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

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1 **ABSTRACT**

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

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

6

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

1 **Introduction**

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

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

17 The planet is experiencing a widespread and pervasive defaunation crisis, highlighting
18 the urgency of improved monitoring of populations, especially of functionally important taxa,
19 including bats (Dirzo et al., 2014). In a recent review, Jones et al. (2009) championed the
20 importance of bats as suitable indicators of biodiversity and global change as they are
21 sensitive and demonstrably respond to a range of environmental stressors related to global
22 climate change, anthropogenic habitat modification, and emerging infectious diseases - key
23 drivers of worldwide bat population declines (Frick et al., 2010; Jones and Rebelo, 2013;
24 Kingston, 2013; Meyer et al., forthcoming; Reeder and Moore, 2013). For instance, novel
25 threats to bats such as the spread of White-Nose Syndrome that has led to swift and

1 precipitous declines of several bat species in North America (Frick et al., 2010), call for well-
2 designed and powerful monitoring schemes capable of rapidly discerning population
3 declines. Given these threats, long-term monitoring of bats for anthropogenic impact
4 assessment is becoming increasingly important. Jones et al. (2009) made a convincing case
5 arguing for the implementation of a global bat monitoring network, a call that since has been
6 reiterated (Willig, 2012). The growing interest in bats as an effective indicator group of
7 global change processes (Flaquer and Puig-Montserrat, 2012) is spurring efforts to widely
8 adopt them along with other commonly monitored taxa such as birds and butterflies in
9 regional monitoring programs (Haysom et al., 2013) whose results could subsequently feed
10 into global assessments. Monitoring efforts for bats are currently biased towards higher
11 latitudes (Meyer et al., 2010; Walters et al., 2013). Well-developed bat monitoring programs
12 at national scales exist across Europe (Battersby, 2010), for instance the United Kingdom's
13 National Bat Monitoring Program (NBMP; Walsh et al., 2003). However, implementation of
14 a global bat monitoring network will require concerted efforts to rapidly scale up monitoring
15 efforts to the global level (Walters et al., 2013). Recent initiatives such as the Indicator Bats
16 Program (iBats), which aims to apply acoustic monitoring techniques to assess trends in bat
17 populations from regional to global scales (Jones et al., 2013b), are undoubtedly an important
18 step forward in this direction.

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

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

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

14 While the use of acoustic methods to globally monitor bats as, for instance, employed
15 by the iBats Program, may constitute an efficient and cost-effective alternative to traditional
16 bat survey methods, their wider application is not without challenges (Walters et al., 2013).
17 All bat surveillance methods are inherently biased in one way or another (Hayes et al., 2009).
18 Especially in the species-rich tropics, where echolocation call similarity is high and
19 consequently species identification is difficult (Walters et al., 2013), and considerable
20 fractions of the bat fauna are difficult to monitor using acoustic detection methods, bat
21 monitoring programs should rely on a range of complementary methods (Meyer et al., 2014).
22 The following discussion is therefore chiefly targeted at the monitoring of bats by direct
23 methods of observation, i.e. through the use of traditional capture methods such as mist nets
24 or harp traps (Kunz et al., 2009). Very similar issues do, however, apply to bat monitoring via
25 acoustic methods (see Frick, 2013; Jones et al., 2013b; Walters et al., 2013) or based on

1 colony counts, the latter being the prevailing method in existing temperate-zone bat
2 monitoring programs (Haysom et al., 2013; Walsh et al., 2003). Throughout this paper, I
3 mostly illustrate my main points with the findings and insights gained from an assessment of
4 the suitability of tropical bats for long-term monitoring (Meyer et al., 2011; Meyer et al.,
5 2010; Meyer et al., 2014). This is in part motivated by the fact that sampling and statistical
6 challenges to monitoring are particularly acute for tropical bat populations and assemblages
7 given their high species richness and large proportion of rare species they are comprised of.
8 Moreover, tropical ecosystems and fauna are among the most imperiled worldwide and are
9 undergoing unprecedented changes as a result of widespread deforestation, land-conversion,
10 and defaunation (Bradshaw et al., 2009; Dirzo et al., 2014; Laurance et al., 2014). Tropical
11 bats are sensitive to these threats and anthropogenic alterations of their environment (García-
12 Morales et al., 2013; Meyer et al., forthcoming), underscoring the pressing need and urgency
13 of monitoring their populations and assemblages in an effort to be able to mitigate human-
14 induced environmental impacts.

