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Addressing multiple sources of uncertainty in the estimation of global parrot abundance from roost counts: A case study with the Vinaceous-breasted Parrot (*Amazona vinacea*)

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ABSTRACT

Population size is a key predictor of extinction risk and is critical to listing species in IUCN threat categories. Assessing population size can be particularly difficult for gregarious species, such as parrots—one of the most threatened bird families—whose ecology and behavior generate multiple sources of uncertainty that need to be addressed in monitoring efforts. To improve estimates of abundance for the endangered Vinaceous-breasted Parrot (*Amazona vinacea*), we combined extensive roost counts over the global range of the species (Argentina, Paraguay, Brazil) with an intensive regional survey designed to address five sources of uncertainty about parrot abundance in western Santa Catarina state (WSC), Brazil, in 2016 and 2017. We estimated abundance at both regional and whole-range scales using N-mixture models of replicated count data, which account for imperfect detection. The regional-scale estimate was 1826 ± 236 and 1896 ± 105 individuals for 2016 and 2017, respectively; global abundance was estimated at 7789 ± 655 and 8483 ± 693 individuals for the same two years. We found no statistical evidence of population change at either scale of the analysis. Although our assessments of abundance and geographic range are larger than those currently reported by the IUCN, we suggest the Vinaceous-breasted Parrot should remain in the 'Endangered' IUCN threat category pending further investigation of population trends. We recommend that roost-monitoring programs for parrots consider and address sources of uncertainty through adequate field protocols and statistical analyses, to better inform assessments of population size, trends, and threat status.

1. Introduction

Population size is arguably the most important state variable in population biology (Gaston, 1994); along with range size, it is the best predictor of extinction risk (Lawton, 1995) and plays a central role in population management (Caughley, 1994; Norris, 2004). Abundance is directly implicated in three of the five IUCN (International Union for the Conservation of Nature) criteria for listing species in threat categories (Mace et al., 2008). Among the animal groups in most urgent need of abundance information, parrots (Psittaciformes) stand out for having the highest number of threatened species of all non-passerine bird orders (Olah et al., 2016). Of 394 extant species of parrots, 117 (29%) are listed as threatened, and 81 of these are declining, according to the IUCN (BirdLife International, 2020). The key causes of parrot population decline are habitat loss—due to deforestation and agroindustrial expansion—, and nest poaching —due to illegal pet trade

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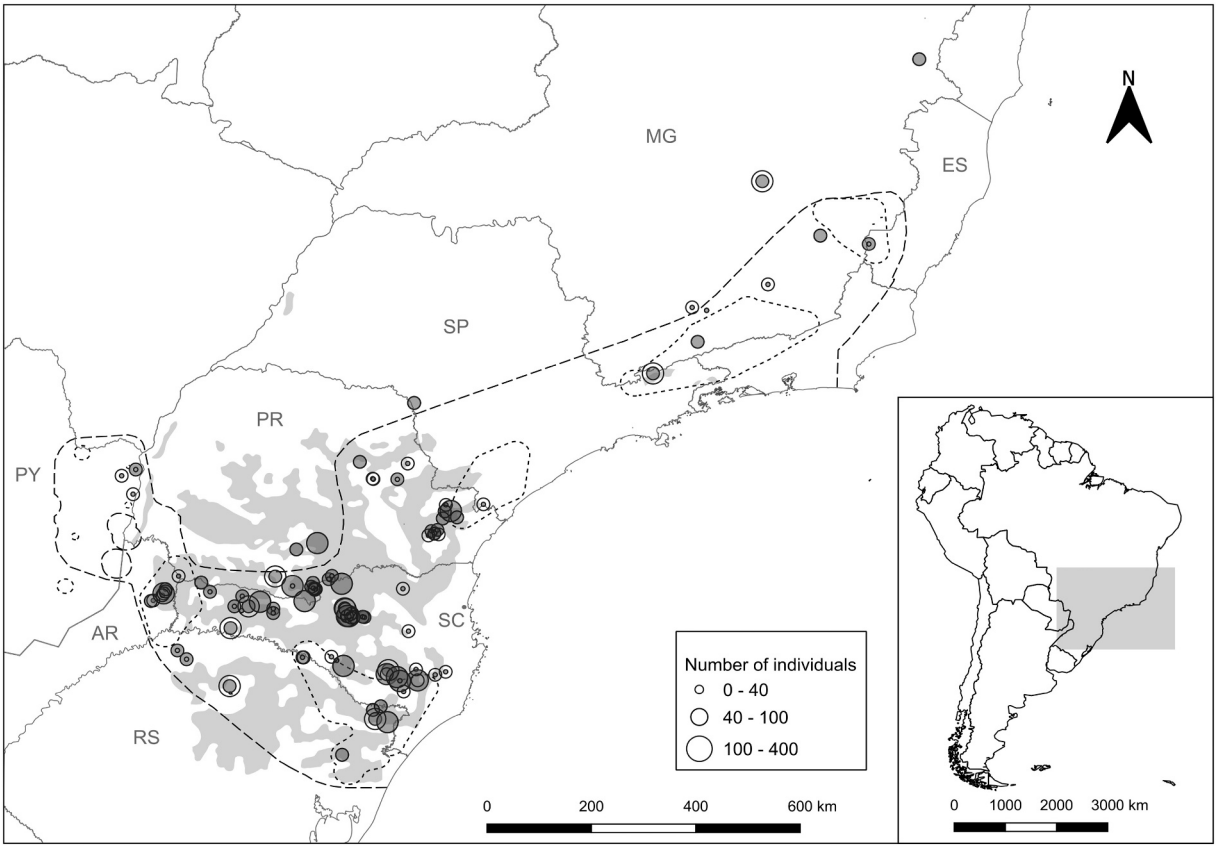

Fig. 1. Estimated number of Vinaceous-breasted Parrots per roost (circles), hypothetical IUCN range areas (dashed polygons), and potential extent of *Araucaria angustifolia* forests (gray polygon). Concentric circles show estimates from 2016 (gray) and 2017 (empty), with sizes corresponding to the abundance classes shown in the legend. When the estimates from both years fall in the same class, the superimposed circles appear as a single gray circle. The set of short-dash polygons represent the IUCN 'Extant' range, while the single, larger, long-dash polygon representes the IUCN 'Possibly Extant' range. Gray, upper-case labels indicate Paraguay (PY), the Argentinian province of Missiones (AR), and the six Brazilian states mentioned in the text: Espírito Santo (ES), Minas Gerais (MG), São Paulo (SP), Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS).

