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Dissertação de Mestrado

Distribuição e abundância de *Amazona vinacea* (papagaio-de-peito-roxo) no oeste de Santa
Catarina

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Porto Alegre, dezembro de 2017

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Resumo

Esse trabalho oferece uma avaliação da abundância do papagaio-de-peito-roxo (*Amazona vinacea*) para 2016 e 2017, combinando contagens em dormitórios ao longo de toda a distribuição da espécie, em escala global, com amostragens replicadas em dormitórios na região oeste de Santa Catarina (WSC), em escala local, Brasil. As contagens em escala global resultaram em 3888 e 4066 indivíduos em 2016 e 2017, respectivamente. As estimativas para o WSC foram de 945 ± 50 e 1393 ± 40 para os mesmos dois anos. Não foi observada nenhuma evidência de crescimento populacional de 2016 para 2017, pois o acréscimo no número de indivíduos foi acompanhado por aumento do esforço amostral em ambas escalas. Quando extrapolamos a abundância no WSC para toda a área de distribuição da espécie, segundo a IUCN, e pressupondo densidade homogênea, obtivemos valores que estão acima da contagem na escala global, mas dentro da mesma ordem de magnitude. Nosso resultado oferece uma base sólida para afirmar que o tamanho populacional global de *A. vinacea* é de milhares de indivíduos, mas não dezenas de milhares. Realizamos um esforço sistemático para considerar as principais fontes de incerteza na estimativa de abundância da espécie. Cada contagem, tanto na escala local quanto na global, incluíram visitas em todos os dormitórios conhecidos dentro de um intervalo de 10 dias, evitando duplas contagens devido ao movimento dos papagaios entre dormitórios. No WSC, a abundância foi estimada usando um N-Mixture Model implementado em contexto Bayesiano. Apesar de nossa estimativa de tamanho populacional e de área de distribuição serem maiores do que as consideradas pela IUCN, sugerimos que *A. vinacea* permaneça na categoria “Em Perigo”, até que sejam realizados estudos sobre tendência populacional.

Palavras-chave: Psittacidae, contagem em dormitórios, detecção imperfeita, N-Mixture Model, espécie ameaçada, critérios da IUCN

Abstract

We offer an assessment of Vinaceous parrot (*Amazona vinacea*) abundance in 2016 and 2017, combining roost counts over the whole range of the species, with a replicated survey of roosts at the local scale, in western Santa Catarina state (WSC), Brazil. The whole range counts amounted to 3888 and 4066 individuals in 2016 and 2017, respectively. The WSC estimates were 945 ± 50 and of 1393 ± 40 individuals, for the same two years. We found no evidence of population growth from 2016 to 2017 because the increase in numbers is accompanied by an increase in observation effort both in WSC and at the whole-range scale. When extrapolating the WSC abundance estimate to the whole IUCN extant range of the species under the simplifying assumption of homogenous population density, we obtain values above the whole-range counts, but within the same order of magnitude. Such result offers a sound basis for putting the global population size of *A. vinacea* in the thousands of individuals, but not in the tens of thousands of individuals. We made a systematic effort to address key sources of uncertainty in parrot abundance estimation. Each count, at the local or whole-range scale, includes visits to all relevant roosts within less than ten days time to avoid double counting due to movement between roosts. At the local scale, we estimated abundance using an N-Mixture Model of replicated count data, implemented in a Bayesian framework. Even though we estimate a larger population size and a bigger geographic range than those currently reported by the IUCN, we suggest that *A. vinacea* should remain in the 'Endangered' IUCN threat category, pending further investigation of population trends.

Key-words: Psittacidae, Roost count, imperfect detection, N-mixture model, endangered species, IUCN criteria

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Introduction

Abundance is arguably the most important state variable in population biology (Gaston 1994); along with range size, it is the most evident correlate of extinction risk (Lawton 1995) and plays a central role in the assessment of any population management strategy (Caughley 1994; Norris 2004). Abundance is also 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 the 398 extant species of parrots, 112 (28%) are listed as threatened (i.e. Vulnerable, Endangered, or Critically Endangered), of which 88 are listed as in decline by the IUCN (BirdLife International 2016). The key causes of parrot population decline are habitat loss, due to deforestation and agricultural expansion, and nest poaching, due to the illegal pet trade (Wright et al. 2001; Olah et al. 2016).

While threatened species do not recognize national borders, environmental regulations do, so it makes sense to ask what countries can contribute most for protecting any given group. Brazil has the highest number of globally threatened parrot species (Olah et al. 2016), and among these, one of the least known, both in terms of organismal biology and population dynamics, is the Vinaceous-breasted Parrot (*Amazona vinacea*). Currently listed in the ‘Endangered’ category of threat, *A. vinacea* is restricted to the Atlantic Forest biome, with a geographic range that falls mostly within Brazil, with small areas of occurrence in the Argentinian province of Misiones and in eastern Paraguay (Cockle et al. 2007; Carrara et al. 2008; Segovia and Cockle 2012; Prestes et al. 2014). Despite an apparent association with the ancient Paraná Pine (*Araucaria angustifolia*; (Collar et al. 2017)), *A. vinacea* is

frequently observed foraging on other trees (Cockle et al. 2007) even when Paraná Pines are fruiting (Prestes et al. 2014); furthermore, its rather uncertain geographic range seems to go well beyond the limits of the Paraná Pine range (Cockle et al. 2007; Carrara et al. 2008). Uncertainty about the geographic range of the species is in large part due to parrot movements, which appear motivated by temporal variation in food availability but whose regularity has yet to be fully uncovered. Unpredictable movements make it difficult to anticipate where the animals are, or whether parrots seen in different places are the same or different individuals, presenting interesting challenges to the estimation of population size.

According to information compiled by the IUCN, the extant geographic range of *A. vinacea* covers an area of 145,700 square kilometers, from Paraguay, in the East, to southern Espírito Santo state, in the west (BirdLife International and Handbook of the Birds of the World 2016). This range consists of five large patches with tens of thousands of square kilometers each, and eleven small patches that have up to a few hundred square kilometers. The discontinuity reflects not only the species' true range, but also the scarcity of information about population structure and movements. Indeed, the IUCN recently updated the range map with a new 'possibly extant' layer that encloses all of the patches above. Part of the challenge in understanding the distribution and abundance of *A. vinacea* comes from its life cycle. Our field observations prior to this work suggest that breeding *A. vinacea* individuals disperse in pairs throughout the range between July and December. Towards the end of the breeding season, from December to January, they start congregating every evening in roosts that they may or may not use throughout the entire non-breeding period. The number of roosting individuals can vary over three orders of magnitude both between roosts and between different days at the same roost during the January-June non-breeding period. When August begins, there are virtually no parrots left at the roosts and the

population is once again dispersed across hundreds of nesting sites whose location is better known to nest poachers than to ornithologists. Despite the difficulty in counting parrots at a roost and the unpredictability of movements during the non-breeding season, roost counts are at present the most effective way of assessing the population size and delimiting the range of the species.

