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REVIEW ARTICLE



Revisiting methods for estimating parrot abundance and population size

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ABSTRACT

Estimating abundance and population size is essential for many ecological and conservation studies of parrots. Achieving these goals requires methods that yield reliable estimates, but parrot traits can make them difficult to detect, count, and capture. We review established and emergent sampling and analytical methods used to estimate parrot abundance and population size, focusing on their assumptions, requirements, and limitations. Roost surveys are cost-effective if all roost locations in a region are known and stable, which is uncommon. Capture–recapture methods incorporate detection probability, but capturing, marking and resighting parrots can be difficult. Distance sampling estimates detection probability and surveys multiple species simultaneously, but is sensitive to the spatial distribution of individuals and excludes birds in flight. Roadside transects can cover large areas and survey multiple species, but habitats near roads may differ from the surrounding areas, biasing abundance estimates. Occupancy surveys and hierarchical models usually require spatially and temporally replicated datasets. Both allow estimation of detection probability; the former dispenses with count data, while the latter is a versatile set of methods that can incorporate multiple processes influencing detection and abundance. Finally, passive acoustic surveys can sample multiple species simultaneously, but identification of vocalisations can be difficult and time-consuming.

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Introduction

Estimating the size of wild populations is essential for quantifying population dynamics and the impacts of different threats, identifying species that require protection, and developing effective management plans and sustainable harvesting targets (IUCN 2016). Given limited funding and the urgency of many conservation undertakings, estimating population size and abundance (i.e. local population size) requires efficient and affordable survey techniques.

Parrots have long been threatened due to extensive habitat loss and fragmentation, persecution, and over-exploitation for the pet trade (Beissinger and Bucher 1992; Tella and Hiraldo 2014; IUCN 2016; Olah *et al.* 2016). Researchers have used information on parrot abundance to understand habitat use (e.g. Mac Nally and Horrocks 2000; Marsden *et al.* 2000; Nunes and Galetti 2007), impacts of natural disturbances (Wunderle 1995), population dynamics (e.g. Beissinger *et al.* 2008), proportions of breeding to non-breeding populations (Tella *et al.* 2013), seed dispersal (Baños-Villalba *et al.* 2017), and how parrots affect ecosystem structure and function (Blanco *et al.* 2015). However,

reliable information on population sizes and trends is lacking for nearly all the world's *ca.* 400 species of parrots (IUCN 2016), and knowledge on how abundance varies in space is even scarcer (Marsden and Royle 2015). Although several methods for estimating abundance and population size exist, their effectiveness differs because parrot behaviour may often violate the basic assumptions of statistical approaches traditionally used (Casagrande and Beissinger 1997).

Twenty years ago Casagrande and Beissinger (1997) evaluated four methods for estimating parrot population size (roost counts, mark-resight surveys, and point and line transects). Their study provided a methodological evaluation that helped many researchers design and carry out their studies of parrot populations (e.g. Rivera-Milán *et al.* 2005; Berg and Angel 2006; Matuzak and Brightsmith 2007), and instigated further investigations (e.g. Marsden 1999; Cougill and Marsden 2004; Legault *et al.* 2013). Since 1997, technological advances have allowed researchers to carry out new types of surveys (e.g. Alquezar and Machado 2015; Figueira *et al.* 2015), while novel statistical methods have dramatically increased the toolbox for analysing survey data from wild populations (Nichols *et al.* 2009).

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We revisit the basic problem facing most parrot researchers – how to accurately estimate abundance and population size – in the context of these new advances. First, we consider how the behaviour and ecology of parrots inform the choice of survey and analytical methods, and how they induce variation and error for different survey methods. Then, we review how methods evaluated by Casagrande and Beissinger (1997) have been applied and developed, and highlight emergent survey and analytical approaches to estimate parrot abundance and population size, focusing on the assumptions, requirements, and limitations of each method. Our aim is to inform parrot researchers of these advances and their limitations so that research and conservation budgets are used effectively, and to ensure that vital conservation efforts are based on the best available information.

Parrot traits hinder estimation of abundance and population size

Parrot populations are challenging to survey for several reasons. Some challenges relate to traits that make parrots difficult to detect, count, or capture, while others are linked to the manner in which parrots use and move in the environment. While none of the challenges are unique to parrots, the combination of traits and behaviours makes parrots difficult to detect or unavailable to be counted.