15

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

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

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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

1 monitoring schemes to establish the extent to which species occupancy patterns effectively
2 capture changes in population abundance.

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

13

14 *Monitoring of assemblage-level attributes*

15 At the assemblage level, most monitoring programs traditionally focus on the
16 taxonomic dimension of biological diversity, i.e. *species richness* (Jones et al., 2013a).
17 However, measures such as *functional diversity* may be more relevant for capturing
18 biodiversity change and how it reflects on ecosystem functioning and services (Yoccoz,
19 2012). Taxonomic and functional metrics of diversity have been shown to often convey
20 complementary information with regard to the responses of a range of animal groups to land
21 use change (Flynn et al., 2009; Vandewalle et al., 2010), and their combined use in
22 monitoring schemes thus offers great potential for improving biodiversity assessments,
23 especially for species-rich assemblages (Vandewalle et al., 2010). Similarly, *phylogenetic*
24 *diversity* is another important component of diversity, arguably more meaningful as
25 biodiversity measure than species richness (Faith, 2013; Rodrigues et al., 2011; Yoccoz,

1 2012). However, despite their potential usefulness as complementary state variables for
2 tracking changes in bat biodiversity, for bats the functional and phylogenetic dimensions of
3 biodiversity, and particularly how they change in response to anthropogenic habitat
4 conversion, remain poorly understood (Cisneros et al., in press; Meyer et al., forthcoming).
5 Finally, *genetic diversity* is yet another important aspect of biodiversity and candidate EBV
6 (Pereira et al., 2013), which given the demonstrated sensitivity of bats to genetic erosion in
7 response to habitat modification (Meyer et al., 2009; Struebig et al., 2011) may likewise
8 prove useful as state variable in long-term monitoring programs.

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

25 Existing temperate-zone bat monitoring schemes at regional, national, or continental

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

17

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

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

25 First, a major design challenge is to collect data from a spatial sample (i.e. sampling

1 sites) that is representative of the wider area or region of interest about which inference is
2 desired (Buckland et al., 2012). Survey site selection should follow a strictly probabilistic
3 sampling design (e.g. random or stratified random), an issue which is neglected in many
4 monitoring programs that still too often are not based on a decent spatial probability sample
5 (Kéry and Schmid, 2008). This should be carefully considered in initiating and implementing
6 new bat monitoring programs, irrespective of whether they are based on capture techniques,
7 acoustic sampling, or colony counts (e.g. Battersby, 2010), although in the latter case
8 stratification of the site sample will often be *post hoc* at the analysis stage (Walsh et al.,
9 2001).

10 The second stochastic process concerns the fact that during field-based wildlife
11 monitoring surveys not all individuals, occupied patches or species are detected, or detected
12 with certainty, at any site sampled, i.e. detection probability (p) is typically < 1 . Detectability
13 is influenced by species and habitat characteristics, survey effort and sampling method, and
14 therefore may vary considerably over both spatial and temporal dimensions (Iknayan et al.,
15 2014).

16 It has long been recognized that species detection is usually imperfect in wildlife
17 surveys, and that this can bias the estimators of ecologically relevant state variables.
18 Imperfect species detection is a pertinent problem in the monitoring of a number of
19 commonly used state variables, species abundance, occupancy, and assemblage-level metrics
20 such as species richness alike (Jones et al., 2013a; MacKenzie and Reardon, 2013). The
21 interpretation of trends based on raw counts for any of these variables is always complicated
22 by imperfect species detection and the fact that detectability rarely remains constant over
23 dimensions of interest (space or time), even when standardized sampling schemes are used
24 (Kéry et al., 2009a; Kéry and Schmid, 2008). The last decade has seen a fast development of
25 statistical models aimed at providing estimates of occupancy, species richness and relative