Roost counts can be obtained in many different ways but they always involve 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 in the area (Casagrande and Beissinger 1997). In order to improve knowledge of the distribution and abundance of *A. vinacea* from roost counts, one should approach these three tasks of locating, timing and counting roosts in a way that minimizes five key sources of uncertainty about the end result. The first and second sources have to do with locating roosts. First, there is uncertainty about the extent of *A. vinacea*'s distribution. When does an isolated patch in the range map represent an isolated population vs. an isolated observation of individuals that use a wide unmapped area? The second source is uncertainty about density of roosts at the local to regional scale. At what point should one stop spending resources on finding more roosts, versus dedicating time to studying the known roosts in detail? The third source of uncertainty pertains to the movement of individuals between roosts and conditions the timing of counts: if roosts or counting sites 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, then such movements have to be accounted for, or counts have to be simultaneous. The fourth and fifth sources of uncertainty relate to the counting technique itself, and address, respectively, false negative and false positive observations of *A. vinacea* individuals. A false negative, or detection failure, happens when

a parrot that is present at a site is not counted because it was not seen. A false positive happens when a parrot is counted twice by mistake.

This paper offers an assessment of *A. vinacea* 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 whole-range scale, we provide a global count of parrots observed in all *A. vinacea* roosts known to us, throughout the entire range of the species. At the local scale, we offer a statistical estimate of the number of *A. vinacea* individuals present in Western Santa Catarina (WSC). We chose to focus the local research on WSC because a) we know the area well, b) it sits between two important *A. vinacea* habitat areas in different countries (Misiones in Argentina and the Araucaria forests of Eastern Santa Catarina in Brazil), and c) being an area of intense agro-industrial activity with no previously published observations of *A. vinacea*, WSC has been left out of the species' IUCN extant map. To connect the local and the whole-range approaches we extrapolate our estimate of abundance in WSC to a global estimate of population size under the simplifying assumption of homogeneous density and compare the extrapolated result with the whole-range counts. The whole-range counts were obtained by a large number of volunteer observers with some variation in methodology; they give us a lower bound for the global *A. vinacea* population size. At the local scale we had closer control of the field methods, and our estimates seek to address all five sources of uncertainty listed in the previous paragraph. The problem of false absences is formally accounted for in the statistical modeling of WSC data; the remaining four sources are reflected in sampling design decisions and in the assumptions of the extrapolation from WSC to the global estimate. We discuss the implications of our results for the listing of *A. vinacea* as an endangered species.

Methods

Study area: Whole-range sampling took place over 59 sites spanning an area from northern *Minas GE* in the north to northeastern *Rio Grande do Sul*, in the south. This area extends west to (and includes) the northeastern Argentina region of Misiones and eastern Paraguay (Fig. 1). One quarter (15) of the count sites were located inside the *A. vinacea*'s IUCN extant range and the remainder (44) was outside. The majority of sites correspond to regularly used roosts, but some are points where parrots regularly fly over at dawn and dusk (Supplemental Table S1). All sites are located within the Atlantic Forest, defined by the southeast, Atlantic portion of the 'tropical and subtropical moist broadleaf forest' ecoregion in South America (Olson et al. 2001).

The local-scale study area was the western part of the Brazilian state of Santa Catarina (WSC; Fig. 2), a rectangle-shaped area of 34,000 km² (IBGE 2015) extending West-East between the Uruguay river (to the South) and the ridgeline that separates the Uruguay and Iguaçu watersheds (to the North). On its West and East ends, the area confines with two relevant patches of forest habitat, respectively, the Atlantic Forest of the Argentinian Province of Misiones, and the Araucaria forests of Eastern Santa Catarina (Fig. 2). Besides the strategic location, WSC is remarkable for having a surprisingly high frequency of *A. vinacea* sightings (Wikiaves 2008) 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, eucalyptus, and pine tree plantations (Fearnside 2001; Baptista and Rudel 2006). The nine WSC sampling

sites are a subset of the whole-range sites. They comprise all known *A. vinacea* roosts in WSC and they all coincide with tall (>10m) Araucaria forest patches. Four of the nine local sites (*Guatambu*, *Campo Erê*, *Abelardo Luz* and *Água Doce*) have very open to non-existent vegetation under the Araucaria canopy (Fig. 2).

Data collection: Sampling at the whole-range scale was carried out by 26 volunteer teams (Supplemental Table S1) coordinated by JM and NPP. Whole-range counts took place from April 29 to May 15, 2016 and from April 24 to May 15, 2017. Each team worked in areas that were familiar to its members, enabling us to cover the whole range in a relatively short period and thus minimize the possibility of double-counting between sampling sites. Of the total 59 sites, 20 were sampled only in 2016, 10 only in 2017, and 29 on both years (Supplemental Table S1). We visited sites at most once per year, counting parrots at the beginning or at the end of the day. Counts started at dawn (30 minutes before sunrise) or dusk (90 minutes before sunset) and lasted until we could not detect parrot movement into or out of the roost for 20 minutes—which always happens within two hours 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 two to ten observers who registered the number of parrots arriving or leaving the area, the flight direction, and the hour. 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.

Fieldwork at the local-scale was carried out by a single team coordinated by VZ. Sampling occurred in two sequences of monthly visits covering two consecutive non-breeding seasons: from December 2015 to July 2016, and from February to June 2016. Having just one team repeating procedures on the same sites inevitably allowed for a much tighter

control and coordination of field technique at the local than at the whole-range scale. On each visit, we spent a day contacting WSC residents and searching for roosts so that the number of sites sampled per visit increased from four to nine, as we discovered new roosts throughout the study period (Fig. 2). We could identify roosting trees on every site, even though occasionally, on some sites, we only saw parrots flying over, without being able to tell exactly where they perched for the night (e.g. *São Domingos, Palma Sola*). Visits lasted from four to eight days, during which we counted the number of individuals present at each site (or roost) between one and four times. Counts started at dawn or dusk, and lasted until we could not detect parrot movements, following the same times and criteria as prescribed for the whole-range counts. We visited every roost before the first count to establish three observation posts per roost, in strategic locations for observing the arrival and departure of parrots. Each count was performed by a team of three observers (one at each post), each equipped with a roost area map, a compass, an audio recorder, and a radio to communicate with other observers about parrots going their way. Every time an observer saw one or more *A. vinacea* individuals, 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 compare their notes and agree on one ‘most reasonable’ (MR) and one ‘highly conservative’ (HC) count result. The difference between MR and HC results 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 result is of eight individuals. Suppose further, however, that one of the observers in the trio heard calls of unseen moving parrots during the time that separates 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 who had left undetected and returned within sight. If that were the case, the HC count result 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 count results addresses one source of uncertainty about *A. vinacea* abundance estimates: the possibility that some animals may be counted more than once. There is, however, a second source of uncertainty that deserves attention, which is the possibility of detection failure, i.e. that some animals are not counted even though they are present at the roost. To address detection failure, we replicated our counts by working simultaneously with two teams of three observers, at the same roost and time. We placed two observers (one from each team of three) at each of the posts, keeping sufficient distance between observers to preclude overhearing radio communications. Furthermore, we ensured that observers from different teams did not exchange any information about their observations until the end of the meeting where each team separately agreed on its count results. We thus treat every team-specific count of a given roost and month, whether at dawn or dusk, as an independent sample of that roost for that month.

