Methodological challenges in monitoring bat population- and assemblage-level changes for anthropogenic impact assessment

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ABSTRACT

Recent years have seen increased attention to bats as an effective bioindicator group for assessing responses to drivers of global change, which concurrently has led to a revived interest in establishing a global bat monitoring network. To be effective and efficient, global-scale monitoring of bats will largely have to rely on integrating data collected as part of a network of regional monitoring schemes. Herein, I highlight and discuss some of the principal challenges faced in the monitoring of population- and assemblage-level changes of bats, focusing mainly on methodological and statistical issues and the selection of suitable state variables for quantifying regional trends in bat biodiversity. Particularly in the tropics, where detailed single-species monitoring is challenging due to high species richness, I recommend that monitoring programs focus on tracking changes in species turnover and composition as more informative measures of anthropogenic impact than species richness. Imperfect species detection is an important source of variation and uncertainty associated with animal count data. Bat monitoring programs need to correct for this, most importantly through the use of sampling protocols that rely on strictly standardized approaches and a well-balanced design, or *a posteriori* by using appropriate statistical models so as to avoid the detection of spurious trends. Multi-species occupancy models that allow for simultaneous assemblage- and species-level inference about occurrence and detection probabilities provide a suitable analysis framework for monitoring data, and are a comparatively low-cost approach that should prove useful especially in the regional monitoring of bats in the tropics. To ensure robust inference about temporal and spatial trend estimates in the state variables of interest, the efficacy of sampling designs should be carefully gauged at the design stage to ensure sufficient statistical power, and data should be collected according to a formal randomized design to allow for regional-scale inference. I stress the importance for long-term bat monitoring programs to have sustained funding, the need to establish trigger points for the

application of appropriate mitigation measures, and for monitoring to be adaptive so as to maximize effectiveness and efficiency based on the data collected. Finally, I argue that to overcome the challenges associated with initiating monitoring networks in tropical countries – a major step towards the realization of global-scale bat monitoring – reliance on citizen scientists and participatory monitoring will be key.

Keywords: detectability; power analysis; occupancy modeling; cost-effectiveness; trend detection; sampling design

Introduction

In the face of unprecedented global environmental changes, monitoring – the process of gathering information about one or several system state variables with the purpose of inferring changes in state over time or space (Yoccoz et al., 2001), is of universally recognized importance for biodiversity conservation (Jones et al., 2013a). In fact, it is nowadays one of the core endeavors of conservation biology (Marsh and Trenham, 2008).

Targets for biodiversity conservation are increasingly established globally and, especially after failure to meet the 2010 Convention on Biological Diversity (CBD) targets (Butchart et al., 2010), global-scale approaches to monitoring biodiversity change, as increasingly advocated by numerous authors (Jones et al., 2011; Pereira et al., 2010; Pereira and Cooper, 2006; Scholes et al., 2008; Scholes et al., 2012), are urgently required. In order to be cost-effective, global-scale monitoring will largely have to rely on integrating data collected as part of a network of regional monitoring schemes (Jones, 2011) and a shift of focus for quantifying biodiversity trends, away from site-scale towards regional-scale approaches, is now apparent (Buckland et al., 2012) and needed as drivers of biodiversity loss tend to operate at larger scales (Jones, 2011).

The planet is experiencing a widespread and pervasive defaunation crisis, highlighting the urgency of improved monitoring of populations, especially of functionally important taxa, including bats (Dirzo et al., 2014). In a recent review, Jones et al. (2009) championed the importance of bats as suitable indicators of biodiversity and global change as they are sensitive and demonstrably respond to a range of environmental stressors related to global climate change, anthropogenic habitat modification, and emerging infectious diseases - key drivers of worldwide bat population declines (Frick et al., 2010; Jones and Rebelo, 2013; Kingston, 2013; Meyer et al., forthcoming; Reeder and Moore, 2013). For instance, novel threats to bats such as the spread of White-Nose Syndrome that has led to swift and precipitous declines of several bat species in North America (Frick et al., 2010), call for well-designed and powerful monitoring schemes capable of rapidly discerning population declines. Given these threats, long-term monitoring of bats for anthropogenic impact assessment is becoming increasingly important. Jones et al. (2009) made a convincing case arguing for the implementation of a global bat monitoring network, a call that since has been reiterated (Willig, 2012). The growing interest in bats as an effective indicator group of global change processes (Flaquer and Puig-Montserrat, 2012) is spurring efforts to widely adopt them along with other commonly monitored taxa such as birds and butterflies in regional monitoring programs (Haysom et al., 2013) whose results could subsequently feed into global assessments. Monitoring efforts for bats are currently biased towards higher latitudes (Meyer et al., 2010; Walters et al., 2013). Well-developed bat monitoring programs at national scales exist across Europe (Battersby, 2010), for instance the United Kingdom's National Bat Monitoring Program (NBMP; Walsh et al., 2003). However, implementation of a global bat monitoring network will require concerted efforts to rapidly scale up monitoring efforts to the global level (Walters et al., 2013). Recent initiatives such as the Indicator Bats Program (iBats), which aims to apply acoustic monitoring techniques to assess trends in bat populations from regional to global scales (Jones et al., 2013b), are undoubtedly an important step forward in this direction.