1 abundance while accounting for imperfect species detection, employing either maximum
2 likelihood or Bayesian approaches (Bailey et al., 2013; Kéry et al., 2009a; Kéry et al., 2009b;
3 MacKenzie et al., 2006; Royle and Dorazio, 2008). Imperfect detection results in false
4 species absences, which, if unaccounted for, will cause species richness, abundance, and
5 occupancy to be underestimated (Kéry and Schmid, 2008; MacKenzie and Reardon, 2013).
6 Consequently, if ignored, imperfect detection may lead to diagnosing spurious trends or mask
7 real patterns and failure to account for detection bias is a major pitfall to quantifying
8 biodiversity change in relation to anthropogenic habitat modification and may misguide
9 management and conservation decisions (Ruiz-Gutiérrez and Zipkin, 2011). For instance,
10 ignoring detectability differences among species and habitats in fragmented landscapes may
11 overestimate turnover rates, distort patterns of species persistence and colonization, and lead
12 to erroneous classification of species as forest specialists and generalists (Ruiz-Gutiérrez and
13 Zipkin, 2011). Monitoring the responses of bats to human-induced habitat loss and
14 modification requires a clear understanding of colonization and persistence patterns and how
15 they are influenced by low and variable detection probabilities across species and habitat
16 types. Problems associated with imperfect detection have long been identified and are
17 regularly taken into account in studies on other vertebrate taxa, particularly birds, through
18 models that adjust for detectability (e.g. Boulinier et al., 1998). In contrast, the application of
19 such detectability models in bat studies is still in its infancy and largely restricted to a few
20 evaluations in the context of acoustic surveys (Clement et al., 2014; Duchamp et al., 2006;
21 Gorresen et al., 2008; Weller, 2008), while the problem has been almost completely ignored
22 in studies using traditional capture methods (but see Rodhouse et al., 2012).

23 Bias in estimates of raw species counts arising from detection errors is especially
24 pronounced in communities that contain a large proportion of rare species (Dorazio et al.,
25 2011) and is thus of particular relevance in the context of bat monitoring in the tropics, where

1 the large number of locally rare species are a fundamental challenge to monitoring efforts. As
2 a case in point, Meyer et al. (2011) demonstrated that mean species detectability in tropical
3 bat surveys rarely approaches unity, averaging $0.76 (\pm 0.8 \text{ SD})$ for a suite of 25 bat
4 assemblages from across the New and Old World tropics. This underscores the fact that
5 considerable proportions of species may regularly be missed in tropical bat surveys, even
6 when several repeat visits are conducted per site. Moreover, there was a clear location effect
7 on mean species detectability, which suggests the potential for large biases to be introduced if
8 monitoring data from geographically disparate locations are compared without accounting for
9 such location-specific differences in mean detectability. As pointed out by Meyer et al.
10 (2011), it will be important for tropical bat monitoring programs that operate over larger
11 geographic scales to be calibrated using location-specific detectability estimates to avoid
12 erroneous inferences about trends in species richness. Species-specific detectability,
13 estimated as the probability of detecting a particular species during two successive surveys,
14 was often considerably lower (mean across 232 species = 0.4) than species-averaged
15 estimates and, importantly, highly heterogeneous across species (range 0.03-0.84),
16 illustrating that raw species counts may often be heavily biased. The analysis further revealed
17 substantial differences in species-level detection probabilities among bat ensembles and
18 sampling methods (Fig. 1). For instance, in the Neotropics aerial insectivorous bats attain
19 fairly high levels of detectability (average 0.71) when sampled with acoustic methods, but
20 have much lower detectability using traditional capture techniques. Gleaning animalivorous
21 phyllostomids, in spite of being adequately sampled with capture methods and a group that is
22 sensitive to habitat modification, are challenging monitoring targets, as most species exhibit
23 low detectability. By comparison, in both the Old and New World tropics, frugivores are
24 somewhat more easily detected (Fig. 1).

25 Tropical bat monitoring programs should generally rely on combining the use of

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

7

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

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

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

1 Recent years have also seen more frequent application of power analysis for assessing the
2 ability of monitoring schemes to detect bat population trends for both temperate-zone and
3 tropical bat species (Battersby, 2010; Jones et al., 2013b; Meyer et al., 2010; Roche et al.,
4 2011; Walsh et al., 2001). Some temperate-zone monitoring programs which relied on power
5 analyses to aid in program planning, such as the UK's NBMP, were shown to have generally
6 high sensitivity to detect population changes, sufficient to detect declines of Amber and Red
7 Alert magnitude (1.14% and 2.73% per year, respectively) after 25 years of monitoring, using
8 data from acoustic field surveys and colony counts (Battersby, 2010; Walsh et al., 2001).
9 Programs such as iBats (Jones et al., 2013b) or car-based bat monitoring schemes in Ireland
10 (Roche et al., 2011) which employ acoustic monitoring have similar levels of sensitivity to
11 detect population changes.

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

1 constitute more challenging monitoring targets than frugivores or nectarivores (Figs. 3 and
2 4).