(Berkunsky et al., 2017; Olah et al., 2016; Wright et al., 2001). However, statistical estimates of parrot population size remain difficult to obtain and are available for very few species (Dénes et al., 2018; Marsden and Royle, 2015).

The globally endangered Vinaceous-breasted Parrot (VBP; *Amazona vinacea*) is restricted to the Atlantic Forest biome, mostly within Brazil but with small areas of occurrence in the Argentinian province of Misiones and eastern Paraguay (Carrara et al., 2008; Cockle et al., 2007; Prestes et al., 2014; Segovia and Cockle, 2012; Fig. 1). VBPs appear to be associated with the ancient Paraná Pine (*Araucaria angustifolia*; Cockle et al., 2019; Collar et al., 2017; Tella et al., 2016), but they also forage and nest in other trees (Bonaparte and Cockle, 2017; Cockle et al., 2007; Prestes et al., 2014), and their incompletely known geographic range extends beyond the current range of *Araucaria* forests (Carrara et al., 2008; Cockle et al., 2007; Collar et al., 2017). As with many other parrot species, incomplete knowledge about the VBP geographic range and population size results in part from movements associated with temporal variation in food availability (Renton et al., 2015; Webb et al., 2014). Seasonal movements reportedly coincide with the fruiting of *Ocotea puberula*, *Podocarpus lambertii*, *Vitex megapotamica*, Juçara palms (*Euterpe edulis*), and *Araucaria* pines (Collar et al., 1992; Forshaw, 2010; Prestes et al., 2014). Unpredictable movements make it difficult to anticipate where parrots will be, or whether parrots seen in different places are the same or different individuals, presenting interesting challenges to the estimation of population size. According to the IUCN, the extant geographic range of the VBP covers approximately 145,700 km^2 (BirdLife International and Handbook of the Birds of the World, 2016; Fig. 1). This range consists of five major patches (>10,000 km^2), and eleven relatively small patches (<1000 km^2). Average distance between major patch centroids is 834 ± 379 km, revealing a discontinuous VBP distribution. Such discontinuity reflects not only the species' true range, but also the scarcity of information about population structure and movements. Accordingly, the IUCN recently updated the range map with a larger, 'possibly extant' layer that encloses all of the patches above (Fig. 1).

One traditional method to assess parrot abundance is to count individuals as they enter or leave communal roosts, a technique used for VBP over the last two decades (Casagrande and Beissinger, 1997; Abe, 2004; Cougill and Marsden, 2004; Cockle et al., 2007; Segovia and Cockle, 2012). Our field observations prior to this work suggest that, as in many parrot species, VBPs disperse in pairs across the species' range while courting and breeding (July–December), begin congregating in communal roosts towards the end of the breeding season (December–January), and may or may not continue to use these roosts throughout the entire non-breeding period (until June). As a result, during the January–June non-breeding period, the number of VBPs can vary from fewer than ten to hundreds of individuals, both among roosts and among days at the same roost (Abe, 2004; VZ, unpublished data). When August begins, there are virtually no parrots left at communal roosts and the population is once again dispersed across hundreds of nesting sites. Despite difficulties inherent to locating roosts and counting the number of individuals, roost counts remain one of the most popular and cost-effective ways of assessing the abundance of parrots (Matuzak and Brightsmith, 2007; Dénes et al., 2018).

Roost count design varies but always involves locating roosts, choosing the appropriate time for counting, and actually counting a

number that is as close as possible to the real number of animals present (Casagrande and Beissinger, 1997). In order to improve knowledge of the distribution and abundance of parrots from roost counts, one should approach the three tasks of locating, timing, and counting in a way that minimizes the magnitude of five key sources of uncertainty about the end result. Although we focus on one parrot species, the same sources of uncertainty arise for researchers assessing the abundance of other gregarious species, such as flamingos (Caziani et al., 2007) or bats (Mohd-Azlan et al., 2001; Walsh and Harris, 1996). The first and second sources have to do with locating roosts. First, there is uncertainty about the extent of the VBP's distribution. When does a gap in the range map represent true absence of the species vs. absence of observations? This problem is well represented by the difference between the IUCN 'Extant' and 'Possibly Extant' ranges in Fig. 1. The second source is uncertainty about density of roosts at the regional scale. At what point should one stop trying to find more roosts to free time for studying known roosts in detail? The third source of uncertainty concerns movement of individuals between roosts and constrains the timing of counts: if roosts correspond to isolated local populations, different roosts could be counted at any time throughout a non-breeding season. If, on the contrary, individuals move between roosts, researchers must account for such movements or count parrots at multiple roosts simultaneously. The fourth and fifth sources of uncertainty relate to the counting technique itself, and address, respectively, false positive and false negative observations of individuals. A false positive happens when by mistake a parrot is counted twice or more. A false negative happens when a parrot that is present at a site is not counted because it was overlooked.

This paper offers an assessment of VBP abundance for the years 2016 and 2017. We follow a two-pronged approach that combines data from two spatial scales, two counting techniques, and two research teams. At the regional scale, we estimate the number of VBPs in Western Santa Catarina/Brazil (WSC; Fig. 2) while seeking to address all five sources of uncertainty listed above. We chose to focus the regional research on WSC because a) being an area of intense agro-industrial activity with no previously published VBP observations, it has been left out of the species' IUCN Extant map; b) it sits between two important VBP habitat areas in different countries (Misiones, in Argentina, and the *Araucaria* forests of Eastern Santa Catarina, in Brazil), and c) based on our previous experience, we expected to find roosts that were not yet documented in WSC. At the whole-range scale, we provide a global statistical estimate of the species based on counts of parrots observed in all VBP roosts known to us, throughout the entire range of the species.