Poorly designed monitoring programs can result in poor decision-making and divert valuable resources from potentially effective interventions (Jones et al., 2013a) and there is now a substantial body of literature dedicated to the do's and don'ts of monitoring (Gitzen et al., 2012; Lindenmayer and Likens, 2010a; Lovett et al., 2007). In their seminal review of methodological and design issues associated with biodiversity monitoring programs, Yoccoz et al. (2001) stressed the need for any such program to be framed around a triad of fundamental questions, a call subsequently echoed repeatedly (e.g. Jones et al., 2013a): (1)

why monitor, (2) what should be monitored and (3) how should monitoring be carried out?

Here, I highlight and discuss some of the major methodological and statistical challenges commonly faced in bat monitoring, i.e. focus on issues related to the “what” and “how” questions, issues which have been discussed on a general level elsewhere (Buckland et al., 2012; Buckland et al., 2005; Jones, 2011; McComb et al., 2010). The importance of targeting monitoring programs to realistic, clearly-defined objectives, i.e. proper appraisal of the purpose of monitoring (the “why” question), essential for guiding program design can, however, not be overstressed (Ferraz et al., 2008; Jones et al., 2013a; Lindenmayer and Likens, 2010b; Nichols and Williams, 2006; Yoccoz et al., 2001). Those responsible for establishing bat monitoring initiatives certainly need to ensure that efforts are guided by carefully posed questions and objectives from the onset of a program. What and how to monitor will generally follow logically from clearly identified objectives and well-articulated questions (Lindenmayer et al., 2012; Yoccoz, 2012).

While the use of acoustic methods to globally monitor bats as, for instance, employed by the iBats Program, may constitute an efficient and cost-effective alternative to traditional bat survey methods, their wider application is not without challenges (Walters et al., 2013). All bat surveillance methods are inherently biased in one way or another (Hayes et al., 2009). Especially in the species-rich tropics, where echolocation call similarity is high and consequently species identification is difficult (Walters et al., 2013), and considerable fractions of the bat fauna are difficult to monitor using acoustic detection methods, bat monitoring programs should rely on a range of complementary methods (Meyer et al., 2014). The following discussion is therefore chiefly targeted at the monitoring of bats by direct methods of observation, i.e. through the use of traditional capture methods such as mist nets or harp traps (Kunz et al., 2009). Very similar issues do, however, apply to bat monitoring via acoustic methods (see Frick, 2013; Jones et al., 2013b; Walters et al., 2013) or based on colony counts, the latter being the prevailing method in existing temperate-zone bat monitoring programs (Haysom et al., 2013; Walsh et al., 2003). Throughout this paper, I mostly illustrate my main points with the findings and insights gained from an assessment of the suitability of tropical bats for long-term monitoring (Meyer et al., 2011; Meyer et al., 2010; Meyer et al., 2014). This is in part motivated by the fact that sampling and statistical challenges to monitoring are particularly acute for tropical bat populations and assemblages given their high species richness and large proportion of rare species they are comprised of. Moreover, tropical ecosystems and fauna are among the most imperiled worldwide and are undergoing unprecedented changes as a result of widespread deforestation, land-conversion, and defaunation (Bradshaw et al., 2009; Dirzo et al., 2014; Laurance et al., 2014). Tropical bats are sensitive to these threats and anthropogenic alterations of their environment (García-Morales et al., 2013; Meyer et al., forthcoming), underscoring the pressing need and urgency of monitoring their populations and assemblages in an effort to be able to mitigate human-induced environmental impacts.

Challenge 1: *What to monitor?* – Selecting (an) appropriate state variable(s)

Selection of (an) appropriate state variable(s) to monitor is one of the central decisions to be made from the outset of a monitoring program and should fundamentally be driven by the specific objectives of the program (Yoccoz et al., 2001). “Laundry-list” approaches to monitoring should be avoided, as they are highly cost-ineffective and too expensive to be sustained financially over the longer term (Lindenmayer and Likens, 2010b). In the context of global monitoring efforts, there is a lack of consensus about what to monitor; however, with the recent delineation of promising candidate Essential Biodiversity Variables (EBVs), capable of capturing major dimensions of biodiversity change, efforts are underway to remedy this (Pereira et al., 2013).