The probability that a parrot is detected during a survey can be considered as the product of four conceptually different components (Nichols *et al.* 2009). The first two components – the probability that its home range or territory partly overlaps a sampling unit (spatial sampling) and the probability that it is present during the survey (presence) – are related to spatial coverage. Parrots are highly mobile and generally do not have all-purpose territories (Forshaw 2010). They often have large home ranges and perform long-distance daily movements between nesting, roosting, and foraging areas. Such movements affect the spatial coverage of parrot surveys because usually the sampling area is small relative to the movements of the species. Individuals may regularly use a surveyed site but be absent at the time of the survey, visiting part of their home range outside of the sample unit. This circumstance, often termed ‘temporary emigration’ or ‘temporary absence’, generates false absences in counts (Chandler *et al.* 2011). Moreover, these movements are highly variable throughout the year, as parrots often track the seasonal availability of their food resources (Renton *et al.* 2015) and, in some species, communal

roosts often change locations (Casagrande and Beissinger 1997).

Seasonal changes in parrot behaviours also affect population and abundance estimations. Some species (e.g. the Red-spectacled Parrot *Amazona pretrei* and Swift Parrot *Lathamus discolor*) perform long-distance, seasonal movements (Forshaw 2010). If surveys are performed at the onset or end of such displacements, when part of the population has already left or arrived, only a portion of the population will be present to count. Whether or not these absences are considered to be false depends on the survey objectives (e.g. whether the goal is to sample the entire population, or the portion that has not yet migrated or arrived). Similarly, during the breeding season, individuals may remain in the nest to incubate or guard, so will not forage socially or join communal roosts, and will less likely be encountered and counted (Luna *et al.* 2017).

The other two components affecting parrot detection are the probability that an individual present during a survey gives a visual or auditory cue and is therefore available for detection (availability), and the conditional probability that available birds are detected (perceptibility). The product of these terms is the overall detection probability (Nichols *et al.* 2009). The gregarious and loud behaviour of most parrot species makes them more easily detected than other groups of medium- and large-sized tropical forest birds, such as raptors, toucans, trogons, or guans. However, as for other bird species, the detection probability of parrots is also influenced by habitat structure (e.g. open savannahs vs. dense cloud forests), time of day (which influences visibility and parrot activity), group size, weather, distance to the observer, and variation between observers (Buckland *et al.* 2001). These factors cause ‘detection error’ or ‘imperfect detection’ – decreasing the probability of detecting individuals – and result in low counts and false absences (Dénes *et al.* 2015).

Parrots often congregate in large flocks and roosts. While this may increase detection probability for the group (i.e. large flocks are noisier and easier to see from afar), it makes accurate tally of the number of individuals more difficult, increasing error in counts and leading to underestimation of group size at larger distances (Buckland *et al.* 2001).

Finally, capturing and marking parrots is difficult (Beissinger and Bucher 1992). Most parrots nest in elevated cavities in trees or cliffs that are difficult to find, reach, and monitor. Capturing parrots outside of their nests is challenging, since most species usually fly high over the canopy and avoid traps, although trapping can be successful at foraging sites (Pires *et al.* 2016). Parrots typically have strong bills and can

remove plastic bands or crush aluminium bands on their legs, leading to injuries. This necessitates using combinations of coloured stainless steel bands or numbered polyvinylchloride (pvc) bands to individually mark most parrots (Meyers 1995). Moreover, the short, hourglass-shaped tarsi of most parrots reduce the number of bands that can be placed on a leg and hinders identification at distance. Senar *et al.* (2012) developed a marking method consisting of a numbered tag hung on a neck collar, and employed it to monitor invasive Monk Parakeets (*Myopsitta monachus*) and Ring-necked Parakeets (*Psittacula krameri*) in Barcelona, Spain. They found a low percentage of tag loss (4.5% and 5.8%, respectively), and neck collars had no adverse effects on individuals of either species. The method has also been tested on amazons and macaws with promising results (Tella unpub. data).

Traditional approaches for estimating parrot abundance and population size

In this section, we review traditional methods to survey and estimate parrot abundance and population size, with a focus on their limitations, assumptions and requirements. We note that methods can be used for estimating abundance (i.e. local population size), density (abundance per area unit), relative abundance indices, or the overall population size (the term ‘census’ is sometimes loosely applied in this case). The latter often relies on extrapolation of local estimates over large areas, and usually implies additional assumptions, which we also discuss below.

