

Long-term monitoring of tropical bats for anthropogenic impact assessment: Gauging the statistical power to detect population change

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ABSTRACT

Bats are ecologically important mammals in tropical ecosystems; however, their populations face numerous environmental threats related to climate change, habitat loss, fragmentation, hunting, and emerging diseases. Thus, there is a pressing need to develop and implement large-scale networks to monitor trends in bat populations over extended time periods. Using data from a range of Neotropical and Palearctic bat assemblages, we assessed the ability for long-term monitoring programs to reliably detect temporal trends in species abundance. We explored the magnitude of within-site temporal variation in abundance and evaluated the statistical power of a suite of different sampling designs for several different bat species and ensembles. Despite pronounced temporal variation in abundance of most tropical bat species, power simulations suggest that long-term monitoring programs (≥ 20 years) can detect population trends of 5% per year or more with adequate statistical power (≥ 0.9). However, shorter monitoring programs (≤ 10 years) have insufficient power for trend detection. Overall, our analyses demonstrate that a monitoring program extending over 20 years with four surveys conducted biennially on five plots per monitoring site would have the potential for detecting a 5% annual change in abundance for a suite of bat species from different ensembles. The likelihood of reaching adequate statistical power was sensitive to initial species abundance and the magnitude of count variation, stressing that only the most abundant species in an assemblage and those with generally low variation in abundance should be considered for detailed population monitoring.

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1. Introduction

Human-induced environmental changes are altering the Earth's biota at unprecedented rates, threatening the long-term persistence of many animal and plant species. Large-scale monitoring networks are critical for understanding and predicting species responses to anthropogenic change and habitat alteration, and ultimately for long-term biodiversity conservation.

Bats (Chiroptera), currently with 1150 recognized extant species (Schipper et al., 2008), are major contributors to mammalian biodiversity, comprising about 20% of mammalian species globally (Simmons, 2005). Bats combine a range of features that make them excellent bioindicators of human-induced changes with respect to climate change and habitat quality, including a cosmopolitan distribution with high functional and taxonomic diversity (Jones et al., 2009). Moreover, many species fulfill key ecosystem services, particularly in tropical ecosystems, as pollinators, seed dispersers, and control agents of arthropod populations (e.g. Kalka et al., 2008; Kelm et al., 2008; Lobova et al., 2009; von Helversen and Winter, 2003; Williams-Guillén et al., 2008). Bats are also excellent indicators of environmental change because they respond to a wide range of global phenomena and environmental stressors such as urbanization, agricultural intensification, forest disturbances (e.g. logging, oil extraction), habitat loss and fragmentation, global climate change, and overhunting. Finally, the responses of bats to habitat disturbance are often associated with those of other taxa (e.g. Bass et al., 2010; Jones et al., 2009).

Worldwide, populations of many bat species are declining, mainly as a consequence of extensive habitat loss and degradation. Globally, almost one fourth of all bat species are considered threatened (Schipper et al., 2008). Thus, many bat species require conservation efforts and there is an urgent need for the implementation of a global network for monitoring bat populations (Jones et al., 2009). However, current monitoring programs for bats are restricted to temperate regions and mostly limited in scope and scale, primarily focusing on single-species at a local level (Betke et al., 2008; Hristov et al., 2010; O'Shea and Bogan, 2003; Walsh et al., 2003). This is despite the fact that in both the Old and New World tropics, many bat species are threatened by rampant deforestation and concomitant loss and fragmentation of habitat (IUCN, 2009; Lane et al., 2006). Thus far, bats have not been included in established long-term monitoring programs in the tropics such as Conservation International's Tropical Ecology, Assessment and Monitoring (TEAM) network (www.teamnetwork.org). Given their importance in tropical ecosystems, their value as bioindicators and their vulnerability (Jones et al., 2009), monitoring of tropical bats to assess population trends over longer time scales is urgently needed. However, implementation of any monitoring program requires scientifically rigorous and statistically defensible efforts to ensure that monitoring data provide reliable results.

Drawing from numerous empirical datasets based on a representative sample of Neotropical and Paleotropical bat assemblages, we herein assess the potential for a monitoring program to reliably detect temporal trends in relative species abundance of tropical bats. Such an assessment should consider the magnitude of change (the effect size) that is thought to be an appropriate threshold, the statistical power needed to confidently detect a particular change, and the sample size. Although evaluating trade-offs between variables of survey design and sample size through *a priori* power analyses should be integral to planning efforts (Fairweather, 1991; Gibbs et al., 1998; Legg and Nagy, 2006; Steidl et al., 1997), statistical power analyses are seldom considered even at the development stage in long-term monitoring programs (Gibbs and Ramirez de Arellano, 2007; Gibbs et al., 1999; Legg and Nagy, 2006; Marsh and Trenham, 2008). Ignoring issues of statistical

power may lead to resources being spent on monitoring programs that have little chance of detecting trends or, conversely, may result in monitoring efforts in excess of what is needed, hence essentially wasting valuable resources by under- or oversampling (Gibbs et al., 1999). In the present study, we use power analyses to determine the necessary sampling effort required to detect biologically significant population trends and to identify appropriate survey techniques and sampling designs for monitoring tropical bat species.

Statistical power is a measure of the confidence with which a statistical test can detect a particular effect when such an effect does indeed exist (Anderson, 1998; Cohen, 1988; Gerrodette, 1987). Thus, statistical power is the probability that a monitoring program will detect a trend in population abundance when such a trend has occurred or is occurring, despite inherent "noise" in the data. The selection of an appropriate monitoring design is largely a question of managing factors that influence Type II error rate (β) (Anderson, 1998). Power ($1 - \beta$) depends on interactions between sample size (number of sites), the duration (years) for which a population is being monitored, the frequency of surveys (within and between years), the magnitude of change (trend) to be detected, variability in the data, and the level of significance (α) of the statistical test being used (Fairweather, 1991; Field et al., 2005; Thompson et al., 1998).

Abundance data often show high variance, thus strategies that can reduce variance are especially important for achieving high statistical power. The decision of which species (or ensembles of species) to focus monitoring studies upon involves a consideration of the repeatability of monitoring data for a particular species. Ideally, species should be targeted that can be consistently measured at an acceptable level of precision (Seavy and Reynolds, 2007).

To this end, we explored the magnitude of within-site temporal variation in abundance at the level of individual bat species and ensembles for a range of datasets. The magnitude of variation can indicate the degree of measurement error in abundance estimates for a particular species, and thus provide information on how reliable such measurements of a given species will be for detecting differences in assemblages. Using mean and variance parameters from a variety of datasets, we evaluated the statistical power of a suite of alternative sampling designs for detecting long-term trends in the relative abundance of bat populations. We explored trade-offs in spatial and temporal allocation of sampling effort needed to achieve reasonable statistical power to detect trends for selected bat species and different ensembles over a range of effect sizes. Specifically, we focused on the trade-offs between number of sampling sites, sampling frequency within and between years, and duration of the monitoring program. Finally, we assessed the efficiency of various sampling strategies by modeling power estimates for designs that can achieve the desired power goal as a function of design characteristics and species attributes.

2. Methods

2.1. Within-site temporal variation in abundance

Within-site temporal variation is the sum of temporal variability in abundance across successive surveys and sample error (methodological) associated with variation in species detectability (Carlson and Schmiegelow, 2002). To assess the consistency of abundance estimates over time for particular species or ensembles, we calculated the coefficient of variation (CV) of relative abundance across repeated surveys for 121 bat species from 24 Neotropical and Paleotropical locations (Appendix). Calculations were based on capture data (mist nets: frugivores, nectarivores, gleaning

animalivores; harp traps: Paleotropical aerial insectivores, relative abundance measured as number of bats captured per square meter net/trap-hour) or acoustic data (Neotropical aerial insectivores, relative activity measured as number of bat passes per minute) from one sampling site per location. To test for differences in the magnitude of CV between ensembles, we fitted a linear mixed model (LMM) with species and location specified as partially crossed random factors using the lme4 package (Bates, 2007) in (R Development Core Team, 2008).