Monitoring of population change - abundance vs. occupancy

Population abundance is the natural choice for state variable, in fact, it is one of the most frequently used in wildlife studies (Marsh and Trenham, 2008; Pollock et al., 2002), and also an important candidate EBV (Pereira et al., 2013). Moreover, local abundance declines within populations are pervasive across a range of taxonomic groups (Dirzo et al., 2014), underscoring the necessity of rigorous population-level monitoring. *Abundance* is the most informative state variable in single-species population monitoring, and is for instance widely used in roost count-based bat monitoring schemes in the temperate zone (Battersby, 2010; Haysom et al., 2013). On the other hand, where monitoring relies on capture or acoustic surveillance methods, landscape-level inference is challenging due to the high costs associated with rigorous abundance estimation for rare species; in fact obtaining precise measures of abundance from field surveys may often not be cost-effective (Joseph et al., 2006; Pollock, 2006). *Occupancy* (i.e. the proportion of sampling units in a landscape occupied by the target species; MacKenzie et al., 2002) may be a useful alternative state variable for landscape-scale monitoring, especially of rare and elusive species, as presence-absence data can be collected at a relatively lower cost than abundance data (Jones, 2011; MacKenzie et al., 2006; MacKenzie and Reardon, 2013). Occupancy may serve as a useful proxy for abundance as the two variables tend to positively co-vary, even though the strength of this association is scale-dependent and frequently non-linear (Buckland et al., 2005; Royle and Dorazio, 2008). Nevertheless, whether occupancy constitutes an appropriate alternative to species abundance monitoring requires careful consideration. Validation of low-cost occupancy vs. more data-intensive abundance-based approaches prior to program implementation is essential, yet rarely realized (Jones, 2011), and empirical assessments of the relationship would be an important step at the planning stages of field survey-based bat monitoring schemes to establish the extent to which species occupancy patterns effectively capture changes in population abundance.

While species-specific trend estimates derived from omnibus surveys often may suffer from poor precision, precision may be increased by combining data from multiple species (Buckland et al., 2011). Multi-species monitoring thus usually involves the use of aggregated population trend indicators or composite diversity indices (Buckland et al., 2005). In this context, the geometric mean index of population abundance has the most favorable statistical properties based on recent evaluations (Buckland et al., 2005; van Strien et al., 2012) and is for instance used in the construction of the pan-European multi-species bat indicator (Haysom et al., 2013). Moreover, it has a clear link to species extinction risk, making it all the more suitable as an appropriate composite index for biodiversity monitoring (McCarthy et al., 2014).

Monitoring of assemblage-level attributes

At the assemblage level, most monitoring programs traditionally focus on the taxonomic dimension of biological diversity, i.e. *species richness* (Jones et al., 2013a). However, measures such as *functional diversity* may be more relevant for capturing biodiversity change and how it reflects on ecosystem functioning and services (Yoccoz, 2012). Taxonomic and functional metrics of diversity have been shown to often convey complementary information with regard to the responses of a range of animal groups to land use change (Flynn et al., 2009; Vandewalle et al., 2010), and their combined use in monitoring schemes thus offers great potential for improving biodiversity assessments, especially for species-rich assemblages (Vandewalle et al., 2010). Similarly, *phylogenetic diversity* is another important component of diversity, arguably more meaningful as biodiversity measure than species richness (Faith, 2013; Rodrigues et al., 2011; Yoccoz, 2012). However, despite their potential usefulness as complementary state variables for tracking changes in bat biodiversity, for bats the functional and phylogenetic dimensions of biodiversity, and particularly how they change in response to anthropogenic habitat conversion, remain poorly understood (Cisneros et al., in press; Meyer et al., forthcoming). Finally, *genetic diversity* is yet another important aspect of biodiversity and candidate EBV (Pereira et al., 2013), which given the demonstrated sensitivity of bats to genetic erosion in response to habitat modification (Meyer et al., 2009; Struebig et al., 2011) may likewise prove useful as state variable in long-term monitoring programs.

Although to date there has been a focus on monitoring temporal changes in biodiversity based on alpha diversity measures such as species richness, there is mounting evidence that temporal turnover metrics that quantify differences in *species composition* across temporal replicates are more sensitive indicators of assemblage-level change than alpha diversity (Magurran and Henderson, 2010). For instance, Dornelas et al. (2014) demonstrated pervasive compositional turnover but found no systematic loss of alpha diversity in a comprehensive analysis of 100 long-term assemblage time series. Their analysis underscores the need for biodiversity studies and monitoring programs to focus greater attention on addressing compositional turnover. In the context of environmental impact assessments, other recent studies also suggest that species richness may generally be less informative as community metric for capturing the impacts of habitat loss and fragmentation (Banks-Leite et al., 2012; Barlow et al., 2007). To fully capture anthropogenically driven biodiversity loss, a focus on changes in diversity metrics alone is clearly insufficient and unlikely to be effective for maintaining adequate ecological function, and monitoring of population declines and compositional changes will be critical as they will generally reflect more on ecosystem function (Dirzo et al., 2014).