Roost surveys

Roost surveys have been used to estimate abundance when parrots are widely dispersed (e.g. Gnam and Burchsted 1991; Casagrande and Beissinger 1997; Pithon and Dytham 1999; Downs 2005; Matuzak and Brightsmith 2007; Burnham *et al.* 2010), and are especially useful to estimate population size when the local and even global populations seasonally concentrate into a few communal roosts (Martinez and Prestes 2008; Tella *et al.* 2013; Pacifico *et al.* 2014; Luna *et al.* 2017). This method requires previous fieldwork to locate the roosts, often facilitated by local knowledge since roost sites are sometimes used for decades (e.g. Martinez and Prestes 2008). Individuals are counted as they enter or leave the roosts around sunset or sunrise, usually by several observers stationed at one or more vantage points. Flock size, time of arrival or departure, and flight direction of birds as they enter or leave roosts are often recorded to reduce double counting

of individuals by different observers (Gnam and Burchsted 1991). For some species (e.g. genus *Amazona*), the size of flocks arriving in roosts may also allow identification of pairs and family groups to make inferences about the proportion of breeders (Berg and Angel 2006; Matuzak and Brightsmith 2007).

Roost sizes vary due to seasonal changes in parrot behaviour, since numbers may diminish gradually as the breeding season advances when breeders roost in nests, and may sharply increase after young fledge. Seasonal changes in the spatial distribution of food resources can also alter roost sizes and locations. Numbers tend to increase when food supply in the surrounding area is high, but may decrease when food supply is more dispersed (Matuzak and Brightsmith 2007; Martinez and Prestes 2008). Cold and rainy weather can also reduce roost sizes for some species because a greater proportion of birds may spend the night in their nest cavities to reduce energy expenditure (Cougill and Marsden 2004). The presence and proximity of neighbouring roosts may also increase daily variation in the counts of the focal roost.

An important factor influencing the ability to accurately observe and count parrots entering or leaving roosts is visibility. Studies have identified significant differences in the time required for parrots to leave roosts in the morning or arrive in the evening (Cougill and Marsden 2004; Matuzak and Brightsmith 2007), which are important because a longer period might mean that some individuals leave or arrive when light levels are too low to allow detection. On the other hand, if too many individuals leave or arrive simultaneously, it may be difficult to accurately count them. Differences in flight behaviour between morning and evening can also affect accuracy of counts. Dawn counts were more accurate for a roost of Red-lored Amazons (*A. autumnalis*) because birds flew closer to the ground than at dusk (Berg and Angel 2006). Naturally, weather (e.g. fog or rain) can drastically impair visibility. In addition, parrots often move around and repeatedly enter and leave the roost, especially in the evenings (Gnam and Burchsted 1991).

Although dawn and dusk roost counts may be equivalent for some species (e.g. Downs 2005; de Moura *et al.* 2010), evidence indicates that this should not be assumed a priori, and that the period most favourable for surveying varies among species, even within a genus (*Amazona*; Cougill and Marsden 2004; Berg and Angel 2006; Matuzak and Brightsmith 2007). Thus, prior to establishing protocols, researchers should evaluate the best period for surveys, considering flight patterns, the time it takes for birds to leave from or arrive at roosts, and the size of

flocks. A simple strategy to reduce double-counting and the count error induced by movement within roosts is to delineate a 'buffer zone' (e.g. a circle of radius ~50 m around the roost centre). Only movements into and out of this space are recorded, and birds leaving are subtracted from the count of birds that entered (Cougill and Marsden 2004).

The potential for high seasonal variation in roost size means that, if the objective of the study is to assess long-term trends, surveys should take place at a similar time of year across sites, with the caveat that breeding seasons can vary between years and locations (Cougill and Marsden 2004). High daily variation in roost size also needs to be accounted for to interpret trends. Cougill and Marsden (2004) tested different counting regimes, and found that a random selection of dates over the month (5–10 days) or counts over successive days (5 days) performed better at estimating roost size than returning to the roost periodically (every 4th day) within the same period. When daily variations are caused by movements of individuals among roosts, this caveat can be avoided if all roost sites can be located – and surveyed simultaneously.