2. Methods

2.1. Whole-range sampling

Whole-range sampling took place over 98 sites spanning an area from northern Minas Gerais, in the north, to northeastern Rio Grande do Sul, 1500 km to the south. The area extends west to, and includes eastern Paraguay, as well as the Argentinian province of Misiones (Fig. 1). Approximately one quarter (22) of the count sites are inside the IUCN Extant range of the VBP, with the remaining three quarters (76) outside. Sites correspond to regularly-used roosts and to points of frequent flyover by parrots at dawn and dusk (Supplemental Material Table S1). Our research team and collaborators identified the count sites, sometimes over decades of VBP observation (e.g. Cockle et al., 2007; Segovia and Cockle, 2012). All sites are located within the Atlantic Forest, defined by the southeast Atlantic portion of the 'tropical and subtropical moist broadleaf forest' eco-region of South America (Olson et al., 2001).

Sampling at the whole-range scale was carried out by 26 volunteer teams (Supplemental Material Table S1) coordinated by NPP and JM. Counts took place in 2016 (24–26 March in Argentina, 29 April to 15 May in Paraguay and Brazil) and 2017 (24 April to 15 May in Paraguay and Brazil only). Each team worked in areas that were familiar to its members, enabling us to cover most of the range in a short period and thus minimize the possibility of double-counting between sites. Of the total 98 sites, 33 were sampled only in 2016, 30 only in 2017, and 35 in both years (Supplemental Material Table S1). We visited sites once per

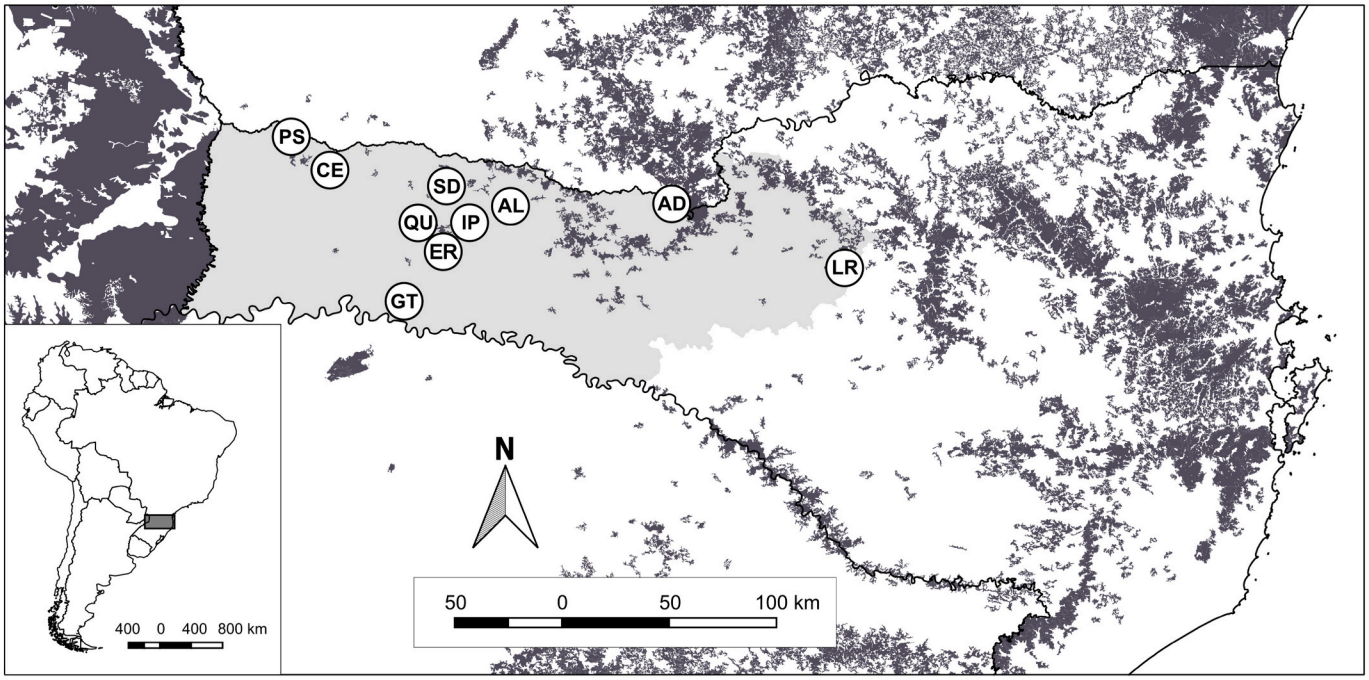

Fig. 2. Regional-scale study area of Western Santa Catarina (light gray). Dark gray indicates every patch of forest (excluding tree plantations) > 5 km^2 in area, according to the Brazilian Ministry of the Environment's *Mapa de Cobertura Vegetal dos Biomas Brasileiros* (MMA, 2007). Circles show the location of all presently known WSC roosts with their name abbreviations: PS (*Palma Sola*), CE (*Campo Erê*), GT (*Guatambu*), QU (*Quilombo*), SD (*São Domingos*), IP (*Ipuaçu*), AL (*Abelardo Luz*), ER (*Entre Rios*), AG (*Água Doce*) and LR (*Lebon Régis*).

year, counting parrots at the beginning or at the end of the day. Counts started at dawn (30 min before sunrise) or dusk (90 min before sunset) and lasted until we could not detect parrot movement into or out of the roost for 20 min—which always happened within 2 h of the beginning of the count. The number of counting posts at each site varied between one and five, located at strategic points for observing movement of flying parrots in and out of the site area. Each count was performed by a team of one to ten observers who registered the number of parrots arriving or leaving the area, the flight direction, and the time. Whenever there was more than one post in a count, observers from different posts met at the end of the count to compare notes and agree on the minimum number of individual parrots seen.