This analysis and the subsequent power calculations involve synthesis of datasets that inevitably encompass certain variation in sampling strategy and that differ to some degree in terms of spatio-temporal scale. Nonetheless, we believe that sampling methods were sufficiently consistent across studies to provide reliable and comparable estimates of temporal variation in population abundance. For datasets originating from fragmented or otherwise disturbed areas, we included only data from control plots in unfragmented or mostly undisturbed forest in the analysis to ensure maximum comparability of datasets.

2.2. Parameters and data sources for power analyses

Power analyses were restricted to a subset of available datasets, covering on average 3.2 (SD 1.4, range 2–6) years of sampling. Specifically, we used estimates of the initial magnitude and variance in relative abundance at a particular sampling transect/plot (i.e. a site within a study location with multiple nets) from five Neotropical and four Paleotropical datasets as input for the power analyses (Appendix). For assessing power to detect trends over 10 or 20 years it would certainly be desirable to use estimates of temporal variance stemming from datasets that cover longer time spans as input for the power calculations, however, such data currently are not available for bats. Nonetheless, we believe that our data incorporate a realistic range of temporal variance in estimates of population abundance and thus can be used to obtain meaningful power estimates. Capture rate, standardized to number of bats captured per 100 m² net hours to account for varying sampling effort between studies, was used as an index of relative population abundance (number of bat passes/min in the case of the one dataset based on acoustic surveys). For each dataset, we performed the power analyses for a spectrum of species covering a range of initial mean estimates of abundance and variance characteristics (34 species total with three to six species per dataset). Additionally, we assessed statistical power at the functional level, pooling species by ensemble (frugivores, nectarivores, gleaning animalivores, aerial insectivores). In each case, we calculated mean estimates of relative abundance and standard deviations for a particular plot based on repeated surveys conducted on the same plot as an estimate of temporal variance. Temporal variances were modeled as a single, pooled estimate of variation (i.e. pooling variation within and between years since it would have been difficult to partition these two sources of variation in a consistent way due to the heterogeneity of the datasets). For survey scenarios involving multiple plots, spatial variation was accounted for by providing different initial mean values for each of the plots being monitored from which trends could then be projected.

2.3. Power simulations

We constructed statistical power curves for various combinations of spatial and temporal replicates using a Monte Carlo simulation approach as implemented in the software MONITOR v. 10.0 (Gibbs and Ramirez de Arellano, 2007). To estimate power in MONITOR, one needs to define the desired sampling design structure (e.g. frequency of surveys, number of survey years, number of plots) and provide estimates of the magnitude and variation in abundance

estimates as input for the program. We used a plot-specific sampling structure in which we specified initial abundance values and sampling variances for each plot. These quantities were derived from several empirical data sets as detailed above. We estimated power for 10 and 20 years of surveys performed annually or biennially along one, three, or five sampling plots and involving two, three, or four repeat surveys per plot per year. Because for trend analysis the risk of missing a significant change can be considered to be at least as important as the risk of finding a significant difference where it does not exist (Anderson, 1998; Di Stefano, 2003), we set the maximum acceptable Type I (α) and Type II (β) error rates both to 0.1 (Di Stefano, 2003; Purcell et al., 2005; Steidl et al., 1997). Consequently, our desired power level ($1 - \beta$) was 0.9, which is often recommended for reliable trend detection (Gibbs and Ramirez de Arellano, 2007; Steidl et al., 1997). Power estimates in MONITOR were based on 1000 iterations and simulations were run using the recommended, default options of exponential trend projection, constant CV over time, and assuming asynchronous spatial autocorrelation for multiple plot designs (Gibbs and Ramirez de Arellano, 2007). The analysis steps implemented in MONITOR differ somewhat depending on whether power is estimated for single- or multiple-plot situations. For survey designs consisting of repeated sampling on a single plot, trends are projected from the initial abundance estimate over the series of previously defined survey occasions. At each survey occasion, sample measures are generated as random deviates drawn from a distribution with mean equal to the projected value at a particular monitoring occasion and with a variance approximated by the standard deviation in initial abundance. Power is then calculated based on the proportion of iterations in which the slope estimates of a least-squares regression of the plot of sample abundances versus survey occasion differ significantly from zero (Gibbs and Ramirez de Arellano, 2007). For monitoring programs consisting of multiple plots, MONITOR uses a 'route regression' approach, whereby trends in sample counts are generated as above for each survey occasion and plot. The slope of a least-squares regression of sample abundances versus survey occasion is determined for each plot and each trend, and then averaged across plots. The proportion of iterations in which the mean slope estimates differ significantly from zero based on a *t*-test is then used to estimate power (Gibbs and Ramirez de Arellano, 2007). We evaluated the significance of a trend based on two-tailed *t*-tests, as we were interested in both negative and positive trends in the populations being monitored. Because two-tailed tests may yield lower power than one-tailed tests (Gibbs and Ramirez de Arellano, 2007), our power estimates can generally be considered as conservative. For any specified sampling scenario, we estimated power for a set of equal interval trends, from a precipitous 25% decline per time unit to a 25% increase, in 5% increments. For example, an effect size of –10% per year with 20 sampling years is equal to a net change of –86.5% over 20 years (=overall trend).

Although low to moderate degrees of temporal autocorrelation are often found in successive estimates of abundance, its effect on power to detect trends appears to be modest, hence assuming independence of sequential values seems reasonable in most cases (Gibbs and Ramirez de Arellano, 2007). We tested this assumption for a subset of the data by performing power simulations with a moderate level of positive serial autocorrelation (0.5) introduced. These analyses confirmed that the influence of temporal autocorrelation on power estimates was typically low (results not shown).

2.4. Determinants of adequate power level

To provide a synthesis of the power simulations, we modeled the probability of reaching the desired power level (0.9) to detect a –25% trend as a function of monitoring design parameters and species characteristics. We fitted a generalized linear mixed-effects

model (GLMM, logit link and binomial errors) to the binary outcome data (1: desired power achieved, ≥ 0.9 ; 0: desired power not achieved, < 0.9), using the lme4 package (Bates, 2007) in (R Development Core Team, 2008). The most complex model included a suite of monitoring design options (number of plots, number of surveys per plot, survey interval, number of survey years) and species attributes (ensemble, initial relative abundance, CV of relative abundance) as fixed effects, and a variance component due to a random effect of species identity. We used likelihood ratio tests to assess the significance of individual model terms (Pinheiro and Bates, 2000). Following model simplification, we tested fixed effects retained in the minimum adequate model (MAM) using Wald tests. Separate GLMMs were performed for Neotropical (ground net data) and Palearctic data sets (ground net and harp trap data, with capture method included as an additional fixed effect in the GLMM).

3. Results

3.1. Within-site temporal variation in abundance

At both the species and ensemble level, the CV of relative abundance was generally high, and varied substantially across species and locations (median CV 1.86, range: 0.211–9.75, Fig. 1 and 2). Only a few species had CV values comparable in magnitude for the majority of locations where they occurred (Fig. 2). CV values were significantly higher for Palearctic than Neotropical species (LMM, $\chi^2 = 3.95$, $df = 1$, $P = 0.047$) and there were significant differences in the magnitude of temporal variation between ensembles (LMM, $\chi^2 = 14.56$, $df = 3$, $P = 0.002$). Nectarivores had significantly higher CV values than frugivores, gleaning animalivores, or aerial

insectivores (multiple comparisons using Tukey contrasts, $z \geq 3.47$, $P < 0.01$). When aerial insectivores were compared separately by region to take into account different sampling methods, Neotropical aerial insectivores that were acoustically sampled had significantly lower CVs than Palearctic species based on captures with mistnets and harp traps (LMM, $\chi^2 = 5.34$, $df = 1$, $P = 0.021$; Fig. 2).

3.2. Power simulations

Results of the power simulations reported below are necessarily a representative sample of the full results, selected to highlight some of the major differences between the survey designs we explored. Although we performed power simulations for both positive and negative trends, we focus here on results that concern the ability to detect negative trends in population abundance, because this is the most relevant issue in long-term, conservation-oriented monitoring programs.