When roost surveys are employed to estimate abundance for a specific area, it is assumed that all roosts in the area are found and sampled. This can be quite difficult, especially when roosts are small, numerous, and change location often (Casagrande and Beissinger 1997). Roost monitoring should be done at a time of year when roosts are stable and birds are sedentary (Cougill and Marsden 2004), which seems to vary among species. For example, roosts of *Amazona* parrots (Gnam and Burchsted 1991; Cougill and Marsden 2004; Berg and Angel 2006; Matuzak and Brightsmith 2007; de Moura *et al.* 2010) appear to be larger and more stable than those of Carnaby's Cockatoo (*Calyptorhynchus latirostris*; Burnham *et al.* 2010) and Green-rumped Parrotlets (*Forpus passerinus*; Casagrande and Beissinger 1997). Determining the 'catchment area' (Cougill and Marsden 2004) of individuals using known roosts in a region with telemetry may be an alternative to finding every roost for estimating population size. Averaging of the catchment area values would allow estimation of the expected number of roosts in the region (number of roosts = total area/average roost area), and the population size could then be estimated by multiplying the expected number of roosts by the average roost size, with appropriate error terms (Casagrande and Beissinger 1997). Moreover, if roosts are surveyed multiple times in periods during which the number of individuals is assumed to be closed, *N*-mixture models and extensions (see below) may be used to obtain population size estimates while accounting for factors affecting detection and abundance.

Mark-resighting surveys

Mark-resight methods used for estimating wildlife abundance (McClintock *et al.* 2014) have rarely been applied to parrots, given the difficulties in capturing and resighting them once marked with combinations of coloured bands. Moreover, the assumption of conventional mark-resighting methods that the marked population is known may be violated due to partial band loss and mortality/emigration of parrots banded in previous years. Casagrande and Beissinger (1997) used a variation of the method for a closed population with an unknown number of marked individuals proposed by Arnason *et al.* (1991) to estimate the abundance of Green-rumped Parrotlets. Resighting data were collected by walking random transects, with surveys limited to 5 days to ensure population closure (i.e. population sampled is closed with respect to mortality, recruitment, immigration, and emigration). The main shortcoming of this mark-resighting method was the large effort necessary to attain precision, because of the low number of observations obtained during the short survey periods (Casagrande and Beissinger 1997). Veran and Beissinger (2009) used a simpler approach to estimate population size over the entire breeding season, following Nichols *et al.* (1994), that corrected the number of marked breeding and non-breeding individuals counted by their resighting rates, which can differ greatly (Sandercock *et al.* 2000).

Analytical methods can address some of these limitations. McClintock and Hoeting (2010) developed a Bayesian binomial logit-normal mixed-effects model that uses data augmentation (*sensu* Royle *et al.* 2007) for estimating abundance when sampling is without replacement (i.e. individuals may only be sighted once per sampling occasion) and the number of marked individuals is unknown. Unlike the method of Arnason *et al.* (1991), this model allows for individual heterogeneity in resighting probabilities. The method is based on a robust sampling design in which surveys are done over one or more primary intervals, within each of which the population is assumed to be closed, and each primary interval is composed of several sampling occasions. The approach performed well in simulations and with real passerine datasets. Sample sizes (25 and 23 marked individuals sighted, respectively; McClintock and Hoeting 2010) were similar to those in Casagrande and Beissinger (1997), but the confidence intervals obtained were 4–10 times narrower.

The identification of individuals marked with combinations of colour bands is often difficult when they are detected during sighting surveys (Casagrande and Beissinger 1997). This major limitation of parrot mark-

resight surveys may be overcome by using numbered patagial tags (Smith and Rowley 1995) or neck collars (Senar *et al.* 2012), which can be read using telescopes from distances of up to 140 m (J. L. Tella pers. obs.). In any case, the incomplete identification of marked individuals is potentially a major source of bias in mark-resight abundance estimators, particularly when there is individual heterogeneity in sighting probability, and ignoring sightings of unidentified marked individuals does not solve the problem (McClintock *et al.* 2014). Fortunately, the new method presented by McClintock *et al.* (2014), based on complete data likelihood and data augmentation, accounts for uncertainty when incomplete individual identifications occur and allows for individual heterogeneity in detection, sampling with or without replacement, and an unknown number of marked individuals. This approach performs well when the probability of identifying an observed marked individual is <90%, individual sighting heterogeneity is non-negligible, and sample sizes are small (McClintock *et al.* 2014).

Other developments of mark-resight surveys that may show promise for parrot studies include spatially explicit models for inference about density in partially marked populations (Chandler and Royle 2013), and a spatial mark-resight model augmented with telemetry data (Sollmann *et al.* 2013).