2.2. Regional-scale sampling

The regional-scale study area is the western part of the Brazilian state of Santa Catarina (WSC; IBGE, 2015; Fig. 2), with approximately 100 by 300 km extending West-East between the Uruguay river (to the South) and the ridgeline that separates the Uruguay and Iguaçú watersheds (to the North). Although mostly deforested, the area adjoins two large patches of forest habitat: the Atlantic Forest of Misiones, to the west, and the *Araucaria* forests of Eastern Santa Catarina, to the east (Fig. 2). WSC is remarkable for having a high frequency of VBP sightings by citizen scientists (Wikiaves, 2018) in an area that is almost entirely (88%) outside the IUCN extant range of the species (Fig. 1). WSC falls within the *Araucaria* forest and the Interior forest biogeographic sub-regions of the Atlantic Forest, which have lost, respectively, 87 and 93% of their forest cover since the onset of European colonization (Ribeiro et al., 2009). Nowadays, the remaining forest patches in WSC (Fig. 2) are surrounded by agro-industrial development, consisting mostly of soybean (*Glycine* max), eucalyptus (*Eucalyptus* sp.), and pine (*Pinus* sp.) plantations (Baptista and Rudel, 2006; Fearnside, 2001). The ten WSC sampling sites are a subset of the whole-range sites. They comprise all known VBP roosts in WSC and they all coincide with *Araucaria* forest patches >10 m tall. Four of the ten regional sites (*Guatambu*, *Campo Erê*, *Abelardo Luz* and *Água Doce*) have very open to non-existent vegetation under the *Araucaria* canopy (Fig. 2).

Fieldwork at the regional-scale was carried out by a single team coordinated by VZ and ESM. Here, we performed monthly visits to each site, across two consecutive non-breeding seasons: from December 2015 to July 2016, and from February to June 2017. By employing the same team for all roost counts of the same month in WSC, we could control and coordinate field technique much more tightly at the regional than at the whole-range scale. To avoid counting the same parrots twice in different roosts during the same month, each visit was performed in the shortest period possible—between four and ten days, depending on the number of roosts sampled. Each roost was sampled at dusk and at dawn of the next day, allowing us to visit two nearby roosts in the same twelve hour period. The shortest distance between roosts was 19 km and the longest single-day displacement recorded for radio-tagged VBPs is 17 km (Prestes et al., 2014). We moved between roosts at the average speed of 45 km per day; therefore, we find the possibility of double counting between roosts to be sufficiently small. In all, we completed 13 visits to WSC, eight during 2015–2016 and five during 2017. To minimize uncertainty about VBP distribution and roost density over the regional-scale, we spent one day per month searching for roosts and interviewing WSC residents that we met in the field. As we discovered new roosts, the number of roosts counted increased from four in December 2015 to five in February 2016, eight in May 2016, and ten in May 2017 (Fig. 2; Supplemental Material Table S2). The *Lebon Régis* and *Entre Rios* sites, also located in WSC, were only visited during the whole-range count of both years. In total, we completed 182 roost counts at the regional scale.

Regional-scale counts started at dusk (77) or dawn (105 counts), and lasted until we could no longer detect parrot movements, following the same times and criteria as described for the whole-range counts. We visited every roost before the first count to establish observation posts in locations suitable for observing the arrival and departure of parrots. Each count was performed by a team of three observers (one per observation post), each equipped with a roost area map, a compass, an audio recorder, and a radio to communicate with team members about parrots going their way. Every time an observer saw one or more VBPs, she recorded the number of individuals, the time, and the direction of flight, as well as any other comments that could help understand the movement of the birds. At the end of each count, the team of three observers met to reconcile their notes and agree on one 'most reasonable' (MR) and one 'highly conservative' (HC) count result. The difference between MR and HC counts lies in how observers treat the possibility of double counting. Suppose, for example, that an observer sees five parrots arriving at a roost and a few minutes later sees another arrival of three individuals. Based on this information, the MR count is eight individuals. Suppose further, however, that one of the observers in the trio determined that there were unseen, but heard, parrots leaving the roost during the time between the two observations above. In this case, the team might judge that there was some, however small, possibility that the second group of three was a subset of the first group of five, which had exited the roost undetected and returned within sight. If that were the case, the HC count should be five and not eight, because five is the absolute minimum number of birds that the team is sure to have seen arriving at the roost.

The consideration of MR and HC counts addresses one source of uncertainty about VBP abundance estimates: the possibility that some animals may be counted more than once within one count. A second source of uncertainty is imperfect detection, i.e. the possibility that some animals are missed. To address imperfect detection, we replicated counts by working simultaneously with two teams of three observers, at the same roost and time, in ten of the thirteen sampling months. Simultaneous replication employed two observers (one from each team of three) per post, keeping sufficient distance between observers to preclude overhearing radio communications. Observers from different teams did not exchange any information about their observations until each team had separately agreed on its count results. We thus treat every team-specific count of a given roost and month, whether at dusk or dawn, as an independent sample of that roost for that month. When working with two teams counting at dusk and dawn we obtained the maximum of four replicate counts for one roost and month. Sometimes it rained and other times we didn't have a second team, but we had more than one count in 90% of the roost*month combinations. The crucial difference between sampling designs at the regional- and whole-range scales was replication. At the regional-scale, we could afford and strove to replicate counts of the same roost and month as much as possible.

2.3. Data analysis

We modeled both regional and whole-range data using an N-mixture model approach (Royle, 2004). N-mixture models account for imperfect detection and estimate the number of individuals per site, given replicated count data. For each spatial scale, we summarized counts in an array C with dimensions S by R by M, where S is the number of roost sites, R is the maximum number of replicate counts per roost in any month, and M is the number of sampling months. Elements C_{ijk} of this array give the number of parrots counted in the j^{th} count of the i^{th} roost in the k^{th} month, with $i = 1, \ldots, S$, $j = 1, \ldots, R$, and $k = 1, \ldots, M$. The N-mixture model represents the true number N_{ik} of individuals in roost i and month k as drawn from a Poisson distribution with parameter λ_k. That is, the number of individuals per roost varies according to a Poisson distribution with mean λ_k, which itself varies through time. We account for imperfect detection by modeling the counts C_{ijk} as the result of a binomial sample with N_{ik} independent trials and probability of success p_k. In short, our models combine the biological variation of abundance among roosts with the sampling process of

parrot detection:

$N_{ik} \sim \text{Poisson}\ (\lambda_k)$

$C_{ijk} \sim Binomial\ (N_{ik}, p_k)$.