Existing temperate-zone bat monitoring schemes at regional, national, or continental scales focus on monitoring temporal trends in population abundance, relying mostly on winter counts at hibernacula or maternity roost counts (Battersby, 2010; Haysom et al., 2013; O'Shea and Bogan, 2003; Walsh et al., 2003). Monitoring changes in bat assemblage-level attributes as discussed above may thus in fact be of limited relevance in the temperate zone. Conversely, it should be of interest in the tropics, where high levels of alpha diversity (e.g. Rex et al., 2008), preclude detailed population monitoring of every species. Here, the monitoring of temporal trends in species diversity and particularly of species composition and turnover could complement the population-level monitoring of a limited set of carefully selected target species (Meyer et al., 2010). In this context, recent developments of composite diversity indices (λ-measures) in conjunction with the geometric mean index, which allow for the separate assessment of trends for common and rare species (Studeny et al., 2013) may prove useful in monitoring trends across species in diverse tropical bat assemblages. Assemblage-wide monitoring of bat biodiversity employing compositional metrics requires establishing a robust baseline against which to monitor future changes. In the tropics this may constitute a considerable challenge given that natural spatiotemporal variability in assemblage composition in unmodified habitats can be substantial (Kingston, 2013).

Challenge 2: *How to monitor?* – Dealing with the problem of imperfect species detection in bat monitoring

In order to be able to draw valid conclusions about trends, managers of regional-scale bat monitoring programs - just like for any other wildlife monitoring program - will have to confront and adequately deal with the two stochastic processes affecting any of the variants of “abundance”, be it the numbers of individuals (abundance), occupancy, or species richness (Kéry and Schmid, 2008).

First, a major design challenge is to collect data from a spatial sample (i.e. sampling sites) that is representative of the wider area or region of interest about which inference is desired (Buckland et al., 2012). Survey site selection should follow a strictly probabilistic sampling design (e.g. random or stratified random), an issue which is neglected in many monitoring programs that still too often are not based on a decent spatial probability sample (Kéry and Schmid, 2008). This should be carefully considered in initiating and implementing new bat monitoring programs, irrespective of whether they are based on capture techniques, acoustic sampling, or colony counts (e.g. Battersby, 2010), although in the latter case stratification of the site sample will often be *post hoc* at the analysis stage (Walsh et al., 2001).

The second stochastic process concerns the fact that during field-based wildlife monitoring surveys not all individuals, occupied patches or species are detected, or detected with certainty, at any site sampled, i.e. detection probability (*p*) is typically < 1. Detectability is influenced by species and habitat characteristics, survey effort and sampling method, and therefore may vary considerably over both spatial and temporal dimensions (Iknayan et al., 2014).

It has long been recognized that species detection is usually imperfect in wildlife surveys, and that this can bias the estimators of ecologically relevant state variables. Imperfect species detection is a pertinent problem in the monitoring of a number of commonly used state variables, species abundance, occupancy, and assemblage-level metrics such as species richness alike (Jones et al., 2013a; MacKenzie and Reardon, 2013). The interpretation of trends based on raw counts for any of these variables is always complicated by imperfect species detection and the fact that detectability rarely remains constant over dimensions of interest (space or time), even when standardized sampling schemes are used (Kéry et al., 2009a; Kéry and Schmid, 2008). The last decade has seen a fast development of statistical models aimed at providing estimates of occupancy, species richness and relative abundance while accounting for imperfect species detection, employing either maximum likelihood or Bayesian approaches (Bailey et al., 2013; Kéry et al., 2009a; Kéry et al., 2009b; MacKenzie et al., 2006; Royle and Dorazio, 2008). Imperfect detection results in false species absences, which, if unaccounted for, will cause species richness, abundance, and occupancy to be underestimated (Kéry and Schmid, 2008; MacKenzie and Reardon, 2013). Consequently, if ignored, imperfect detection may lead to diagnosing spurious trends or mask real patterns and failure to account for detection bias is a major pitfall to quantifying biodiversity change in relation to anthropogenic habitat modification and may misguide management and conservation decisions (Ruiz-Gutiérrez and Zipkin, 2011). For instance, ignoring detectability differences among species and habitats in fragmented landscapes may overestimate turnover rates, distort patterns of species persistence and colonization, and lead to erroneous classification of species as forest specialists and generalists (Ruiz-Gutiérrez and Zipkin, 2011). Monitoring the responses of bats to human-induced habitat loss and modification requires a clear understanding of colonization and persistence patterns and how they are influenced by low and variable detection probabilities across species and habitat types. Problems associated with imperfect detection have long been identified and are regularly taken into account in studies on other vertebrate taxa, particularly birds, through models that adjust for detectability (e.g. Boulinier et al., 1998). In contrast, the application of such detectability models in bat studies is still in its infancy and largely restricted to a few evaluations in the context of acoustic surveys (Clement et al., 2014; Duchamp et al., 2006; Gorresen et al., 2008; Weller, 2008), while the problem has been almost completely ignored in studies using traditional capture methods (but see Rodhouse et al., 2012).