Distance sampling (DS) using point counts and line transects

A common approach to estimate parrot abundances and densities is to conduct point count or line transect surveys using DS (e.g. Lambert 1993; Casagrande and Beissinger 1997; Marsden 1999; Marsden *et al.* 2000, 2016; Rivera-Milán *et al.* 2005; Lee and Marsden 2012; Rodríguez *et al.* 2012). Distance sampling methods estimate abundance under the hypothesis that detectability is related primarily to the distance between animals and the observer (Buckland *et al.* 2001). The distribution of distances from the observer to detected individuals is used to estimate a detection function, which is modelled to decline with increasing distance from the point or transect line (distance = 0). This function, together with the average group size, allows estimation of abundance and density (dividing abundance by the sampled area) at the point or along the transect line. Extensions of DS models also allow modelling of covariate effects on detection (Marques and Buckland 2003) and abundance (Johnson *et al.* 2010).

Distance sampling is one of the most used methods to estimate wildlife abundance, and relies on six central

assumptions: (i) individuals on the line or point are detected with certainty; (ii) individuals are detected at their initial locations and do not move in response to the observer before detection; (iii) measurements of distances from the point or transect line to detected individual(s) are exact; (iv) the position of detected individuals is independent of the survey point or line; (v) cluster sizes are recorded without error; and (vi) detections are independent events. Violations of these assumptions may result in biased estimates (Buckland *et al.* 2001), and they may frequently be violated when surveying parrots (Casagrande and Beissinger 1997). Parrots are often detected while flying and vocalising in flocks as they move between locations. Including such individuals in survey counts violates multiple premises discussed above and will overestimate density generated from DS (Buckland *et al.* 2008). Thus, flying birds should be excluded from density estimation, but that often limits detections, especially when surveying open habitats and making canopy counts. Many parrots inhabit forests where visibility is poor, hindering their detection, and their cryptic coloration often inhibits detection until they are disturbed by the observer and move. Marsden (1999) suggested a large number of points was required for uncommon species (e.g. 2000), and even this might not be sufficient for rare species. Finally, accurate enumeration of cluster size can be difficult for large flocks of parrots, especially if they are composed of mixed species (Chapman *et al.* 1989).

Taken together, these limitations suggest that researchers should be prudent in their application of distance sampling for estimating parrot population size. Marsden *et al.* (2016) suggested using encounter rates as a surrogate for density estimation derived from point counts for parrots. *N*-mixture models discussed below may offer another option.

Roadside transects

Roadside transects are useful for sampling very large areas, which is advantageous because increasing spatial representation helps accounting for the large home ranges, mobility, and scarcity of many parrot species. Two or more observers usually drive slowly (20–40 km/h) through unpaved or secondary low-traffic roads, during the hours of maximum parrot activity (Tella *et al.* 2013). When parrots are detected, stops are made if needed to identify the species and count individuals, resulting in data that can be interpreted as an abundance index (i.e. number of recorded individuals per km surveyed) that does not account for detectability. This method has been applied in many surveys of species that naturally occur in low densities, such as

raptors (e.g. Sanchez-Zapata *et al.* 2003; Carrete *et al.* 2009), waterfowl (Pagano and Arnold 2009), wild turkeys (Butler *et al.* 2007), and also parrots (Tella *et al.* 2013, 2016a; Blanco *et al.* 2015). Habitat composition and configuration near roads may differ from the surrounding areas (Buckland *et al.* 2008), thus biasing the estimates of abundance and compromising their extrapolation to larger areas. On the other hand, road survey data are less problematic when used to estimate differences in parrot abundance among land uses (Tella *et al.* 2013), seasons (Tella *et al.* 2016b) or species within single habitats (Tella *et al.* 2016a), especially when abundances differ to the point that they overcome sources of sampling error (i.e. differences in detectability among species or land uses).

Rigorous survey design and analysis may increase the reliability of abundance indices derived from roadside transects. New statistical methods for temporally replicated surveys can account for presence, availability and detection processes over large areas, and the single-visit method may also prove useful (see sections below). On the other hand, DS may still be useful in road surveys to account for detectability loss due to distance, depending on the roads, habitats and parrot species surveyed (Blanco *et al.* 2015; Baños-Villalba *et al.* 2017). Roadside abundance indices and abundance estimates derived from DS were obtained simultaneously for two parrot communities from very different habitats (Andean dry forests; Blanco *et al.* 2015; and flooded Amazonian savannahs; Baños-Villalba *et al.* 2017, with 6823 and 734 km surveyed, respectively), resulting in highly correlated values for both communities (Spearman correlations, $r_s > 0.9$; Tella *et al.* 2016a). More research is needed to ascertain to what extent roadside abundance indices can be considered as a surrogate of actual parrot densities.