The duration of monitoring was clearly important in determining whether population trends could be detected. In many instances, 10 years of monitoring were insufficient to detect a significant decline in relative abundance with adequate power, in particular with effect sizes of lower magnitude (e.g. -10%). Even the maximum number of visits (four) and plots (five) typically provided inadequate power to detect annual declines of 5% or 10% with only 10 years of sampling. Conversely, 20 years of sampling yielded adequate power to detect decreases in abundance for most species (see Figs. 3 and 4 for examples).

The large degree of between-site spatial variation in surveys on multiple plots made trend-detection more difficult compared to monitoring of single plots, thus requiring a larger number of

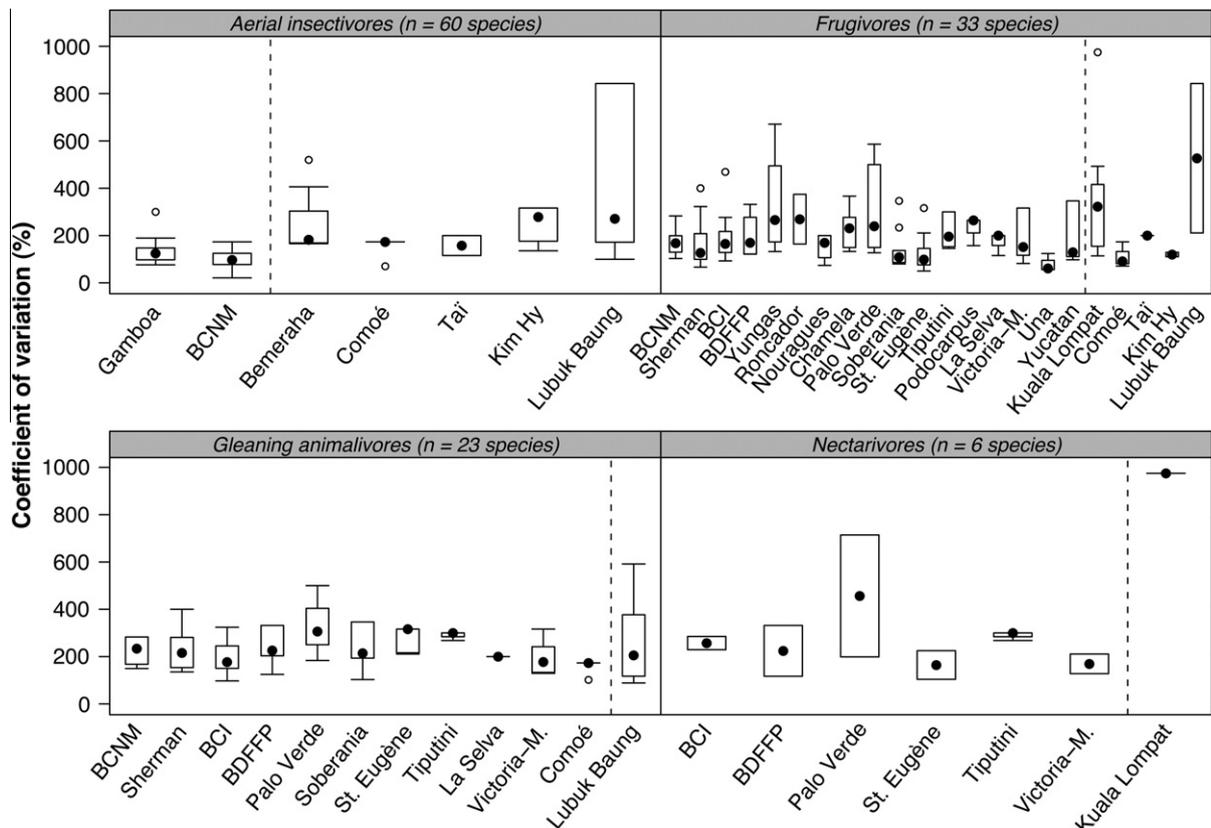


Fig. 1. Boxplots showing temporal variation in relative abundance of bats, expressed as coefficient of variation (CV), across a range of Neotropical and Palearctic locations, with species pooled by ensemble. In each panel, the dotted line separates Neotropical (left) from Palearctic datasets (right). Plots shown are based on acoustic data (Gamboa and BCNM, Panama), harp trapping (Lubuk Baung, Malaysia) and mist netting data (all other locations) and include data from one sampling site per location and from at least two species per location and ensemble.

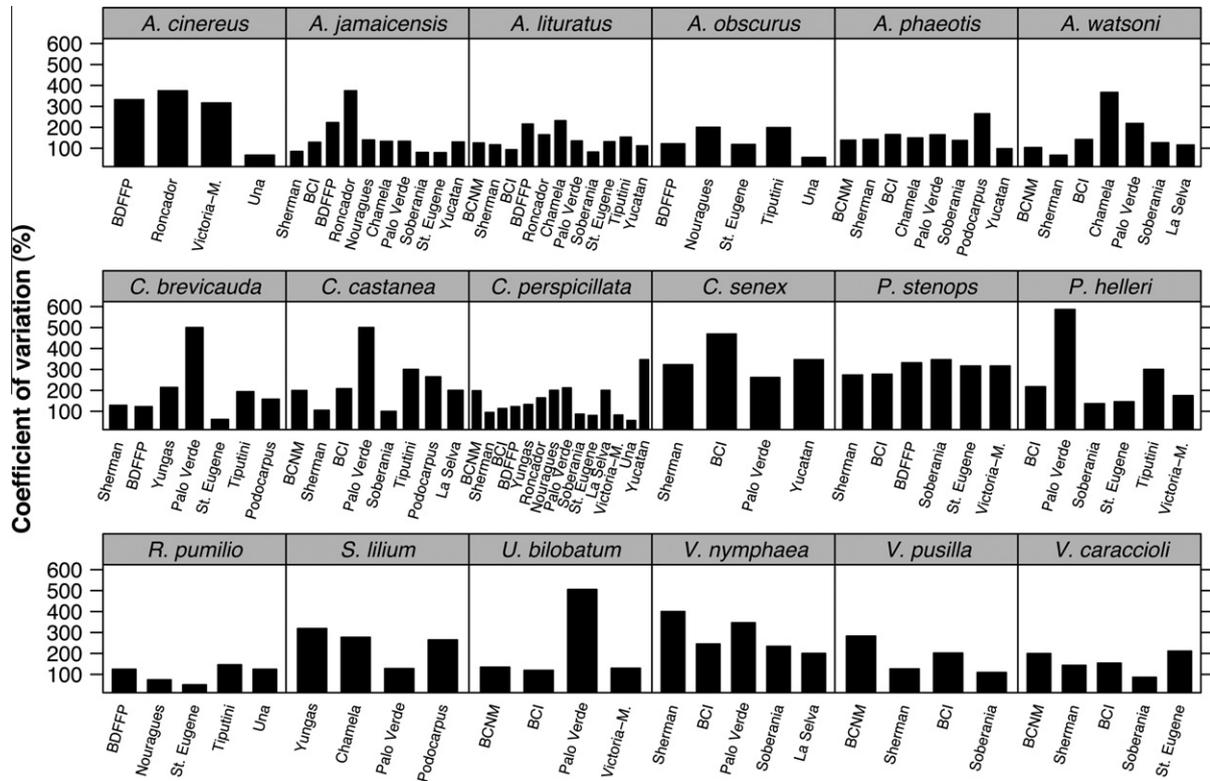


Fig. 2. Within-site temporal variation in relative abundance, expressed as coefficient of variation (CV), for 18 frugivorous bat species from several Neotropical locations. Plots are based on ground-level mist netting data from one sampling site per location and species present at a minimum of four separate locations.