Bias in estimates of raw species counts arising from detection errors is especially pronounced in communities that contain a large proportion of rare species (Dorazio et al., 2011) and is thus of particular relevance in the context of bat monitoring in the tropics, where the large number of locally rare species are a fundamental challenge to monitoring efforts. As a case in point, Meyer et al. (2011) demonstrated that mean species detectability in tropical bat surveys rarely approaches unity, averaging 0.76 (± 0.8 SD) for a suite of 25 bat assemblages from across the New and Old World tropics. This underscores the fact that considerable proportions of species may regularly be missed in tropical bat surveys, even when several repeat visits are conducted per site. Moreover, there was a clear location effect on mean species detectability, which suggests the potential for large biases to be introduced if monitoring data from geographically disparate locations are compared without accounting for such location-specific differences in mean detectability. As pointed out by Meyer et al. (2011), it will be important for tropical bat monitoring programs that operate over larger geographic scales to be calibrated using location-specific detectability estimates to avoid erroneous inferences about trends in species richness. Species-specific detectability, estimated as the probability of detecting a particular species during two successive surveys, was often considerably lower (mean across 232 species = 0.4) than species-averaged estimates and, importantly, highly heterogeneous across species (range 0.03-0.84), illustrating that raw species counts may often be heavily biased. The analysis further revealed substantial differences in species-level detection probabilities among bat ensembles and sampling methods (Fig. 1). For instance, in the Neotropics aerial insectivorous bats attain fairly high levels of detectability (average 0.71) when sampled with acoustic methods, but have much lower detectability using traditional capture techniques. Gleaning animalivorous phyllostomids, in spite of being adequately sampled with capture methods and a group that is sensitive to habitat modification, are challenging monitoring targets, as most species exhibit low detectability. By comparison, in both the Old and New World tropics, frugivores are somewhat more easily detected (Fig. 1).

Tropical bat monitoring programs should generally rely on combining the use of multiple sampling methods in order to increase detection rates (Meyer et al., 2011). Recent versions of occupancy models allow for the estimation of method-specific detection probabilities (Nichols et al., 2008), information which can be used to optimize study design in multi-species bat occupancy surveys. Figure 2 illustrates this approach, providing method-specific detection probabilities for four species of phyllostomid bats sampled by two methods, ground- and canopy-level mist netting.

Challenge 3: *How to monitor?* – Ensuring adequate statistical power for reliable detection of trends in bat abundance or occupancy

Although abundance or some index thereof is the state variable of primary interest in most wildlife monitoring programs, establishing with a high level of confidence whether a population is increasing or decreasing is riddled with challenges. Assessing the effects of anthropogenic environmental changes on bat populations requires data at appropriate spatial and temporal resolutions to ensure sufficient statistical power to detect population-level changes or trends. Statistical power is the probability that an analysis will correctly reject a null hypothesis that is indeed false or, in the context of monitoring, the probability that an analysis will correctly identify an ongoing population trend of a specified magnitude under a given survey design (Gerrodette, 1987). Power is sensitive to a range of factors, most importantly the magnitude of population change over time to be detected (effect size), the duration and frequency of monitoring, the number of sites surveyed, the risk of a false positive (i.e. Type I error), and the precision in abundance estimates (Di Stefano, 2001).

Although an issue that had long been overlooked, prospective power analysis is now increasingly recognized and applied as a crucial tool to aid in the development of suitable monitoring designs that are capable of yielding statistically robust population trend estimates, thus avoiding that valuable resources are being wasted (Jones, 2013; Legg and Nagy, 2006).

Recent years have also seen more frequent application of power analysis for assessing the ability of monitoring schemes to detect bat population trends for both temperate-zone and tropical bat species (Battersby, 2010; Jones et al., 2013b; Meyer et al., 2010; Roche et al., 2011; Walsh et al., 2001). Some temperate-zone monitoring programs which relied on power analyses to aid in program planning, such as the UK's NBMP, were shown to have generally high sensitivity to detect population changes, sufficient to detect declines of Amber and Red Alert magnitude (1.14% and 2.73% per year, respectively) after 25 years of monitoring, using data from acoustic field surveys and colony counts (Battersby, 2010; Walsh et al., 2001). Programs such as iBats (Jones et al., 2013b) or car-based bat monitoring schemes in Ireland (Roche et al., 2011) which employ acoustic monitoring have similar levels of sensitivity to detect population changes.

Meyer et al. (2010) explored the potential for a monitoring program of tropical bats to reliably detect trends in population abundance by evaluating the statistical power of a range of different survey design options, specifically focusing on the trade-offs between number of sampling sites, sampling frequency within and between years, and duration of the monitoring program. A key finding was that for most species a monitoring program would perform poorly in detecting trends in abundance if the program were of short duration. Monitoring for only a few (< 10) years was found to be clearly insufficient in terms of statistical power to reliably infer population changes, especially those of lower magnitude (5% annual declines; Fig. 3). On the other hand, a program extending over at least 20 years would have sufficient power (≥ 0.9) to detect annual population declines of 5% or more. In this regard, the most cost-effective sampling scheme identified was one consisting of four surveys conducted every other year on five plots per monitoring site. Such a design was demonstrated to be effective at detecting population changes of fairly low magnitude (5%) for a range of species from different bat ensembles, although gleaning animalivorous phyllostomid bats generally constitute more challenging monitoring targets than frugivores or nectarivores (Figs. 3 and 4).