Potential for applying recent statistical and technological advances

In this section, we consider new options for estimating parrot abundance and population size based on recent statistical or technical advances. Most have yet to be tested with parrots, or have received few applications to date. We think they offer important opportunities if applied thoughtfully.

Estimating abundance from occupancy surveys

MacKenzie *et al.* (2002) and Tyre *et al.* (2003) developed occupancy models with temporally replicated surveys of detection and non-detection data to estimate the portion of sites occupied (i.e. containing ≥ 1

individual), while estimating site-level detection probability (i.e. the probability of detecting at least one individual at a site). Note that this probability of detection differs from the individual-level detection probability. If individuals are detected independently, under binomial sampling these two probabilities can be related (equation 1 in Royle and Nichols 2003). Royle and Nichols (2003) proposed a method (hereafter, the RN model) to estimate abundance from binary observations of detection and non-detection of the species at a site, assuming that site-specific detection probabilities are functionally dependent on local abundance. In other words, it obtains information about local abundance directly from the apparent heterogeneity in detection probability among sites actually induced by variation in abundance (Royle and Dorazio 2008)

In the RN model, the detection frequencies for each site, defined as the number of times the species was detected in the repeated samples, are assumed to follow a binomial distribution with number of trials equal to the number of temporal replicates, and the site-specific detection probability, which depends on the unknown underlying abundance, specified as a Poisson-distributed random variable. Measurable covariates that may influence detection at the individual level and abundance can be added to the model. We believe this method may prove to be a useful addition for estimating parrot abundance, especially for surveys when distance measurements are imprecise and/or when there is ambiguity in the number of birds detected.

Hierarchical (N-mixture) models for unmarked populations

Hierarchical modelling is an extremely versatile approach for analysing count data and estimating abundance and detection probability of marked and unmarked populations while incorporating different processes influencing these quantities (Kéry and Royle 2016). In their simplest forms, hierarchical abundance models handle variation in the observed count data as a result of explicit observation and state process components. The approaches for unmarked populations generally require temporally and spatially replicated surveys combined with DS or ancillary covariate data.

The basic N -mixture model for count data combines a binomial GLM (for the observed counts) and a standard count model (Poisson or negative binomial GLM). It assumes that the population sampled is closed during the sampling period (Royle 2004), that detections at a site are independent, and that all individuals recorded at a given site and time have the same detection probability. Counts at each sampled unit are

regarded as a binomial process dependent upon the detection probability and the underlying abundance, modelled as a Poisson (or negative binomial) random variable. Covariates can be included in both the abundance and the detection models using standard GLM techniques. The method generates parameter estimates of the abundance distribution across sites that allow evaluation of temporal changes or geographic comparisons. Total abundance can be estimated posteriorly if the sample units are of known area (Royle 2004).

Extensions of the basic N -mixture formulation allow incorporation of additional processes often associated with parrots, such as temporary emigration, correlated detection of individuals and uncertainty in species identification, and also population dynamics and multi-species modelling. See Dénes *et al.* (2015) for a recent overview and Kéry and Royle (2016) for an extensive treatise. Below, we describe a variant of the N -mixture approach for single-visit datasets, followed by the integration of the basic N -mixture model (and some of the extensions mentioned above) with DS.

Single-visit N -mixture models

Increasing spatial representation of surveys can help account for parrots' large home ranges and mobility. With limited budgets, this often means reducing temporal replication, a requirement of multiple-visit N -mixture models. Detection error in counts can be modelled from only a single visit to each sampled site if covariates that affect detection and abundance are available (Sólymos *et al.* 2012). The binomial-zero-inflated Poisson mixture model for analysing single-visit count data replaces both the need for repeated visit data and the assumption of population closure required by multiple-visit approaches with the use of non-overlapping sets of covariates that affect detection and/or abundance. When appropriate covariates are available, conditional likelihood can be used to estimate the regression parameters of a binomial-zero-inflated Poisson mixture model and correct for detection error (Sólymos *et al.* 2012). Zero-inflated negative binomial mixtures can also be used instead of their Poisson counterpart, which can help to model aggregations of individuals (Dénes *et al.* 2017). Most parrot studies designed to compare abundance between different conditions or sampling periods are likely to collect detection and abundance covariates. For example, detection covariates often include time of day, weather, habitat and observer, which are frequently available for most datasets. This approach has been employed to model raptor abundance over large scales (>300 000 km²) based on

single-visit surveys (Dénes *et al.* 2017), and may also prove useful for parrot research.