Data analysis: We statistically modeled the local-scale data to estimate abundances for each roost site and month using an N-mixture model (Royle 2004). We analyzed MR and HC counts as separate data sets, each summarized by a data array C with dimensions S by K by T , where $S = 9$, the number of roosts, $K = 4$, the maximum number of counts per roost in any visit, and $T = 14$, the number of sampling months. Elements C_{ijk} of this three-dimensional array give the number of parrots counted at the j^{th} count of the i^{th} roost in the k^{th} month, with $i = 1, \dots, S$, $j = 1, \dots, K$, and $k = 1, \dots, T$. The N-mixture model represents the number N_{ik} of individuals in roost i and month k as drawn from a Poisson distribution

with parameter λ_k . For simplicity, we drop the subscript k from the notation below, but we do model each month separately and therefore have monthly estimates of the Poisson parameter and of the number of parrots at each roost. The most straightforward implementation of Royle's (2004) model accounts for imperfect detection by modeling the counts C_{ij} as the result of a binomial sample with N_i independent trials and probability of success p (which also takes a different value every month). The Binomial distribution, however, implies that the probability p of detecting one individual parrot is independent of the other parrots; this would be reasonable if parrots moved about independently of each other, but they don't, they form groups of variable sizes where large, more noisy groups are easier to detect than small groups. To address this problem, we followed Martin et al. (2011)'s approach of modeling detection as a Beta-binomial distribution, with parameters N_i , p and ρ , where ρ is a correlation parameter that accounts for heterogeneity in detection probability. In practice, this solution amounts to using a Binomial distribution with a random p , which comes from a Beta distribution. In short, our model combines the biological variation of abundance among roosts with the sampling process of parrot detection:

$$N_i \sim \text{Poisson}(\lambda)$$

$$C_{ij} \sim \text{Binomial}(N_i, p, \rho).$$

We fit this model to each month's and to each type of count result (MR or HC) in a Bayesian framework, using non-informative priors. The model implementation used the BUGS language (Lunn et al. 2000) running on JAGS (Plummer 2003), using code adapted from Kéry and Royle (2015, chap. 6; Supplemental Appendix 1). To draw from the posterior probability distribution of the parameters, we used an MCMC algorithm with

three chains, 25,000 iterations and a burn-in of 5000 implemented in the software JAGS. All chains converged to $R\text{-hat} < 1.1$.

Even though the detection part of our local-scale model accounts for variation in detection probability between parrots of different-sized groups, it still assumes constancy of the detection parameters (p and ρ) among sites and counts of the same visit. We see this as a fair-enough assumption for the local-scale counts, which were always coordinated by the same individual, consistently applying the same technique. At whole-range scale, however, the sparsity of the data and heterogeneity of counting teams are such that we find it unreasonable to assume constancy of detection parameters. We believe this puts us too close to the limits of applicability of N-mixture models (Barker et al. 2017) and thus will present the whole-range count results as raw counts as they were reported by each team. The whole-range count for each year is the sum total of counts from all sites, including some of the local-scale counts from WSC. As an exercise, we divide the estimate of population size obtained at the local scale by the WSC area to obtain an estimate of WSC density, extrapolate this density estimate for the area of the whole range and compare the result with the whole-range count.

Results

The whole-range counts added up to 3888 and 4066 individuals, respectively, in 2016 and 2017 (Table 1). Due to logistic difficulties, the 2017 counts do not include numbers from Argentina and Paraguay. Brazil sites accounted for 93% of individuals in 2016, and the totality in 2017. The total number increased by 9% from the first to the second year, even though there were ten fewer sites visited in 2017 (68 sites) than in 2016 (78). If one accounts only for the sites that were visited in both years (Supplemental Table S1),

however, the total goes down by 16.3%, from 2938 in 2016, to 2460, in 2017. The distribution of counting sites extends well beyond the IUCN extant range of the species (Fig. 1), with three quarters (44) of the sites falling outside the area. The highest number of individuals counted at one site was 356 in 2016 and 364 in 2017. The two counts come from sites approximately 150 km apart, both in the Brazilian state of *Santa Catarina* and both from the month of May, toward the end of the non-breeding season. *Santa Catarina* had the highest subtotal count in Table 1, with more than 60% of individuals in both years; followed by *Paraná*, with approximately 20%, and Rio Grande do Sul, with 8-10%. *Santa Catarina* was also the state with the highest average number of parrots counted per site, on both years, with 111 individuals per site in 2016 and 174 in 2017.

The local-scale results were obtained in 13 field visits to WSC, eight during the first and five during the second year. We started out by sampling four roosts in December 2015, increased to five in February 2016, seven in May 2016, and nine in May 2017 (Supplemental Table S2). The *Lebon Régis* site was only visited during the whole-range count of both years. In total, we completed 179 roost counts, with an average of 2.2 counts per roost per trip (minimum of 1 and maximum of 4). Comparison of the MR and HC results from each count reveals that while MR values were always higher, as expected, they were also less variable (Supplemental Table S2). Accordingly, when fitting models to MR and HC results separately, estimates of detection probability (p) and the precision of abundance estimates (N) were generally higher for the MR than for the HC results. We will, for this reason, focus on the MR results in the remainder of the paper. We will refer to MR counts simply as ‘counts’, and specify ‘HC counts’ when we refer to the highly conservative results.

Looking at the aggregate of all roosts, we found the lowest number of individuals in the two extremes of the non-reproductive period (Supplemental Table S2; Fig. 3): in December 2015, with a maximum count of 265 and N estimate of 286 ± 8 , and in July 2016 with a maximum count of 321 and N estimate of 396 ± 22 individuals. The highest aggregate WSC count (1151 individuals) and N estimate (1393 ± 40 individuals) were obtained in May 2017. In 2016, the maximum aggregate estimate of N was 936 ± 40 individuals. The maximum aggregate estimate went up by almost 50% from 2016 to 2017, but if one accounts only for WSC roosts that were counted in both years, the maximum aggregate estimate, with respective standard error and 95% credibility interval, goes from 945 ± 52 [859, 1066] in 2016 to 1068 ± 44 [994, 1164] in 2017.

Five of the nine WSC roosts – *Guatambu*, *Ipuacu*, *Abelardo Luz*, *Água Doce* and *Lebon Régis* - reached 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. The lowest, as the highest N , were obtained in different months depending on the 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. Looking at the spatial distribution of roosts in Figure 2, and the distribution of N estimates in Supplemental Table S2, it becomes apparent that, in 2016, the northeast of the study area (*Abelardo Luz* and *Água Doce*) concentrated between 56 and 90% of the population during the last three months of the sampling period. However, this tendency was not apparent in 2017, when the same roosts concentrated between 31 and 34% of the population during May and June.