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

16 Temporal and spatial variation in population counts due to environmental variation
17 (process variation) and variability in abundance estimates due to sampling inaccuracies
18 (observation error) are the dominant sources of error in population count data (Clark and
19 Bjørnstad, 2004) and important causes of unreliable identification of a species’ population
20 status (d’Eon-Eggertson et al., 2014). Both of these sources of variability may mask the
21 existence, or alter the magnitude and direction of underlying population trends. Meyer et al.
22 (2010) assessed within-site temporal variation in estimates of relative abundance, i.e. the
23 combined effect of both process variation and observation error, for 121 bat species from 24
24 Neotropical and Paleotropical locations. Precision in abundance estimates, expressed as the
25 coefficient of variation across repeat visits to the same survey site, was generally low as

1 indicated by high CV values (mean CV = 231%, range 101 - 500%), which varied
2 substantially among species and locations. This high among-survey variability in abundance
3 estimates reduces statistical power for trend detection, an effect that in most cases could only
4 be compensated for by substantially increasing the duration of monitoring (Figs. 3 and 4).
5 Further complicating matters, the likelihood of achieving adequate (≥ 0.9) statistical power
6 was not only dependent on the magnitude of temporal variation in abundance estimates, but
7 also on how common or rare a species generally was (Meyer et al., 2010). For rare species,
8 which comprise a sizable portion of tropical bat assemblages (Meyer et al., 2014), the amount
9 of effort required to obtain adequate sample sizes to ensure sufficient power to detect changes
10 in abundance over time can be daunting. The fact that rare species are simultaneously the
11 ones for which strong inferences about trends are most needed and those for which that
12 information is most difficult to obtain represents a formidable challenge in population
13 monitoring (MacKenzie et al., 2005). Species rarity will generally aggravate the problems in
14 dealing with both spatial sampling variation and detectability issues in the estimation of
15 abundance (MacKenzie et al., 2005). For rare bat species, monitoring of trends in abundance
16 via field surveys will often be practically impossible and prohibitively costly. Where
17 abundance is an infeasible metric, species occupancy may be a useful alternative (see above),
18 offering practical advantages over traditional abundance estimates in addition to being
19 regarded a more reliable metric for landscape-level inference due to being more robust to
20 local effects and stochasticity than local abundance estimates (MacKenzie and Reardon,
21 2013).

22 In recent years, considerable progress has been made in the development of analytical
23 methods for estimating occupancy (Bailey et al., 2013), and free software is available such as
24 the program PRESENCE (Hines, 2006) or the R package unmarked (Fiske and Chandler,
25 2011), facilitating their application also in bat monitoring programs. Moreover, in the context

1 of occupancy studies, general survey design recommendations have been devised which can
2 assist managers of bat monitoring programs in finding the optimal allocation of survey effort
3 in terms of number of sampling sites vs. number of temporal replicates (Guillera-Arroita et
4 al., 2010; MacKenzie and Royle, 2005). Choosing the number of repeat visits based on these
5 guidelines also appears to be a suitable approach to optimizing statistical power for detecting
6 temporal differences in occupancy under imperfect detection (Guillera-Arroita and Lahoz-
7 Monfort, 2012). Just as with abundance monitoring, power analyses should inform decisions
8 as to whether to adopt occupancy as state variable in bat monitoring programs and should
9 form the basis for devising appropriate sampling schemes. Guillera-Arroita and Lahoz-
10 Monfort (2012) provide tools for conducting power analyses to assess design trade-offs in
11 occupancy surveys, which can provide valuable guidance, especially for choosing an
12 appropriate and powerful design for monitoring trends in occupancy patterns for rare tropical
13 bat species, for most of which abundance monitoring would be prohibitively costly and
14 infeasible.

15

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

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

21 Even though monitoring occupancy instead of abundance may result in a considerable
22 increase in efficiency and reduce costs, species-level monitoring at the landscape scale
23 remains challenging in situations where many species are involved (Noon et al., 2012), as is
24 the case with highly diverse tropical bat assemblages. Although detailed abundance
25 monitoring of some carefully selected target species - those which are reasonably common