When evaluating the suitability of population monitoring based on power analyses, bat monitoring programs should heed concerns about setting inadequate levels of Type I and Type II error, specifically the widespread application of the “five-eighty convention”, i.e. setting significance and power levels at 0.05 and 0.8, respectively (Di Stefano, 2001; Di Stefano, 2003). In the context of monitoring for environmental impact assessment, costs associated with wrongly concluding that there is no population decline when in fact there is a trend (false negative, Type II error) are arguably greater than concluding that there is an effect when it does not exist (false positive, Type I error). Therefore, following the precautionary principle, it is imperative that Type II error levels are set to more stringent levels (e.g. 0.1) so as to avoid that management inaction has potentially dire consequences for threatened populations (Di Stefano, 2001; Jones, 2013; Mapstone, 1995). Power evaluations in the context of bat monitoring programs so far have taken inconsistent approaches in this regard (Jones et al., 2013b; Meyer et al., 2010; Roche et al., 2011; Walsh et al., 2001).

Temporal and spatial variation in population counts due to environmental variation (process variation) and variability in abundance estimates due to sampling inaccuracies (observation error) are the dominant sources of error in population count data (Clark and Bjørnstad, 2004) and important causes of unreliable identification of a species’ population status (d’Eon-Eggertson et al., 2014). Both of these sources of variability may mask the existence, or alter the magnitude and direction of underlying population trends. Meyer et al. (2010) assessed within-site temporal variation in estimates of relative abundance, i.e. the combined effect of both process variation and observation error, for 121 bat species from 24 Neotropical and Paleotropical locations. Precision in abundance estimates, expressed as the coefficient of variation across repeat visits to the same survey site, was generally low as indicated by high CV values (mean CV = 231%, range 101 - 500%), which varied substantially among species and locations. This high among-survey variability in abundance estimates reduces statistical power for trend detection, an effect that in most cases could only be compensated for by substantially increasing the duration of monitoring (Figs. 3 and 4). Further complicating matters, the likelihood of achieving adequate (≥0.9) statistical power was not only dependent on the magnitude of temporal variation in abundance estimates, but also on how common or rare a species generally was (Meyer et al., 2010). For rare species, which comprise a sizable portion of tropical bat assemblages (Meyer et al., 2014), the amount of effort required to obtain adequate sample sizes to ensure sufficient power to detect changes in abundance over time can be daunting. The fact that rare species are simultaneously the ones for which strong inferences about trends are most needed and those for which that information is most difficult to obtain represents a formidable challenge in population monitoring (MacKenzie et al., 2005). Species rarity will generally aggravate the problems in dealing with both spatial sampling variation and detectability issues in the estimation of abundance (MacKenzie et al., 2005). For rare bat species, monitoring of trends in abundance via field surveys will often be practically impossible and prohibitively costly. Where abundance is an infeasible metric, species occupancy may be a useful alternative (see above), offering practical advantages over traditional abundance estimates in addition to being regarded a more reliable metric for landscape-level inference due to being more robust to local effects and stochasticity than local abundance estimates (MacKenzie and Reardon, 2013).

In recent years, considerable progress has been made in the development of analytical methods for estimating occupancy (Bailey et al., 2013), and free software is available such as the program PRESENCE (Hines, 2006) or the R package unmarked (Fiske and Chandler, 2011), facilitating their application also in bat monitoring programs. Moreover, in the context of occupancy studies, general survey design recommendations have been devised which can assist managers of bat monitoring programs in finding the optimal allocation of survey effort in terms of number of sampling sites vs. number of temporal replicates (Guillera-Arroita et al., 2010; MacKenzie and Royle, 2005). Choosing the number of repeat visits based on these guidelines also appears to be a suitable approach to optimizing statistical power for detecting temporal differences in occupancy under imperfect detection (Guillera-Arroita and Lahoz-Monfort, 2012). Just as with abundance monitoring, power analyses should inform decisions as to whether to adopt occupancy as state variable in bat monitoring programs and should form the basis for devising appropriate sampling schemes. Guillera-Arroita and Lahoz-Monfort (2012) provide tools for conducting power analyses to assess design trade-offs in occupancy surveys, which can provide valuable guidance, especially for choosing an appropriate and powerful design for monitoring trends in occupancy patterns for rare tropical bat species, for most of which abundance monitoring would be prohibitively costly and infeasible.

Challenge 4: *How to monitor?* – Maximizing program effectiveness and efficiency

We live in a resource-constrained world and due to its long-term nature monitoring is inherently a costly enterprise (Jones, 2013). Bat monitoring programs need to strike a balance between collecting data of high-enough quality to ensure robust conclusions about trends on the one hand and cost-effectiveness on the other.