Considering the area of WSC and the 95% credibility interval for the maximum aggregate estimate of abundance in each year ($N = 945 \pm 50$ [859, 1066] in February 2016, and $N = 1,393 \pm 40$ [1323, 1477] in May 2017), we estimate the density of *A. vinacea* in WSC to be between 0.025 and 0.031 individuals per square kilometer in 2016, and between 0.039 and 0.043 in 2017. Extrapolating this density to the entire area of the IUCN extant geographic range ($\sim 145,700 \text{ km}^2$), we obtain an estimated global population size of 4050 individuals in 2016 (c.i. = [3681, 4568]) and of 5969 (c.i. = [5669, 6329]) individuals in 2017.

Discussion

We estimate a WSC population size of 945 ± 50 *A. vinacea* individuals in 2016 and 1393 ± 40 in 2017. These values, extrapolated to the entire IUCN extant range of the species, result in average global population estimates of 4,050 individuals in 2016 and of 5969 in 2017.

Comparing with the whole-range counts, the extrapolation for 2016 exceeds the whole-range count of 3888 by 162 individuals, yet its 95% credibility interval of 3681 to 4568 includes the whole-range count by a wide margin. In 2017, the extrapolated whole-range estimate of 5969 individuals exceeds the whole-range count of 4066 by almost 50% with a credibility interval of [5669, 6329], which excludes the whole-range count. Despite the differences between methods and years, the whole-range counts and the extrapolated estimates are all within the same order of magnitude, providing strong evidence that the *A. vinacea* global population consists of thousands, yet not tens of thousands of individuals.

The WSC population estimates and the whole-range counts, as well as the extrapolated whole-range estimates, increased from 2016 to 2017. We find no evidence, however, that such change is a result of population growth. The increase is largely due to the addition of two new roosts to the WSC sample, one of them (*Ipuacu*) with more than 300 individuals

estimated for 2017. There is an almost 50% increase between years in the WSC estimate, with non-overlapping credibility intervals; however, when we compare yearly estimates based on data from the same seven roosts that were sampled in both years the posterior mean increases by less than 15%, with widely overlapping credibility intervals. Likewise, the whole range count, which goes up by 4.6% when all sites are summed, goes down by more than 16% if one accounts only for sites that were counted on both years. We conclude that the increase in estimates from 2016 to 2017 is due mostly to improved coverage of the species range and stress the importance of further improving coverage.

The IUCN criterion C for the classification of species in the ‘Endangered’ threat category states that a species should be considered endangered if its population is ‘estimated to number fewer than 2500 mature individuals’ *and* it fulfills either of two conditions about inferred population trend (BirdLife International 2001). Given the short temporal scope of our study, we will not examine the trend conditions, but we can ask whether the 2016 and 2017 population is below the threshold of 2500 mature individuals. To do this, we must specify what proportion of the estimated population consists of mature individuals. From the IUCN’s range of ‘precautionary’ numbers for total and mature population size, we derive a range of proportions of mature individuals from 0.60 to 0.68. If, taking the midpoint of that range, one considers a proportion of 0.64 and multiplies that proportion by the 2016 and 2017 whole-range results, the estimate of the number of mature individuals becomes 2488 in 2016 and 2602 in 2017, both very close to the IUCN threshold. Applying the same reasoning to the extrapolated results, the global number of mature individuals becomes 2592 with a 95% c.i. of 2430 to 2754 in 2016, and 3820 with a 95% c.i. of 3582 to 4059 in 2017. The 2017 extrapolation exceeds the threshold, but precaution suggests it is no sound basis for proposing a category change. For one, the number is based on the

assumption of homogenous density throughout the range and on a guessed mature/immature ratio of approximately 2:1. We apply this ratio for consistency with the IUCN, but we have not found a demographic analysis of the *A. vinacea* that supports this or any other choice. Furthermore, the IUCN attributes 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 either of the five criteria for that level. Non-fulfillment of the conditions under criterion C requires examinations of range and population dynamic conditions under the other criteria, which are beyond the scope of this abundance study. We suggest that the species should remain in the ‘Endangered’ IUCN threat category pending a study of population growth, 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.

Clearly, the assessment of extinction risk can only be as good as the underlying estimates of population size. Our estimate for WSC and its extrapolation are far from perfect, but they address a variety of sources of uncertainty that ought to be accounted for as formally as possible in future monitoring efforts. At the broadest level, there is uncertainty about the range of the species, both within and beyond WSC. We tried to reduce this uncertainty within WSC by dedicating eight days in each year to searching for new roosts. The effort returned a 125% increase in the number of sampling sites over the duration of the study, but we covered the northern half of the region in more detail than the southern half, which has only one known roost (*Guatambu*; Fig. 2). One should expect more roosts in the north, because it has more *Araucaria* forest and a higher density of large ($\geq 5 \text{ km}^2$) forest patches; yet, judging from the distribution of sightings in WikiAves (Wikiaves 2008) and verbal

reports from the area, we believe there are more regular roosting sites to be found in the southern part of WSC. Considering that many Vinaceous Parrots detected in this study were observed outside the IUCN range, uncertainty about range extends well beyond the limits of WSC. The small dots suggestive of isolated populations in the IUCN range map (Fig. 1) may be a useful starting point for improving knowledge about the species distribution. Most of these dots are likely part of larger areas of continuous use by *A. vinacea* individuals.

A second source of uncertainty is the possible variation in density (individuals per unit area) across the species' range. This is particularly relevant to our extrapolated global estimate, as mentioned above, because the validity of the extrapolation relies on the assumption of homogenous density. There are two good reasons to question this assumption. The first is that densities tend to be low at the edge of distribution ranges (Brown et al. 1995; Gaston 2009). Such pattern is supported by the relatively lower counts found in Argentina and Paraguay (Cockle et al. 2007; Segovia and Cockle 2012) when compared with those of eastern Santa Catarina (Prestes et al. 2014) . A second reason is the substantial difference in number of known roosts per unit area (roost density) between WSC and the IUCN range. Roost density may give a biased impression of individual density because the number of individuals counted per roost varies over three orders of magnitude (Supplemental Table S1); nonetheless, roost density numbers weigh against the homogeneity assumption because there are, on average, many more roosts per unit area in the IUCN range than in WSC. Dividing the IUCN area by the 59 whole-range sites outside WSC (most of which are roosts), one obtains an average of $2,5 \times 10^3$ km² per site in the IUCN range; in WSC, the corresponding area is bigger, at $3,8 \times 10^3$ km². In light of this information, if the number of individuals per roost is sufficiently stable across the range,

our extrapolation should be an underestimate of the true global population. Since the whole-range counts do not correct for imperfect detection and estimates of detection probability range from 0.64 to 0.89 (Table 2), the sum of counts is likely to be an underestimate as well. Lacking more robust information about population density outside WSC, we find it reasonable to draw a first estimate of global population size based on the assumption of homogenous density. It is important, however, that this first estimate is taken as what it is—a rough approximation. Replication of counts within short periods over a larger part of the species range will certainly help account for geographic changes in density and improve knowledge of global population size.