When a roost i is not sampled in month k, we impute an estimate of N_{ik} based on the estimate of λ_k for that month. Such imputation accounts for the temporal variation in effort and implies that differences between abundance estimates from different months are not a result of variation in the number of roosts counted. In the way we set up the analysis, this imputation is a by-product of our Bayesian model fitting using MCMC methods (see below).

To analyze regional-scale data, we used two arrays C, of HC and MR counts, with dimensions $S = 10$ sites, $R = 4$ counts, and $M = 13$ months. The first eight months correspond to December 2015 through July 2016, while the last five correspond to February-June 2017. Because our counts in WSC were often replicated at different times of the day, we modeled a binary effect of time of day (dawn vs. dusk) on logit(p), to account for possible differences in visibility or parrot behavior between dawn and dusk counts. Models were fit in a Bayesian framework using gamma-distributed vague priors for λ and p parameters. We implemented models in the BUGS language (Lunn et al., 2000) running on JAGS (Plummer, 2003) with code adapted from Kéry and Royle (2016, chap. 6; Supplemental Material Appendix A). Regional-scale inference is based on draws from the posterior probability distribution of model parameters using an MCMC algorithm with three chains, 25,000 iterations and a burn-in stage of 5000 iterations.

Analysis of the whole-range data was based on the same model used for the regional scale, with some adjustments to model and data structure. We organized data into an array C with dimensions $S = 98$ sites, $R = 4$ counts, and $M = 2$ 'months'. The first 'month' of whole-range counts spans the period of late March to early May 2016, the second is May 2017. The main limitation of the whole-range data is lack of replicated counts within the same site and month outside WSC and one of the Misiones sites, i.e. in 87 out of 98 sites. While applying an N-mixture model to such data, we rely on information from only a few sites to infer detection probability everywhere else. This is not ideal but is the best we could do at present with the available data. To avoid demanding too much from limited information on detection we took two precautions. First, we simplified the detection model by estimating p as a constant value through time, across 'months'. Second, we included environmental information—area of remaining *Araucaria* forest—as a covariate of λ. We measured *Araucaria* forest as standardized cover in a circular buffer with 17 km radius around each roost, which amounts to an area of 907 km^2. We also tried buffer radiuses of 5 and 50 km in exploratory analyses, but elected to use a 17-km buffer because it corresponds to the longest single-day displacement recorded for radio-tagged VBPs (Prestes et al., 2014), and indeed resulted in the highest (positive) slope for the relationship between *Araucaria* cover and λ. *Araucaria* forest cover data resulted from the intersection of two maps: a map of the potential range of South American *Araucaria* Forest drawn by Hueck (1966) and georeferenced by Hasenack et al. (2017), and Ribeiro et al.'s (*in prep.*) map of existing Atlantic Forest remnants that are larger than 30-by-30 meters in area. To explore the consequences of the environmental covariate on our assessment of global population size, we built two alternative models, one without (*Model 1*) and the other with (*Model 2*) a year-dependent effect of *Araucaria* Forest cover on λ, the average roost population size. All regional-scale counts used in the whole range analysis were MR counts. As at the regional scale, we fit models in a Bayesian framework using vague priors. Whole-range inference was based on an MCMC algorithm with three chains, 50,000 iterations and a burn-in of 1000 iterations. At both regional and whole-range scales, we ran the MCMC until obtaining a value of the convergence criterion R-hat lower than 1.1 for all parameters.

To assess the Goodness of Fit (GoF) of our models, we applied leave-one-out cross-validation (Conn et al., 2018) and a Bayesian p-value approach (Gelman et al., 1996) on a chi-squared discrepancy statistic T. For both the regional and the whole-range analysis, the former indicated that our models predicted the observed counts about right on average, but the latter indicated severe overdispersion. The Bayesian p-value, reflecting the frequency with which discrepancy is higher for replicated data (T_{rep}) than for observed data (T_{obs}), was zero for both analyses. This was not unexpected, since parrots often travel in pairs, thus violating the independence assumption of the model. To accommodate this, we had experimented with the beta-binomial variant of the model developed by Martin et al. (2011) and Dorazio et al. (2013) for group-living animals, which yielded acceptable GoF results, but completely unrealistic (too high) abundance estimates. This 'good fit/bad prediction dilemma' (Kéry and Royle, 2016) is observed not rarely with N-mixture models and so far does not have a formal remedy.

Thus, we had to decide between choosing an analysis that ignored detection error (e.g., some GLMM; Barker et al., 2018) and a simple N-mixture model that accommodates that key consideration when estimating abundance, but resulting in lack of fit, or overdispersion. We conducted a simple simulation (see Supplemental Material Appendix B), where we simulated replicated counts that resembled our data in the regional analysis. Our simulation randomly varied the degree of overdispersion at the site-level in both λ and p, and of site-by-occasion level in p. We then analysed the data set using an intercepts-only N-mixture model that ignored the resulting lack of fit and estimated the total population size. As an alternative, p-ignorant method we simply added up the maximum count across sites. We simulated 1000 data sets and found that the root mean squared error (RMSE) of the overdispersion-naive N-mixture model was 25% reduced compared to the p-ignorant method of adding maximum counts. This led us to choose the formal estimation method of the N-mixture model.

To accommodate the additional uncertainty stemming from the lack of fit or overdispersion detected in the GoF test, we chose an ad hoc way of increasing the uncertainty in our estimates by 'stretching' the posterior distributions around their mean. This was motivated by the frequent adoption of variance inflation by some overdispersion factor c-hat in frequentist analyses of count data, see e.g., Chapter 5 in Cooch and White (2020) for Cormack-Jolly-Seber models. We estimated the degree of overdispersion c-hat by the ratio $T_{\text{obs}} / T_{\text{rep}}$, from above, at 5.6 for the regional and 5.8 for the whole-range scale. To make the posterior distributions more dispersed, we first subtracted from all posterior samples of a parameter its mean, multiplied the result by our estimate of c-hat and then added back the original mean. All uncertainty assessments such as posterior SDs or credible intervals were then based on this 'stretched' sample of the posterior of a parameter. In our simulation, the coverage of this approach for total abundance summed across roosts was on average only 0.67 and thus considerably lower than the nominal level of 0.95, but much better than the coverage of 'unstretched' CRIs would have been. Therefore, to be conservative, we chose the stretching procedure despite its lack of theoretical underpinning.