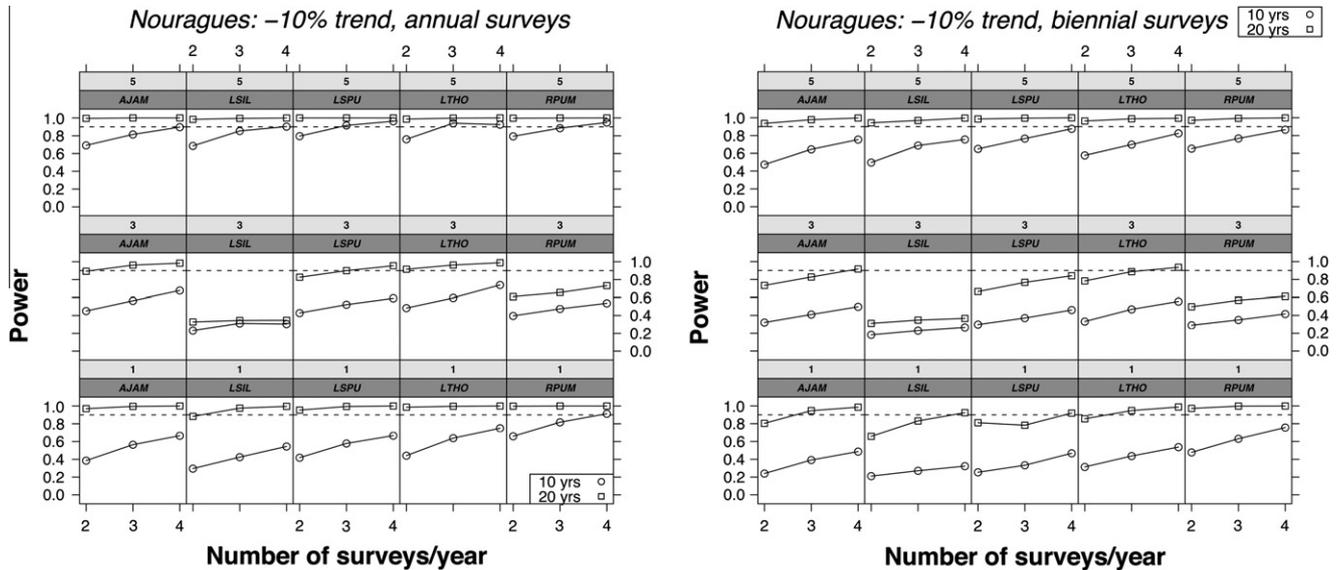


Fig. 3. Influence of number of survey occasions per year for annual (left) and biennial surveys (right) along different numbers of sampling plots (one, three, and five) on power to detect a 10% decrease over 10 or 20 years, respectively, for five bat species sampled with ground-level mist nets at Nouragues, French Guiana. The dotted line indicates the desired power level at 0.90 ($\beta = 0.10$). AJAM = *Artibeus jamaicensis*; LSIL = *Lophostoma silvicolum*; LSPU = *Lionycteris spurelli*; LTHO = *Lonchophylla thomasi*; RPUM = *Rhinophylla pumilio*.

plots to be surveyed to compensate for this effect. This is reflected in the fact that power was often lower in the case of three plots compared to only one or five plots (Figs. 3–5). Even 20 years of monitoring on three plots were insufficient to attain adequate power for the majority of species included in the simulations, in particular for a 5% declining trend per year (Table 1). With three plots, varying the magnitude of the projected trend generally had

a large effect on power estimates. While the desired power level was reached at least for a variety of species for annual population declines of 10% or 25% per year, annual declining trends of 5% could only be detected for two species (Table 1). Increasing the number of repeat surveys from two to four in these three-plot sampling designs had comparatively little effect on power estimates.

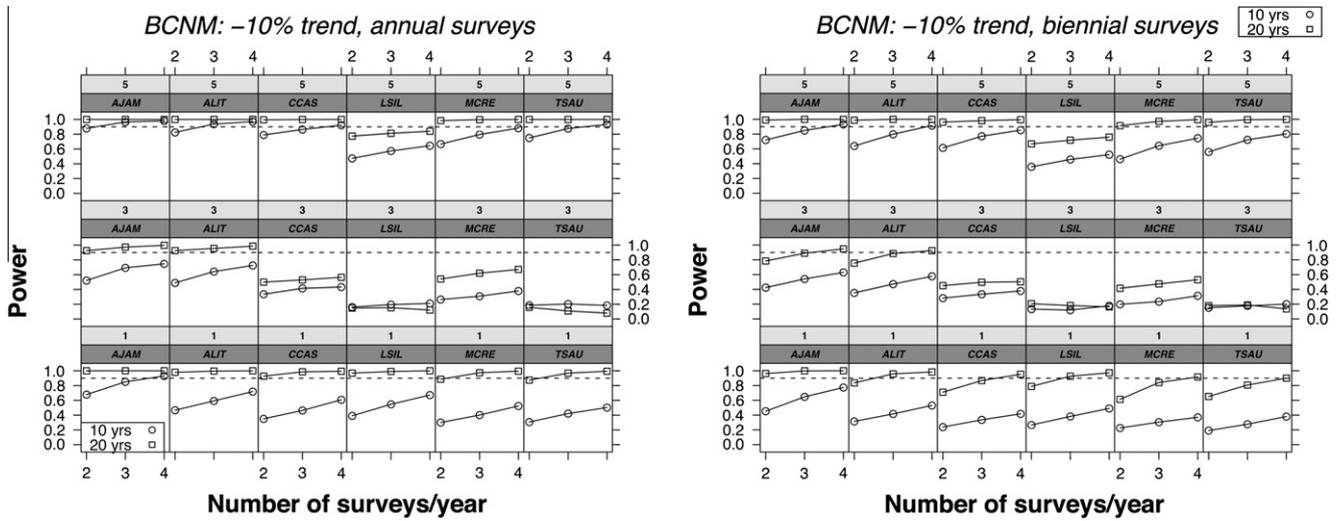


Fig. 4. Influence of number of survey occasions per year for annual (left) and biennial (right) surveys along different numbers of sampling plots (one, three, and five) on power to detect a 10% decrease over 10 or 20 years, respectively, for six bat species sampled with ground-level mist nets in the Barro Colorado Nature Monument, Panama. The dotted line indicates the desired power level at 0.90 ($\beta = 0.10$). AJAM = *Artibeus jamaicensis*; ALIT = *A. lituratus*; CCAS = *Carollia castanea*; LSIL = *Lophostoma silvicolium*; MCRE = *Mimon crenulatum*; TSAU = *Tonatia saurophila*.