Homogenous or non-homogenous, the distribution of *A. vinacea* individuals throughout the species's range is certainly dynamic. Such dynamism is unequivocally supported by the disappearance of individuals from roosts during the breeding season and by the variation in WSC roost estimates throughout the study (Supplemental Table S2). This brings up a third source of uncertainty, about movement of individuals between roosts, which we tried to address in this work. We estimated the lowest numbers of individuals on all WSC roosts in December 2015 and July 2016 (Table 2), the first and last months of the sampling period of 2016, but the variation of abundance through time (Supplemental Table S2) was far from synchronous across roosts. Indeed, the roosts at *São Domingos* and *Abelardo Luz* had their lowest estimates in January and March in 2016, respectively—not at the extremes of the sampling period. If there were a gradual accumulation and subsequent loss of individuals from all roosts with a peak somewhere in the middle of the non-breeding period, we would be inclined to believe that each roost aggregates individuals that breed in the surrounding area. The irregularity of temporal variation in roost size, however, suggests that *A. vinacea* individuals probably 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 counts in as short a period as possible, both in our monthly WSC counts and in the whole-range counts.

So far, we discussed three sources of uncertainty that are mostly biological in nature – uncertainty about range limits, about spatial distribution of abundance, and about movements between roosts. Another two sources of uncertainty – double counting and detection failure – are more methodological in nature, but they also guided relevant decisions of our study design and data analysis. In the context of this study, 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 consideration of MR and HC counts was an attempt to evaluate the consequences of being less or more conservative about the possibility of double counting. The consequences were negligible: the 95% credibility intervals of the MR and HC-based estimates for WSC overlapped in all but six months (March, June and July of 2016; February, April and May of 2017). In those months, the difference was on average 82 individuals, with a standard deviation of 58.6. The tendency for higher precision in MR than HC estimates stems from a greater agreement among MR, than among HC counts of the same roost and month. This is no proof that MR counts are indeed closer to the true value, but it does strengthen our reliance on the MR estimates.

The second methodological source of uncertainty is the recurrent failure to detect some of the parrots that are present at a site. Despite all our efforts to surround the roosts, work with three-observer teams, and connect observers within each team by radio, the counts taken by different teams at the same place and time still differed. We believe that this is not a problem to be eradicated—as it cannot possibly be—but to be accounted for. It is reassuring to see that detection probability (p) was estimated to be always greater than 0.6, but its variation through time makes it clear that detection failure can't be measured once and used to correct all the counts from then on. Under our modeling approach at the local-scale, the fact of $p < 1$ should be addressed by replicating counts and estimating p during every time period for which we want to estimate N . It should be noted that p did not go up monotonically from the beginning to the end of the WSC sampling period, as part of the field team got more experienced with the species, the sites, and the logistics. On the contrary, p varied from month to month without any apparent trend, reaching its maximum in March 2016 and its minimum in April 2016 (Table 2). This suggests that detection failure is not just a matter of observer experience, but also a matter of atmospheric conditions, observer luck, and unpredictable parrot movements.

The very real pressures of habitat loss (Ribeiro et al. 2009) and nest poaching (Wright et al., 2001) caused an obvious but poorly documented decline of the *A. vinacea* population. Any efforts to protect the species will benefit from improved knowledge of population size and structure. We hope that our approach to estimating population size in WSC will motivate others to obtain replicated counts of roosts elsewhere in the species range. In an attempt to coordinate observers and gather count information, 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 local and global population estimates, however, is still high enough to justify monitoring the species with a wide variety of observation techniques. On one front, citizen science networks such as WikiAves, Xeno-Canto, and eBird can offer valuable information for mapping the species range and reproductive areas. On the other, molecular analysis of parrots across the range can help understand seasonal movements and the spatial structure of the population. Progress on both fronts will require formal integration of different types of data into one statistical model of the species distribution and abundance. Any progress on the molecular front will require development of effective and safe techniques for obtaining *A. vinacea* DNA without endangering the sampled individuals.

Acknowledgments

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Tables and figures

Table 1. Number of parrots counted in Argentina, Brazil, and Paraguay during the whole-range counts of 2016 and 2017. Cells with dashes denote changes in the distribution of effort. In 2017 we added point counts in *Espírito Santo* but were not able to cover Argentina and Paraguay.

Country	Region	Number Counted	
		2016	2017
Argentina	Misiones	252	–
Brazil	Espírito Santo	–	2
	Minas Gerais	58	135
	Paraná	803	805
	Rio Grande do Sul	335	409
	Santa Catarina	2324	2606
	São Paulo	93	109
Paraguay		23	–
TOTAL		3888	4066

Table 2. Estimated number of WSC individuals (N) and their detection probability (p), by month, for the aggregate of all roosts sampled. The numbers in parentheses show aggregate count, based on the sum of the highest count of each roost for the corresponding month. The two rows per month separate estimates based on the ‘most reasonable’ (MR) and the ‘highly conservative’ (HC) count results. Boldface numbers identify the highest N estimate of each year.

Month	2016		2017	
	N	p	N	p
December	(MR)	286±8 (265)	0.87±0.03	
	(HC)	275±11 (244)	0.79±0.03	
January	(MR)	440±28 (335)	0.69±0.04	
	(HC)	387±28 (297)	0.67±0.05	
February	(MR)	945±52 (696)	0.67±0.03	544±19 (426)
	(HC)	954±56 (670)	0.62±0.04	463±18 (374)
March	(MR)	678±9 (639)	0.89±0.01	696±27 (587)
	(HC)	611±7 (588)	0.92±0.01	719±41 (529)
April	(MR)	729±28 (562)	0.64±0.02	559±18 (493)
	(HC)	750±35 (538)	0.58±0.03	498±22 (418)
May	(MR)	936±33 (790)	0.77±0.03	1393±40 (1151)
	(HC)	1006±50 (758)	0.64±0.03	1195±27 (1060)
June	(MR)	840±13 (761)	0.81±0.01	891±42 (639)
	(HC)	797±13 (724)	0.81±0.01	917±57 (588)
July	(MR)	396±22 (321)	0.74±0.04	
	(HC)	353±19 (286)	0.75±0.04	

Figure 1. Extant geographic range of *Amazona vinacea* according to the IUCN Red List of Threatened Species (dark gray), our local-scale study area of Western Santa Catarina (light gray), and the whole-range count sites for 2016 and 2017. Diamonds represent sites visited only in 2016, triangles only in 2017, and filled circles in both years. For ease of representation, sites located less than fifteen kilometers from each other are shown by only one symbol.