Hierarchical distance sampling (HDS) and multi-species models

Royle *et al.* (2004) proposed an HDS model that treats counts as a function of detection probability and site-specific abundance. In this approach, counts are a function of the detection probability – estimated using the DS framework – and of the underlying abundance, modelled as a Poisson (or negative binomial) GLM random effect. Sillett *et al.* (2012) extended this approach to include site-specific covariate effects on the detection function, and Chandler *et al.* (2011) included accounting for processes such as temporary emigration that induce additional variation in counts. This is accomplished by employing zero-inflated mixture distributions (e.g. zero-inflated Poisson) to model abundance and temporary immigration simultaneously (see also Wenger and Freeman 2008; Joseph *et al.* 2009 for implementations with temporally replicated surveys). Hierarchical distance sampling can also be integrated with density surface models (reviewed in Miller *et al.* 2013), which can be used to assess the effects of environmental variables on the spatial distribution of individuals, and to generate spatial predictions of abundance over larger or different areas from those originally surveyed.

Sollmann *et al.* (2016) employed HDS in a community modelling framework (Dorazio *et al.* 2006), which is an approach for jointly analysing multi-species datasets and sharing information across species while maintaining the ability to model species-specific parameters (i.e. detection probability, abundance, and covariate effects). Information is shared across species by assuming a common underlying distribution for species-specific parameters. These distributions, in turn, are governed by hyperparameters, which reflect community-level patterns and processes. The main benefit of using a community model over a single-species model lies in the ability to obtain estimates of occurrence, abundance and other parameters of species observed so rarely that they cannot be modelled individually. Many parrot species are known to occur in low densities, which results in low sample sizes precluding modelling of abundance and detection probability. Data on multiple species are often collected during parrot surveys (e.g. Marsden 1999; Marsden *et al.* 2000; Lee and Marsden 2012). Multi-species approaches, which can also be applied for temporally replicated surveys and tailored for tropical settings marked by low abundance patterns (Gomez *et al.* 2017), may prove extremely useful.

Passive (autonomous) acoustic surveys

As an alternative to survey methods based on visual observations and physical capture, passive acoustics is an emerging field in biodiversity monitoring (Marques *et al.* 2013). Passive acoustic methods may be advantageous because

unlike (most) visual surveys, passive acoustic surveys can operate under any light conditions (e.g. both day and night, or in fog), being less affected by weather conditions; and passive acoustics is highly amenable to automated data collection and processing, so large amounts of data can readily be analysed. (Marques *et al.* 2013, p. 3)

Passive recording units allow surveys to sample repeatedly and simultaneously a large number of sites, something that in most cases is logistically impracticable with human observers. Lastly, acoustic recorders provide a voucher record of detections, like a specimen, that can be reviewed and re-reviewed to minimise false-positive and -negative detections. Analytical methods used with recorder data include *N*-mixture, DS, mark-recapture, and spatially explicit models, or combinations thereof (Marques *et al.* 2013).

Passive acoustic recorders have been used in studies of occupancy or abundance of different groups of highly vocal species, including cetaceans, anurans and birds (Dawson and Efford 2009; Marques *et al.* 2013; Furnas and Callas 2015; Sedláček *et al.* 2015; Stevenson *et al.* 2015), but its use for surveying parrot populations is still incipient. Alquezar and Machado (2015) compared the data obtained with autonomous acoustic recordings and avian point counts in open woodland savannah in Brazil, including seven parrot species ranging in size from parrotlets to macaws. For all seven species both methods had similar detection efficacy, indicating that passive recorders can be effective in sampling parrot assemblages in open vegetation areas. Passive acoustic recorders were also used to survey parrots in Amazonian forests (Figueira *et al.* 2015), and the data obtained were analysed using multi-state occupancy models (Nichols *et al.* 2007) to investigate habitat use by nine parrot species. These two studies illustrate that passive acoustic recorders have great potential for surveying parrots. However, neither study attempted to generate abundance or density estimates, which constitutes a major analytical challenge in this emerging field, especially for highly mobile species (Stevenson *et al.* 2015). Generalised random encounter models (Lucas *et al.* 2015) are a