3. Results

Comparison of most reasonable (MR) and highly conservative (HC) results from the regional-scale data suggest a small but consistent difference between counts. Whereas MR counts were always greater than or equal to HC counts of the same roost and month, they were also less variable between replicates within the same roost and month (Supplemental Material Table S2). Accordingly, estimates of detection probability (p) tended to be higher for MR than for HC results; this was true in nine out of thirteen months for the whole WSC region (Table 1). Likewise, MR-based estimates of abundance tended to be more precise than their HC counterparts: roost and month-specific estimates based on MR counts were as precise or more precise than those based on HC counts in 95 of 130 cases (Supplemental Material Table S2). Spatial and

Table 1
Western Santa Catarina estimates of the number of Vinaceous-breasted Parrots (*N*) in all known roosts and the average probability (p_{dawn}) of detecting one parrot present at those roosts that were visited, at dawn, by month. Values preceded by the '±' sign are standard deviations of the posterior distribution of the parameter in question. Numbers in parentheses show the sum of the highest counts from each roost sampled in the corresponding month. MR and HC indicate estimates based on, respectively, 'most reasonable' and 'highly conservative' count results. Boldface numbers identify the highest *N* estimate of each year.

Month	*2015–2016*		*2017*	
	N	p_{dawn}	*N*	p_{dawn}
December (MR)	714 ± 92 (265)	0.87 ± 0.06		
(HC)	686 ± 106 (244)	0.78 ± 0.08		
January (MR)	1091 ± 190 (335)	0.69 ± 0.10		
(HC)	956 ± 183 (297)	0.68 ± 0.12		
February (MR)	**1826 ± 236 (696)**	0.67 ± 0.08	893 ± 90 (426)	0.68 ± 0.06
(HC)	1825 ± 270 (670)	0.63 ± 0.09	754 ± 87 (374)	0.70 ± 0.07
March (MR)	1364 ± 100 (639)	0.87 ± 0.03	1151 ± 121 (587)	0.78 ± 0.08
(HC)	1229 ± 99 (588)	0.91 ± 0.03	1175 ± 176 (529)	0.62 ± 0.10
April (MR)	1482 ± 173 (562)	0.61 ± 0.06	940 ± 98 (493)	0.79 ± 0.08
(HC)	1546 ± 218 (538)	0.53 ± 0.07	859 ± 131 (418)	0.70 ± 0.11
May (MR)	1522 ± 166 (997)	0.72 ± 0.10	**1896 ± 105 (1627)**	0.76 ± 0.06
(HC)	1755 ± 336 (965)	0.55 ± 0.13	1693 ± 74 (1517)	0.82 ± 0.05
June (MR)	1397 ± 89 (761)	0.80 ± 0.04	11,092 ± 121 (639)	0.64 ± 0.07
(HC)	1329 ± 91 (724)	0.78 ± 0.04	1100 ± 161 (588)	0.53 ± 0.09
July (MR)	655 ± 96 (321)	0.73 ± 0.09		
(HC)	580 ± 90 (286)	0.74 ± 0.10		

temporal variation is qualitatively similar between types of counts, with MR and HC counts resulting in the same maximum-abundance month (March 2017) and the same maximum-abundance roost (*Lebon Régis*). We also found a small but measurable effect of the time of day on detection probability, with dusk counts having detection probability on average 0.03 above dawn counts. The 95% credible interval of the negative 'dawn' coefficient excludes zero for both MR and HC data. For simplicity, we focus on MR results for any WSC-related content in the remainder of the paper.

Temporal variation in estimated abundance for WSC (summed across roosts) shows the lowest number of individuals in the two extremes of the non-reproductive period (Table 1): in December 2015, with an estimated 714 ± 92 individuals (posterior mean ± standard deviation), and in July 2016 with 655 ± 96 individuals. The highest aggregate WSC count (1627 individuals) and *N* estimate (1896 ± 105 individuals) were obtained in May 2017. Spatial variation among WSC roosts shows five of ten roosts – *Guatambu*, *Ipuaçu*, *Abelardo Luz*, *Água Doce* and *Lebon Régis* – reaching *N* estimates in excess of 200 at some point during the sampling period. All roosts showed substantial variation in *N* between months in both years, but there was no obvious synchrony in the temporal variation of the number of individuals at different roosts. As with the highest estimates of *N*, the lowest were obtained in different months depending on roost. For example, while *Água Doce* peaked in March 2016 and May 2017, *Guatambu* did so in April 2016 and February 2017. *Abelardo Luz* was the only roost that peaked both years in the same month, in June.

The posterior mean global abundance of VBPs varied slightly between models and years, but was always smaller than 10,000 individuals. *Model 1* estimated 7789 ± 655 individuals (95% Bayesian credible interval 6586–9184) for 2016, and 8483 ± 693 (7181–9977) for 2017. *Model 2* estimated 8012 ± 714 individuals (6779–9507) for 2016, and 9039 ± 779 (7641–10,677) for 2017. Estimates from *Model 2*, which includes a relationship between λ and *Araucaria* forest cover, were slightly higher than those from *Model 1*, but the 95% credible intervals from different models in the same year clearly overlap. Both counts and abundance estimates increased from 2016 to 2017, but there was overlap between 95% credible intervals of estimates from the same model in different years. The average probability of detecting a parrot that is present at a visited roost was 0.70 ± 0.05 under *Model 1* and 0.67 ± 0.05 under *Model 2*. There was a smaller difference between models within year than between years within model, but little statistical support for temporal change in global abundance. The positive effect (a logit-scale slope parameter) of *Araucaria* forest cover on λ, estimated by *Model 2*, differed between years and was higher in 2016 (0.43 ± 0.04) than in 2017 (0.16 ± 0.04). Such effects amount to a tripling of abundance as *Araucaria* cover increases from 20% to 80% of the buffer in 2016, but only to a 1.3-factor increase accompanying the same cover change in 2017.