Figure 2. Local-scale study area of Western Santa Catarina (light gray) and regional forest cover (dark gray). Dark gray areas represent every patch of forest (excluding tree farms) with more than five square kilometers, according to the Brazilian Ministry of the Environment's *Mapa de Cobertura Vegetal dos Biomas Brasileiros* (MMA 2007). The 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 (*Ipuacu*), AL (*Abelardo Luz*), AG (*Água Doce*) and LR (*Lebon Régis*).

Figure 3. Monthly estimates of the number of *Amazona vinacea* individuals in WSC in 2016 and 2017 according to the 'most reasonable' (MR) count results. Error bars show 95% credibility intervals around the estimated number of individuals.

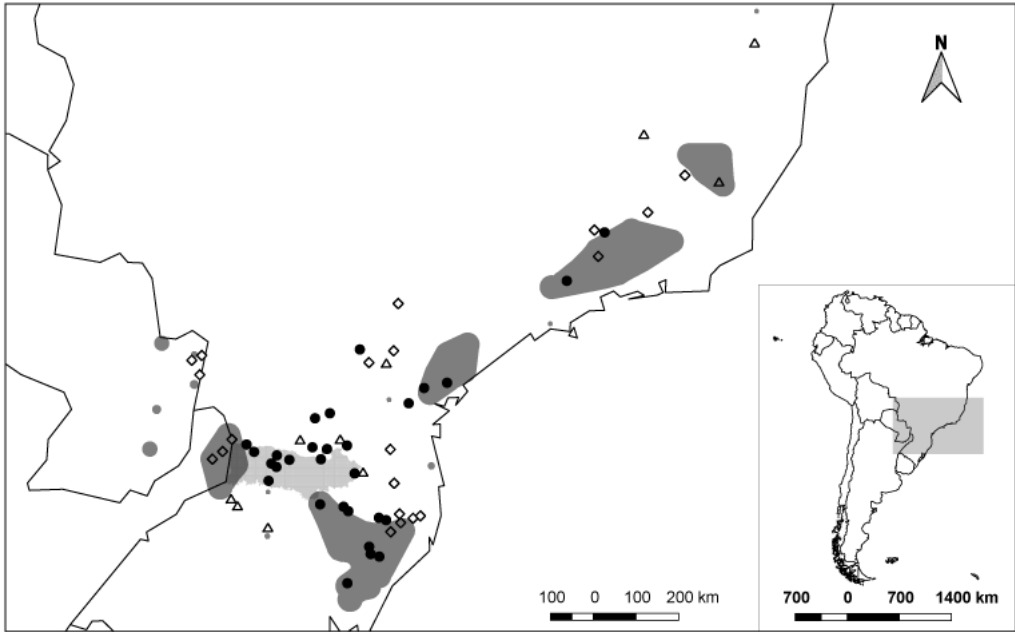


Figure 1

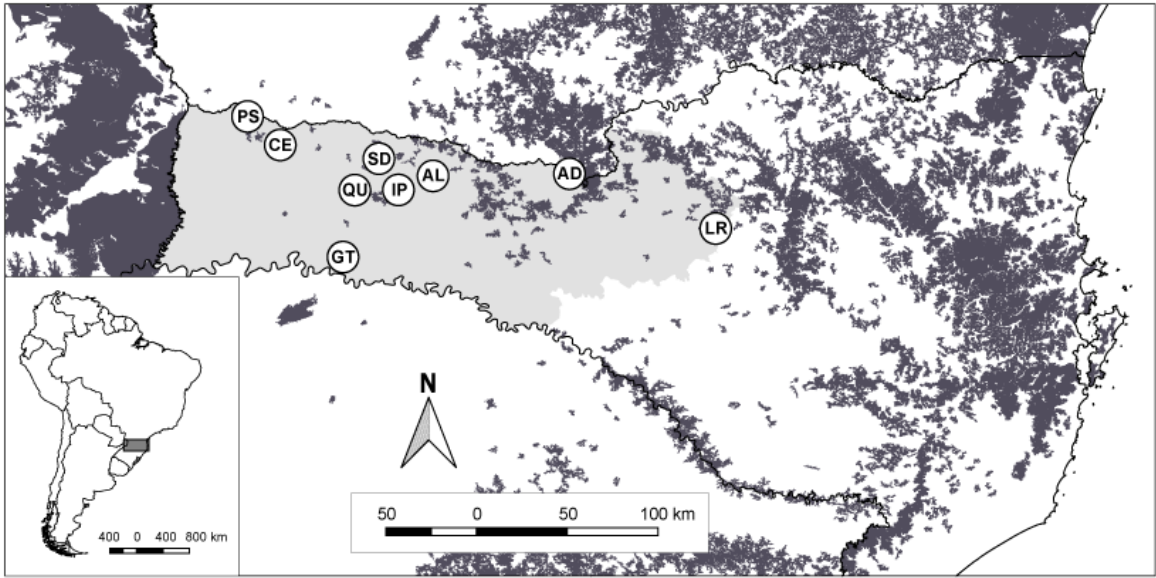


Figure 2

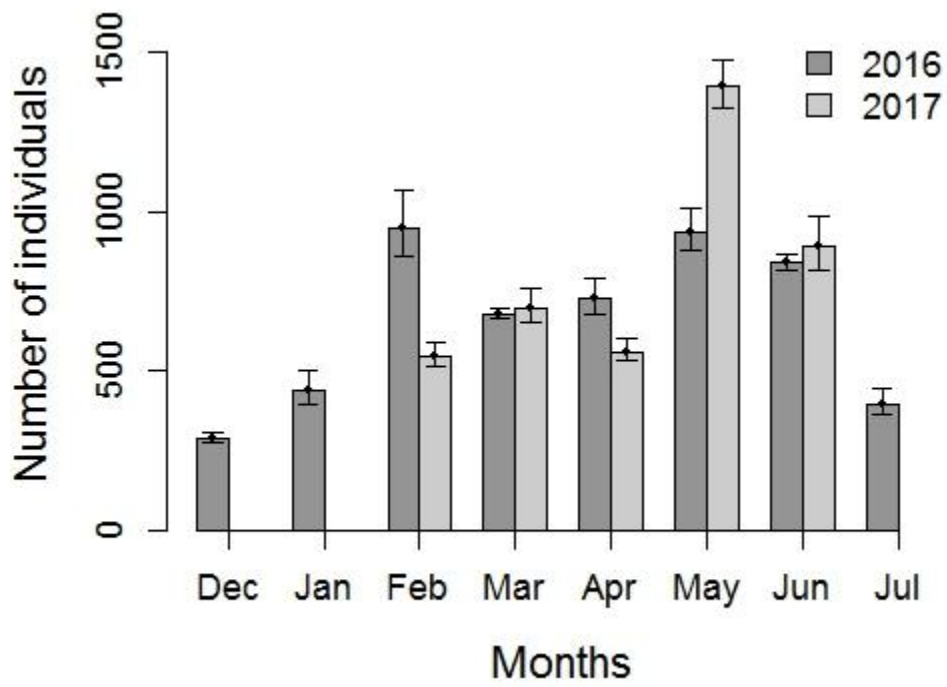


Figure 3

Supplemental Information

Supplemental Table S1. Whole-range count sites by country and region, with team leader, type of record (R = Roost, F = Flyover site), and the year sampled. Sites located within less than 15 kilometers from each other were grouped under the same heading identified by a whole number; it is the headings that are represented on Figure 1.