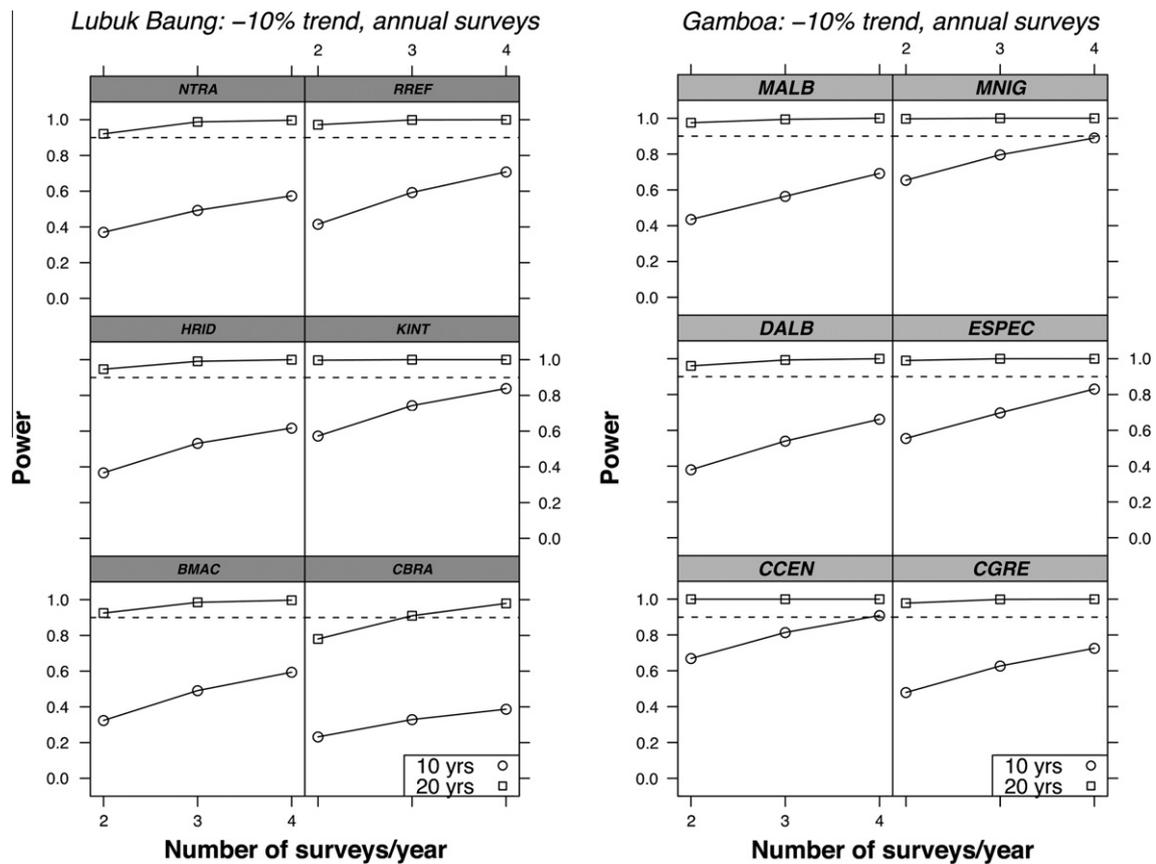


Fig. 5. Influence of number of survey occasions per year for annual surveys conducted on one sampling plot on power to detect a 10% decrease over 10 or 20 years, respectively, for 12 bat species sampled with harp traps at Lubuk Baung, Malaysia (left), and acoustically in Gamboa, Panama (right). The dotted line indicates the desired power level at 0.90 ($\beta = 0.10$). BMAC = *Balionycteris maculata*; CBRA = *Cynopterus brachyotis*; CCEN = *Centronycteris centralis*; CGRE = *Cynomops greenhalli*; DALB = *Diclidurus albus*; ESPEC = *Eumops spec.*; HRID = *Hipposideros ridleyi*; KINT = *Kerivoula intermedia*; MALB = *Myotis albescens*; MNIG = *M. nigricans*; NTRA = *Nycteris tragata*; RREF = *Rhinolophus refulgens*.

For a monitoring program that extends over 20 years, increasing the number of plots to five would allow reliable trend detection even for annual changes in population levels of -5% or -10% (Table 2, Figs. 3 and 4). Moreover, in the latter case, using biennial surveys would suffice to attain adequate power to detect a 10% decline

for almost all species included in the simulations with only two repeat visits per plot, and even smaller changes of -5% would be detectable by increasing the number of sampling occasions per plot to four (Table 2). Depending on the desired effect size, a statistically robust monitoring program based on two-four repeat visits

Table 1

Power to detect population decreases per unit time of 5%, 10%, or 25% over 20 years on three plots with surveys conducted annually for 21 species of tropical bats. Cases in which the desired power level (0.9) was reached are highlighted in italics.

Species	Ensemble ^a	Location ^b	Trend: –5%			–10%			–25%		
			No. of surveys			No. of surveys			No. of surveys		
			2	3	4	2	3	4	2	3	4
<i>Artibeus jamaicensis</i>	FRUG	BCNM, Panama	0.72	0.82	0.89	0.93	0.97	1.00	0.96	0.98	0.99
<i>A. jamaicensis</i>	FRUG	Nouragues, French Guiana	0.64	0.77	0.84	0.89	0.96	0.98	0.94	0.98	1.00
<i>A. jamaicensis</i>	FRUG	St. Eugène, French Guiana	0.33	0.31	0.28	0.28	0.28	0.26	0.30	0.25	0.24
<i>A. lituratus</i>	FRUG	BCNM, Panama	0.67	0.80	0.87	0.93	0.96	0.99	0.94	0.98	0.99
<i>A. obscurus</i>	FRUG	Una, Brazil	0.55	0.61	0.63	0.67	0.68	0.73	0.64	0.72	0.73
<i>Carollia castanea</i>	FRUG	BCNM, Panama	0.43	0.48	0.49	0.50	0.53	0.56	0.51	0.53	0.54
<i>C. perspicillata</i>	FRUG	Una, Brazil	0.82	0.90	0.95	0.98	1.00	1.00	0.99	1.00	1.00
<i>Micropteropus pusillus</i>	FRUG	Comoé, Ivory Coast	0.19	0.21	0.19	0.22	0.20	0.20	0.20	0.21	0.21
<i>Nanonycteris veldkampii</i>	FRUG	Comoé, Ivory Coast	0.46	0.52	0.58	0.60	0.62	0.69	0.63	0.65	0.73
<i>Rhinophylla pumilio</i>	FRUG	Nouragues, French Guiana	0.48	0.56	0.58	0.61	0.66	0.73	0.65	0.71	0.76
<i>R. pumilio</i>	FRUG	St. Eugène, French Guiana	0.56	0.62	0.64	0.67	0.71	0.77	0.69	0.76	0.77
<i>R. pumilio</i>	FRUG	Una, Brazil	0.45	0.59	0.62	0.67	0.78	0.82	0.70	0.82	0.87
<i>Choeroniscus minor</i>	NECT	St. Eugène, French Guiana	0.24	0.32	0.33	0.35	0.39	0.38	0.37	0.39	0.43
<i>Lionycteris spurelli</i>	NECT	Nouragues, French Guiana	0.53	0.69	0.78	0.83	0.90	0.96	0.87	0.93	0.97
<i>Lonchophylla thomasi</i>	NECT	Nouragues, French Guiana	0.66	0.81	0.85	0.92	0.96	0.99	0.95	0.99	1.00
<i>L. thomasi</i>	NECT	St. Eugène, French Guiana	0.24	0.26	0.23	0.21	0.17	0.16	0.22	0.17	0.15
<i>Lophostoma silvicolum</i>	GLANIM	BCNM, Panama	0.19	0.18	0.17	0.15	0.15	0.12	0.17	0.11	0.12
<i>L. silvicolum</i>	GLANIM	Nouragues, French Guiana	0.29	0.33	0.33	0.33	0.34	0.35	0.34	0.36	0.34
<i>Mimon crenulatum</i>	GLANIM	BCNM, Panama	0.35	0.45	0.49	0.54	0.62	0.67	0.55	0.65	0.74
<i>M. crenulatum</i>	GLANIM	St. Eugène, French Guiana	0.49	0.59	0.69	0.70	0.79	0.85	0.76	0.80	0.87
<i>Nycteris arge</i>	GLANIM	Comoé, Ivory Coast	0.71	0.80	0.85	0.88	0.94	0.97	0.92	0.96	0.99
<i>N. arge</i>	GLANIM	Taï, Ivory Coast	0.95	0.98	0.99	1.00	1.00	1.00	1.00	1.00	1.00
<i>N. macrotis</i>	GLANIM	Comoé, Ivory Coast	0.42	0.49	0.57	0.59	0.66	0.68	0.60	0.68	0.72
<i>Tonatia saurophila</i>	GLANIM	BCNM, Panama	0.19	0.21	0.16	0.16	0.11	0.08	0.14	0.09	0.05
<i>T. saurophila</i>	GLANIM	St. Eugène, French Guiana	0.32	0.35	0.38	0.38	0.41	0.44	0.39	0.40	0.44
<i>Rhinolophus alcyone</i>	AEINS	Comoé, Ivory Coast	0.77	0.86	0.90	0.92	0.97	0.98	0.95	0.98	0.99
<i>R. alcyone</i>	AEINS	Taï, Ivory Coast	0.33	0.37	0.41	0.42	0.46	0.52	0.44	0.47	0.54
<i>Scotophilus viridis</i>	AEINS	Comoé, Ivory Coast	0.54	0.64	0.75	0.78	0.85	0.89	0.80	0.89	0.90

^a FRUG = frugivore, NECT = nectarivore, GLANIM = gleaning animalivore, AEINS = aerial insectivore.

^b BCNM = Barro Colorado Nature Monument.

Table 2

Power to detect a population decrease per unit time of 5% and 10%, respectively, over 20 years on five plots with surveys conducted annually or biennially for 13 species of tropical bats. Cases in which the desired power level (0.9) was reached are highlighted in italics.