Even though monitoring occupancy instead of abundance may result in a considerable increase in efficiency and reduce costs, species-level monitoring at the landscape scale remains challenging in situations where many species are involved (Noon et al., 2012), as is the case with highly diverse tropical bat assemblages. Although detailed abundance monitoring of some carefully selected target species - those which are reasonably common locally and whose abundance can be estimated with fairly high levels of precision - is feasible on statistical grounds if data are collected over a sufficiently long time span (Figs. 3 and 4; Meyer et al., 2010), I argue that the sheer number and diversity of species in tropical bat assemblages makes single-species monitoring ineffective, cost-inefficient, and thus unrealistic to implement at larger scales. Instead, multi-species monitoring and hierarchical assemblage-level modeling frameworks based on presence-absence data, which have recently emerged as efficient and cost-effective approaches to track the influence of environmental changes on biological communities (DeWan and Zipkin, 2010; Dorazio and Royle, 2005; Dorazio et al., 2006), offer a promising alternative for the regional-scale monitoring of tropical bats. These newly developed hierarchical multispecies occupancy models enable simultaneous monitoring of multiple species and are especially useful for assemblages that include many rare species. Compared to the application of single-species occupancy models, a major advantage of these models is that they allow for simultaneous assemblage-level and species-level inference with regard to probabilities of occurrence and detection and can readily accommodate survey-, site-, and species-level covariates that differentially affect the detection of species or individuals in the estimation process (e.g. Iknayan et al., 2014; Kéry et al., 2009b; Zipkin et al., 2010). It thus constitutes an innovative, comprehensive, cost-effective analysis framework to obtaining robust estimates of occurrence for both individual species and assemblages (DeWan and Zipkin, 2010), whose potential should be fully exploited in the implementation of a tropical network of regional-scale bat monitoring programs. This integrated approach would also be suitable to monitor the occurrence status of certain target groups of species, for instance bat ensembles with demonstrably high functional importance and sensitivity to habitat disruption and disturbance such as Neotropical gleaning animalivorous bats (García-Morales et al., 2013; Kalka et al., 2008; Meyer et al., forthcoming).

Sustained long-term funding is crucial to the success of a bat monitoring program to ensure sufficient statistical power for reliable trend detection, yet undoubtedly constitutes a prime challenge (Jones et al., 2013b). However, long-term funding alone is not enough. Lindenmayer et al. (2013) pointed out that many species are being monitored to the point of extinction, reflecting the fact that most monitoring programs lack pre-planned interventions and effective mitigation strategies if a monitored species is in decline. The authors call attention to the importance for monitoring programs to establish well-defined thresholds of population change that would trigger mitigation measures in accordance with the observed level of decline. I argue that such trigger points for conservation action (e.g. an *a priori* established percentage population decline) should likewise be adopted as an integral part of any bat monitoring program.

While the implementation of a network of regional-scale bat monitoring programs undoubtedly requires that the initial program design is well thought-through and statistically robust, monitoring should be adaptive so as to maximize effectiveness and efficiency based on the data collected (Lindenmayer and Likens, 2009). Periodic reevaluations are crucial to determine whether sampling needs to be re-allocated in space or time to optimize the use of financial and human resources (Levine et al., 2014). Reductions in sampling effort over the course of a monitoring program may often be possible without forfeiting statistical power for trend detection, and thus provide opportunities for reducing costs. The necessity of adaptive sampling schemes was also highlighted by Meyer et al. (2014) who argued that such a flexible approach would be essential to avoiding misallocation of valuable resources in tropical bat monitoring programs aimed at tracking assemblage-level changes. The authors investigated the surrogate effectiveness of species subsets for adequately capturing changes in bat species richness and composition. On the one hand they found that focusing on surveying only a reduced subset of species that excluded the rarest ones in an assemblage (ca.

85% of the full set) could in many instances reduce monitoring costs by requiring fewer site visits. On the other hand, species subset performance depended on structural assemblage characteristics, which are site-specific. This highlights the need for rigorously validating surrogate performance of species subsets on a site-by-site basis prior to program implementation and throughout the monitoring process. More generally it stresses the importance of adaptive sampling schemes that spatially prioritize effort so as to ensure reliable and statistically robust inference about patterns of change over larger spatial scales.

There has been growing interest in the potential of participatory monitoring schemes to decrease the costs involved (Jones, 2013). For instance, much of the success of well-established bat monitoring programs in the temperate zone, most notably the UK's NBMP, stem from their reliance on a large network of volunteers (Jones et al., 2013b; Walsh et al., 2003). Although citizen science monitoring of bats in the tropics in the foreseeable future is unlikely to attain levels of participation anywhere close to these, I argue that the successful implementation of a larger network of regional monitoring schemes in developing countries will also critically hinge on involving to a large extent local populations and volunteers. Indeed, in view of recent studies demonstrating that participatory monitoring in developing tropical countries can be a success (Danielsen et al., 2014; Holck, 2008), there is a clear and as of yet unrealized potential for involving local people in developing countries in bat monitoring efforts, provided specialist training in survey methods is given. Although concerns are often raised over the reliability of data collected by volunteers, by correcting for detection bias, modern statistical approaches, specifically occupancy models, can simultaneously adjust for observation and reporting bias inherent in opportunistic citizen science data (Kéry et al., 2010; van Strien et al., 2013).