Country and Region	Site	Team leader	T	Year Sampled	
				2016	2017
ARGENTINA					
Misiones	1. San Pedro	KC	R	X	
	1.1 San Pedro – Cerro Suizo	KC			
	1.2 San Pedro – Parque A	KC			
	1.3 San Pedro – Parque B	KC			
	1.4 San Pedro – Terminal	KC			
	1.5 San Pedro – Centro	KC			
	2. San Pedro	KC	R	X	
	2.1 San Pedro – Cruce Caballero A	KC			
	2.2 San Pedro – Cruce Caballero B	KC			
	2.3 San Pedro – Cruce Caballero C	KC			
	2.4 San Pedro – Cruce Caballero D	KC			
	2.5 San Pedro – Cruce Caballero E	KC			
	2.6 San Pedro – Tobuna A	KC			
	2.7 San Pedro – Tobuna B	KC			
	2.8 San Pedro – Fernandes	KC			
	2.9 San Pedro – Victor Prestes	KC			
	3.0 San Pedro – Santa Rosa	KC			
	3.1 San Pedro – Amadeu dos Santos	KC			
	3.2 San Pedro – Teresa Oliveira	KC			
3. Irigoyen	3.1 Irigoyen A	KC	R	X	
	3.2 Irigoyen B	KC			
BRAZIL					
Espírito Santo	4. Dores do Rio Preto	Tatiane Pongiluppi	F		X
Minas Gerais	5. Minas Gerais	Sérgio Carvalho	F	X	
	6. Carrancas e Minduri	Kassius Santos	F	X	X
	7. Paipendi	Manu	F	X	
	8. Santo Antônio do Grama	Leonardo Miranda	F	X	
	9. Luminárias	Kassius Santos	F	X	
	10. Serra do Cipó	Lucas Carrara	F		X
	11. Crisólita	Marina Somenzari	F		X

Supplemental Table S1: (cont.)

Country and Region	Site	Team leader	T	Year Sampled	
				2016	2017
Paraná	12. General Carneiro	NPP and JM	F	X	X
	12.1 Bituruna	NPP and JM			
	12.2 General Carneiro B	NPP and JM			
	12.3 General Carneiro C	NPP and JM			
	12.4 General Carneiro D	NPP and JM			
	12.5 General Carneiro E	NPP and JM			
	13. Curitiba	Roberto Boçon	F	X	X
	13.1 Curitiba B	Romulo da Silva			
	13.2 Curitiba C	Rafael Sezerban			
	13.4 Curitiba D	Roberto Boçon			
	13.5 Curitiba E	Roberto Boçon			
	13.6 Curitiba F	Rafael Sezerban			
	14. Bocaiúva do Sul	Elenise Sipinski	R	X	X
	14.1 Bocaiúva do Sul B	Romulo da Silva			
	14.2 Tunas do Paraná	Roberta Boss			
	14.3 Bocaiúva do Sul/Tunas do Paraná	Pedro Scherer-Neto			
	14.4 Bocaiúva do Sul C	Patricia Serafini			
	15. Castro/Pirai do Sul/Jaguariaíva	Tony Teixeira	R		X
	16. Jaguariaíva	Tony A. Bichinky	R	X	
	17. Tibagi	Romulo da Silva	F	X	
	17.1 Tibagi B	Romulo da Silva			
	18. Coronel Domingos Soares	NPP and JM	F		X
	19. Inácio Martins	NPP and JM	R	X	X
	20. Palmas	NPP and JM	F	X	X
	21. Pinhão	NPP and JM	F	X	X
	22. Telêmaco Borba	Roberto Boçon	R	X	X
	23. União da Vitória	NPP and JM	F		X
	23.1 Porto União	NPP and JM			
Rio Grande do Sul	24. Barracão	NPP and JM	R	X	X
	24.1 Sarandi	NPP and JM			
	25. Coqueiros do Sul	NPP and JM	F		X
	26. Canela	NPP and JM	R	X	X
	27. Bom Jesus	NPP and JM	R	X	X
	28. Bom Jesus B	NPP and JM		X	X

Supplemental Table S1: (cont.)

Country and Region	Site	Team leader	T	Year Sampled	
				2016	2017
Rio Grande do Sul	29. São José dos Ausentes	NPP and JM	R	X	X
	30. Miraguaí	NPP and JM	F		X
	31. Dois Irmãos da Missão	NPP and JM	F		X
Santa Catarina	32. Cerro Negro	NPP and JM	R	X	X
	32.1 Abdon Batista	NPP and JM			
	33. Abelardo Luz	VZ and ESM	R	X	X
	33.1 Passos Maia	Vanessa Kannan			
	33.2 Ponte Serrada	Vanessa Kannan			
	34. Água Doce	VZ and ESM	R	X	X
	35. Anitápolis	NPP and JM	F	X	
	36. Anitápolis B	NPP and JM	F	X	
	37. Bom Retiro	NPP and JM	F	X	
	38. Campo Belo do Sul	NPP and JM	R	X	X
	39. Campo Erê	VZ and ESM	R	X	X
	40. Entre Rios	VZ and ESM	R	X	X
	40.1 Ipuacu	VZ and ESM			
	41. Guatambu	VZ and ESM	R	X	X
	42. Irineópolis	NPP and JM	F	X	X
	43. Itaiópolis	NPP and JM	F	X	
	44. Lebon Régis	NPP and JM	R	X	X
	44.1 Lebon Régis B	NPP and JM			
	44.2 Lebon Régis C	NPP and JM			
	44.3 Lebon Régis D	NPP and JM			
44.4 Lebon Régis E	NPP and JM				
44.5 Lebon Régis F	NPP and JM				
44.6 Lebon Régis G	NPP and JM				
44.7 Lebon Régis H	NPP and JM				
44.8 Lebon Régis I	NPP and JM				
45. Lorentino	Miguel Angelo Biz	F	X		
46. Palma Sola	Paulo A. Neto, VZ e ESM	R	X	X	
47. Urupema	NPP and JM	R	X	X	
47.1 Urupema	NPP and JM				
47.2 Pained	NPP and JM				

Supplemental Table S1: (cont.)