The spatial distribution of *Model 1* abundance estimates across regions of the whole range (Table 2) reveals that Brazil accounted for

Table 2
Roosts visited, total number counted and Model 1 estimates of the number of Vinaceous-breasted Parrots in Argentina, Brazil, and Paraguay during the whole-range counts of 2016 and 2017. Estimates are given as mean ± standard deviation of the posterior distribution. Dashes denote absence of counts in the corresponding location and year.

Country	Region	2016			2017		
		Roosts visited	Count	M1 estimate	Roosts visited	Count	M1 estimate
Argentina	Misiones	7	252	426 ± 56	0	–	605 ± 78
Brazil	Espírito Santo	0	–	80 ± 23	1	2	28 ± 14
	Minas Gerais	5	58	336 ± 60	3	135	558 ± 70
	Paraná	16	803	2112 ± 198	17	805	2050 ± 205
	Rio Grande do Sul	6	335	717 ± 75	9	409	642 ± 71
	Santa Catarina	28	2324	3860 ± 285	31	2606	4197 ± 296
	São Paulo	3	93	164 ± 27	2	109	247 ± 35
Paraguay	Alto Paraná	3	23	94 ± 27	2	18	156 ± 36
Total		68	3888	7789 ± 655	65	4084	8483 ± 693

>90% of the estimated population size in both years. The Brazilian state of Santa Catarina had the highest number of roosts (41), as well as the highest estimated population size of all Brazilian regions, accounting for 50% of the total population in both years. Paraná had the second highest estimates among regions, accounting for approximately 25% of the total population. Looking at the spatial variation of abundance estimates per roost, Santa Catarina came out on top again, with an average of 94 to 102 individuals per roost. The highest number of individuals estimated at one site was 380 in 2016 and 390 in 2017. The two estimates came from sites approximately 180 km apart, both in Santa Catarina and both in May, towards the end of the non-breeding season. The spatial distribution of *Model 2* estimates was qualitatively similar to that of *Model 1*. We focus on Model 1 for simplicity and because it provides the most conservative abundance estimates.

4. Discussion

We developed a counting technique and associated statistical analysis to estimate VBP abundance at two spatial scales: regional and whole-range. Our approach sought to address five sources of uncertainty about parrot abundance related to range limits, roost density, movement between roosts, false positive—these addressed by our count technique, and false negative observations—addressed by our statistical analysis. Based on estimates of abundance for 2016 and 2017, we provide evidence that the global VBP population consists of a few thousand, but definitely not more than ten thousand individuals. Comparison between global abundance estimates from the two years reveals that even though average estimates were greater in 2017 than in 2016 under both models, there is no statistical evidence that such increase resulted from population growth.

Global population estimates are approximately twice the maximum number of individuals counted in whole-range counts (Table 2). Since never >70% of the total known roosts were counted, summed counts are bound to result in underestimates of the global population size. Nonetheless, we strongly emphasize that our estimates do not warrant proposing a category change for the species. The IUCN assigns threat levels based on a combination of five criteria (Mace et al., 2008). In order to qualify for one level, a species must meet conditions from any of the five criteria for that level. Thus, non-fulfillment of one criterion does not warrant category change. More specifically, non-fulfillment of the conditions under criterion C (Small population size and decline) would require examination of range and population dynamic conditions under the other criteria, which are beyond the scope and possibilities of our two-year analysis of roost counts. We suggest that the species should remain in the 'Endangered' IUCN threat category pending demographic studies and analysis of the conditions under criteria A, B, D and E. Ideally, given appropriate coverage of the species range and understanding of population dynamics, one should be able to assess an extinction risk for the species, which is demanded by criterion E.

The assessment of extinction risk can only be as good as the underlying estimates of population size. Our regional and global estimates point out some of the ways in which researchers can address sources of uncertainty when monitoring VBP and other parrots. At the broadest level, there is uncertainty about species' ranges. We tried to reduce uncertainty about the VBP range by searching for new roosts 8 days/year in WSC, which returned a 150% increase in the number of sampling sites over the 2 years of the study. We covered the northern half of WSC in more detail than the southern half, which has only one known roost (*Guatambu*; Fig. 2), because it has more *Araucaria* forest and a higher density of large ($\geq$5 km^2) forest patches; yet, judging from verbal reports and the distribution of sightings in WikiAves (Wikiaves, 2018) we believe there are more roosts to be found in the southern part of WSC. Only one-quarter of the counting sites in the whole-range counts were inside the IUCN range, showing that range uncertainty extends well beyond the limits of WSC (Fig. 1). The small areas suggestive of isolated populations in the IUCN Extant range (e.g., Fig. 1) may be part of larger areas of continuous use and may be useful starting points for improving knowledge about the species' distribution.

From the abundance estimates and the spatial distribution of roosts, it appears that the number of both roosts and individuals per unit area increases towards the interior of the distribution range (Fig. 1). Roosts with more than one hundred individuals counted are located in the three southernmost states of Brazil, in agreement with the pattern of higher densities towards the center of species' ranges reported by Brown et al. (1995) and Gaston (2009). The non-homogenous density of individuals also appears related to the distribution of *Araucaria* forest cover, which is centered in southern Brazil (Fig. 1) and offers VBPs an important food source during the autumn and winter months (Collar et al., 2017; Prestes et al., 2014; Tella et al., 2016). *Model 2* results suggest that the relationship between *Araucaria* forest cover and parrot abundance may change substantially through time, as it decreased by >50% from 2016 to 2017. Such change is likely due to variability in the amount, spatial distribution and temporal distribution of *Araucaria angustifolia* seed production (Mantovani et al., 2004). When *Araucaria* seed production coincides with winter-scarcity of alternative resources, *Araucaria* could become a more important food source and a stronger driver of VBP distribution.