Species	Ensemble ^a	Location ^b	Annual surveys						Biennial surveys					
			Trend: –5%			–10%			Trend: –5%			–10%		
			No. of surveys			No. of surveys			No. of surveys			No. of surveys		
			2	3	4	2	3	4	2	3	4	2	3	4
<i>Artibeus jamaicensis</i>	FRUG	BCNM, Panama	0.97	0.99	1.00	1.00	1.00	1.00	0.87	0.95	0.99	0.99	1.00	1.00
<i>A. jamaicensis</i>	FRUG	Nouragues, French Guiana	0.88	0.96	0.98	1.00	1.00	1.00	0.67	0.81	0.90	0.94	0.98	1.00
<i>A. lituratus</i>	FRUG	BCNM, Panama	0.96	0.99	1.00	1.00	1.00	1.00	0.84	0.92	0.97	0.99	1.00	1.00
<i>A. obscurus</i>	FRUG	Una, Brazil	0.97	0.99	1.00	1.00	1.00	1.00	0.88	0.95	0.98	0.99	1.00	1.00
<i>Carollia castanea</i>	FRUG	BCNM, Panama	0.89	0.95	0.98	1.00	1.00	1.00	0.77	0.87	0.92	0.96	0.98	1.00
<i>C. perspicillata</i>	FRUG	Una, Brazil	0.99	1.00	1.00	1.00	1.00	1.00	0.91	0.97	0.99	1.00	1.00	1.00
<i>Rhinophylla pumilio</i>	FRUG	Nouragues, French Guiana	0.94	0.99	0.99	1.00	1.00	1.00	0.80	0.90	0.93	0.97	0.99	1.00
<i>R. pumilio</i>	FRUG	Una, Brazil	0.98	1.00	1.00	1.00	1.00	1.00	0.89	0.96	0.99	1.00	1.00	1.00
<i>Lionycteris spurelli</i>	NECT	Nouragues, French Guiana	0.94	0.99	1.00	1.00	1.00	1.00	0.80	0.93	0.96	0.99	1.00	1.00
<i>Lonchophylla thomasi</i>	NECT	Nouragues, French Guiana	0.91	0.96	0.99	0.99	1.00	1.00	0.76	0.86	0.94	0.96	0.99	0.99
<i>Lophostoma silvicolum</i>	GLANIM	BCNM, Panama	0.62	0.70	0.72	0.77	0.81	0.84	0.49	0.56	0.59	0.67	0.72	0.76
<i>L. silvicolum</i>	GLANIM	Nouragues, French Guiana	0.86	0.94	0.98	0.98	1.00	1.00	0.68	0.82	0.89	0.94	0.97	1.00
<i>Mimon crenulatum</i>	GLANIM	BCNM, Panama	0.84	0.93	0.98	0.98	1.00	1.00	0.66	0.78	0.87	0.91	0.97	1.00
<i>Tonatia saurophila</i>	GLANIM	BCNM, Panama	0.90	0.98	0.99	1.00	1.00	1.00	0.75	0.89	0.93	0.96	1.00	1.00
<i>Nycteris arge</i>	GLANIM	Taï, Ivory Coast	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00	1.00
<i>Rhinolophus alcyone</i>	AEINS	Taï, Ivory Coast	0.96	0.99	1.00	1.00	1.00	1.00	0.87	0.93	0.97	0.99	1.00	1.00

^a FRUG = frugivore, NECT = nectarivore, GLANIM = gleaning animalivore, AEINS = aerial insectivore.

^b BCNM = Barro Colorado Nature Monument.

to five sampling plots surveyed every second year would provide adequate power with minimal expense.

3.3. Determinants of adequate power level

GLMM modeling showed that for the Neotropical datasets the probability of achieving the desired power level of 0.9 was sensi-

tive to each sample effort parameter and, in addition, differed significantly between ensembles (Table 3). In contrast, there was no such effect for Paleotropical datasets (Table 4). The likelihood of reaching adequate power was significantly lower for Neotropical gleaning animalivores compared to frugivorous and nectarivorous species. Moreover, for Neotropical datasets the probability of achieving adequate power was positively related to the initial

Table 3

Results from GLMM analyses assessing the probability of reaching the desired statistical power (0.9) to detect a 25% decline per unit time in a monitoring program for Neotropical bats as a function of survey design and species characteristics. Parameter estimates for the fixed effects retained in the minimum adequate model are given.

Source of variation	L-ratio χ^2	df	P
<i>Fixed effects</i>			
Ensemble	6.351	2	0.042
CV of relative abundance	2.230	1	0.135
Initial relative abundance	15.38	1	<0.0001
No. of survey years	74.91	1	<0.0001
Survey interval	45.57	1	<0.0001
No. of surveys per interval	35.74	2	<0.0001
No. of plots	471.8	2	<0.0001
	Estimate (SE)	z	P
Intercept	2.905 (0.837)	3.471	0.001
Ensemble_GLANIM	-3.591 (1.25)	-2.872	0.004
Ensemble_NECT	-1.412 (1.252)	-1.128	0.259
Initial rel. abundance	1.801 (0.487)	3.698	0.000
No. survey years_20	2.946 (0.411)	7.164	0.000
Survey interval_2	-2.207 (0.366)	-6.031	0.000
No. plots_3	-7.057 (0.63)	-11.209	0.000
No. plots_5	1.115 (0.443)	2.516	0.012
No. surveys_3	1.689 (0.401)	4.213	0.000
No. surveys_4	2.242 (0.425)	5.276	0.000

Table 4

Results from GLMM analyses assessing the probability of reaching the desired statistical power in a monitoring program for Paleotropical bats as a function of survey design and species characteristics. Parameter estimates for the fixed effects retained in the minimum adequate model are given.

Source of variation	L-ratio χ^2	df	P
<i>Fixed effects</i>			
Ensemble	2.856	3	0.414
CV of relative abundance	18.99	1	<0.0001
Initial relative abundance	0.023	1	0.880
No. of survey years	38.38	1	<0.0001
Survey interval	15.00	1	0.0001
No. of surveys per interval	19.92	2	<0.0001
No. of plots	80.66	2	<0.0001
	Estimate (SE)	z	P
Intercept	4.127 (1.409)	2.929	0.003
CV	-1.913 (0.462)	-4.144	0.000
No. survey years_20	4.65 (0.983)	4.729	0.000
Survey interval_2	-3.349 (1.084)	-3.089	0.002
No. plots_3	-8.043 (1.432)	-5.615	0.000
No. plots_5	-1.81 (1.397)	-1.296	0.195
No. surveys_3	3.108 (1.172)	2.652	0.008
No. surveys_4	3.494 (0.926)	3.774	0.000

relative abundance. In contrast, for the Paleotropical datasets, the CV of relative abundance was a strong predictor, with the ability to attain adequate power decreasing with increased temporal variation in species abundance.

4. Discussion

We compared the effectiveness of various sampling designs for detecting temporal trends in relative abundance of tropical bats as a prerequisite for establishing long-term monitoring programs. Our power simulations revealed a pronounced effect of the duration of a monitoring program on the ability to detect trends in bat species abundance. Monitoring over a period of only 10 years had, in many cases, insufficient power to detect annual declines of five or 10%. In contrast, 20 years of sampling yielded adequate power to detect decreases in abundance for many more species.

This suggests that a monitoring program aimed at reliably detecting population trends for many tropical bat species would need to be implemented for a minimum of 20 years.

One of the prime considerations when designing a monitoring program concerns the number of plots to be sampled at a particular location. Space should be sampled in a manner that permits inference about the entire area of interest, based on the selected sampling units (Pollock et al., 2002). To minimize sample error, sampling multiple plots at a site is thus preferable to multiple within-year visits to the same plot. The same plots then need to be revisited during each survey to eliminate the plot-to-plot variation from the estimates of trend precision (Sims et al., 2006). Our power simulations for the three-plot design showed that several repeat visits per year are for the most part insufficient to detect species declines with adequate statistical power. Thus, we conclude that efforts should be directed at sampling more plots rather than increasing the number of visits per plot. Conducting sampling on five plots yielded adequate power levels to reliably detect trends for most species examined. In the latter case, efficiency could be increased with little loss of statistical power by reducing survey effort to every other year. An alternative monitoring approach for decreasing costs would be to perform annual surveys during the early stages of the program, and then reduce the frequency of monitoring (e.g. after 10 years) to a biennial sampling scheme.