Conclusions and recommendations

Monitoring requires a clear understanding of “what” and “how” should be monitored to ensure that the data collected allow robust inference about temporal and spatial trend estimates. To monitor bats effectively and efficiently as part of a future global network of regional-scale monitoring programs bat ecologists will have to grapple with a number of challenges inherent to essentially all wildlife monitoring programs.

I advocate that state variables monitored as part of a bat monitoring network adhere as closely as possible to those established within the EBV framework in order to be able to better integrate trends with those for other taxa. Furthermore, state variables that represent dimensions of diversity other than the taxonomic one should be carefully considered for inclusion. In the tropics, where high species richness and levels of species rarity greatly limit detailed single-species monitoring, a focus on tracking changes in species turnover and compositional metrics appears particularly useful. Reliance on lower-cost approaches that yet are able to provide robust information about trends such as multi-species occupancy monitoring is an avenue that regional-scale bat monitoring programs, particularly in the tropics, should pursue in an effort to curtail costs.

For reliable quantification of regional trends, bat monitoring programs should ensure adequate spatial replication throughout the survey region, whereby the critical sample size is the number of randomly selected sampling sites, and sufficient data to allow average detectability across sites within the region of interest to be estimated for each species (Buckland et al., 2012). Bat researchers are lagging quite far behind much of the rest of the ecological research community in applying corrective measures for imperfect species detection in contexts where they are clearly needed - including monitoring - and I advocate that greater attention be paid to this issue. Bat monitoring programs should embrace and take advantage of recent advances in statistical modeling and analysis techniques, specifically hierarchical occupancy models that account for detectability, which are an important and flexible toolkit for the analysis of monitoring data. Notwithstanding the indisputable usefulness of such statistical models that allow adjusting for imperfect species detection, Banks-Leite et al. (2014) recently cautioned against their uniform application, and called attention to the fact that carefully planned sampling designs that *a priori* try to minimize the effects of covariates of detectability are just as important. I echo their call and argue that bat monitoring programs should first and foremost control for covariates of detection probability through a well-balanced study design and highly standardized sampling, and not rely exclusively on *a posteriori* statistical detectability adjustments.

Irrespective of whether the focus is on monitoring of bat abundance or species occupancy, the efficacy of sampling designs should be carefully evaluated during the initial stages of a program to ensure sufficient statistical power for trend detection. Besides, while securing sustained funding will be a major challenge for a network consisting of a large number of individual regional-scale monitoring programs, it will be critical to ensure its long-term success. Adaptive sampling schemes in this regard are fundamental to increase program efficiency and to help minimize costs. Finally, I contend that increasing reliance on citizen scientists to aid in collecting empirical data will be of fundamental importance in initiating and implementing large-scale bat monitoring initiatives in tropical countries.

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FIGURE CAPTIONS

Fig. 1 Estimates of species-level detectability derived from a generalized linear mixed-effects model estimating the probability of detecting a particular species in two successive surveys. Detection probabilities are given for several bat ensembles and sampling methods, using data for 128 and 104 Neotropical and Paleotropical bat species, respectively. AEINS = aerial insectivores, FRUG = frugivores, GLANIM = gleaning animalivores, NECT = nectarivores; CN = canopy nets, GN = ground nets, HT = harp traps. Figure adapted from Meyer et al. (2011).

Fig. 2 Method-specific detection probabilities $\hat{p}$ estimated from fitting a single-season multi-method occupancy model (Nichols et al., 2008) to bat capture data collected at 17 sites in the Barro Colorado Nature Monument (continuous forest) and on adjacent forested islands in Gatún Lake, Panama (see Meyer and Kalko, 2008). Given are detection probability estimates and associated standard errors for four species of phyllostomid bats sampled with canopy-level (CN) and ground-level (GN) mist nets during two site visits during the wet season. Models were fitted in the program PRESENCE (Hines, 2006) and included a fragmentation effect (continuous forest vs. islands) as a covariate for occupancy ψ, while modeling detection probabilities as different between methods. For this purposely-simple example to illustrate the approach only one of several possible models was fitted.

Fig. 3 Variation in statistical power to detect bat population declines of different magnitude (5 and 10% annually), contingent upon the number of annual visits, the number of sites monitored, and the number of survey years. For each bat ensemble, power values represent means (± SD) for a range of bat species from various Neotropical locations. The dotted line indicates the desired power level at 0.9. Maximum acceptable rates of Type I (false positive) and Type II (false negative) error in the analysis were both set to 0.1. Modified from Meyer et al. (2010).

Fig. 4 Statistical power to detect 10% annual abundance declines for three species each of frugivorous and gleaning animalivorous phyllostomid bats. Power was calculated for surveys conducted biennially at five sampling plots using data based on ground-level mist netting from the Barro Colorado Nature Monument, Panama (Meyer and Kalko, 2008). The dotted line indicates the desired power level at 0.9. Modified from Meyer et al. (2010).