Spatiotemporal variability in environment and demography necessarily lead to temporal variation in VBP distribution. Such dynamism is evident in WSC from the disappearance of VBPs from roost sites during the breeding season, and from the variation in roost estimates throughout the study (Supplemental Material Table S2). We estimated the lowest numbers of VBPs during December 2015 and July 2016 (Table 1)—the first and last months of the sampling period of 2016. Nonetheless, temporal variation of abundance was far from synchronous across roosts (Supplemental Material Table S2). Indeed, estimates for *São Domingos* and *Abelardo Luz* were lowest in January and March of 2016, respectively, neither month being the first or last of the sampling period. If individuals were breeding in surrounding areas and aggregating at centrally-located roosts for the non-breeding season, we would expect a gradual accumulation of individuals at all roosts with a peak in the middle of the non-breeding season. Instead, we observed irregular temporal variation in roost size, suggesting that VBPs move well beyond the immediate surroundings of one roost as they track resources during the non-breeding season (see also Forshaw, 2010; Prestes et al., 2014). As a result, individuals counted at one roost in a given month may very well be present at a different roost in another month. This is why we based our WSC estimate on the month with the highest estimate of each year (February 2016 and May 2017) and not on a sum of each roost's highest monthly estimate. Uncertainty about movement is also the reason behind concentrating monthly counts in as short a period as possible. We cannot be certain that VBPs don't move further than the reported maximum daily displacement of 17 km (Prestes et al., 2014); nonetheless, our own displacement between roosts was 2.6 times faster. Only two of the ten roosts (Ipuaçu and São Domingos) have two neighboring roosts within 30 km of distance, and these were always sampled on consecutive days minimizing the possibility of parrot movement between counts. Ideally, one would have different observers counting all the roosts at the same time, but barring that possibility we believe that our design is one acceptable compromise.

Two further sources of uncertainty originate within counts. These are double counting (false positive) and imperfect detection (false negative). They are more methodological in nature, but should also guide decisions of study design and data analysis for estimating population sizes. In parrot roost counts, double counting happens when observers overestimate the number of parrots in a flock, and when parrots move out of sight and are mistakenly counted as different individuals when they reappear. Our comparison of MR and HC results was an attempt to evaluate the consequences of being less or more conservative about the possibility of double counting. The consequences were negligible: 95% credible intervals of the MR and HC-based estimates for WSC

overlapped in all but one month (May 2017). In this month, the difference was 197 individuals. The tendency for higher precision in MR than HC estimates stems from a greater agreement among MR, than among HC results for the same roost and month. All else being equal, greater similarity of counts fed into an N-mixture model results in higher estimates of detection probability and therefore greater precision of the abundance estimate. This is no proof that MR counts are indeed closer to the true value, but it does support our reliance on the MR estimates. We suggest that by including MR and HC estimates in monitoring efforts for other parrots, researchers can assess the potential effects of double-counting on population estimates.

Despite all our efforts to surround the roosts, work with three-observer teams, and connect each team's observers by radio, the WSC counts taken by different teams at the same place and time still differed. This problem of imperfect detection cannot be completely eradicated, but it should be accounted for. Detection probability (p) was always estimated to be >0.6 on MR estimates, which is reassuring; however, its variation through time makes it clear that p can't be estimated once and subsequently used to correct all counts from then on. Researchers can address imperfect detection by replicating counts and estimating p during every time period for which they want to estimate N. Furthermore, the temporal variation in estimated p suggests that it is more than a simple function of observer experience. Part of the field team gained experience with the species, the sites, and the logistics over the course of the study in WSC, but p did not increase monotonically from the beginning to the end of the sampling period. Instead, p varied from month to month without any apparent trend, reaching its maximum in March 2016 and its minimum in April 2016 (Table 1). Detection at dawn was slightly (though measurably) lower than at dusk, likely due to mist forming more frequenly during the morning than in the afternoon, but such intra-day variation was an order of magnitude lower than the variation between months. We conclude that failure to detect parrots at roost counts is largely a matter of chance, weather, and unpredictable parrot movements—not a matter of observer experience.

The difference between the number of parrots estimated and counted over the whole range is not just due to the failure to detect some parrots at roosts that were visited. Only 69% of known roosts were visited in 2016 and 66% in 2017. The Bayesian MCMC-based implementation of our model accounts for this incomplete coverage by imputing values of N for each roost that was not visited, in agreement with the value of λ estimated across roosts for the corresponding year. Multiplying the coverage of 0.66–0.69 by the average detection probability of 0.67–0.70 estimated by models 1 and 2, one obtains products of 0.45–0.47, which approximate the ratios of counted to estimated individuals in Table 2. We thus conclude that the improvement of data quality for whole-range estimates should benefit more from increasing the number of sites surveyed than from attempting to increase detection at each roost, which may be beyond our control.

Habitat loss and nest poaching have caused alarming but poorly documented declines of many Neotropical parrot populations, including VBPs (Berkunsky et al., 2017; Ribeiro et al., 2009; Wright et al., 2001). Any efforts to protect these species will benefit from improved knowledge of population size and structure. We hope that our approach to estimating population size of VBPs in WSC and beyond will motivate others to obtain replicated counts of parrot roosts for this and other species and to improve on both our survey design and analyses. In an attempt to coordinate observers and gather count information for VBPs, we set up an online count-reporting tool where users can access existing data and contribute their own. The current version is available in Portuguese at: http://vivianezulian.azurewebsites.net. The uncertainty surrounding regional- and whole-range population estimates, however, is still high enough to justify employing a wide variety of observation techniques in monitoring Vinaceous-breasted, and other Neotropical parrots. On one front, citizen science networks such as WikiAves, Xeno-Canto, and eBird can offer valuable information for mapping species ranges and reproductive areas. On the other, molecular analysis of parrots across their range would help understand seasonal movements and the spatial structure of populations. Progress will require formal integration of different types of data into one statistical model of species distribution and abundance. Molecular data collection will require effective and safe techniques for obtaining parrot DNA without endangering the sampled individuals. Our study illustrates key sources of uncertainty about parrot abundance estimates, and how they can be addressed through monitoring protocols and statistical analysis. Critically, by addressing and estimating uncertainty, parrot monitoring efforts can move beyond minimum or average roost counts to a broader understanding of what we do and do not know about parrot numbers. On that basis, one can produce reliable assessments of population trends over time.

Credit author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary materials to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108672.

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