For a five-plot sampling scheme with biennial surveys, the frequency of repeat visits per plot ultimately depends on the desired sensitivity of the monitoring program (i.e. the magnitude of change to be detected). Our results for the range of species studied suggest that two repeat visits/plot would suffice to detect declines in the 10% range, whereas four visits to a plot may be necessary for detecting annual changes of lower magnitude such as 5%. Negative population trends of a magnitude as low as 1–2% per year may result in unacceptable probabilities of extinction in many animals (Mace and Lande, 1991). Thus, conservation-oriented monitoring programs should aim for being able to detect relatively small annual population declines. Power analyses performed as part of the UK's National Bat Monitoring Program (NBMP) suggest that NBMP sampling schemes should be able to detect annual declines in the eight selected target species as small as 1–2% at power levels over 90% (Walsh et al., 2003). However, this program is based on monitoring many sites (ca. 2000) and relies on a large volunteer force of >800 people to provide adequate geographical coverage. Moreover, NBMP data largely stem from surveys of maternity colonies and hibernation sites in temperate regions and thus are inherently different from monitoring data that would be obtained from a plot or transect-based sampling scheme. Trends of a magnitude as low as 1–2% per year may be very difficult to detect for species that are characterized by high variance in abundance estimates, as is the case for most tropical bat species (see below). Nonetheless, our results are reassuring insofar as a monitoring program extending over 20 years with four surveys conducted biennially on five plots would have the potential for detecting a 5% change in abundance per time unit for a variety of bat species from different ensembles. The ability to detect meaningful trends may be thwarted by large variation in species detectability, which increases sampling error. Considering the fact that a certain number of repeat surveys is essential if reliable detectability estimates are to be obtained (MacKenzie and Kendall, 2002; Royle and Nichols, 2003), four visits per plot probably represent a good balance between what is required for sound statistical inference and for detecting change of a magnitude that is biologically meaningful, and what could be achieved in practice. In general, monitoring efforts for bats could feasibly be combined in space and time with those for other taxa such as birds, which would help to minimize financial costs.

Monitoring of bats will be complicated by the fact that several tropical bat species exhibit seasonal, probably mostly short-distance habitat shifts (Stoner, 2001, 2005) and a few species even migrate over longer distances (Fleming and Eby, 2003; Thomas, 1983). However, detailed knowledge of seasonal habitat shifts currently exists for only a handful of bat species and/or for only a few tropical localities (Fleming and Eby, 2003). Trend detection requires that a constant fraction of the population is encountered over time intervals for making reliable comparisons (MacKenzie et al., 2005) and trend estimates may thus be confounded if seasonal shifts in relative abundance occur, for instance, along with a declining trend. This suggests that the seasonal time window for sampling should be restricted to the same period during all monitoring years.

We found that the likelihood of reaching an adequate power level was sensitive to initial estimates of species abundance and temporal variation. In line with other studies (Seavy and Reynolds, 2007; Sims et al., 2006), our results emphasize the importance of considering the magnitude of this variation in a power analysis because design decisions depend on the relative magnitude of these variance components. Prospective power analyses should be complemented by an assessment of the precision of population estimates, and monitoring programs should set acceptable levels of precision (Seavy and Reynolds, 2007). Low statistical power in population monitoring protocols is primarily due to high variability associated with measures of population size (Gibbs et al., 1998). Gibbs et al. (1998) summarized data from 512 studies and found average CV values to vary substantially across the 24 taxonomic and ecological groups examined, ranging between 14% and 131% (median 57%) overall, and averaging 93% for studies on bats. Thus, with a mean of 231% (range 101–500%) across 24 studies, our observed CV values were well above the variability indices for other published studies. At the level of ensembles, our data suggest that aerial insectivorous bats in the Neotropics would make good candidates for monitoring using acoustic sampling techniques due to comparatively low temporal variation. Conversely, gleaning animalivores and phytophagous bats constitute more challenging monitoring targets owing to higher average CV values and greater variation among species and locations. Based on their analysis, Gibbs et al. (1998) recommended longer time periods for monitoring to compensate for high temporal variability and low statistical power. Indeed, as our analyses showed, increasing the number of monitoring years from 10 to 20 can successfully offset the generally low precision in estimates of abundance and in most cases yield adequate statistical power.

Species that can be monitored effectively will likely differ between sites and regions, as species that are abundant in one location may be less abundant or rare elsewhere. This was borne out to some degree in the power simulations, especially for sampling schemes involving three plots. Here, power estimates for particular species (e.g. *Artibeus jamaicensis*, *Lonchophylla thomasi*, *Lophostoma silvicolum*) sometimes varied quite substantially between locations, suggesting that a species may be reliably monitored at one location but not at another (Tables 1 and 2).

Ubiquitous species are easiest to monitor, however, such species also typically have broader habitat requirements that buffer them from spatial and temporal environmental variation, suggesting normally less sensitivity to disturbance, which then reduces their value for monitoring (Carlson and Schmiegelow, 2002). Conversely, rare species, although inherently of greater monitoring interest, will require increased sampling effort to compensate for high sampling error and high natural variability that often results from specialized habitat requirements. Costs associated with monitoring such species may be excessive. In such instances, it has been advocated to select target species for monitoring that are sensitive to disturbance, yet exhibit relative temporal stability in esti-

mates of abundance (Carlson and Schmiegelow, 2002). Based on these criteria, phytophagous species such as *Carollia perspicillata* or *Rhinophylla pumilio* may be examples of efficient targets for monitoring. Likewise, certain gleaning animalivores such as *Lophostoma silvicolum*, *Trachops cirrhosus*, and *Nycteris arge* also constitute potentially important species for monitoring.

For certain target species long-term monitoring of day roosts may constitute a suitable complementary approach to relative abundance estimates based on capture or acoustic data, which may strongly reduce the variance in estimates of population abundance. This could for instance be a feasible strategy for colonial flying fox species such as *Eidolon helvum* in Africa or *Pteropus* spp. in South East Asia, or cave-roosting species (Epstein et al., 2009; Newson et al., 2009).

While power analyses are most appropriately employed prior to implementation of a monitoring program for determining optimal study design, the detection of trends can be improved by the use of statistical models that include covariates that effectively remove some of the 'noise' that may otherwise obscure trends (e.g. to account for habitat effects or site variability; Fewster et al., 2000; Purcell et al., 2005). We generally advocate that such an approach be taken with the data generated from bat monitoring programs.

Methods for estimating abundance and detection probabilities on sample units can be expensive in both time and effort. One potential approach to reducing effort in large-scale monitoring programs involves a shift from count surveys to presence-absence data obtained on sampling units (MacKenzie et al., 2005). Presence-absence surveys, which are generally relatively easy and efficient to conduct, have become more commonly the focus of monitoring programs in recent years (Marsh and Trenham, 2008). Estimation approaches developed for occupancy surveys incorporate detection probability directly into the estimation process (MacKenzie and Kendall, 2002; MacKenzie et al., 2005; Nichols et al., 2008; Royle and Nichols, 2003) and thus deal appropriately with this fundamental component of estimating animal abundance. Extensions of these models have recently been developed also for count data (Kéry et al., 2009; Kéry and Royle, 2010). Although presence-absence data may provide an adequate indicator (Joseph et al., 2006), its sensitivity in diagnosing population change depends on the relationship between abundance and occupancy (Holt et al., 2002). It is likely, for example, that changes in presence-absence are not detected until a precipitous decline in abundance has already occurred. Thus, trend detection based on abundance data may be more statistically powerful than presence-absence data, but also potentially more expensive (Field et al., 2005). Quantitative guidelines for choosing between presence-absence surveys and count surveys depend on the biological and logistical constraints governing a conservation monitoring effort. A recent study by Pollock (2006) suggests that presence-absence surveys work best when there is little variability in abundance among survey sites and the target species is rare and difficult to detect so that the time spent getting to each survey site is less than or equal to the time spent surveying each site; count surveys work best otherwise. Although we did not specifically evaluate species occupancy as a potentially appropriate state variable for a bat monitoring program, we recommend that occupancy analyses be incorporated into any monitoring data analyses and the relative benefits and drawbacks of such an approach relative to an abundance-based approach be considered.