Country and Region	Site	Team leader	T	Year Sampled	
				2016	2017
Santa Catarina	48. São Joaquim	NPP and JM	R	X	X
	48.1 Painei	NPP and JM			
	49. Quilombo	VZ and ESM	R	X	X
	50. Santa Cecília	NPP and JM	R		X
	50.1 Santa Cecília B	NPP and JM			
	50.2 Santa Cecília C	NPP and JM			
	51. São Domingos	VZ and ESM	R	X	X
	52. Urubici	NPP and JM	R	X	
	53. Urubici	NPP and JM	R	X	
	São Paulo	54. Timburi	Fernando Zurdo	F	X
55. São Paulo		Fernando Zurdo	F	X	X
56. Campos do Jordão		Luís Fábio Silveira	F	X	X
PARAGUAI					
Canindeyú	57. Refúgio Biológico Carapá	AL	F	X	
	58. Reserva Privada Itabó Rivas	AL	F	X	
Alto Paraná	59. Reserva Biológica de Limoy	AL	R	X	

Supplemental Table S2. Monthly counts and estimates of the number of individuals in each roost throughout the study period based on ‘highly conservative’ (HC) and ‘most reasonable’ (MR) count results. Numbers in parentheses show the highest count for the corresponding roost and month. Roost order in the table is longitudinal from East to West. The Abelardo Luz, Campo Erê, Ipuacu, Quilombo and Lebon Régis roosts have fewer months of data because they were discovered after the beginning of the sampling period.

Year	Month\Roost	Palma Sola	Campo Erê	Guatambu	Quilombo	São Domingos	Ipuacu	Abelardo Luz	Água Doce	Lebon Régis	
2016	December	(MR)	12±2 (10)	-	165±4 (155)	-	83±3 (75)	-	26±1 (25)	-	
		(HC)	12±2 (8)	-	157±5 (143)	-	81±4 (71)	-	25±2 (22)	-	
	January	(MR)	87±7 (65)	-	222±11 (175)	-	27±6 (10)	-	104±7 (85)	-	
		(HC)	73±7 (53)	-	194±11 (158)	-	25±6 (10)	-	95±7 (76)	-	
	February	(MR)	133±9 (101)	-	194±12 (141)	-	104±8 (77)	-	140±13 (77)	374±16 (300)	-
		(HC)	132±10 (94)	-	195±13 (137)	-	107±9 (75)	-	149±14 (77)	371±17 (287)	-
	March	(MR)	74±2 (68)	-	60±2 (51)	-	31±2 (25)	-	19±2 (14)	494±4 (481)	-
		(HC)	66±2 (63)	-	50±2 (47)	-	27±2 (24)	-	16±1 (14)	452±4 (440)	-
	April	(MR)	28±5 (5)	-	244±9 (197)	-	58±4 (39)	-	77±6 (48)	322±9 (273)	-
		(HC)	36±7 (5)	-	252±11 (191)	-	63±5 (35)	-	78±8 (42)	321±11 (265)	-
	May	(MR)	41±5 (25)	41±4 (25)	61±5 (40)	-	75±5 (58)	-	135±6 (114)	208±7 (184)	375±8 (344)
		(HC)	52±7 (21)	53±7 (24)	71±8 (36)	-	74±8 (45)	-	147±9 (110)	213±10 (178)	396±11 (344)
	June	(MR)	5±2 (0)	5±2 (0)	41±3 (29)	-	33±3 (24)	-	449±5 (433)	307±5 (275)	-
		(HC)	5±2 (0)	5±2 (0)	38±3 (26)	-	31±3 (22)	-	428±5 (409)	290±5 (267)	-
July	(MR)	37±3 (31)	57±4 (46)	20±3 (12)	-	57±4 (45)	-	168±7 (143)	57±4 (44)	-	
	(HC)	34±3 (30)	46±4 (37)	15±3 (8)	-	53±4 (42)	-	157±7 (131)	48±4 (38)	-	
2017	February	(MR)	174±6 (131)	23±2 (17)	201±6 (184)	-	54±5 (32)	-	64±4 (42)	28±3 (20)	-
		(HC)	152±6 (124)	22±2 (17)	166±6 (150)	-	41±4 (25)	-	60±4 (42)	23±2 (16)	-
	March	(MR)	199±7 (177)	27±4 (18)	153±7 (125)	-	68±5 (54)	-	203±7 (174)	46±4 (39)	-
		(HC)	196±9 (162)	38±6 (18)	167±10 (118)	-	64±7 (41)	-	200±10 (155)	54±7 (35)	-
	April	(MR)	155±5 (135)	28±2 (23)	175±6 (157)	-	42±3 (35)	-	134±5 (122)	25±3 (21)	-
		(HC)	144±6 (126)	30±3 (22)	130±6 (113)	-	36±4 (23)	-	133±6 (115)	25±3 (19)	-
	May	(MR)	50±5 (34)	35±4 (20)	185±7 (147)	39±5 (25)	43±5 (27)	329±8 (289)	266±7 (242)	171±7 (132)	275±8 (235)
		(HC)	42±3 (34)	28±3 (20)	153±5 (135)	26±3 (19)	30±3 (22)	304±6 (280)	207±5 (193)	146±5 (122)	259±6 (235)
	June	(MR)	123±5 (84)	44±8 (5)	119±7 (84)	34±5 (12)	77±7 (45)	16±5 (2)	352±8 (320)	126±8 (87)	-
		(HC)	113±8 (81)	57±10 (5)	126±9 (77)	38±7 (8)	86±9 (41)	23±7 (0)	341±11 (295)	133±10 (81)	-

Supplemental Appendix 1: BUGS language specification of the model used in estimating *Amazona vinacea* abundance in Western Santa Catarina. The model was based on Royle (2004) and Kéry and Royle (2015), adapted according to Martin et al. (2011) to include a Beta-Binomial distribution for detection probability. See references in main text.

```

library (jagsUI)

sink("modell.txt")
cat("
model{

## Priors
lambda ~ dgamma(0.001, 0.001)
alpha.p ~ dgamma(0.01, 0.05)
beta.p ~ dgamma(0.01,0.05)
p ~ dbeta(alpha.p, beta.p)      # p follows a beta distribution

## Biological model for true abundance

for(i in 1:site){              # loop over sites
N[i] ~ dpois(lambda)          # estimate of the true abundance

## Observed data at replicated counts
for(j in 1:visit){            # loop over visits in each site
data1[i,j] ~ dbin(p, N[i])    # counts follow a beta-binomial
distribution
} # counts
} # sites

## Derived quantities
totalN <- sum(N[])            # Estimate total population size across
all sites
p.derived <- alpha.p/(alpha.p+beta.p)    # derived detection
probability
rho.derived <- 1/(alpha.p+beta.p+1)      # derived correlation
coefficient
}

",fill = TRUE)
sink()

## Initial Values
Nst <- apply(data1, 1, max, na.rm=TRUE)
inits <- function(){list(N=Nst)}

## Params monitored
params <-
c("lambda","totalN","N","alpha.p","beta.p","p","p.derived","rho.derive
d")

## MCMC settings
nc <- 3
nb <- 5000
ni <- 25000
nt <- 20

## Call JAGS
fm2 <- jags(bugs.data, inits, params, "modell.txt", n.chains = nc,
n.thin = nt, n.iter = ni, n.burnin = nb) #run model
print(fm2, dig = 2) #print results

```