of 200 iterations.
This view does not rule out the possibility of changes in the occupancy rate in the future. Suitable areas may become vacant if their resident groups collapse and are not replaced. The amount of suitable habitat may decrease if the reserve undergoes additional logging, forest fires or deforestation. The opposite is also possible as the amount of suitable habitat may increase as previously degraded areas recover from disturbance. Continuous monitoring is needed to reveal future trends, while additional studies may indicate the maximum attainable population size in the reserve and what factors may be limiting population growth and expansion.

Observed trends should be interpreted with caution, as the study duration was relatively short. Five years is just a little longer than the average tenure of a dominant individual over a group (Sherman 1995b), and approximately equivalent to the estimated generation length of the Black-winged Trumpeter (Bird et al. 2020). For example, the guidelines for using the IUCN Red List categories and criteria require information on population reduction over 10 years or three generations (Rodrigues et al. 2006), which for the Black-winged Trumpeter corresponds to 15 years (Bird et al. 2020). Therefore, more years of monitoring are needed for robust conclusions on trends for the species.

The apparent stable trumpeter population at Gurupi provides hope for the species within this protected area. However, the conservation prospects for the species remain highly precarious as a large but unknown fraction of its remaining population resides in unprotected forest patches that continue to be lost at alarming rates (Silva Junior et al. 2020). Furthermore, even protected areas are prone to habitat degradation from logging, fires, and climate change (de Moraes et al. 2020). We reinforce the main recommendations already provided for the conservation of the species, such as expanding the network of protected areas and improving the management of existing ones (BirdLife International 2018, Silveira 2018). We also recommend continued monitoring at Gurupi to further clarify trends in this key area for the species, as well as additional studies to provide reliable estimates of population size in the reserve and in other areas.

Supplementary Material
To view supplementary material for this article, please visit https://doi.org/10.1017/S0959270922000077

Acknowledgements
We thank the managers of Gurupi Biological Reserve for logistical support. W.M. Silva, M. C. de Lima, F. C. Braga and C. R. D. V. Melo assisted in fieldwork. Ronaldo G. Morato commented on an earlier draft of this manuscript. This work was funded by ARPA – Programa Áreas Protegidas da Amazônia.

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