4.1. Conclusions and recommendations

The detection of temporal patterns in population abundance is an issue central to most monitoring programs (Marsh and Trenham, 2008). So far, approaches to vertebrate monitoring in the tropics have been mostly limited to birds and in a few cases

to small or large, non-volant mammals. Our findings suggest that inclusion of bats as a group of crucial ecological importance in tropical ecosystems into long-term monitoring programs is feasible given that temporal changes in species abundance can be assessed with an adequate level of statistical power for a range of species from different functional groups. Based on our results, we make the following recommendations on study design for a long-term monitoring program of tropical bats:

(1) Given that the time frame over which monitoring is carried out is crucial for achieving adequate power for detection of long-term population trends, we recommend that monitoring data be collected over a time span of at least 15 years and we encourage studies of 20 years' duration to ensure that reliable trend analysis will be possible for a larger number of species. We would advise against sampling for fewer years unless the number of plots being monitored and the number of visits per plot is increased considerably beyond the values examined in this study.

(2) Cost-effectiveness is an important consideration in long-term monitoring programs (Gardner et al., 2008). Given the limited budget of most conservation projects, we propose a biennial sampling scheme, which would still allow for reliable trend detection while providing considerable savings in terms of survey costs.

(3) Based on our results, we recommend conducting monitoring surveys on at least five spatial replicates per monitoring location.

(4) The interpretation of trends from raw species counts is always complicated by imperfect detectability (Kéry et al., 2009). Optimal survey design thus requires a sufficient number of temporal replicate observations on the same monitoring plot. Species detectability was found to be highly variable in our datasets (Meyer et al., unpublished data). For a monitoring program we would therefore recommend four within-year visits per plot, which we suggest should be timed to coincide with the major seasonal periods (typically the peak dry and wet seasons, as well as corresponding transitional periods). Such a sampling scheme would allow for reliable estimation of species detectability and the detection of seasonal, annual, and multi-annual trends also of lower magnitude (5% changes). It would further ensure that newly developed hierarchical mixture models that explicitly correct for imperfect detection (Kéry et al., 2009; Kéry and Royle, 2010) can be applied at the analysis stage.

(5) Species that provide useful data for detailed population monitoring (e.g. indicator species for habitat quality) need to be carefully selected. We recommend that choices of species on the local scale be based on reasonably high abundance and low CV as well as on important ecological functions. *A priori* site-specific knowledge of the ecology and abundance of species based on field data and/or a literature search will thus be essential for a reasoned pre-selection of species for the analysis of population trends.

(6) Relatively low temporal variation in abundance measures (this study) and high species detectability (Meyer et al., unpublished data) suggest that aerial insectivorous bats constitute a suitable target group for monitoring. We therefore recommend complementing mist net captures with acoustic surveys (Flaquer et al., 2007; Kunz and Parsons, 2009), especially since the latter have been shown to be indispensable for maximizing inventory completeness in tropical bat surveys (Furey et al., 2009; MacSwiney et al., 2008). Moreover, advances in acoustic technology now make acoustic sampling increasingly efficient and affordable. In this context, we advocate the application of transect-based sampling using acoustic point counts to maximize the output of acoustic surveys in terms of species detection (Estrada Villegas et al., 2010).

(7) Because many species are seldom captured in ground-based mist nets we advocate the use of multiple capture methods. Canopy nets and, particularly in the Paleotropics, also harp traps have been successfully employed in a number of recent studies (e.g. Clarke et al., 2005; Fahr and Kalko, 2010; Furey et al., 2010; Kings-

ton et al., 2006; Meyer and Kalko, 2008) and are an important means of increasing the detection of rare and uncommon species.

(8) We emphasize the importance of standardizing sampling design and sampling effort as much as possible during monitoring surveys.

From our results it is obvious that in order to be statistically defensible the successful implementation of a long-term monitoring program for tropical bats would entail considerable efforts in terms of both substantial monetary costs and time investment. We are aware that this may discourage potential funding bodies from becoming involved in such an endeavor, particularly in light of the general underfunding of conservation-oriented research in the tropics (Balmford and Whitten, 2003). Nonetheless, given the enormous potential of bats as indicators of human-induced changes in climate and habitat quality (Jones et al., 2009), we believe it is hard to overstate the importance of incorporating bats into long-term monitoring schemes so the potential of this highly diverse and ecologically important group of mammals as a sensitive indicator group for the status of tropical forests can be fully realized.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.07.029.

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Appendix. Datasets from tropical bat assemblages used for assessing within-site temporal variation in relative species abundance and for evaluating the statistical power of different sampling designs. This list summarizes the sampling methods used and the number of sampling years covered by each dataset. The datasets used in the power analyses include the number of sampling plots for which the simulations were run and the number of species for which the power calculations were performed.

	<i>Country</i>	<i>Location¹</i>	<i>Sampling method²</i>	<i>No. of sampling years</i>	<i>Temporal variation in abundance</i>	<i>Power simulations</i>	<i>No. of plots</i>	<i>No. of species analyzed</i>	<i>Data source³</i>
<i>Neotropics</i>	Mexico	Yucatan	GN	2	x				MacSwiney et al., 2007;2008
	Mexico	Chamela ^{a)}	GN	2	x				Stoner, 2005
	Costa Rica	Palo Verde ^{a)}	GN	2	x				Stoner, 2005
	Costa Rica	La Selva	GN	1	x				Rex et al., 2008
	Panama	Fort Sherman	GN	2	x				Weise, 2007
	Panama	BCNM	GN	2	x	x	1, 3, 5	6	Meyer and Kalko, 2008
	Panama	BCNM	AS	1	x				Estrada Villegas et al., 2010
	Panama	BCI	GN	2	x				Weise, 2007
	Panama	BCI	GN	2	x				von Staden, 2002
	Panama	BCI	GN	2	x				Weise, 2007
	Panama	Soberanía	GN	3	x				von Staden, 2002; E. Kalko, unpublished data
	Panama	Gamboia	AS	2	x	x	1	6	Jung and Kalko, 2010
	Trinidad	Victoria-Mayaro	GN	2	x				Clarke et al., 2005a;b
	French Guiana	St. Eugène	GN	6	x	x	1, 3, 5	6	Cosson et al., 1999; Pons and Cosson, 2002; Henry et al., in press
	French Guiana	Nouragues	GN	4	x	x	1, 3, 5	5	Delaval et al., 2005; Henry and Kalko, 2007; M. Henry, unpublished data
	Ecuador	Podocarpus	GN	1	x				Rex et al., 2008
	Ecuador	Tiputini	GN	1	x				Rex et al., 2008
	Brazil	Una	GN	3	x	x	1, 3, 5	3	Faria, 2006
	Brazil	Roncador ^{b)}	GN	1	x				L. Aguiar, unpublished data
Brazil	BDFFP	GN	3	x				Sampaio, 2001	
Bolivia	Yungas de La Paz	GN	2	x				Moya et al., 2008	

Paleotropics	Malaysia	Lubuk Baung	HT	2	x	x	1	6	Kingston et al., 2006
	Malaysia	Kuala Lompat	CN	4	x	x	1	5	Hodgkison et al., 2004
	Vietnam	Kim Hy	GN	1	x				Furey et al., 2010
	Ivory Coast	Comoé ^{c)}	GN	4	x	x	1, 3	6	Fahr and Kalko, 2010
	Ivory Coast	Taï	GN	2	x	x	1, 3, 5	3	Fahr and Kalko, 2010
	Madagascar	Bemaraha ^{a)}	GN	2	x				Kofoky et al., 2007

¹ forest/habitat type other than tropical wet/moist forest: a) tropical dry forest, b) Cerrado, c) biome transition (forest-savanna mosaic)

BCNM = Barro Colorado Nature Monument, BCI = Barro Colorado Island, BDFFP = Biological Dynamics of Forest Fragments Project

² sampling methods: GN = ground nets, CN = (sub)canopy nets, HT = harp traps, AM = acoustic survey

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