1 locally and whose abundance can be estimated with fairly high levels of precision - is feasible
2 on statistical grounds if data are collected over a sufficiently long time span (Figs. 3 and 4;
3 Meyer et al., 2010), I argue that the sheer number and diversity of species in tropical bat
4 assemblages makes single-species monitoring ineffective, cost-inefficient, and thus
5 unrealistic to implement at larger scales. Instead, multi-species monitoring and hierarchical
6 assemblage-level modeling frameworks based on presence-absence data, which have recently
7 emerged as efficient and cost-effective approaches to track the influence of environmental
8 changes on biological communities (DeWan and Zipkin, 2010; Dorazio and Royle, 2005;
9 Dorazio et al., 2006), offer a promising alternative for the regional-scale monitoring of
10 tropical bats. These newly developed hierarchical multispecies occupancy models enable
11 simultaneous monitoring of multiple species and are especially useful for assemblages that
12 include many rare species. Compared to the application of single-species occupancy models,
13 a major advantage of these models is that they allow for simultaneous assemblage-level and
14 species-level inference with regard to probabilities of occurrence and detection and can
15 readily accommodate survey-, site-, and species-level covariates that differentially affect the
16 detection of species or individuals in the estimation process (e.g. Iknayan et al., 2014; Kéry et
17 al., 2009b; Zipkin et al., 2010). It thus constitutes an innovative, comprehensive, cost-
18 effective analysis framework to obtaining robust estimates of occurrence for both individual
19 species and assemblages (DeWan and Zipkin, 2010), whose potential should be fully
20 exploited in the implementation of a tropical network of regional-scale bat monitoring
21 programs. This integrated approach would also be suitable to monitor the occurrence status of
22 certain target groups of species, for instance bat ensembles with demonstrably high functional
23 importance and sensitivity to habitat disruption and disturbance such as Neotropical gleaning
24 animalivorous bats (García-Morales et al., 2013; Kalka et al., 2008; Meyer et al.,
25 forthcoming).

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

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

1 85% of the full set) could in many instances reduce monitoring costs by requiring fewer site
2 visits. On the other hand, species subset performance depended on structural assemblage
3 characteristics, which are site-specific. This highlights the need for rigorously validating
4 surrogate performance of species subsets on a site-by-site basis prior to program
5 implementation and throughout the monitoring process. More generally it stresses the
6 importance of adaptive sampling schemes that spatially prioritize effort so as to ensure
7 reliable and statistically robust inference about patterns of change over larger spatial scales.

8 There has been growing interest in the potential of participatory monitoring schemes
9 to decrease the costs involved (Jones, 2013). For instance, much of the success of well-
10 established bat monitoring programs in the temperate zone, most notably the UK's NBMP,
11 stem from their reliance on a large network of volunteers (Jones et al., 2013b; Walsh et al.,
12 2003). Although citizen science monitoring of bats in the tropics in the foreseeable future is
13 unlikely to attain levels of participation anywhere close to these, I argue that the successful
14 implementation of a larger network of regional monitoring schemes in developing countries
15 will also critically hinge on involving to a large extent local populations and volunteers.
16 Indeed, in view of recent studies demonstrating that participatory monitoring in developing
17 tropical countries can be a success (Danielsen et al., 2014; Holck, 2008), there is a clear and
18 as of yet unrealized potential for involving local people in developing countries in bat
19 monitoring efforts, provided specialist training in survey methods is given. Although
20 concerns are often raised over the reliability of data collected by volunteers, by correcting for
21 detection bias, modern statistical approaches, specifically occupancy models, can
22 simultaneously adjust for observation and reporting bias inherent in opportunistic citizen
23 science data (Kéry et al., 2010; van Strien et al., 2013).

24

25 **Conclusions and recommendations**

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

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

16 For reliable quantification of regional trends, bat monitoring programs should ensure
17 adequate spatial replication throughout the survey region, whereby the critical sample size is
18 the number of randomly selected sampling sites, and sufficient data to allow average
19 detectability across sites within the region of interest to be estimated for each species
20 (Buckland et al., 2012). Bat researchers are lagging quite far behind much of the rest of the
21 ecological research community in applying corrective measures for imperfect species
22 detection in contexts where they are clearly needed - including monitoring - and I advocate
23 that greater attention be paid to this issue. Bat monitoring programs should embrace and take
24 advantage of recent advances in statistical modeling and analysis techniques, specifically
25 hierarchical occupancy models that account for detectability, which are an important and

1 flexible toolkit for the analysis of monitoring data. Notwithstanding the indisputable
2 usefulness of such statistical models that allow adjusting for imperfect species detection,
3 Banks-Leite et al. (2014) recently cautioned against their uniform application, and called
4 attention to the fact that carefully planned sampling designs that *a priori* try to minimize the
5 effects of covariates of detectability are just as important. I echo their call and argue that bat
6 monitoring programs should first and foremost control for covariates of detection probability
7 through a well-balanced study design and highly standardized sampling, and not rely
8 exclusively on *a posteriori* statistical detectability adjustments.

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

18

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23

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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 Palearctic 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 (\pm 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).