promising approach to overcoming this problem. Random encounter models use encounter rates and independent data on average group size and day range (i.e. movement speed) to obtain density estimates without relying on fitting a statistical (e.g. DS or *N*-mixture) model to estimate detection probability. Instead, they explicitly model the detection process, with animals being detected only if they approach the sensor from a suitable direction (Lucas *et al.* 2015), and other processes that affect detection probability also modelled. Key advantages of the approach are that it is robust to multiple detections of the same individual and is not sensitive to the spacing of sensors relative to the size of animal home ranges, and therefore can be applied more flexibly across a wide range of species, including parrots. Description of the method, its assumptions and limitations is extensive, so we refer readers to the original articles for details (Rowcliffe *et al.* 2008; Lucas *et al.* 2015).

Conclusions

Twenty years after the work by Casagrande and Beissinger (1997), estimating parrot abundance and population size remains a challenge. We provide here an extensive toolbox, including survey methods and analytical approaches (Table 1), some of which have yet to be applied to parrots. All of the estimation methods presented have both explicit and implicit assumptions. When applying these methods, researchers should gauge the extent that assumptions are met and discuss the consequences of their possible failure.

The suitability of methods for estimating abundance or population size for a given research project depends on the scale and objectives of the study, the species sampled, whether surveys can be temporally replicated, and the availability and feasibility of collecting ancillary data (Table 1). Moreover, sampling design guidance (i.e. number and size of sample units, number and duration of visits) for most analytical methods described here is very sensitive to context (Dénes *et al.* 2015). Rather than readily replicating from studies in different contexts, we encourage researchers to evaluate a range of designs using simulations tailored to anticipated sampling conditions and/or pilot studies of their own systems, as well as to explore new survey methods (e.g. passive acoustics), while continuing to test and improve established approaches (e.g. roost counts). Finally, methods can also impose differing financial and logistical costs, depending on survey design requirements (Table 1). Researchers should be

Table 1. Key concerns, sampling and logistic challenges, and advantages of sampling and analytical methods for estimating parrot abundance and population size.

Method	Key concerns	Sampling and logistic challenges	Advantages
Roost surveys	Roost size and number of roosts can vary daily and seasonally; roosts may change location	Locating roosts; visibility and counting of individuals leaving and/or arriving at roosts	Highly cost-effective if roost locations are fixed and known in advance
Mark-resighting surveys	Number of marked individuals when resampling the population is unknown	Capturing individuals; feasibility of using and reading bands, tags, or collars	Allows identification of individuals; explicitly estimates detection probability
Distance sampling using point and line transects	Non-random distribution of individuals in relation to survey point or line; flying individuals should be excluded from sample	Accurate measurements of detection distances and counts of large groups of individuals	Explicitly estimates detection probability; surveys multiple species simultaneously
Roadside transects	Non-random distribution of individuals in relation to road; habitats along roads may not be representative of study area	Requires low-traffic roads; often 4 × 4 vehicles	Can survey large areas and multiple species; may be combined with analytical methods (e.g. DS, HDS, N-mixture models)
Occupancy surveys	Assumes that local abundance directly influences site-level detection probability	Requires spatially and temporally replicated surveys, large sample sizes	Uses binary occupancy data to estimate abundance; explicitly estimates site-level detection probability
Hierarchical N-mixture models (including single-visit, HDS and multi-species models)	Methods rely on multiple assumptions (e.g. closed population during sampling period, individuals at a given site and time have equal detection probability)	Usually requires spatially and temporally replicated surveys, requires large sample sizes	Explicitly estimate detection probability; versatile set of methods with extensions that can incorporate temporary emigration, correlated detection, population dynamics, multi-species modelling
Passive (autonomous) acoustic surveys	Estimation of abundance or density relies on multiple assumptions or independent data on average group size and movement speed (in generalised random encounter models)	Identification of vocalisations (species and number of individuals) can be difficult and time-consuming	Autonomous recorders can sample sites repeatedly and simultaneously; survey multiple species simultaneously; and provide voucher record of detections

aware of these differences when designing studies, so that limited funds and effort are spent efficiently.

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